The Salton Sea

Proceedings of the Salton Sea Symposium,
held in Desert Hot Springs, California, 13–14 January 2000

Edited by

Douglas A. Barnum[1], John F. Elder[2], Doyle Stephens[3] & Milton Friend[2]

[1] *U.S. Geological Survey, Sacramento, CA, U.S.A.*
[2] *U.S. Geological Survey, Madison, WI, U.S.A.*
[3] *Formerly of U.S. Geological Survey, Salt Lake City, UT, U.S.A.*

Reprinted from Hydrobiologia, volume 473 (2002)

Kluwer Academic Publishers
Dordrecht / Boston / London

Library of Congress Cataloging-in-Publication Data

A C.I.P. Catalogue record for this book is available from the Library of Congress.

ISBN 1-4020-0555-5

Published by Kluwer Academic Publishers,
P.O. Box 17, 3300 AA Dordrecht, The Netherlands

Sold and distributed in North, Central and South America
by Kluwer Academic Publishers,
101 Philip Drive, Norwell, MA 02061, U.S.A.

In all other countries, sold and distributed
by Kluwer Academic Publishers Group,
P.O. Box 322, 3300 AH Dordrecht, The Netherlands

Printed on acid-free paper

All Rights reserved
© 2002 Kluwer Academic Publishers

No part of the material protected by this copyright notice may be reproduced or utilized in any form or by any means, electronic or mechanical, including photocopying, recording or by any information storage and retrieval system, without written permission from the copyright owner.

Printed in the Netherlands

TABLE OF CONTENTS

Preface
M. Friend vii–xii

Chemical and physical characteristics of the Salton Sea, California
G. Chris Holdren, Andrew Montaño 1–21

Chemical evolution of the Salton Sea, California: nutrient and selenium dynamics
Roy A. Schroeder, William H. Orem, Yousif K. Kharaka 23–45

Characteristics and contaminants of the Salton Sea sediments
Richard A. Vogl, Ryan N. Henry 47–54

Reconstruction of prehistoric Lake Cahuilla in the Salton Sea Basin using GIS and GPS
Joseph E. Buckles, Kazuyuki Kashiwase, Timothy Krantz 55–57

Simulation of wind-driven circulation in the Salton Sea: implications for indigenous ecosystems
Christopher B. Cook, Gerald T. Orlob, David W. Huston 59–75

Preliminary studies of cyanobacteria, picoplankton, and virioplankton in the Salton Sea with special attention to phylogenetic diversity among eight strains of filamentous cyanobacteria
A. Michelle Wood, Scott R. Miller, W.K.W. Li, Richard W. Castenholz 77–92

Flagellate *Cryptobia branchialis* (Bodonida: Kinetoplastida), ectoparasite of tilapia from the Salton Sea
Boris I. Kuperman, Victoria E. Matey, Steven B. Barlow 93–102

Metazooplankton dynamics in the Salton Sea, California, 1997–1999
Mary A. Tiffany, Brandon K. Swan, James M. Watts, Stuart H. Hurlbert 103–120

Freeliving nematodes from the Salton Sea
R. M. Warwick, D.M. Dexter, B. Kuperman 121–128

Cryptomonads from the Salton Sea, California
S.B. Barlow, P. Kugrens 129–137

The benthic invertebrates of the Salton Sea: distribution and seasonal dynamics
P.M. Detwiler, Marie F. Coe, Deborah M. Dexter 139–160

Naked amoebae (Protozoa) of the Salton Sea, California
Andrew Rogerson, Gwen Hauer 161–177

The diatom flora of the Salton Sea, California
Carina B. Lange, Mary Ann Tiffany 179–201

Invertebrates of the Salton Sea: a scanning electron microscopy portfolio
Boris I. Kuperman, Victoria E. Matey, Deborah M. Dexter, Mary Ann Tiffany 203–216

Skeletal development in *Hermesinum adriaticum* Zacharias, a flagellate from the Salton Sea, California
M.A. Tiffany 217–221

Summer movements of desert pupfish among habitats at the Salton Sea
Ronald J. Sutton 223–228

Fish biology and fisheries ecology of the Salton Sea, California
Ralf Riedel, Lucille Caskey, Barry A. Costa-Pierce 229–244

Biology and migration of Eared Grebes at the Salton Sea
Joseph R. Jehl, Jr., Robert L. McKernan 245–253

The Salton Sea as critical habitat to migratory and resident waterbirds
W. David Shuford, Nils Warnock, Kathy C. Molina, Kenneth K. Sturm 255–274

Possible importance of algal toxins in the Salton Sea, California
Kristen M. Reifel, Michael P. McCoy, Tonie E. Rocke, Mary Ann Tiffany, Stuart H. Hurlbert, D. John Faulkner 275–292

Avian disease at the Salton Sea
Milton Friend 293–306

Hydrobiologia **473:** vii–xii, 2002.
D.A. Barnum, J.F. Elder, D. Stephens & M. Friend (eds), The Salton Sea.

Preface

This issue of *Hydrobiologia* brings together a series of papers resulting from an intensified effort to describe the current status of the physical and biological conditions present at California's Salton Sea. Most of the studies were contract investigations that were part of a project initiated in January 1998 to pursue the improvement of environmental conditions at the Salton Sea. The remainder are independent investigations resulting in information of importance for the Salton Sea Restoration Project. The information provided by those investigations is the most holistic assembly of scientific knowledge about the Salton Sea ever brought together in a single publication. The resulting findings provide an important foundation of knowledge for what has been stated to be, ". . . one of the worlds' most dynamic salt lakes . . ." (Hart et al., 1998). We hope this publication will serve as a catalyst to stimulate additional scientific investigations that will further enhance understanding of the dynamics of this unique ecosystem. The purpose for these introductory comments is to place the scientific investigations reported on and the Salton Sea Restoration Project in context as entities, and to one another.

The Salton Sea

The Salton Sea was formed by floodwaters of the Colorado River during the period of 1905–1907 (Kennan, 1917). This waterbody is the largest lake in California. It is approximately 58 km long, 14 to 22 km wide and has a surface area of 980 km^2 (Hart et al. 1998). The Salton Sea is located in the center of the Colorado Desert (Arnal, 1961) in southern California and lies approximately 227 feet below sea level within the Salton Trough. At the time of formation the Salton Sea was a freshwater lake but by 1929 had become almost as saline as ocean water because of evaporation and the solution of salts present on the basin floor prior to lake formation (Arnal, 1961). The current salinity of the Salton Sea is approximately 44 g l^{-1} (Hart et al., 1998) and continuing to rise.

The formation of the Salton Sea created a large oasis within the desert that soon became a focal point for land development associated with recreational opportunities afforded by this waterbody. Land developers also touted the Salton Sea as a retirement haven (Kennan, 1917; du Buys & Myers, 1999). The "boom" for shoreline development and public use of the Salton Sea that began during the 1930's started to wane during the mid-1960's and collapsed during the 1970's. To a large extent that shift in fortunes was due to rising water levels that flooded shoreline properties, increasing salinity and other factors. The State Water Quality Control Board contracted with a private firm in 1964 to prepare preliminary plans for controlling water quality, primarily salinity, and secondarily to consider algal blooms. Stabilization of water levels was also to be considered (USDI & RCA, 1969). That action was followed by a series of evaluations and reports without any actions being taken (USDI & RCA, 1969; 1974; Ormat, 1989; Ogden, 1996; Bureau of Reclamation et al., 1997; USDI, 1998).

The Salton Sea Restoration Project

An increasing occurrence of avian disease at the Salton Sea prompted an unsuccessful attempt by the Director of the National Wildlife Health Center to stimulate the development of an ecosystem health project to address those problems (U.S. Geological Survey, 1996). However, the unprecedented 1996 type C avian botulism mortality event involving American white pelicans (*Pelecanus erythrorhynchos*) and California brown pelicans (*P. occidentalis*) (National Wildlife Health Center Epizootic Database) served to focus prolonged national media attention on the Salton Sea. In August 1997 the U.S. Fish and Wildlife Service and Bureau of Reclamation sponsored a workshop in Palm Springs, California to develop a process to address the natural and cultural resource issues, and research and investigation needs for any proposed engineering solutions to repair the Salton Sea (U.S. Fish and Wildlife, 1997). In December 1997, the Secretary of the U.S. Department of the Interior announced a collaborative agreement between Interior and other stakeholders for a Salton Sea Restoration Project focused on improving the

environmental quality of the Sea (USDI, 1997). The U.S. Bureau of Reclamation was designated as the project federal co-lead and the Salton Sea Authority was designated as the co-lead for the State of California.

Project initiation in January 1998 had two major conditions. An independent Science Subcommittee was established to provide objective, enhanced scientific information about the Salton Sea ecosystem to serve as a foundation for management decisions by the co-lead agencies relative to restoration actions to be pursued. In addition, the co-lead agencies were required to comply with National Environmental Policy Act (NEPA) and California Environmental Quality Act (CEQA) processes in developing their recommendations. They were also required to provide their findings to the Secretary of the Interior by December 1999 for his transmittal to the Congress by January 2000. The Science Subcommittee pursued its task through contracting for a series of reconnaissance studies to describe the current state of the Salton Sea. Because of imposed time constraints the maximum amount of time that could be allocated for individual studies was twelve months. The collective highlights from those studies were presented at a January 2000 symposium held at Desert Hot Springs, California. Symposium presentations also included reports from independent studies with information relevant for the restoration project.

Rather than being an end-point, the reconnaissance investigations are just the beginning of scientific needs associated with the Salton Sea Restoration Project. Additional scientific investigations have been initiated to begin addressing some of the specific problems that must be overcome for goal achievement. Those goals are to:

- maintain the Sea as a repository of agricultural drainage;
- provide a safe, productive environment at the Sea for resident and migratory birds and endangered species;
- restore recreational uses at the Sea;
- maintain a viable sport fishery at the Sea; and
- enhance the Sea to provide economic development opportunities.

A Strategic Science Plan was developed to guide an integrated, continuing science effort (Fig. 1). That Plan calls for the development of a Science Office to serve restoration project needs (Salton Sea Science Subcommittee, 2000). In keeping with that Plan, in February 2000 the Science Subcommittee was replaced with an interim Science Office. It is anticipated that a permanent Science Office will be authorized as part of Congressional approval and funding for a large-scale restoration project.

Overview

Presenters at the January 2000 symposium were not required to provide manuscripts for publication. As a result, several of those presentations are not included in this issue of *Hydrobiologia*. Nevertheless, the papers that are provided address a broad spectrum of subject areas and clearly illustrate the dynamic nature of the Salton Sea and the richness of biodiversity present. Symposium papers included within this overview are cited without dates.

Prehistoric and Native American peoples were closely associated with the large waterbodies that occupied the Salton Trough and left behind cultural resources that are part of the richness of the area considerations. Buckles et al. (this volume) delineated the prehistoric shorelines of those lakes as a foundation for archaeological and cultural resources. Those factors are important in evaluating restoration alternatives for the Salton Sea and are themselves areas for scientific investigations (Darnell, 1959; Schaefer et al., 2000; Wilke & McDonald, 1989).

Cook et al. (this volume) investigated the circulation of the Salton Sea and developed a mathematical model for describing water movement. They noted that circulation is driven primarily by wind stresses imposed on the water surface and that those patterns affect the ecology of the Sea. Therefore, proposed actions that change the bathymetry and configuration of the Sea can be expected to impact the environmental quality and existing ecological relations of the Salton Sea. Continued enhancement of the circulation model for predictive impact purposes remains an important area for scientific investigation.

The current chemical and physical conditions of the Salton Sea were evaluated by Holdren & Montano (this volume). This investigation included water quality parameters, nutrients, trophic state variables, major cations and anions, trace metals, organic compounds and provides comparisons with the classic publications of Arnal (1961) and Walker (1961). Failure of Holdren & Montano to detect high levels of pesticides and other anthropogenic chemical contaminants (other than nutrients) within the water column was counter to expectations. The distribution

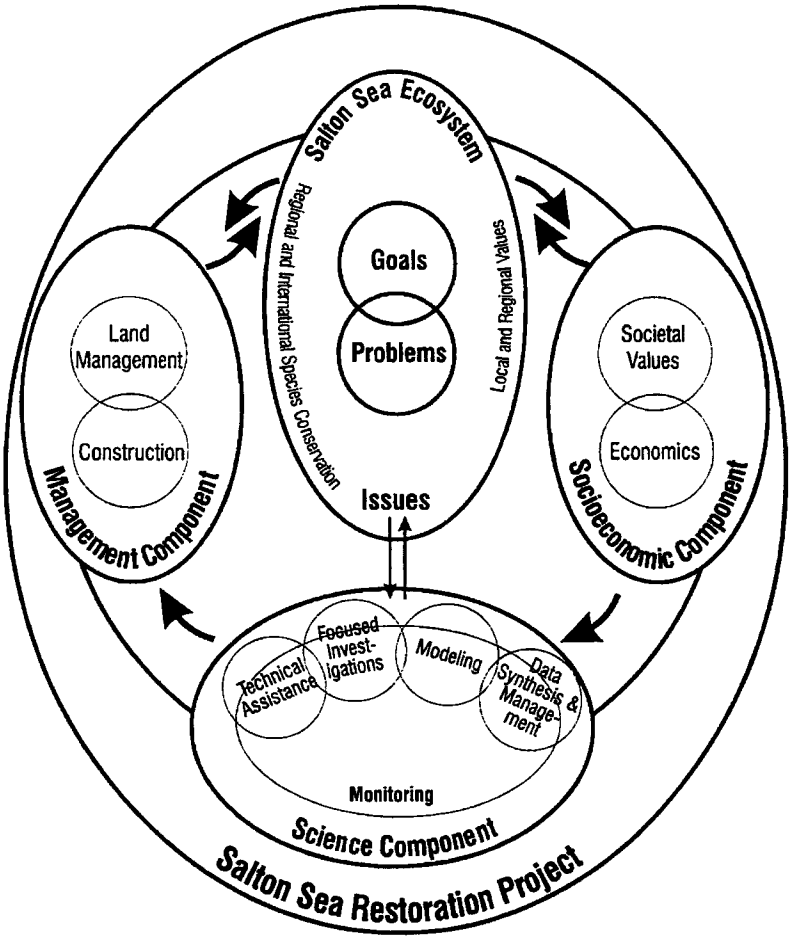


Figure 1.

of sediment types and sediment contaminants throughout the Salton Sea were also investigated. Vogl et al. (this volume) found an absence of elevated concentrations of organic chemicals such as dichlorodiphenyltrichloethane (DDT) despite several decades of heavy DDT use in the surrounding agricultural areas. Those findings also differed from expectations. Several heavy metals and selenium were found at elevated levels within some sediments but not at other locations. The pattern of metal and selenium deposition also differed from expectations with the most elevated levels seen in deep water areas rather than within the shallow delta area receiving input waters.

Other contaminant investigations have also resulted in unexpected findings. For example, Fialkowski & Newman (1998) concluded from their studies of barnacles (*Balanus amphitrite*) that the Salton Sea has not been significantly polluted with heavy metals or that those metals are bring transferred from the water column to the sediments. The lack of clear findings relative to contaminants are an indication of the need for greater understanding of the fate, transport and biological effects of chemicals within the Salton Sea ecosystem.

The most comprehensive evaluations included in this publication are those for the limnology of the Salton Sea. Those findings document far greater numbers of nonvertebrate species than the earlier studies of Arnal (1958, 1961) and the publication by Walker (1961). Many of the approximately 400 species found have not previously been described within the scientific literature.

Investigations on the dynamics of metazooplankton populations extended existing studies to provide a three-year evaluation (Tiffany et al., this volume). Those studies disclosed two major changes in metazooplankton dynamics since 1954–56 investigations by Carpelan (1961). Eight genera of cryptomonads from the Salton Sea

were recorded for the first time and one putative genus that may represent a new taxon remains under investigation (Barlow & Kugrens, this volume). The authors note that the genera and species identified are typical of marine rather than freshwater environments and may play an important role in primary productivity and as preferred food organisms for zooplankton. The first investigations of the naked amoeboid protozoa of the Salton Sea disclosed 45 different morphospecies (considered to be species), approximately 40% of which are new to science (Rogerson & Hauer, this volume). The authors postulate that amoebae may be important in the cycling of carbon and nutrients in the Salton Sea.

A high diversity of diatoms was also found. Ninety-four taxa were distinguished. Those taxa constituted four general categories of diatom assemblages associated with plankton, benthos and algal mats, an epiphytic community and freshwater assemblages at inflow points to the Sea (Lange & Tiffany, this volume). Even greater numbers of Cilophora were found. One hundred and forty-one species within nine classes of citiates were collected from eleven different shoreline sites around the perimeter of the Salton Sea. A follow-up collection resulted in an additional thirty-five species. Those investigations by Small and others are documented within the Salton Sea database (Salton Sea Science Office) but are not included within these proceedings.

The macroinvertebrates of the Salton Sea include only a few species and the investigations of Detwiler et al. (this volume) add several new species for this waterbody. The pileworm (*Neanthes succinea*) may be a key food item for the fish of the Sea and also for a number of bird species. Area-weighted estimates of standing stock of this invertebrate were two orders of magnitude less than biomass estimates made during 1956 investigations (Carpelan & Linsley, 1961). Thirteen species of freeliving nematodes have been found, doubling the number of multicelluar invertebrates known to occur at the Salton Sea (Warwick et al., this volume). Scanning electron microphotographs of 16 Salton Sea invertebrates including foraminiferans, a flatworm, a rotifer, annelids, crustaceans and insects are provided along with comments on the morphology and function of structures visible in the images (Kuperman et al., this volume). Scanning electron microscopy was also used to study the skeletal development of *Hermesinum adricaticum*, a rarely reported unicellular biflagellated organism with a solid siliceous skeleton (Tiffany, this volume).

Cyanobacterial diversity in the Salton Sea is also great. Eighty-four pure strains, including filamentous and unicellular forms were isolated from the water column and benthos. Those isolates fall within 11 described genera except for two strains that do not conform to any currently recognized genus (Wood et al., this volume). The authors note that among those taxa are five known toxin producing species and they suggest that cyanobateria should be considered as possible causes for some of the bird and fish mortality occurring at the Salton Sea. Initial studies of algal toxicity showed a low level of activity in the brine shrimp lethality assay but an absence of activity in the mouse bioassay (Reifel et al., this volume). Additional investigations are being pursued under funding provided by the Salton Sea Restoration Project.

Three of the four primary fishes of the Salton Sea are species from the Gulf of California. Orangemouth corvina, *Cynoscion xanthulus*, sargo, *Anisotremus davidsoni*, and bairdiella, *Bairdiella icistius*, are the result of 1950 and 1951 introductions by the California Department of Fish and Game (Walker, 1961). Tilapia, *Oreochromis mossambicus*, an exotic species for North America was introduced more recently by unknown means and has become a dominant species.

Massive fish kills involving hundreds of thousands to millions of fish occur at the Salton Sea and are a subject for concern and debate relative to causes. Studies on the ecology and biology of the fishes of the Salton Sea are reported by Riedel et al. (this volume). They note fish population abundance, that dissolved oxygen influences movement patterns for reproduction and feeding, and that the fish species present grow faster and have shorter life spans than co-specifics elsewhere and for Salton Sea species of five decades ago. Young tilapia were found by Kuperman et al. (this volume) to be infested by the flagellate parasite *Cryptobia branchialis*. The authors postulate that mortality of young tilapia may arise from decreased gill function in response to *Cryptobia* infestation. The study by Sutton (this volume) provides information on summer movement behavior of desert pupfish (*Cyprinodon macularius*), an endangered species and the only native fish present in the Salton Sea.

The abundance of fish at the Salton Sea, the foodbase provided in adjacent agricultural fields, the geographic location of the Salton Sea within the Pacific Flyway and drainage of more than 90 percent of historic interior wetland acreage in California (Dahl, 1990) has resulted in the Salton Sea becoming California's crown jewel of avian biodiversity and one of the crown jewels of North American avian biodiversity. The Salton Sea is of regional

or national importance for species from several groups of birds and provides habitat for a number of important taxa (Shuford et al., this volume). The eared grebe (*Podiceps nigricollis*) is one of the species for which the Salton Sea is of great importance with perhaps 75% or more of the population passing through the Salton Sea during spring migration (Jehl & McKerran, this volume).

Avian disease is one of the reasons for the focus on restoration efforts at the Salton Sea. The history of avian disease at the Salton Sea extends back at least until 1917 (Kalmbach & Gunderson, 1934). Nevertheless, the variety of diseases present as well as the magnitude of losses have both intensified during the 1990's (Friend, this volume). Minimizing losses from disease is an area for focus by the restoration program.

Prognosis

Can the Salton Sea Restoration Project Goals be achieved? The only certainty is that failure is assured without a sound scientific basis to guide the restoration effort through what is largely "unchartered waters". The challenge is a contemporary one involving the management of wastewater to achieve direct benefits for human society and the conservation of avian biodiversity. Science will become increasingly important as the restoration effort moves forward. A major first step has been accomplished through the investigations already undertaken but much remains to be done.

MILTON FRIEND, *Chief Scientist*
Salton Sea Science Office

References

Arnal, R. E., 1958. Rhizopoda from the Salton Sea, California. Cushman Found. for Foram. Res. 9: 36–45.

Arnal, R. E., 1961. Limnology, sedimentation, and microorganisms of the Salton Sea, California. Geological Soc. Amer. Bull. 72: 427–478.

Bureau of Reclamation, Salton Sea Authority & California State Department of Water Resources, 1997. Salton Sea area study, alternative evaluation appraisal report, final draft. Boulder City, NV, 221 pp. (+ appendices).

Carpelan, L. H., 1961. Zooplankton. In Walker, B. W. (ed.), The Ecology of the Salton Sea, California in Relation to the Sport Fishery. Calif. Fish and Game, Fish Bull. 113: 49–62.

Carpelan, L. H. & R. H. Linsley, 1961. The pile worm, *Neanthes succinea* (Frey and Levekart). In Walker, B. W. (ed.), The Ecology of the Salton Sea, California in Relation to the Sport Fishery. Calif. Fish and Game, Fish Bull. 113: 63–76.

Dahl, T. E., 1990. Wetland losses in the United States 1780's to 1980's. U.S. Fish and Wildlife Service, Washington, D.C., 13 pp.

Darnell, W. I., 1959. The Imperial Valley: its physical and cultural geography. M.S. Thesis, San Diego State University, San Diego, 127 pp.

du Buys, W. & J. Myers, 1999. Salt Dreams. University of New Mexico Press, Albuquerque, 307 pp.

Fialkowski, W. & W. A. Newman, 1998. A pilot study of heavy metal accumulations in a barnacle from the Salton Sea, Southern California. Marine Pollution Bull. 36: 138–143.

Hart, C. M., M. R. Gonzáles, E. P. Simpson & S. H. Hurlbert, 1998. Salinity and fish effects on Salton Sea microecosystems: zooplankton and nekton. Hydrobiologia 381: 129–152.

Kalmbach, E. R. & M. F. Gunderson, 1934. Western duck sickness a form of botulism. U.S. Dept. Agriculture, Tech. Bull. 411: 82 pp.

Kennan, G., 1917. The Salton Sea: an account of Harriman's fight with the Colorado River. Macmillan, New York, 106 pp.

Ogden Environmental and Energy Services Co., Inc., 1996. Salton Sea management project evaluation of salinity and elevation management alternatives. Project No. 313561000, San Diego, CA, 117 pp. (+ appendices).

Ormat Technical Services, Inc., 1989. Salton Sea Project + preliminary study, Sparks, NV, 118 pp. (+ appendices).

Salton Sea Science Subcommittee. 2000. Strategic science plan Salton Sea restoration project. Salton Sea Science Office, La Quinta, CA, 122 pp.

Schaefer, J., D. Huntley, S. Reddy, K. Gobalet, K. Hardin, L.S. Cummings & P. Mitchell, 2000. Archaeological investigations at a protohistoric fish camp on the receding shoreline of ancient Lake Cahuilla, Imperial County, California. ASM Affiliates, Inc, Encinitas, CA, 113 pp.

Walker, B. W. (ed.), 1961. The Ecology of the Salton Sea, California, in Relation to the Sport Fishery. Calif. Fish and Game Bull. 113: 1–204.

U.S. Department of the Interior (USDI), 1997. Statement by Interior Secretary Bruce Babbitt after meeting with governmental agencies involved in Salton Sea issues, Dec. 19. News, USDI, Washington, D.C., 5 pp.

U.S. Department of the Interior (USDI), 1998. Salton Sea alternatives – final preappraisal report. Bureau of Reclamation, Lower Colorado River Region. Boulder City, NV, 108 pp.

U.S. Department of the Interior (USDI) & The Resources Agency of California (RCA), 1969. Salton Sea Project Federal – State Reconnaissance Report, Washington, D.C., 160 pp.

U.S. Department of the Interior (USDI) & The Resources Agency of California (RCA), 1974. Salton Sea Project Federal – State Feasibility Report, Washington, D.C., 5 vols.

U.S. Fish and Wildlife Service, 1997. Proceedings of Saving the Salton Sea: a needs assessment workshop. U.S. Fish and Wildlife Service, Portland, OR.

U.S. Geological Survey, 1996. Salton Sea Ecosystem Initiative: Salton Sea Workshop, October 22–23, National Wildlife Health Center, Madison, WI, 14 pp.

Wilke, P. & A. M. McDonald, 1989. Prehistoric use of rock-lined cache pits: California deserts and southwest. J. Calif. And Great Basin Anthrop. 11: 50–73.

Hydrobiologia **473:** 1–21, 2002.
D.A. Barnum, J.F. Elder, D. Stephens & M. Friend (eds), The Salton Sea.
© 2002 *Kluwer Academic Publishers. Printed in the Netherlands.*

Chemical and physical characteristics of the Salton Sea, California

G. Chris Holdren & Andrew Montaño
Bureau of Reclamation, P.O. Box 25007 (D-8220), Denver, CO 80225, U.S.A.

Key words: Salton Sea, saline lakes, nutrients, nitrogen, phosphorus, ionic composition, dissolved solids, geochemical modeling

Abstract

A 1-year sampling program was conducted to assess current chemical and physical conditions in the Salton Sea. Analyses included general physical conditions and a suite of water quality parameters, including nutrients, trophic state variables, major cations and anions, trace metals and organic compounds. Samples were collected from three locations in the main body of the lake and from the three major tributaries. Nutrient concentrations in the Salton Sea are high and lead to frequent algal blooms, which in turn contribute to low dissolved oxygen concentrations. The tributaries consist primarily of agricultural return flows with high nutrient levels. Concentrations of trace metals and organic compounds do not appear to be of major concern. Two geochemical models, PHRQPITZ and PHREEQC, were used to evaluate potential chemical reactions limiting the solubility of selected water quality variables. Modeling indicated that the Salton Sea is supersaturated with respect to calcite, gypsum, and other minerals. Precipitation of these minerals may serve as a sink for phosphorus and limit the rate of salt accumulation in the Salton Sea.

Introduction

Water quality has been of concern in the Salton Sea since its formation in 1905–1907. With no surface outflows, salinity in the Sea continues to increase and is of major concern for planned restoration efforts. Excess nutrient levels, low dissolved oxygen concentrations and elevated levels of selenium and organic pesticides have all been noted as potential water quality problems by previous reports. Although the Sea has been extensively studied over the years, the extent and quality of existing water quality data are not known (Thiery, 1999).

High nutrient levels lead to extensive algal blooms, which interfere with fishing and other recreational uses of the lake. Odors caused by decaying organic matter also have adverse impacts on economic development in the area. The high algal populations also contribute to oxygen depletion in the hypolimnion of the lake during the summer months.

The last major study on water quality in the Sea (Setmire et al., 1993) reported on field work that occurred in 1990. Salinity has continued to increase since that time and major reductions in water inflows are proposed. Because nutrients and salinity are of particular concern for planned management efforts at the Salton Sea, a completely new characterization of water quality was required to provide current information to fulfill the requirements of an Environmental Impact Statement and Environmental Impact Report recently prepared for the Salton Sea project (Salton Sea Authority/USBR, 2000).

This study was conducted as part of a year-long effort to produce current scientific data on the Sea. General physical conditions and a suite of water quality parameters, including nutrients, major ions, trace metals and organic compounds, were measured to provide information on key physical and chemical characteristics of the Salton Sea, including mixing processes, nutrient dynamics, trophic state variables and general water quality conditions.

Review of existing data

In light of recent interest in the area, there is a surprising paucity of published historical water quality data on the Salton Sea. Although several agencies have per-

formed chemical analyses on the Salton Sea, much of this information is unpublished (Thiery, 1999). Thiery indicated that the unpublished information has been collected from different locations over the years and at differing levels of quality.

Major ions

The earliest water quality data on the Salton Sea were presented by MacDougal (1907) and Ross (1915). MacDougal compared the major ion composition of the Salton Sea in 1907 to normal seawater. Ross presented data on cations and anions, as well as total and dissolved solids information, collected in May or June each year from 1907 to 1914. The composition of the Salton Sea underwent dramatic changes during the period when the Sea was forming in 1905–1907 as a result of dissolution of flooded salt deposits. Ross (1915) concluded that leaching of salts from the lake bottom had been completed by 1911. Since that time, fluctuations in water level and continued concentration of salts by evaporation have been the driving forces in changing the salinity of the Salton Sea.

Results collected along several transects in the Salton Sea from November 1953 to January 1955 were reported by Arnal (1961). Arnal compared data from 1907 (MacDougal, 1907), 1913 (Ross, 1915), 1929 (Coleman, 1929) and 1955 (Arnal, 1961) to examine changes in composition over time and to determine salt budgets for the Sea, but indicated that the data presented by Coleman were not very accurate. Arnal also presented data on turbidity and Secchi depth (0.10–3.05 m during the study), as well as data on currents, sediments and micro-organisms.

Some historical data on the major ion (Ca, Mg, Na, K, $CO_3^{=}$, HCO_3^{-}, $SO_4^{=}$, and Cl^{-}) composition of the Salton Sea was summarized by Carpelan (1958, 1961). These reports also provided detailed information on temperature, dissolved oxygen and nutrients (ammonia, nitrate and phosphate) for the period July/August 1954 to June/July 1956. Profiles for temperature, dissolved oxygen and pH were presented, as well as data on chlorinity and sulfide.

Historical chemical analyses of Salton Sea water were summarized by Hely et al. (1966). Data from a variety of sources provided information on major ion analyses (Ca, Mg, Na, K, HCO_3^{-}, $SO_4^{=}$, and Cl^{-}) for the years 1907–1916, 1923, 1929 and 1945–1964. In addition, Hely et al. (1966) calculated salinity for each year in which data was available, as well as water volume (millions of acre-ft) and mineral content (millions of tons) in the Sea.

Setmire et al. (1990) presented major ion concentrations from the Salton Sea area as part of a larger, comprehensive study. Results reported included specific conductance, pH, temperature, Ca, Mg, Na, K, alkalinity, $SO_4^{=}$, Cl^{-}, F^{-}, silica, and dissolved solids from nine tile drains, the Alamo and New River outlets and a composite sample from the Salton Sea. Single samples were collected at each location from 12 to 14 August 1986. Ogden (1996) also reported cation and anion concentrations collected from three stations near the center of the Salton Sea in April 1994.

Water and salt balances in the Salton Sea from its formation through 1989 were examined by Tostrud (1997) using published data, as well as unpublished data from the Imperial Irrigation District (IID) and the Coachella Valley Water District (CVWD). Tostrud estimated that 80 million tons of salt had dissolved from flooded salt deposits and were added to Sea water by 1914. He concluded that calcium, bicarbonates and sulfates have precipitated out of the Sea. The Sea apparently reached saturation with respect to bicarbonate within the first year after its formation. The Sea became saturated with respect to calcium in about 1950 and with respect to sulfate in about 1980. Some sodium has apparently been precipitated. Tostrud suggested that precipitation of $CaCO_3$, $CaSO_4$ and Na_2SO_4 would account for the observed results. Similar results were presented by Ormat (1989, cited in Ogden, 1996). Ormat evaluated analyses of Salton Sea water collected by IID from 1981 to 1987. Ormat concluded that the Salton Sea was saturated with respect to $CaCO_3$ and $CaSO_4$ and that Na_2SO_4 would also precipitate as Salton Sea water is concentrated. Amrhein (2001) is currently using X-ray diffraction to assess mineral formation in Salton Sea sediments, but has not positively identified any minerals that could explain the observed loss of sodium noted by Ormat (1989) and Tostrud (1997).

Nutrients

Carpelan (1958, 1961) measured nitrate-N, ammonia-N and phosphate-P concentrations in surface and bottom samples at four locations in the Salton Sea in 1954–1955, although he indicated absolute values for both nitrate and phosphate were questionable because of the low concentrations present. Average reported concentrations for the four stations ranged from 0.075 to 0.172 mg l^{-1} for ammonia-N, 0.011–0.107 mg l^{-1}

for nitrate-N, and 0.015–0.035 mg l^{-1} for phosphate-P. In all cases, lower concentrations were from mid-Sea stations and the highest concentrations were from a site off Mullet Island affected by the inflow from the Alamo River. Bottom water concentrations for both ammonia-N and phosphate-P were higher than surface concentrations.

The Federal Water Quality Administration (FWQA, 1970) presented information on nutrients in Sea inflows, water and sediment from both the FWQA and the California Department of Water Resources. Data from the period 1963 to 1969 were included in the report, which characterized the Sea as 'objectionably eutrophic'. Information on internal loading and biological characteristics, including fish, invertebrates and phytoplankton was also presented. High algal growth led to dissolved oxygen super-saturation in surface waters and oxygen depletion at the bottom of the water column. Algal growth studies conducted as part of the study indicated nutrients were generally not limiting algal growth, with only one sample showing evidence of phosphorus limitation.

Results from current research being conducted by San Diego State University were presented by Watts et al. (1999). Investigations of nutrient loadings and nutrient concentrations in the Salton Sea compared results from 1967 to 1968 and 1996 to 1997. Total P concentrations were similar for the two periods, averaging 0.095 mg l^{-1} in 1967–1968 and 0.091 mg l^{-1} in 1996–1997. Nitrogen concentrations more than doubled during the same period, with total N increasing from 2.1 mg l^{-1} to 5 mg l^{-1}. Reported concentration ranges for the 1996–1997 period were 0.050–0.200 for total P and 1.6–5.0 mg l^{-1} for total N.

Metals

There is detailed information on selenium, and to a lesser extent boron, in the Salton Sea area (Setmire et al., 1990; Setmire et al., 1993; Setmire & Schroeder, 1998), but there is a lack of routine monitoring data. Setmire et al. (1990) analyzed trace elements (As, Ba, B, Cd, Cr, Cu, Fe, Pb, Mn, Hg, Mo, Ni, Se, Ag, V, Zn) from nine drains, the Alamo and New River outlets and a composite sample from the Salton Sea collected on 12–14 August 1986. Detailed analyses of Se and B in water, sediment and biota samples were presented by Setmire et al. (1990, 1993). The 1993 report contained data collected from 1988 to 1990. A more detailed analysis of Se results, including data from 1994 to 1995, was presented by Setmire & Schroeder (1998).

Pesticides

Irwin (1971) reported results of pesticide analyses for selected tributaries to the Salton Sea collected from August 1969 to June 1970. DDT and its metabolites and dieldrin were found in all samples at the stations from the New (Westmorland, CA) and Alamo (Niland, CA) Rivers closest to the Salton Sea at concentrations up to 11 $\mu g\ l^{-1}$ for the individual metabolites, while dieldrin was found concentrations of 0.01–0.03 $\mu g\ l^{-1}$ at both stations. Methyl parathion, 2,4-D and Silvex were also found in nearly all samples from the two stations. Maximum observed concentrations were 0.03, 0.65, 19 and 1.7 $\mu g\ l^{-1}$ in the Alamo River and 0.19, 1.6, and 0.84 $\mu g\ l^{-1}$ in the New River for methyl parathion, 2,4-D and Silvex, respectively. Endrin, lindane, parathion and 2,4,5-T were detected in some samples at both locations, while aldrin, heptachlor and heptachlor epoxide were not found in any of the samples.

Hogg (1973) examined chlorinated hydrocarbon pesticides in water, sediment and tissue samples from the Salton Sea in 1970–1971. Hogg found DDT and its metabolites in 146 of the 159 samples examined, and dieldrin and its metabolites in 66 of the 159 samples. Total DDT in the water samples was found at a level of 0.006 mg l^{-1} while dieldrin was not detected. In general, pesticide residue concentrations were higher in samples collected from the southern part of the Sea.

Results of organochlorine pesticide analyses were also presented by Setmire et al. (1990, 1993). Those studies included results from sediment and biota samples, but did not measure pesticides in Salton Sea water. Although the use of DDT was banned in the U.S. in 1972 and in Mexico in 1983, its metabolites were still detected in most samples analyzed by Setmire et al. (1993).

Methods

Water quality samples were collected from three lake stations (North Basin, SS-1; Mid-Lake, SS-2; and South Basin, SS-3), as well as from the three main rivers entering the lake (Whitewater River, Alamo River, and New River) (Fig. 1). Salton Sea sampling locations were located using a Rockwell HNV-560B PLGR global positioning system (GPS). The Alamo

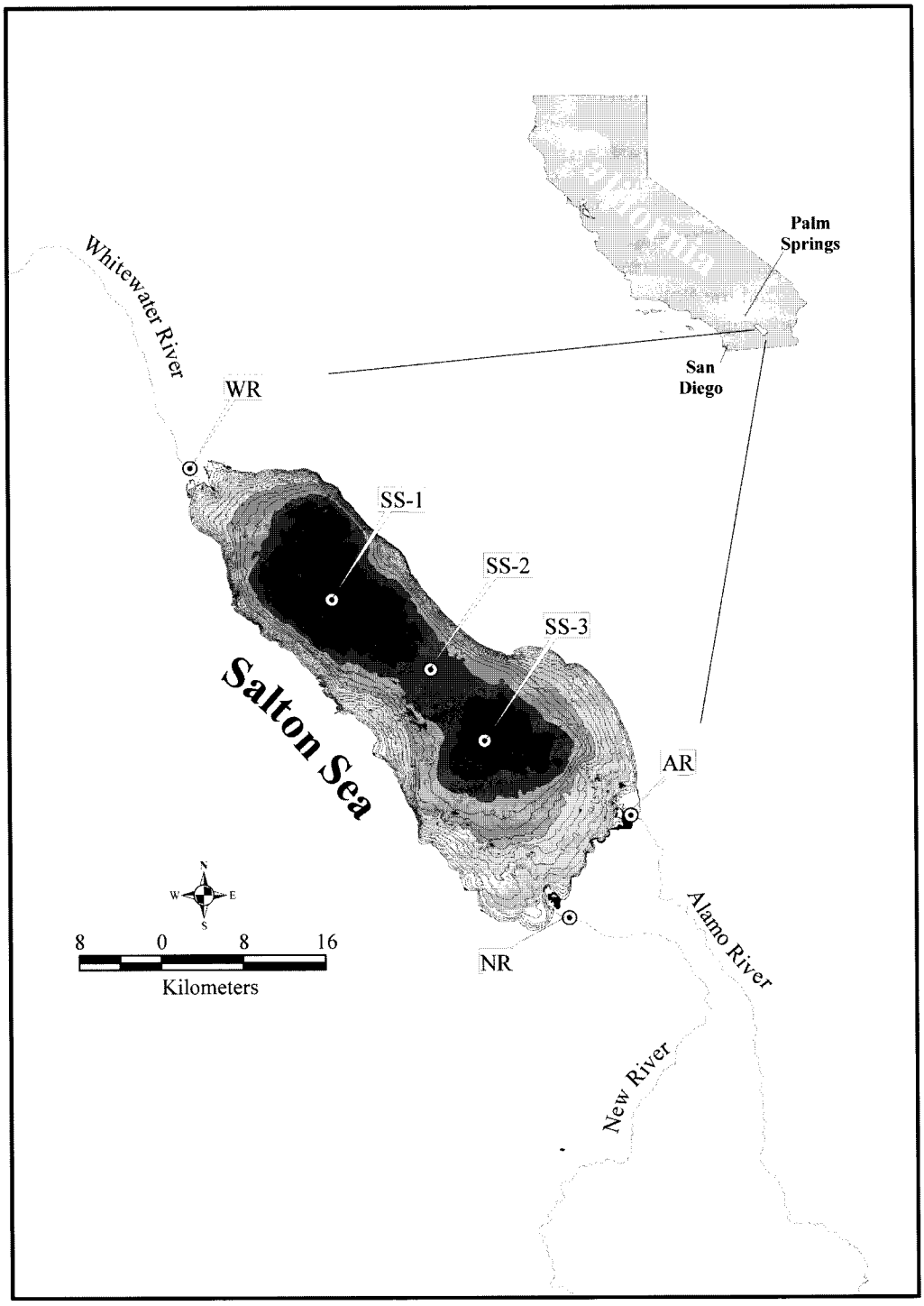


Figure 1. Locations of sampling stations.

River (AR) site was located at the Garst Road bridge just downstream of USGS Station Number 10254730. The New River (NR) site was located west of Lack Road at USGS Station Number 10255550. The Whitewater River (WR) sampling site was located at the Lincoln Street crossing west of USGS Station 10259540.

Samples were collected as surface grabs from the river stations and the lake surface, and with a Kemmerer sampler at other depths. Profiles were measured at 1-m intervals for general chemical and physical variables (temperature, dissolved oxygen concentration, pH, conductivity, turbidity, and oxidation-reduction potential). Samples for other variables were collected at the surface and bottom of the water column from January to March and October to December, and from the surface, bottom of epilimnion, top of hypolimnion, and bottom from April through September.

The sampling program included monthly measurements from January to March and October to December, and biweekly measurements from April through September 1999 for general chemical and physical variables (temperature, dissolved oxygen, pH, conductivity, oxidation-reduction potential, turbidity), light penetration (Secchi depth and 1% light level), and nutrients (soluble orthophosphate, total phosphorus, nitrate+nitrite-N, ammonia-N, total Kjeldahl nitrogen, dissolved organic carbon, and dissolved silica). Major ions were measured in February, May, August, October, and December. All major ion samples included major cations (Ca, Mg, Na, K) and anions ($CO_3^=$, HCO_3^-, $SO_4^=$, Cl^-). In addition, F^-, Sr and B were added for the March, October and December samples. Trace metals (Al, As, Ba, Cd, Cr, Co, Cu, Fe, Pb, Mn, Hg, Mo, Ni, Se, Ag, V, and Zn) and organic compounds (semi-volatile organics and chlorinated pesticides) were measured once in March and once in October.

Profiles were measured with a Hydrolab Surveyor 4 calibrated following manufacturer's instructions. The probe corrects dissolved oxygen readings for salinity with the equation:

$$F = 1 - C \times (3.439 \times 10^{-3} + 0.361/(22.1 + T)^2), \quad (1)$$

where F is the factor correcting dissolved oxygen readings for salinity, C is the specific conductance and T is the temperature in degrees Celsius. The factor F calculated from Equation (1) was approximately 0.8 for conditions at the Salton Sea and agrees to within about 1% with salinity correction factors published by Weiss (1970).

Nutrients were analyzed with a Perstorp segmented flow analyzer. Cations/metals were analyzed with a Thermo-Ash Model ICP-61E or a Varian Techtron Model SpectrAA-220Z atomic absorption spectrophotometer using serial dilution techniques to minimize salt interference. Arsenic, selenium and mercury were analyzed by Frontier Geosciences, Inc., Seattle, WA. Arsenic and selenium were analyzed by hydride generation and mercury was analyzed by oxidation, purge and trap, cold vapor atomic fluorescence spectrometry. A Dionex Model DX-500 ion chromatograph was used for the analysis of $SO_4^=$ and Cl^- and an ion selective electrode was used for F^- analyses. Alkalinity was measured in the field by titration with 0.02 N H_2SO_4 and in the laboratory with a Metrohm Brinkmann Model 716 Auto-Titrator, which was also used for the determination of carbonate and bicarbonate. Semivolatile Organics (EPA Methods 8270/3540) and chlorinated pesticide and PCBs (EPA Methods 8080/3540) were analyzed by gas chromatography using a mass spectrophotometric detector. Light penetration was determined using a Li-Cor LI-1000 data logger equipped with LI-190SA and LI-192SA quantum sensors. Total dissolved solids (TDS) and total suspended solids (TSS) were determined gravimetrically after drying at 180 °C and 103–105 °C, respectively.

Summary results for nutrients, major ions, and solids (Table 1) are presented as whole lake average concentrations. Summary concentrations were calculated by multiplying measured concentrations of samples collected at all depths and stations on each sampling date by corresponding volume increments obtained from current hypsometric factors for the Salton Sea (Bureau of Reclamation, 2000, modified from Ferrari & Weghorst, 1997). Values for months with more than one sampling date were averaged to produce a single observation from each month for both lake and river nutrient samples.

Results and discussion

Temperature

Temperatures followed expected seasonal patterns (Fig. 2), with the maximum surface temperature of 36.5 °C observed at Station SS-3 on 24 August 1999. The maximum observed temperatures for all lake stations were reached on that date. Minimum surface

Table 1. Summary data for 1999

Variable (concentrations in mg l^{-1})	Location			
	Salton Sea	Alamo River	New River	Whitewater River
Ortho-P	0.021	0.408	0.697	0.710
Total P	0.069	0.719	1.11	0.865
Ammonia-N	1.16	1.26	3.72	0.729
Nitrate+Nitrite-N	0.12	6.42	3.55	14.3
Total Kjeldahl N	3.5	2.8	4.7	2.0
Dissolved Organic C	40.9	4.2	8.8	7.6
Dissolved Si	4.60	5.89	7.30	8.62
Calcium	944	166	177	122
Magnesium	1400	83.0	82.8	32.2
Sodium	12 370	389	566	303
Potassium	258	8.17	12.6	9.0
Strontium	22.0	2.88	3.20	1.94
Boron	11.1	0.560	0.879	0.632
Chloride	17 240	443	724	235
Sulfate	10 500	762	716	527
Bicarbonate	245	259	300	245
Carbonate	2	<1	<1	<1
Fluoride	2.1	1.2	1.8	2.6
Total Dissolved Solids	44 090	2020	2440	1550
Total Suspended Solids	36.6	357	217	95.7

temperatures were observed in the Salton Sea on 22 January 1999, with Station SS-3 having the lowest temperature of 14.2 °C. Temperature differences between the top and the bottom of the water column ranged from 1 to 3 °C during the cooler months and from 3 to 9 °C during the summer.

Temperatures in the river samples were generally slightly lower than Salton Sea surface samples. The maximum observed temperatures of 30.5 °C and 30.4 °C for the Alamo and New Rivers, respectively, were observed on 25 August 1999. The maximum observed temperature of 29.6 °C for the Whitewater River was observed on 24 August 1999. The minimum observed temperatures of 11.4, 12.7, and 14.7 °C for the Alamo, New, and Whitewater Rivers, respectively, all occurred on 14 December 1999, when lake surface temperatures were also at minimum levels.

Dissolved oxygen and pxidation reduction potential

Oxygen levels in the Salton Sea are characteristic of a highly eutrophic system. Surface oxygen levels during several months were often greater than 200% of saturation, while some oxygen depletion was observed in the bottom waters of the Salton Sea throughout the year. Hypolimnetic dissolved oxygen concentrations were often severely depleted, with observed concentrations at the lake bottom usually less than 2 mg l^{-1} from April through November. The zone of severe oxygen depletion ranged up to the surface in both August and September (Fig. 3). The maximum observed surface dissolved oxygen concentration at Station SS-1 was less than 1 mg l^{-1} on both September sampling dates. The August and September surface oxygen minima coincided with extensive fish kills.

Dissolved oxygen levels in the rivers flowing into the Salton Sea also exhibited some oxygen depletion, with nearly all measured concentrations below the 90% saturation level. Dissolved oxygen concentrations averaged 77.3, 66.2 and 73.2% of saturation in the Alamo, New, and Whitewater Rivers, respectively.

As expected, oxidation-reduction potential (ORP) closely followed dissolved oxygen concentrations (Fig. 4). The ORP was usually in the range of 200–300 mV at the surface, but dropped to a minimum of −12 mV at the surface at Station SS-1 during the extreme low oxygen event that occurred on 8 September 1999.

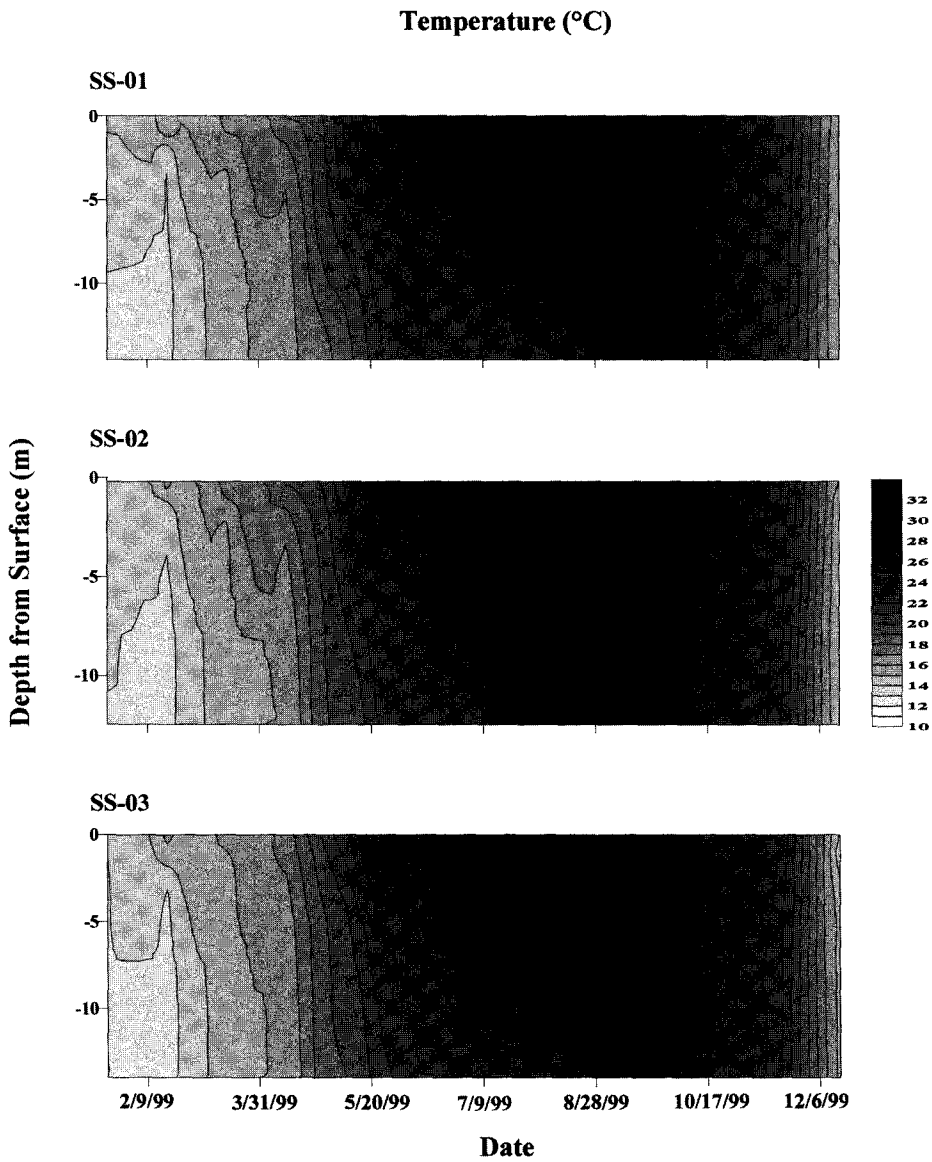


Figure 2. Salton Sea temperature summary for 1999.

Conductivity and total dissolved solids

Conductivities in the Salton Sea exhibited little temporal and spatial variability. Changes in conductivity with depth were also small and inconsistent. Average levels over the entire year were 55.11, 55.19, and 55.23 mS cm^{-1} for Stations SS-1, SS-2, and SS-3, respectively. The minor differences between the stations are less than expected instrumental variation.

Conductivities in the river samples were more variable than those in the Sea, with differences between maximum and minimum values ranging from 26% in the New River to 49% in the Alamo River. Average conductivities were 3.12, 4.09, and 2.17 mS cm^{-1} for the Alamo, New, and Whitewater Rivers, respectively.

Total dissolved solids concentrations were measured both by evaporation at 180 °C and by calculating the sum of the major cations and anions (Ca, Mg, Na, K, $CO_3^{=}$, HCO_3^{-}, $SO_4^{=}$, Cl^{-}). The mean measured TDS concentrations for the Alamo River, New River, and Whitewater Rivers (Table 1) were within 2–8% of the calculated TDS concentrations: 2060, 2520, and 1430 mg l^{-1}, respectively. Directly measured and calculated TDS concentrations for the Salton Sea were

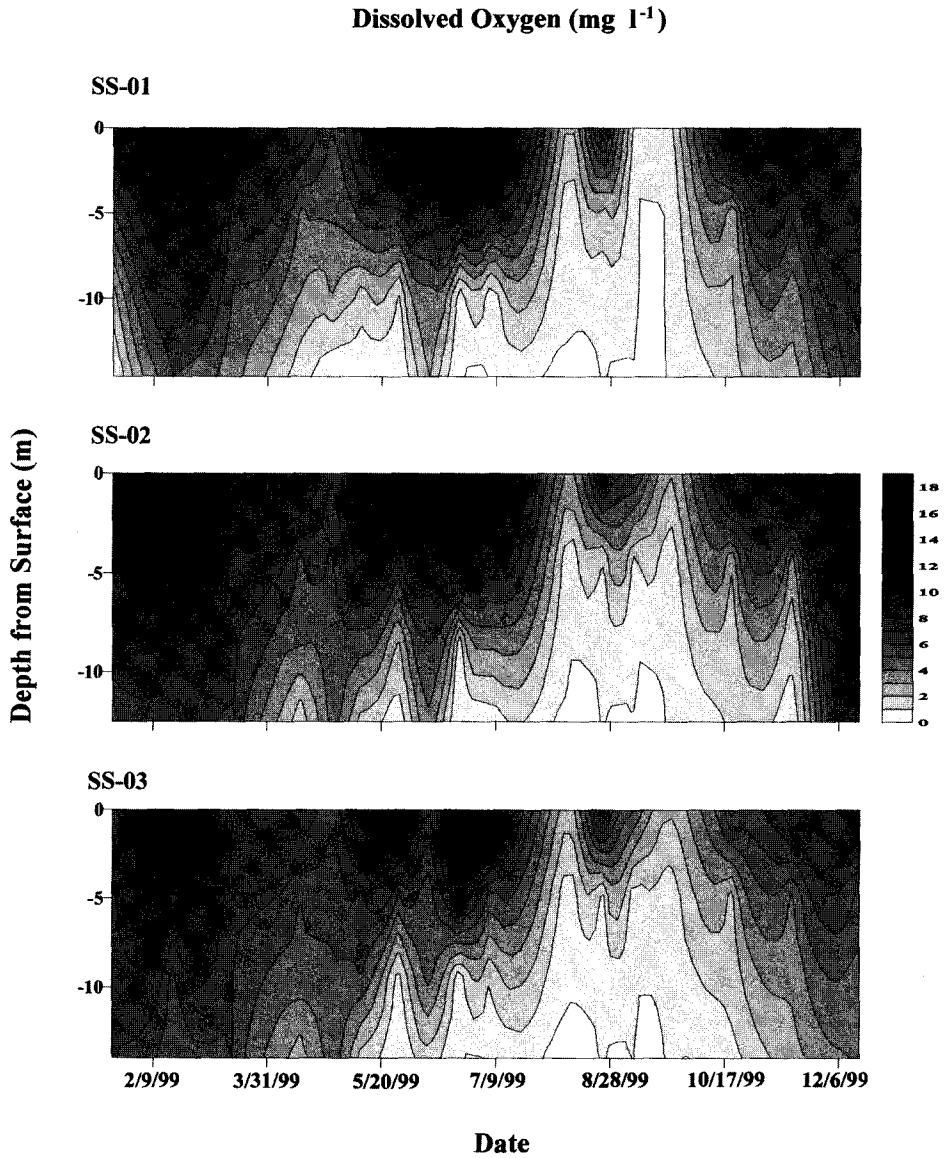


Figure 3. Salton Sea dissolved oxygen concentrations.

43 940 and 42 160 mg l^{-1}, respectively. Note that this measured value of 43 940 mg l^{-1} was based on all measurements made during the sampling program and therefore differs slightly from the weighted mean of 44 090 mg l^{-1} calculated in Table 1.

The difference between calculated and measured TDS concentrations were generally within expected analytical error. The measured concentrations of TDS for the Salton Sea were higher than calculated concentrations, even if minor ions are included. The difference of about 4% could be partially the result of analytical error. Standard Methods (1998) indicates that drying at 180 °C removes most physically occluded water, but water of crystallization may not be completely removed, especially in waters, like the Salton Sea, that are high in sulfate. Many historic analyses at the Salton Sea relied on drying at 103–105 °C. Under those conditions, the occlusion of water during the drying process would lead to even higher reported values for TDS and may represent a significant source of error in older work.

Possible seasonal differences were examined by calculating average TDS concentrations for the summer (June through August), fall (September through

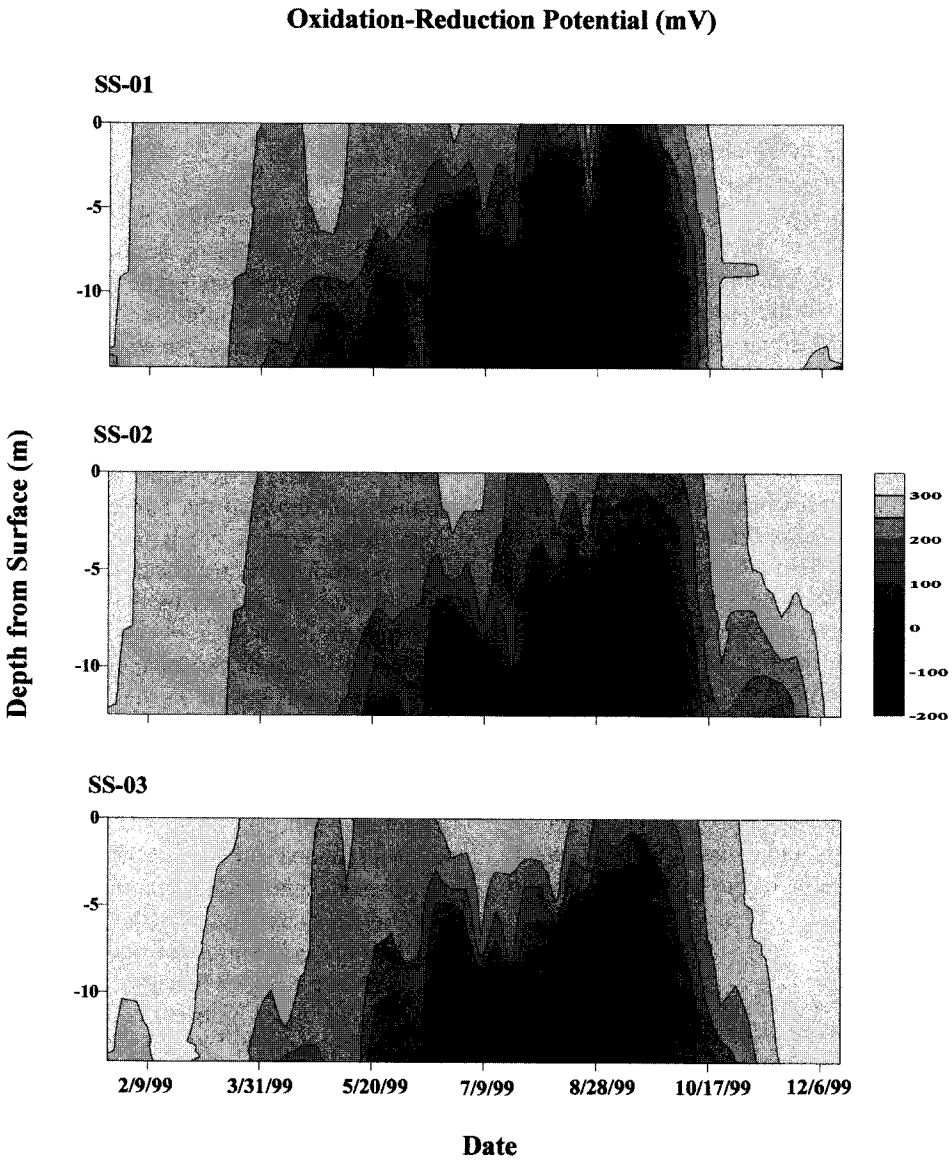


Figure 4. Oxidation-Reduction Potential in the Salton Sea.

November), winter (December through February) and spring (March through April) months. Concentrations were averaged for months with more than one sampling date so as not to skew the seasonal averages. In general, seasonal differences in conductivity and TDS varied by less than 10% from mean annual values and showed no consistent patterns.

Total suspended solids

Total suspended solids levels were high in the river samples (Table 1). The Alamo and New Rivers were always very turbid, with TSS levels ranging from 237 to 480 mg l^{-1} in the Alamo River, and from 87 to 332 mg l^{-1} in the New River. Levels of TSS in the Whitewater River were lower, with a range of 40 to 188 mg l^{-1}.

Concentrations of TSS showed little change during the summer, winter, and spring for the Alamo and New Rivers, with averages of about 360 mg l^{-1} for the Alamo River and 210 mg l^{-1} for the New River during those months. The TSS concentrations were approximately 50 mg l^{-1} lower during the fall months for both rivers. Seasonal variations in the Whitewater

River were more apparent. The summer TSS concentration of 121 mg l^{-1} was over twice as high as the winter concentration of 58 mg l^{-1}, although the change in concentration between the summer and fall months is similar to that of the other two rivers. Seasonal changes in TSS may be related to agricultural operations, with less irrigation during the fall and winter.

As expected, levels of TSS in the Salton Sea were much lower that those in the rivers, indicating that the suspended sediment load rapidly settles out in the Sea. TSS levels in the Sea were also more variable than those in the rivers. Observed TSS concentrations ranged from 9 to 179 mg l^{-1} during the sampling program and *in situ* turbidity measurements ranged from 0 to 479 NTU. In contrast to the river samples, algal cells are expected to be an important component of the TSS levels in the Salton Sea.

Some variations with both season and depth in the water column were noted. In contrast to the river samples, TSS levels in the Salton Sea were highest during the winter and spring, with whole-lake average TSS concentrations of 46 mg l^{-1} and 43 mg l^{-1}, respectively. Lower levels were observed during the fall and summer, with average concentrations of 31 mg l^{-1} and 25 mg l^{-1}, respectively. Surface TSS levels, which averaged 42 mg l^{-1}, were higher than TSS levels at the bottom of the water column, where the average was 26 mg l^{-1}.

pH

There was little variation in pH levels in river samples and only small temporal and spatial variations in samples from the Salton Sea. The pH for the river samples was usually between 7.5 and 7.65, with ranges of only 0.4 units between the high and low values at each station. The surface pH at all three lake stations averaged about 8.2. As is typical of eutrophic lakes, the pH at the surface was frequently more than 1 pH unit higher than the pH at the bottom of the water column.

Secchi depth and light penetration

Secchi depths in the Salton Sea were low, ranging only from 0.4 to 1.4 m. Secchi depths often varied widely between stations on the same sampling date and there were no clear seasonal changes. Light penetration in the Salton Sea was greater than expected based on the low Secchi depths. The depth of 1% light penetration ranged from 1.8 to 4.8 m and was strongly correlated ($\alpha < 0.01$, n=54) with Secchi depth. Average ratios of the depth of 1% light penetration to Secchi depth were 4.2:1 for all three sampling stations.

Nutrients

Nutrient concentrations in the tributaries were much higher than those in the Salton Sea (Table 1). High nutrient concentrations in the river samples originate from intense agricultural activity in the Salton Sea watershed and from wastewater treatment plant discharges, which are especially important for the New River where some of the wastewater is untreated.

Total phosphorus concentrations in the river samples were approximately an order of magnitude higher than those in the Salton Sea (Table 1). Sedimentation, chemical precipitation and burial following incorporation of phosphorus into aquatic organisms are all possible causes of the observed decrease in phosphorus in the Sea.

Relatively high percentages of the phosphorus in the river samples were in the form of soluble orthophosphate, which accounted for 54, 61, and 82% of the total phosphorus in the Alamo, New, and Whitewater Rivers, respectively. As expected, the fraction of soluble orthophosphate was inversely related to the total suspended solids concentrations in the rivers.

Seasonal phosphorus concentrations varied among the three river inflows. The Alamo River had the lowest nutrient concentrations and the greatest seasonal nutrient variation, while the New and Whitewater Rivers had higher nutrient concentrations and lower seasonal variability. This likely occurs because the Alamo River contains primarily agricultural return flows, while the New and Whitewater Rivers also contain wastewater treatment plant effluents. Soluble orthophosphate concentrations were generally lowest during the summer months, with the largest drop occurring in the Alamo River. Total phosphorus concentrations were highest in the winter and spring in the Alamo and New Rivers and in the fall in the Whitewater River.

Concentrations of soluble orthophosphate were frequently below the detection limit of 0.005 mg l^{-1} in the Salton Sea. These low concentrations were observed in one or more of the Sea locations in January and in every month from April through September. This is reflected in the low whole lake averages observed during the spring and summer months (Table 2). Orthophosphate concentrations were highest during the winter months when biological activity is at its

Table 2. Seasonal nutrient concentrations in Salton Sea and tributary samples (all concentrations in mg l^{-1})

Variable	Summer	Fall	Winter	Spring	Annual Mean
Alamo River					
Soluble ortho-P	0.230	0.456	0.492	0.454	0.408
Total P	0.530	0.583	0.744	1.02	0.719
NO_3+NO_2-N	5.00	6.84	6.94	6.91	6.42
NH3-N	0.890	0.629	1.57	1.97	1.26
TKN	2.3	1.6	3.4	4.0	2.8
New River					
Soluble ortho-P	0.548	0.928	0.773	0.537	0.697
Total P	1.01	1.11	1.16	1.15	1.11
NO_3+NO_2-N	2.50	3.41	4.08	4.21	3.55
NH3-N	5.23	3.36	3.55	2.74	3.72
TKN	5.3	4.4	4.7	4.5	4.7
Whitewater River					
Soluble ortho-P	0.632	0.709	0.823	0.675	0.710
Total P	0.753	0.920	0.899	0.889	0.865
NO_3+NO_2-N	15.8	15.4	12.2	13.9	14.3
NH3-N	0.450	0.396	1.52	0.551	0.729
TKN	1.8	1.5	3.1	1.7	2.0
Salton Sea					
Soluble ortho-P	0.010	0.020	0.042	0.011	0.021
Total P	0.053	0.026	0.107	0.088	0.069
NO_3+NO_2-N	0.10	0.05	0.19	0.16	0.12
NH3-N	1.45	1.27	1.17	0.76	1.16
TKN	4.1	4.1	2.3	3.6	3.5

lowest. Total P concentrations were also highest during the winter months, with the lowest concentrations observed in the fall.

Total nitrogen concentrations in the river samples were 30–120 times greater than those in the Salton Sea (Table 1). This difference can be attributed primarily to the high nitrate+nitrite-N concentrations in the rivers, which were more than one to two orders of magnitude greater than concentrations in the Sea. Nitrate+nitrite-N was the major form of nitrogen in the Alamo and Whitewater Rivers, comprising 70 and 88% of the total nitrogen, respectively, for these rivers. In contrast, oxidized nitrogen accounted for only 43% of the total nitrogen in the New River and ammonia concentrations were higher than nitrate+nitrite concentrations. The presence of untreated wastewater in the New River may explain this observation.

Oxidized nitrogen represented far less than 1% of the total nitrogen present in the Salton Sea. In contrast, ammonia-N contributed 32% of the total nitrogen. Ammonia concentrations also varied with depth, with bottom concentrations averaging about 50% higher (1.47 vs. 1.05 mg l^{-1}) than surface concentrations. The higher concentration near the bottom may be indicative of internal nitrogen loading or decomposition of organic matter falling through the water column.

Because nitrate and ammonium salts are generally soluble, uptake by aquatic organisms and denitrification are expected to be the major sinks for nitrogen in the Salton Sea. However, nitrogen levels far exceed those of phosphorus, so biological uptake will be limited by the supply of phosphorus (see below) and cannot explain the large losses of oxidized nitrogen that were observed. As a result, denitrification is the most likely explanation for the observed decreases in oxidized nitrogen in the Salton Sea relative to the inflowing rivers.

Ammonia levels in the Salton Sea exceed water quality standards. The California Ocean Plan (SWRCB, 1997) lists a 6-month median of 0.6 mg l^{-1} and a daily maximum of 2.4 mg l^{-1} as objectives for ammonia (as N) to protect marine aquatic life. The whole-lake mean ammonia-N concentration for 1999 of 1.15 mg l^{-1} was nearly twice the allowable 6-month median. In addition, the daily maximum was exceeded for bottom samples at Stations SS-1 and SS-3. The U.S. EPA (1976) listed an un-ionized ammonia concentration of 0.02 mg l^{-1} (as NH_3, or 0.016 mg l^{-1} as N) as the criterion for freshwater aquatic life. This value was based on observed toxic effects on some species in the range of 0.20–2.0 mg l^{-1}.

There is little information available on the toxicological effects of ammonia on marine species, but ammonia levels in the Salton Sea are higher than the applicable standards and may be contributing to fish toxicity. The sampling event on 10 August 1999 coincided with a major fish kill at Station SS-1. Un-ionized ammonia concentrations for this station and date were calculated following procedures outlined by Messer et al. (1984) and adapted for the high salinity of the Salton Sea by use of the Lewis equations to calculate activity coefficients. The fraction of un-ionized ammonia was estimated from the formula:

$$(M_{NH_3})/[(M_{NH_3}) + (M^{+}_{NH_4})] = 1/[1 + 10^{(pK_{a,T} - pH - s)}], \quad (2)$$

where (M_{NH_3}) is the concentration of un-ionized ammonia; $(M_{NH_3}) + (M^{+}_{NH_4})$ is the analytical concentration of ammonia; $pK_{a,T}$ is the ionization constant of ammonia adjusted for ionic strength, calculated as 9.40, and pH was 8.23. The factor s is a salinity correction term, which was calculated from the Lewis equation:

$$s = -A \times [I^{1/2}/(1 + I^{1/2})] - 0.2\, I, \quad (3)$$

where A is a coefficient that if a function of the dielectric constant and temperature of water and I is the ionic strength of the solution, calculated for the Salton Sea as 0.76 moles l^{-1} from the PHREEQC model (Parkhurst & Appelo, 1999). Although the Lewis equation is generally considered applicable to an ionic strength range of 0.3–0.7 moles l^{-1}, it should be able to provide a reasonable estimate for the slightly higher ionic strength observed in the Salton Sea. The coefficient A was calculated from the formula:

$$A = 1.82483 \times 10^{6} \times [E \times (T + 273.16)]^{-1.5}, \quad (4)$$

where T is the temperature in degrees Celsius (29.35) and E was calculated from the following formula presented by Truesdell & Jones (1974):

$$E = 87.74 - 0.4008 \times T + 9.398 \times 10^{-4} \times T^{2} - 1.41 \times 10^{-6} \times T^{3}. \quad (5)$$

From the above considerations and the analytical ammonia concentration of 1.39 mg l^{-1}, the concentration of un-ionized ammonia at Station SS-1 during the 10 August 1999 fish kill was calculated as 0.054 mg l^{-1}. This value exceeds the U.S. EPA (1976) criterion for un-ionized ammonia. While this concentration is below levels observed to cause toxic effects in freshwater systems, EPA indicated that the toxicity of un-ionized ammonia does increase with salinity. As a result, it is possible that relatively high concentrations of un-ionized ammonia, which represent another stress to fish in the Salton Sea, in addition to the high temperatures, low dissolved oxygen concentrations and high sulfide levels associated with algal blooms, may be contributing to the observed fish kills.

Dissolved silica (Si) concentrations were lower in the Salton Sea than in the river samples. Concentrations of dissolved Si averaged 5.89, 7.30, and 8.62 mg l^{-1} for the Alamo, New, and Whitewater Rivers, respectively. In contrast, the average concentration in the Salton Sea was 4.60 mg l^{-1}. The settling of suspended particulate matter is one probable explanation for the observed decrease, although the highest Si concentrations were found in the Whitewater River, which has the lowest suspended solids load. Differences in soil chemistry between the northern and southern parts of the watershed are the likely reason for this observation.

Inorganic carbon decreased slightly in the Sea relative to levels in the rivers. Average bicarbonate concentrations of varied from 245 mg l^{-1} in the Whitewater River to 300 mg l^{-1} in the New River. Bicarbonate concentrations were relatively constant in the Sea, with a range in whole lake average concentrations of 224–255 mg l^{-1} and a mean of 245 mg l^{-1}.

In contrast to other nutrient concentrations, dissolved organic carbon concentrations increased significantly in the Sea relative to the river concentrations.

Table 3. Nitrogen–phosphorus ratios in Salton Sea and tributary samples

Variable	Summer	Fall	Winter	Spring	Annual Mean
Alamo River					
TN:TP	17.2	16.3	14.3	10.8	14.6
TIN:SOP	27.6	19.2	29.4	19.8	24.0
New River					
TN:TP	8.1	7.7	7.9	7.6	7.8
TIN:SOP	14.6	7.5	12.5	13.3	12.0
Whitewater River					
TN:TP	25.0	19.3	17.0	17.6	19.7
TIN:SOP	28.5	23.3	18.6	21.9	23.1
Salton Sea					
TN:TP	334	316	24.4	100	194
TIN:SOP	479	112	154	165	228

DOC concentrations averaged 4.2, 8.7, and 7.6 mg l^{-1} for the Alamo, New, and Whitewater Rivers, respectively, and 40.9 mg l^{-1} in the Salton Sea.

Limiting nutrient

Nitrogen and phosphorus are the nutrients that usually limit algal growth in natural waters, and relative concentrations of nitrogen and phosphorus are just as, if not more, important than absolute concentrations in structuring phytoplankton communities (Schindler, 1977; Reynolds, 1986). The average N:P ratio of healthy, growing algal cells is 7 to 1 by weight (or between 15 and 16 by atomic ratio). This value, known as the Redfield ratio, is generally assumed to be the ratio in which these nutrients are ultimately required by algal cells (Reynolds, 1986). Generally, large N:P ratios (>7) indicate that growth will be limited by the supply of phosphorus present, while small N:P ratios (<7) indicate that growth will be limited by nitrogen (Schindler, 1977). The ratios of total inorganic nitrogen (TIN=nitrate-N, nitrite-N and ammonia-N) to soluble orthophosphate (SOP) may be more meaningful than the ratio of total nitrogen to total phosphorus because the inorganic nutrient forms are more directly available to support the growth of aquatic organisms. Nitrogen–phosphorus ratios in both the influent rivers and in the Salton Sea were large as a result of low phosphorus concentrations and relatively high nitrogen concentrations (Table 3).

Calculated N:P ratios were similar for the Alamo and Whitewater Rivers, with the highest ratios of both TN:TP and TIN:SOP observed during the summer months and all ratios indicating phosphorus limitation. The N:P ratios for the New River were much lower than for the other two rivers, possibly reflecting the presence of untreated wastewater in the New River. The highest ratios again occurred during the summer, but the lower values observed did not clearly indicate the limiting nutrient.

The N:P ratios in the Salton Sea were extremely high (Table 3). The highest ratios were observed during the summer months when algal growth would be at a maximum. Annual N:P ratios were near 200:1 for both TN:TP and TIN:SOP. The winter TN:TP ratio of 24.4, resulting from relatively high TP levels and low TKN levels, was the only ratio less than 100:1. These high levels clearly indicate that phosphorus is the limiting nutrient in the Salton Sea.

Trophic state indices

A trophic state index provides a relative expression of the biological productivity of a lake. The Trophic State Index (TSI) developed by Carlson (1977) is among the most commonly used indicators of lake trophic state. A TSI of less than 35 indicates oligotrophic conditions, a TSI between 35 and 50 indicates mesotrophic conditions, and a TSI greater than 50 indicates eutrophic conditions. Hypereutrophic, or excessively productive lakes, have TSI values greater than 70.

Higher numbers are associated with increased probabilities of encountering nuisance conditions, such as excessive macrophyte growth and algal scums.

The Carlson TSI was developed from a data set on lakes primarily from the Great Lakes region of the United States and from Northern Europe. As a result, application of these indices to the Salton Sea may be questionable; however, these indices have been widely applied (and misapplied) to many other lake systems and can at least provide some indication of the trophic state of the Salton Sea.

Trophic state indices for the Salton Sea were calculated using data collected during the months of May through September because Carlson (1977) suggested that summer average values might produce the most meaningful results. The average concentrations during these months of 0.049 mg l^{-3} and 0.89 m for total phosphorus and Secchi depth, respectively, result in trophic state indices of 60 and 62, which place the Salton Sea in the eutrophic range.

Major ions

Concentrations of major ions in the Salton Sea have undergone many changes since the Sea was formed (Fig. 5). Major ion concentrations increased dramatically from the time the Sea was formed to the mid-1920s as a result of dissolution of salts from underlying soils and concentration resulting from volume loss by evaporation. Slight decreases were observed in the 1940s and 1950s as the volume of the Sea expanded with increasing agricultural runoff. Concentrations have increased from the 1960s to present as a result of evaporative concentration and relatively stable water levels.

Concentrations of nearly all major ions are higher in the Sea than in the rivers. The only exception is bicarbonate, which has a slightly lower concentration in the Sea than in a flow-weighted average of river concentrations. The most soluble ions, sodium, potassium and chloride, are enriched in the Sea by factors of 25–30 over river concentrations. Magnesium concentrations are about 17 times as high in the Sea compared to the rivers and sulfate concentrations are 14 times as high.

Cation concentrations show less relative variation with time than anion concentrations. Relative potassium concentrations have remained fairly constant, comprising 0.7 and 0.6% of the total ions in 1907 and 1999, respectively. Relative sodium concentrations decreased from 32.0 to 28.8% percent and relative calcium concentrations decreased from 2.9 to 2.2% of the total ion concentration between 1907 and 1999. In contrast, magnesium concentrations have increased from 1.9 to 3.3% of the total. The observed changes in relative cation concentrations are a function of both individual ion solubilities and loadings from the Colorado River.

Bicarbonate has undergone the greatest relative change of the major ions, decreasing from 1.6% of the total major ion concentration in 1916 to 0.6% in 1999. A decrease in bicarbonate would be expected if the Sea became saturated with respect to bicarbonate within a year after its formation as suggested by Tostrud (1997), because concentrations of other, more soluble ions would continue to increase at a faster rate than bicarbonate.

Sulfate has increased from 13.7% of the total ions in 1907 to 24.4% in 1999. The increase in sulfate is partially balanced by a decrease in chloride from 48.9% of the total in 1907 to 40.1% in 1999. This change can be attributed to the composition of Colorado River water, which contributed over 2.5 times more sulfate than chloride to the Salton Sea basin between 1905 and 1989 (Tostrud, 1997).

At present, the major ion composition of the Salton Sea is different from most other saline lakes because of the relatively large concentration of sulfate. If the Sea has indeed reached saturation with respect to sulfate, as suggested by Ormat (1989), Tostrud (1997), and geochemical modeling conducted during this study (see below), two significant changes will occur. First, the increase in salinity will be less than predicted by current models because sulfate minerals should begin to precipitate, and second, the long-term trends of relative concentrations of increasing sulfate and decreasing chloride should eventually reverse.

Trace metals and organic compounds

Trace metal concentrations were all low (Table 4). This is not surprising because of relatively high concentrations of sulfide in the Salton Sea and the low solubility of most heavy metal sulfides.

The only metals with high concentrations were total iron and aluminum. The concentration of dissolved iron was nearly two orders of magnitude lower than the total iron concentration and the concentration of dissolved aluminum was at or below the detection limit of 30 $\mu g\ l^{-1}$. This indicates that both of these metals were associated with soil particles in the river samples.

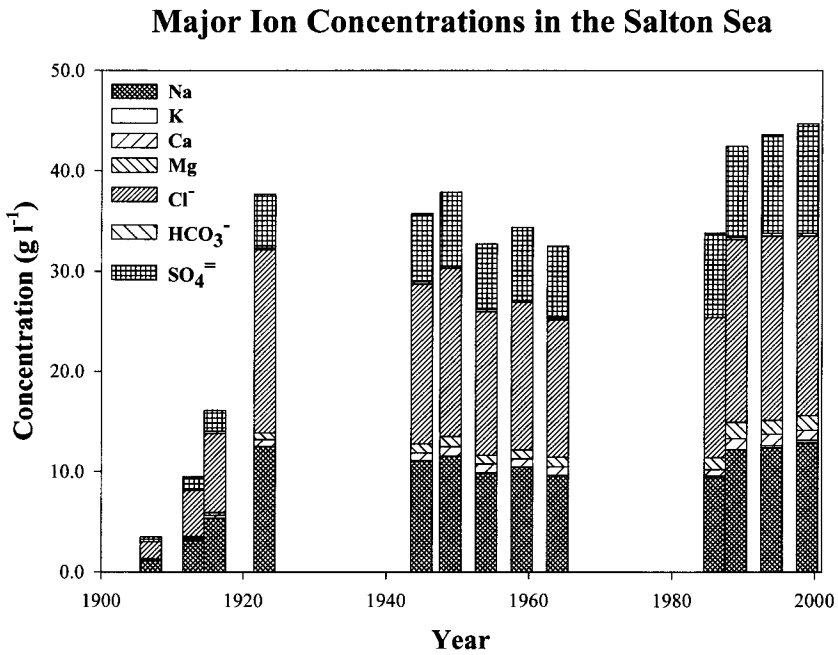


Figure 5. Major Ion Concentrations in the Salton Sea. Data from Ross, 1915 (1907 and 1913); Hely et al., 1966 (1916, 1923, 1945, 1949, 1954, 1959, 1964); Setmire et al., 1990 (1986), Tostrud, 1997 (1989), Ogden, 1996 (1994) and this study (1999). Hely et al. (1966) and Tostrud (1997) presented only a sum for sodium and potassium, which was plotted as sodium; Ross (1915) did not report bicarbonate for the 1907 data set and Setmire et al. (1990) did not include bicarbonate concentrations for the 1986 data set.

Selenium is of concern for many water bodies in the southwest, but was not present at elevated concentrations in the Salton Sea. Like all of the other trace metals, selenium concentrations were lower in the Salton Sea than in the rivers (Table 4), and the Salton Sea concentration of 1.1–2.1 $\mu g\ l^{-1}$ is well below levels of concern for aquatic life.

Semi-volatile organics and chlorinated pesticides were not detected in the river inflows during the current study. Two pthalate esters, di-n-octylphthalate and bis(2-Ethylhexyl)phthalate were present at concentrations of 5.4 and 46 $\mu g\ l^{-1}$, respectively, at Station SS-1 on the 20 October 1999 sampling date. The former compound was present just above the detection limit of 5 $\mu g\ l^{-1}$ and the latter result is in question because the analyte was also detected in the method blank. These compounds are widely used as plasticizers and their presence at these low levels is not a water quality concern. The lack of organic compounds in the Salton Sea is consistent with previous studies and is not surprising given the low solubility of these compounds in water.

Nutrient and solids loadings

Data from the sampling program was used in conjunction with discharge data to calculate loadings from runoff for total P, total N, total suspended solids and total dissolved solids. The average annual inflow to the Salton Sea was reported as 1346 000 acre-ft in the Salton Sea Restoration Draft EIS/EIR (Salton Sea Authority/USBR, 2000). This total is composed primarily of 620 000 acre-ft from the Alamo River (46.1% of the total), 438 000 acre-ft from the New River (32.5%), 79 000 acre-ft from the Whitewater River (5.9%), and 106 000 acre-ft from agricultural drains (7.9%). Other inflows include groundwater (3.7%), direct precipitation (3.5%), San Felipe Creek (0.4%), Salt Creek (0.1%) and other (1.3%). The first four sources listed account for 92.4% of the average annual inflow to the Salton Sea and may be expected to account for an even higher percentage of the total pollutant loading.

Actual discharge data for 1999 for the three influent rivers (Rockwell et al., 2000, and provisional data) and the average data from the agricultural drains were used to calculate nutrient and solids loads for 1999. The measured discharges were 617 130 acre-ft measured at USGS Station Number 10254730, Alamo River near Niland, CA; 488 080 acre-ft measured at

Table 4. Trace metal concentrations in Salton Sea and river samples collected on 15–16 March and 19–20 October 1999

Variable	Location (total metal concentrations in $\mu g\ l^{-1}$)			
	Salton Sea	Alamo River	New River	Whitewater River
Aluminum	<30	14 900–18 800	4340–7530	2070–3590
Arsenic	1.55–9.95	5.33–6.98	4.23–6.74	6.05–7.35
Barium	65–80	162–176	104–146	58–75
Cadmium	<4	<4	<4	<4
Chromium	<4	10–14	4.5–6.1	<4
Cobalt	<3–3.4	3.8–7.9	<3	<3
Copper	<4	7.4–10.9	4.3–4.7	<4–4.1
Iron	8.3-65	8070–9320	2160–4220	1910–3230
Lead	<30	<30	<30	<30
Manganese	17–59	186–253	190–205	87–91
Mercury	0.001–0.030	0.009–0.011	0.017–0.017	0.006–0.006
Molybdenum	<10–12	<10-13	12–17	33–39
Nickel	<10	<10–15.1	10–12.5	<10
Selenium	1.1–2.1	5.9–6.6	3.4–3.5	2.4–2.5
Silver	<4	<4	<4	<4
Vanadium	<4–7.5	30–31	12–16	16–18
Zinc	<4–4.1	28-40	14–18	16–31

USGS Station Number 10255550, New River near Westmorland, CA; and 52 984 acre-ft measured at USGS Station Number 10259540, Whitewater River near Mecca, CA. Discharges for the Alamo and Whitewater Rivers were below the long-term averages and the New River discharge was higher; however, the total discharge from the three rivers of 1158 200 acre-ft was less than 2% above the long-term average.

Although there was a general tendency for concentrations of both nutrients and solids to increase with increasing flow, there were no consistently strong correlations with flow for all three of the major inflows, and differences in flow varied by less than a factor of three between maximum and minimum flows for all of the three major rivers. As a result, data from the 18 sampling dates were multiplied by river flows on those dates to determine daily loadings. The calculated daily loadings were averaged and multiplied by 365 to determine the annual load. Loadings from the agricultural drains were calculated by assuming those loads were in proportion to the flows from the agricultural drains and the Alamo River because both discharges are draining land with similar uses (Setmire, 2000).

The calculated total dissolved solids loading of 3 434 000 tonnes yr^{-1} (Table 5) is only 73% of the loading projected from the average TDS inflow concentration of 2800 mg l^{-1} reported in the Salton Sea EIS/EIR (Salton Sea Authority/USBR, 2000). However, our estimate is consistent with a recent examination of salt loads by Weghorst (2001), who found an average salt loading of 3290 000 tonnes yr^{-1} for 1985–2000.

Watts et al. (1999) presented nitrogen and phosphorus loadings for the periods 1967–1968 and 1997–1998, and Cagle (1998) calculated nutrient loadings using data collected by the California Regional Water Quality Control Board from 1980–1992. These results were compared with nutrient loadings from this study (Table 6). Some variations in both concentration and loading were expected because the different studies have used different sampling sites and frequencies, and different methods for evaluating results. It is clear, however, that nutrient loadings to the Salton Sea have been increasing, but their impacts on nutrient concentrations in the Sea are variable.

Watts et al. (1999) found no difference in nitrogen loading to the Salton Sea between the 1967–1968 and 1996–1997 time periods, but reported that total nitrogen concentrations more than doubled. In contrast, both Cagle (1998) and this study found higher nitrogen loadings than those reported by Watts et al. (1999). This study found lower total nitrogen concentrations than those reported by Watts et al. (1999) for 1996–1997, but still showed a significant increase over the

Table 5. 1999 nutrient and solids loadings for the Salton Sea

Source	Pollutant (annual load, tonnes yr^{-1})			
	Total P	Total N	TSS	TDS
Alamo River	574	7080	281 100	1 584 000
New River	660	4960	132 700	1 480 000
Whitewater River	52	1030	6020	96 600
Agricultural Drains	99	1220	48 300	272 000
Total	1385	14 300	468 100	3 434 000

Table 6. Current and previous nutrient loadings and concentrations for the Salton Sea

Dates	Total P		Total N	
	Concentration (mg l^{-1})	Annual load (tonnes yr^{-1})	Concentration (mg l^{-1})	Annual load (tonnes yr^{-1})
1967–1968[a]	0.095	663	2.1	11 400
1980–1992[b]	–	1135	–	12 500
1996-1997[a]	0.091	1515	5	11 400
1999[c]	0.069	1385	3.6	14 300

[a] Watts et al. (1999).
[b] Cagle (1998).
[c] This study.

1967–1968 levels. It appears the total nitrogen load to the Salton Sea has increased between 0 and 25% over the past 30 years, accompanied by an increase of total nitrogen concentrations of between 70 and 140%.

In contrast to the nitrogen results, total P loadings to the Sea have apparently doubled over the past 30 years, but total P concentrations in the Sea are apparently decreasing. As noted previously, sedimentation, chemical precipitation and burial following incorporation into aquatic organisms are all possible phosphorus sinks. Some phosphorus is undoubtedly lost through sedimentation of soil particles entering the Sea, but it is unlikely that the rate of sedimentation has changed dramatically. Geochemical modeling (see next section) indicates the Sea is often supersaturated with respect to hydroxyapatite [$Ca_5(PO_4)_3OH$], as well as other phosphate minerals. While direct precipitation of hydroxyapatite is known to be kinetically hindered, it often forms initially on the surface of calcite crystals (Stumm & Morgan, 1981) and should be forming in the Salton Sea. The incorporation of phosphorus in fish tissue and bone and in the shells of aquatic invertebrates would be another means of phosphorus removal. Once incorporated into bone or shell material, the insolubility of hydroxyapatite would prevent re-dissolution of the precipitated phosphorus to provide a permanent removal mechanism.

Geochemical modeling

The geochemical programs PHRQPITZ (Plummer et al., 1988) and PHREEQC (Parkhurst & Appelo, 1999) were used to evaluate the equilibrium conditions that may affect the concentrations of various ions in the Salton Sea. PHRQPITZ uses the Pitzer virial coefficient approach for activity coefficient corrections. It was designed for geochemical calculations in brines and other electrolyte solutions with high concentrations. The database used for the program has been partially validated for the system Na-K-Mg-Ca-H-Cl^--$SO_4^=$-OH^--HCO_3^--$CO_3^=$-CO_2-H_2O, and extended with largely untested data for Fe, Mn, Sr, Ba, Li and Br and provisions for temperatures other than 25 °C. Because the temperature dependence on the solubility of many minerals in the PHRQPITZ database is not known, large errors could result for calculations at temperatures other than 25 °C. PHREEQC is a more versatile program; however, it uses ion-association and Debye-Huckel expressions to account for the non-ideality of aqueous solutions. These corrections may

Table 7. Input data for geochemical models

Variable	Location (concentrations in mg l^{-1})					
	Salton Sea			River composite		
	Average	1/22/1999	8/24/1999	Average	1/21/1999	8/25/1999
Ortho-P	0.021	0.003	0.003	0.510	0.624	0.392
NH_3-N	1.16	0.858	1.13	2.22	2.13	2.58
NO_3+NO_2-N	0.12	0.174	0.076	5.45	5.80	5.00
Si (as SiO_2)	9.84	10.8	8.13	14.0	12.3	17.5
Ca	944			168		
Mg	1400			80.8		
Na	12 400			454		
K	258			9.9		
Sr	22.0			2.97		
B	11.1			0.686		
Cl^-	17 200			543		
$SO_4^=$	10 500			734		
HCO_3^-	245			274		
$CO_3^=$	2			0		
F^-	2.1			1.5		
Temp. (°C)	23.0	14.3	29.9	22.6	15.4	30.3
PH	8.12	8.24	7.97	7.58	7.56	7.71
Pe	3.09	5.06	0.085	5.02	4.99	5.51
DO	5.48	7.41	2.71	6.41	7.30	4.34
Density (kg l^{-1})	1.04			1.0		

break down for ionic strengths in the range of seawater and above, particularly in systems, like the Salton Sea, which are not dominated by sodium chloride.

Both models were used to evaluate the equilibrium status of minerals within the Salton Sea and the precipitation of minerals resulting from salt loading from the rivers. Weighted mean concentrations of major ion profiles for the Salton Sea and a composite river concentration, calculated by flow-weighting mean concentrations for the Alamo, New and Whitewater Rivers, with flows from the agricultural drains added to the Alamo River flow, were used as model inputs (Table 7). Profiles for the dates with the maximum (24 August 1999) and minimum (22 January 1999) observed temperatures were used to evaluate the impacts of temperature on chemical equilibria.

Results from the two programs were similar, although greater solubilities were predicted by PHRQPITZ, primarily as a result of lower calculated activities for Ca^{++} and $SO_4^=$. More mineral phases were available for evaluation through PHREEQC, particularly when the database from the program Wateq4f was used. These programs were used to determine which minerals should be precipitating under current conditions in the Salton Sea.

Both programs indicated that the Salton Sea is currently super-saturated with respect to calcite ($CaCO_3$), gypsum ($CaSO_4 2H_2O$), magnesite ($MgCO_3$) and dolomite [$CaMg(CO_3)_2$]. The larger database for PHREEQC also indicated super-saturation with respect to celestite ($SrSO_4$), huntite [$CaMg_3(CO_3)_4$], and several silicate minerals. Saturation levels were exceeded for the phosphate minerals, hydroxyapatite [$Ca5(PO_4)_3OH$] and fluorapatite [$Ca5(PO_4)_3F$], for phosphate concentrations greater than 0.005 mg l^{-1}. Both programs also predicted that the composite river sample was super-saturated with respect to calcite, dolomite, and magnesite, and PHEEQC also calculated super-saturation with respect to hydroxyapatite and fluorapatite in the rivers.

While the geochemical programs predict that the Salton Sea is super-saturated with respect to the minerals listed above, they do not provide proof of precipitation. Kinetics and other unknown factors can influence precipitation. The problem of super-saturation with respect to hydroxyapatite was mentioned earlier, however, it is likely that both hydroxyapatite and fluorapatite are forming in the Salton Sea, and their formation would provide a sink for phosphorus. Celestite is found mostly as a minor constituent in limestones but

may form in the sulfate-rich environment of the Salton Sea. The prevalence of dolomite super-saturation has been widely discussed in the geochemical literature (Berner, 1971; Krauskopf, 1979). Seawater and many saline lakes are super-saturated with respect to dolomite, but this mineral is not known to form except under extreme saline conditions and is not expected to be forming in the Salton Sea. Likewise, it is unlikely that either magnesite or huntite are forming in significant amounts.

Calcite readily forms in lake systems and is expected to be forming in the Salton Sea. Several independent observations also support gypsum formation. These include direct observations of gypsum crystals in Salton Sea sediments by principal investigators of other reconnaissance studies on the Salton Sea (LFR Levine Fricke, 1999; Dexter & Hurlbert, 2000; Amrhein, 2001) and precipitation of gypsum in unpreserved samples stored in this laboratory after analysis.

Although both Ormat (1989) and Tostrud (1997) postulated precipitation of a sodium sulfate mineral to account for the ion balance in the Sea, PHREEQC indicated this was unlikely. Saturation indices were -1.75 for mirabilite ($Na_2SO_4 10H_2O$) and -2.69 for thenardite (Na_2SO_4), indicating that neither of these minerals is close to saturation. In addition, sodium sulfates do not form in seawater (Krauskopf, 1979), except as evaporites. This leaves substitution in other minerals, the adsorption of Na^+ on clay minerals, or formation of some other unidentified mineral, as possible explanations for the observed sodium loss.

Additional evaluations of chemical equilibria in the Salton Sea were made by using the geochemical programs to equilibrate Sea water with calcite and gypsum, the two minerals that currently exceed saturation levels that are the most likely to be forming at the present time, as well as with atmospheric carbon dioxide. The amount of these minerals that would need to precipitate to establish equilibrium was calculated for a mixture of Salton Sea water and composite river water (Table 7), followed by evaporation to the original volume to mimic current conditions of salt loading to the Sea, as well as for average Sea water alone.

Each program produced similar results for the two scenarios, although in both cases greater amounts of salt were calculated to precipitate under the PHREEQC program because of the higher ion activities for calcium and sulfate with PHRQPITZ. The total dissolved solids concentration of Salton Sea water in equilibrium with calcite, gypsum, and atmospheric carbon dioxide was calculated as 42.1 g l^{-1} by PHREEQC and 42.3 g l^{-1} by PHRQPITZ, salinity levels that were reached in the Salton Sea in about 1989 (Weghorst, 2001). The amount of $CaCO_3$ and $CaSO_4 2H_2O$ precipitation required to reach these levels from the current concentration of 43.1 g l^{-1} calculated from the average concentrations of the major ions was also calculated from both programs. In order to reach equilibrium with calcite and gypsum, PHREEQC required precipitation of about 1.1 g l^{-1} of calcite and gypsum (water of hydration was not included for gypsum) and PHRQPITZ required precipitation of 0.7 g l^{-1}. When applied to the entire volume for the Salton Sea of 9.41×10^9 m^3, these values correspond to 1.1×10^{10} and 6.6×10^9 kg, respectively, for the two programs, or 1.5–2.5% of the total salt in solution and 2–3 times the calculated annual salt load from the rivers.

The above considerations indicate that the Salton Sea is not at equilibrium with respect to the formation of calcite and gypsum, but that these minerals may be precipitating in the Sea. Precipitation of calcite, and particularly gypsum, would slow the rate of salt accumulation in the water column, which is of major concern for proposed restoration alternatives. Additional evidence for precipitation was provided by Tostrud (1997), who evaluated salt inputs from Colorado River water and the amounts of salt in the Sea water in 1989, to predict a drop in salt gain of about 1/3 of the inflow beginning in 1980. This drop resulted from salt precipitation, which was calculated to be about 1.469 million tons/yr from 1980 through 1996.

Conclusions

The Salton Sea is a eutrophic saline lake characterized by very low oxygen concentrations leading to frequent fish kills during the summer months. Nutrient ratios indicate that algal growth in the Sea should be phosphorus limited and management efforts should focus on phosphorus removal. Although phosphorus loadings to the Salton Sea have doubled over the past 30 years, phosphorus concentrations appear to have decreased. Both biotic mechanisms, such as incorporation of phosphorus in fish tissue and bone and in the shells of aquatic invertebrates, and abiotic mechanisms, such as sedimentation and precipitation of hydroxyapatite, may account for this observation.

Nitrate concentrations are high in the influent rivers but very low in the Sea. Denitrification is the

most likely explanation for this decrease. In contrast, ammonia concentrations show little reduction relative to river concentrations and remain high in the Salton Sea. Ammonia levels are high enough to lead to un-ionized ammonia concentrations above regulatory limits. Ammonia toxicity represents an additional stress that may have synergistic effects with low oxygen levels and high temperatures to lead to fish kills.

The Salton Sea is currently super-saturated with respect to several minerals, including calcite, gypsum, celestite, hydroxyapatite and fluorapatite. Formation of the first three of these minerals may lead to precipitation of calcium, strontium and some of the sulfate entering the Sea, while formation of the apatites could provide a sink for phosphorus.

The geochemical models PHREEQC and PHRQPITZ indicated that precipitation of 1.5–2.5% of the total amount of salt currently in the Sea, or 2–3 times the average annual salt inflow, would be required for the Salton Sea to reach equilibrium with respect to calcite and gypsum. Depending on the rate and extent of the precipitation actually occurring, salt levels are expected to rise at a slower rate in the future than in the period prior to about 1989 when the gypsum saturation level was reached.

Acknowledgements

Funding for the project was provided to the U.S. Bureau of Reclamation through grant number R826552-01 from the U.S. EPA to the Salton Sea Authority. Logistical support was provided by North Shore State Park and the Sonny Bono Salton Sea National Wildlife Refuge. The Yuma Area Office and the Denver Technical Service Center of the U.S. Bureau of Reclamation provided sampling support for the project. David Parkhurst, USGS, Denver, CO, provided assistance with the geochemical modeling.

References

Amrhein, C., 2000. Personal communication, January 2001. Chris Amrhein, University of California-Riverside, and G. Chris Holdren, U.S. Bureau of Reclamation.

Arnal, R. E., 1961. Limnology, sedimentation and microorganisms of the Salton Sea, California. Geol. Soc. am. Bull. 72: 427–478.

Berner, R. E., 1971. Principles of Chemical Sedimentology. McGraw-Hill Book Company, New York.

Bureau of Reclamation, 2000. Salton Sea Restoration Project, Draft Alternatives Appraisal Report. Bureau of Reclamation, Lower Colorado Region, Boulder City, NV.

Cagle, F., 1998. Geomedicine in the Salton Basin. In Lowell, L. (ed.), Geology and Geothermal Resources of the Imperial and Mexicali Valleys. San Diego Association of Geologists: 169–187.

Carlson, R. E., 1977. A trophic state index for lakes. Limnol. Oceanogr. 22: 361–369.

Carpelan, L. H., 1958. The Salton Sea. Physical and chemical characteristics. Limnol. Oceanogr. 3: 373–386.

Carpelan, L. H., 1961. Physical and chemical characteristics. In Walker, B. W. (ed.), The Ecology of the Salton Sea, California, in Relation to the Sportfishery. Cal. Dept. Fish Game, Fish Bull. 113: 17–32.

Coleman, G. A., 1929. (cited by R.E. Arnal, 1961). A biological survey of the Salton Sea. Calif. Fish and Game 15(2): 218–227.

Dexter, D. & S. Hurlbert, 2000. Personal communication, January, 2000. Deborah Dexter and Stuart Hurlbert, San Diego State University, and G. Chris Holdren, U.S. Bureau of Reclamation.

Ferrari, R. L. & P. Weghorst, 1997. Salton Sea 1995 Hydrographic GPS Survey. Bureau of Reclamation, Water Resources Services, Technical Service Center, Denver, CO.

FWQA, 1970. Salton Sea, California. Water Quality and Ecological Management Considerations. U.S. Department of the Interior, Federal Water Quality Administration, Pacific Southwest Region.

Hely, A. G., G. H. Hughes & B. Irelan, 1966. Hydrologic regimen of Salton Sea, California. Water resources of Lower Colorado River-Salton Sea area. A study of the variations in water level and water quality and their causes. Geological Survey Professional Paper 486-C. U.S. Government Printing Office, Washington.

Hogg, N. D., 1973. Chlorinated Hydrocarbon Pesticide Residues, Salton Sea, California. M.S. Thesis. California State Polytechnic University, Pomona, CA.

Irwin, G. A., 1971. Water quality data for selected sites tributary to the Salton Sea, California, August 1969–June 1970. USGS Open File Report 7414-10.

Krauskopf, K. B., 1979. Introduction to Geochemistry, Second Edition. McGraw-Hill Book Company, New York.

LFR Levine Fricke, 1999. Environmental Reconnaissance of the Salton Sea: Sediment Contaminants. Riverside and Imperial Counties, California. LFR Levine Fricke Report No. 6824.00-03, submitted to the Salton Sea Authority, La Quinta, CA.

MacDougal, D. T., 1907. Desert basins of the Colorado Delta. Am. Geog. Soc. Bull. 39:705–729.

Messer, J., J. Ho & W. J. Grenney, 1984. Ionic strength correction for extent of ammonia ionization in freshwater. Can. J. Fish. aquat. Sci. 41: 811–815.

Ogden, 1996. Salton Sea management project: Evaluation of salinity and elevation management alternatives. Report prepared for the Salton Sea Authority by Ogden Environmental and Energy Services Co., Inc., San Diego, CA.

Ormat, 1989. Salton Sea project: Preliminary study. Report prepared by Ormat Technical Services, Sparks, NV.

Parkhurst, D. L. & C. A. J. Appelo, 1999. User's Guide to PHREEQC (Version 2) – A Computer Program for Speciation, Batch-Reaction, One-Dimensional Transport, and Inverse Geochemical Calculations. Water-Resources Investigations Report 99-4259. U.S. Department of the Interior, U.S. Geological Survey, Denver, CO.

Plummer, L. N., D. L. Parkhurst, G. W. Gleming & S. A. Dunkle, 1988. A Computer Program Incorporating Pitzer's Equations for Calculation of Geochemical Reactions in Brines. U.S. Geological Survey Water-Resources Investigations Report 88-4153. U.S. Geological Survey, Reston, VA.

Reynolds, C. S., 1986. The Ecology of Freshwater Phytoplankton. Cambridge University Press, New York.

Rockwell, G. L., S. W. Anderson & J. Agajanian, 2000. Water Resources Data – California, Water Year 1999. Volume 1 – Southern Great Basin from Mexican Border to Mono Lake Basin, and Pacific Slope Basins from Tijuana River to Santa Maria River. USGS.

Ross, W. H., 1915. The chemical composition of the water of the Salton Sea, and its annual variation in concentration. In Cory, H. T. (ed.), The Imperial Valley and the Salton Sea, John J. Newbegin, San Francisco: 37–41.

Salton Sea Authority/USBR, 2000. Draft Salton Sea Restoration Project Environmental Impact Statement/Environmental Impact Report. Report prepared for the Salton Sea Authority and the U.S. Department of the Interior, Bureau of Reclamation, by Tetra Tech, Inc.

Schindler, D. W., 1977. Evolution of Phosphorus Limitation in Lakes. Science 195: 260–262.

Setmire, J. G., 2000. Personal communication, September, 1999. James Setmire, U.S. Bureau of Reclamation and G. Chris Holdren, U.S. Bureau of Reclamation.

Setmire, J. G., J. C. Wolfe & R. K. Stroud, 1990. Reconnaissance Investigation of Water Quality, Bottom Sediment, and Biota Associated with Irrigation Drainage in the Salton Sea. U.S. Geological Survey Water-Resources Investigations Report 89-4102. USGS, Sacramento, CA.

Setmire, J. G., R. A. Schroeder, J. N. Densmore, S. L. Goodbred, D. J. Audet & W. R. Radke, 1993. Detailed Study of Water Quality, Bottom Sediment, and Biota Associated with Irrigation Drainage in the Salton Sea Area, California, 1988–1990. USGS Water-Resources Investigations Report 93-4014. USGS, Sacramento, CA.

Setmire, J. G. & R. A. Schroeder, 1998. Selenium and salinity concerns in the Salton Sea area of California. In Frankenberger, W. T. Jr. & R. A. Engberg (eds), Environmental Chemistry of Selenium, Marcel Dekker, Inc., New York·Basel·Hong Kong: 205–221.

Standard methods for the analysis of water and wastewater, 20th Edition, 1998. Am. Public Health Assoc., Am. Water Works Assoc., Water Env. Fed., Washington, DC.

Stumm, W. & J. J. Morgan, 1981. Aquatic Chemistry, 2nd edn. Wiley-Interscience, New York.

SWRCB, 1997. California Ocean Plan. Water Quality Control Plan. Ocean Waters of California. State of California, State Water Resources Control Board, Sacramento, CA.

Thiery, R., 1999. Personal communication, February, 1999. Richard Thiery, Coachella Valley Irrigation District and G. Chris Holdren, U.S. Bureau of Reclamation.

Tostrud, M. B., 1997. The Salton Sea, 1906–1996, Computed and Measured Salinities and Water Levels. Draft Report, Colorado River Board of California.

Truesdell, A. H. & B. F. Jones, 1974. WATEQ, a computer program for calculating chemical equilibria of natural waters. J. Res. U.S. Geol. Surv. 2: 233–274.

U.S. EPA, 1976. Quality Criteria for Water. U.S. Environmental Protection Agency, Washington, DC.

Watts, J. M., M. Tiffany, J. R. Verfaillie & S. H. Hurlbert, 1999. Nutrient loadings to the Salton Sea: past, present and the future. Presented at the American Society of Limnology and Oceanography conference, February 1–5, 1999, Santa Fe, NM.

Weghorst, P. A., 2001. Historic salinity increases in the Salton Sea and solids precipitation and/or reduction. Draft Report, U.S. Bureau of Reclamation, Denver, CO.

Weiss, R. F., 1970. The solubility of nitrogen, oxygen and argon in water and seawater. Deep-Sea Res. Vol. 17: 721–735.

Hydrobiologia **473:** 23–45, 2002.
D.A. Barnum, J.F. Elder, D. Stephens & M. Friend (eds), The Salton Sea.
© 2002 *Kluwer Academic Publishers. Printed in the Netherlands.*

Chemical evolution of the Salton Sea, California: nutrient and selenium dynamics

Roy A. Schroeder[1], William H. Orem[2] & Yousif K. Kharaka[3]
[1]*U.S. Geological Survey, 5735 Kearny Villa Road, Suite O, San Diego, CA 92123, U.S.A.*
E-mail: raschroe@usgs.gov
[2]*U.S. Geological Survey, Mail Stop 956, U.S. Geological Survey, 12201 Sunrise Valley Drive, Reston, VA 20192, U.S.A.*
E-mail: borem@usgs.gov
[3]*U.S. Geological Survey, Mail Stop 427, 345 Middlefield Road, Menlo Park, CA 94025, U.S.A.*
E-mail: ykharaka@usgs.gov

Key words: nutrients, selenium, bottom sediments, interstitial water, closed lakes, Salton Sea

Abstract

The Salton Sea is a 1000-km^2 terminal lake located in the desert area of southeastern California. This saline (~44 000 mg l^{-1} dissolved solids) lake started as fresh water in 1905–07 by accidental flooding of the Colorado River, and it is maintained by agricultural runoff of irrigation water diverted from the Colorado River. The Salton Sea and surrounding wetlands have recently acquired substantial ecological importance because of the death of large numbers of birds and fish, and the establishment of a program to restore the health of the Sea. In this report, we present new data on the salinity and concentration of selected chemicals in the Salton Sea water, porewater and sediments, emphasizing the constituents of concern: nutrients (N and P), Se and salinity. Chemical profiles from a Salton Sea core estimated to have a sedimentation rate of 2.3 mm yr^{-1} show increasing concentrations of OC, N, and P in younger sediment that are believed to reflect increasing eutrophication of the lake. Porewater profiles from two locations in the Sea show that diffusion from bottom sediment is only a minor source of nutrients to the overlying water as compared to irrigation water inputs. Although loss of N and Se by microbial-mediated volatilization is possible, comparison of selected element concentrations in river inputs and water and sediments from the Salton Sea indicates that most of the N (from fertilizer) and virtually all of the Se (delivered in irrigation water from the Colorado River) discharged to the Sea still reside within its bottom sediment. Laboratory simulation on mixtures of sediment and water from the Salton Sea suggest that sediment is a potential source of N and Se to the water column under aerobic conditions. Hence, it is important that any engineered changes made to the Salton Sea for remediation or for transfer of water out of the basin do not result in remobilization of nutrients and Se from the bottom sediment into the overlying water.

Introduction

The Salton Sea, located in the desert area of southeastern California, is a large (1000 km^2) shallow (mean depth = 8 m) saline (about 44 000 mg l^{-1}total dissolved solids) lake whose shoreline is currently at an elevation of 69 m below sea level (Fig. 1). It was formed as a fresh water lake in 1905–07 as a result of accidental flooding from the Colorado River and has subsequently been maintained largely by runoff (currently about 1.7 km^3 annually) from agricultural irrigation in the Salton Sea Basin. Because Salton Sea is a closed-basin lake with minimal ground–water interaction and is located in an arid region (precipitation only 7 cm yr^{-1}) of high evapotranspiration (about 1.8 m yr^{-1}), it has been accumulating soluble salts in its water and insoluble constituents in its bottom sediment for nearly 100 years (e.g. Setmire & Schroeder, 1998). These accumulations together with accelerated eutrophication have been implicated in the periodic deaths of millions of tilapia and over 200 000 migratory water birds (Jehl, 1996; Kaiser, 1999). Restoring

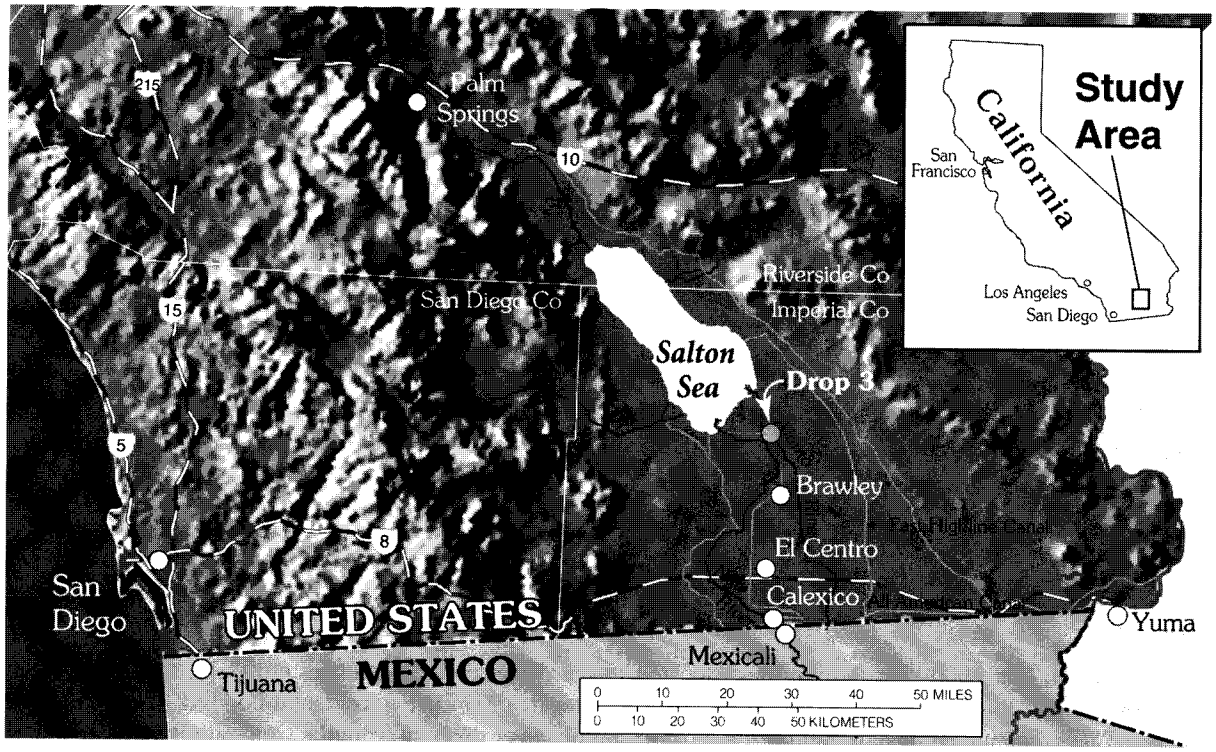


Figure 1. Salton Sea Basin and surrounding area of California, U.S.A. and Mexico.

the ecological health of the Sea is of paramount importance because the Sony Bono Salton Sea National Wildlife Refuge (NWR), a major waterfowl stopover for millions of migratory birds on the Pacific Flyway that also supports five endangered species, is located in the southern end of the Sea (Setmire & Schroeder, 1998). Historical and technical information on the Salton Sea and Salton Sea Basin are available from Dowd (1956), Hely et al. (1966), Setmire et al. (1990, 1993), Tolstrud (1997) and Setmire & Schroeder (1998) and references therein, and from other reports in this volume.

Nutrients (nitrogen and phosphorus) and selenium (Se) are among those constituents that, in addition to water salinity, threaten the health of Salton Sea (Kaiser, 1999; Schroeder & Orem, 2000). The concentration of total nitrogen (N) in irrigation water diverted from the Colorado River is relatively low (1.0 mg l^{-1}as NO_3), and fertilizer use is the primary source of N, which is delivered to the Sea with agricultural runoff (e.g. Setmire & Schroeder, 1998). Municipal and domestic wastewater, in addition to agricultural runoff, are the important sources of P (Federal Water Quality Administration, 1970). The addition of nutrients and abundant sunlight are responsible for the excessive biological productivity (eutrophication) of the Salton Sea that is evidenced by the lake's frequent algal blooms, large fish population, and high organic-carbon (OC) content in the water column and bottom sediment (Jehl, 1996; Setmire & Schroeder, 1998; Kaiser, 1999). The initial source of Se is marine pyritic shales that outcrop in the Upper Colorado River Basin and relatively high concentrations of Se (2.5 $\mu g\ l^{-1}$), mainly as selenate, is delivered to the Salton Sea Basin in irrigation water obtained from Colorado River (Engberg, 1999; Kharaka et al., 2001).

In this report, we present new data on the salinity and concentration of nutrients, Se and selected other chemicals in the Salton Sea water, porewater and (or) sediments. These results are combined with historical data from the Salton Sea Basin, results of one laboratory experiment and geochemical computer simulations to investigate the chemical evolution, and the fate and the cycling of N, P and Se in this saline lake. Understanding the physical and chemical evolution of the Salton Sea is important to the success of the various plans being considered to remediate the major ecological problems of the Sea.

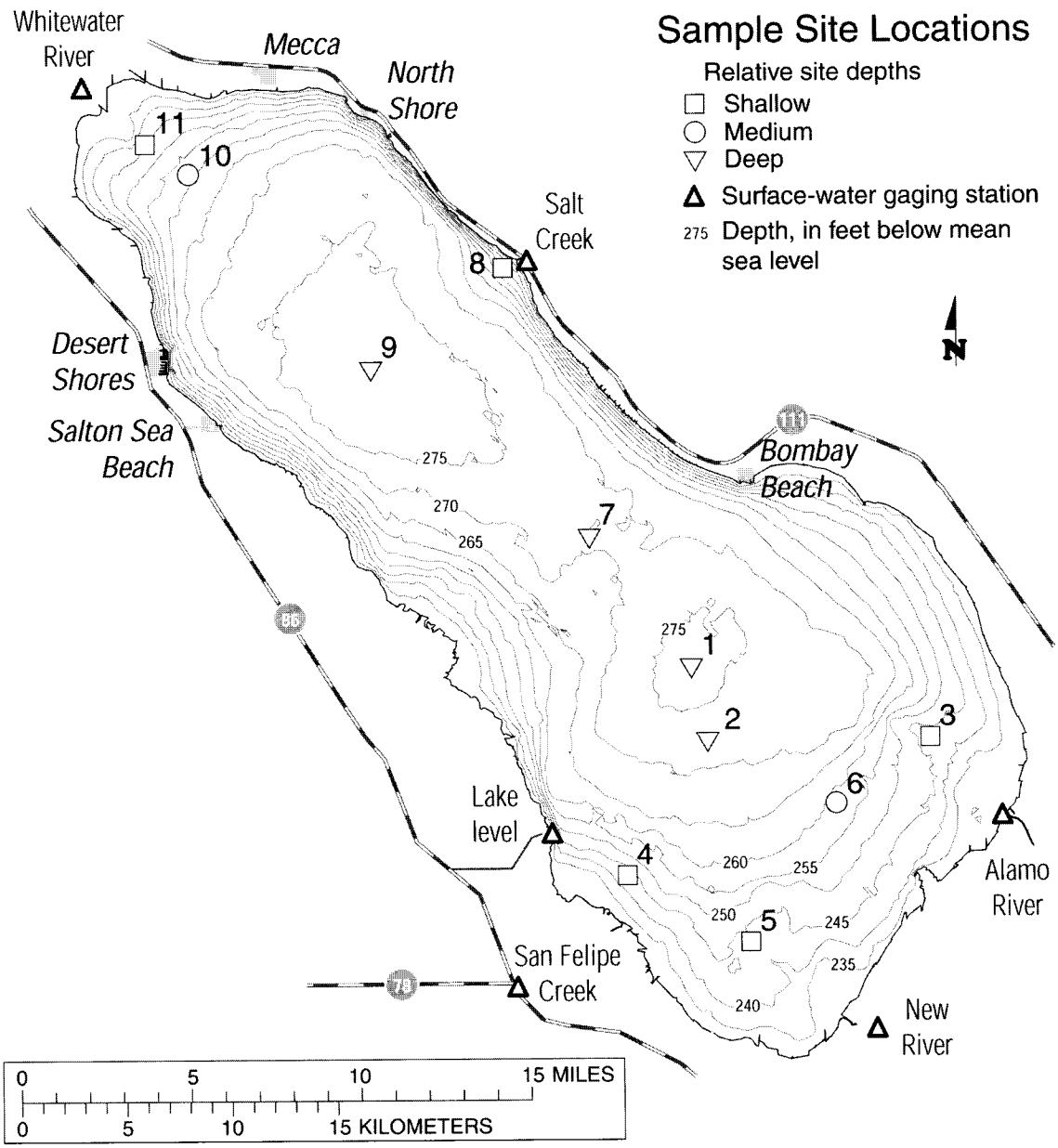


Figure 2. Sampling locations in the Salton Sea, 1998–99.

Sampling sites, materials and methods

Surface sediment and water-column and bottom-water samples were collected from 11 sites in the Salton Sea during July 20–22, 1998 (Fig. 2). Sediment cores, porewater and water-column samples were collected from two of the 1998 sites (Sites 9 and 10) on April 26–27, 1999. The sites for coring were selected in the center of the north basin (deepest part of the Sea) and between this basin and the Whitewater River delta (Fig. 2). Because of the distance from the major sources of input at the south end of the Sea, the sediment at these sites has uniformly fine texture, allowing for successful recovery of 0.5-m cores. Sediment samples were squeezed for pore water and processed for other tests described below almost immediately after collection. Some core samples, not processed immediately, were stored under anoxic con-

ditions in the sealed core liner. Sediment samples were stored at 4 °C prior to processing to minimize bacterial activity.

Bottom sediment and water

The 11 sites from which grab samples of bottom sediment were collected in 1998 (Fig. 2) were chosen to represent the range in depositional environments and to span lake depths from shallow (4.6 m) to medium (9 m) and to deep (14–15 m). The shallow sampling depth of 4.6 m was chosen because these sites could become the new shore if inflow to the Salton Sea is reduced annually by 0.37 km^3 (300 000 acre-ft), an amount that represents a commonly anticipated water-conservation scenario (Pacific Institute, 2001). Shallow sites were sampled in the deltas at each of the five perennial streams that discharge to the Salton Sea (Sites 3, 4, 5, 8 and 11). Deep sites were sampled at four locations – in the center of the north (Site 9) and south (Site 1) basins, in the saddle between the basins (Site 7) and near the center of the south basin (Site 2). The remaining two sites that were sampled are in the coalesced deltas of the New and Alamo Rivers (Site 6), and between the Whitewater River and the lake's north basin (Site 10). Grab samples of bottom sediment (top 10–15 cm) were obtained with a 23-cm stainless-steel Ekman dredge, which was lowered to within 2–3 m of the bottom then allowed to free-fall into the sediment. The top 3 cm of sediment (about 1.5 kg wet weight) was transferred into a glass bowl and homogenized before transfer into small plastic and glass containers for chemical and particle-size analyses. The remaining sediment was sieved and visually inspected onboard for presence of macroinvertebrates. Sieves and hydrometers were used to determine the grain-size distributions (Guy, 1969).

The sediment grab samples were analyzed for about 50 inorganic elements at the USGS's Analytical Facility in Denver using ICP-MS, and hydride generation for Se. Sediment samples were also analyzed for polycyclic aromatic hydrocarbons (PAHs) and organochlorine compounds by GC-MS at the USGS's National Water Quality Laboratory (NWQL) in Denver. Nutrient analyses on sediment and porewater samples were done by Orem's laboratory in Reston, Virginia, using procedures described in the following section. Sediment analyses were done on material from which large shells and debris had been removed using either 850-μm or 2-mm sieves.

Dissolved oxygen (DO), pH, specific conductance (surrogate for salinity), and temperature profiles were determined electrometrically by lowering a Hydrolab™ containing suitable probes through the water column. In addition, a bottom-water sample was collected at each site using a Van Dorn sampler lowered to a depth about 30 cm above the sediment–water interface. Water samples were filtered through a 0.45-μm capsule membrane and analyzed for alkalinity, silica, orthophosphate (PO_4), dissolved hydrolyzable P, NO_3, NO_2, NH_4, ON, and DOC (using a 0.45-μm membrane silver filter). All bottom water samples collected in 1998 were analyzed by the NWQL in Denver.

Sediment cores and porewater

Sediment cores from the Salton Sea were collected at Sites 9 and 10 (Fig. 2) using a Benthos gravity corer with a 5-cm o.d. plastic core liner. Multiple cores were collected at each site to provide samples for solid phase and porewater analyses. In most instances, the gravity core penetrated through the soft surface mud into the underlying material that predates the 1905–07 creation of the Salton Sea. Once recovered, the core liners were removed, capped on both ends, and taped shut until returned to shore. At the NWR, cores were vertically extruded in 2-cm intervals and stored for analyses. Cores for porewater studies were extruded into a porewater-squeezing barrel using a plastic coupling device (Orem et al., 1997). Filtered (0.45-μm Gelman Acrodisc™) porewater samples, collected from selected depth intervals, were stored frozen and later analyzed for reactive P and NH_4 within 5 days (Strickland & Parsons, 1973; EPA, 1979). Water-column samples from the core sites were similarly analyzed (Orem et al., 1997). Precision is ± 2% for both.

Sediment grab samples collected in 1998 for analysis of nutrients (C, N and P) were lyophilized and sieved (850 μm) to remove large shells, sand, and rocks. Sediment samples collected by coring in 1999 were sieved (62 μm), which at these sites removed very little material. The sieved samples were milled to a powder, and prior to analysis, were dried overnight at 60 °C to remove adsorbed water. Total C, OC and N were determined using a Leco 932 CHNS Analyzer™ (Leco Corp., St. Joseph, Mich.); OC was determined after removal of carbonates (Orem et al., 1999). Total P was determined by baking ~0.5 g of dried sediment at 550 °C, extracting the residue in 1 M HCl, and ana-

lyzing the extracted TP (Strickland & Parsons, 1973; Aspila et al., 1976). Precision is ±1% for TC and TN, ±2% for OC, and ±3% for P.

Results and discussion

Only selected data collected during 1998 and 1999, discussed below, are included in this article because of space limitations. Additional data available but not included herein are: (1) numerous organic compounds whose concentrations were below the method reporting level (MRL) from grab sediment at 11 sites, (2) more than 40 elements in grab sediment from 11 sites and in sediment from about 20 samples at 2-cm intervals in cores from two sites, and (3) profiles of temperature, salinity, DO, and pH at nine of the 11 sites sampled in 1998. These data can be obtained from the NWIS public website (http://water.usgs.gov/ca/nwis/qwdata/), using the station ID numbers listed in Table 1, or directly from the senior author.

Water quality

The specific conductance values (Table 2) measured in bottom water samples collected from the 11 sites sampled in 1998 ranged from 54 300 to 54 800 μS cm^{-1} at 25 °C, a range that is within the measurement error of ±1%, indicating an essentially constant salinity for the bottom water. Measured residue-on-evaporation (ROE) at 180 °C on the same bottom-water samples ranged from 40.8 to 43.1 g l^{-1} (Table 2), indicating constant salinity within the analytical precision of ±3%. Profiles of salinity, expressed as ROE and calculated from field conductance measurements at all 11 sites exhibit considerably more variation with depth at a given site and differences in surface water between sites (profiles from Sites 1 and 9 shown in Fig. 3). Salinity differences in near-surface water between sites illustrate the local effect of dilution from the large freshwater sources (the Alamo and New Rivers) that discharge at the south end of the Sea (Fig. 3). The profiles indicate salinity increases with depth, especially in deeper parts of the Sea, as a result of thermal density stratification that is typical of summertime conditions (Fig. 3).

These results indicate that water samples for lake chemistry should be taken from near the lake bottom and preferably near the center of the lake to minimize the effect of spatial inhomogenity, if the purpose is to ascertain short-term interannual salinity trends. For evaluating trends and validating geochemical-model predictions of mineral precipitation, it would also be helpful to have annual analyses of all the major ions.

Historically there have been numerous chemical analyses of water from the Salton Sea, but these are restricted largely to determination of salinity (total dissolved solids) and major constituents. The Salton Sea started as a fresh water lake in 1905–1907, but water salinities increased (water levels declined after the initial rise) rapidly due to the high evaporation rate, reaching a value of about 50 000 mg l^{-1} in 1935 (Fig. 4). Water salinities decreased substantially between 1935 and 1955 as water levels rose from increased input of irrigation water. Salinities then show a general increase with time (currently about 44 000 mg l^{-1}), even though water levels remain essentially unchanged since about 1980 (Fig. 4), indicating a dynamic steady state between evaporation and irrigation input.

Salinity of the Salton Sea is increasing because it is a terminal lake with minimal ground–water interaction (Hely et al., 1966) and large amounts of salts, ≈4.5 million metric tons annually, are carried in surface-water discharges. However, the salinity increase is significantly less than would be expected on the basis of mass balance, indicating precipitation of some of the less-soluble salts (Tostrud, 1997). Computer simulations were run on chemical data collected in the late 1980s from source waters and from water in the Salton Sea to calculate saturation indices (departure from equilibrium) for minerals using thermodynamic information in the geochemical code PHREEQC (Parkhurst, 1995). Results indicate that precipitation of calcite is likely and that precipitation of gypsum is probable within the lake (Fig. 5). Incorporation of large amounts of calcite in bottom sediment is confirmed by x-ray diffraction on the bottom sediment (B. Jones, 2001, written communication) and by finding as much as 40% by weight in sediment from deepwater sites in the 1998 grab samples (calculated from IC data in Table 4). Gypsum precipitation also is confirmed by x-ray diffraction on the bottom sediment (B. Jones, 2001, written communication). Calcite and gypsum precipitation also are indicated from temporal trends in the concentrations of Ca, HCO_3, and SO_4 relative to Cl, in water from the Salton Sea (Tostrud, 1997).

The effect of biological production and summer stratification is evident on DO profiles (Fig. 3). Oxygen is present in surface water at all 11 sites, but is vir-

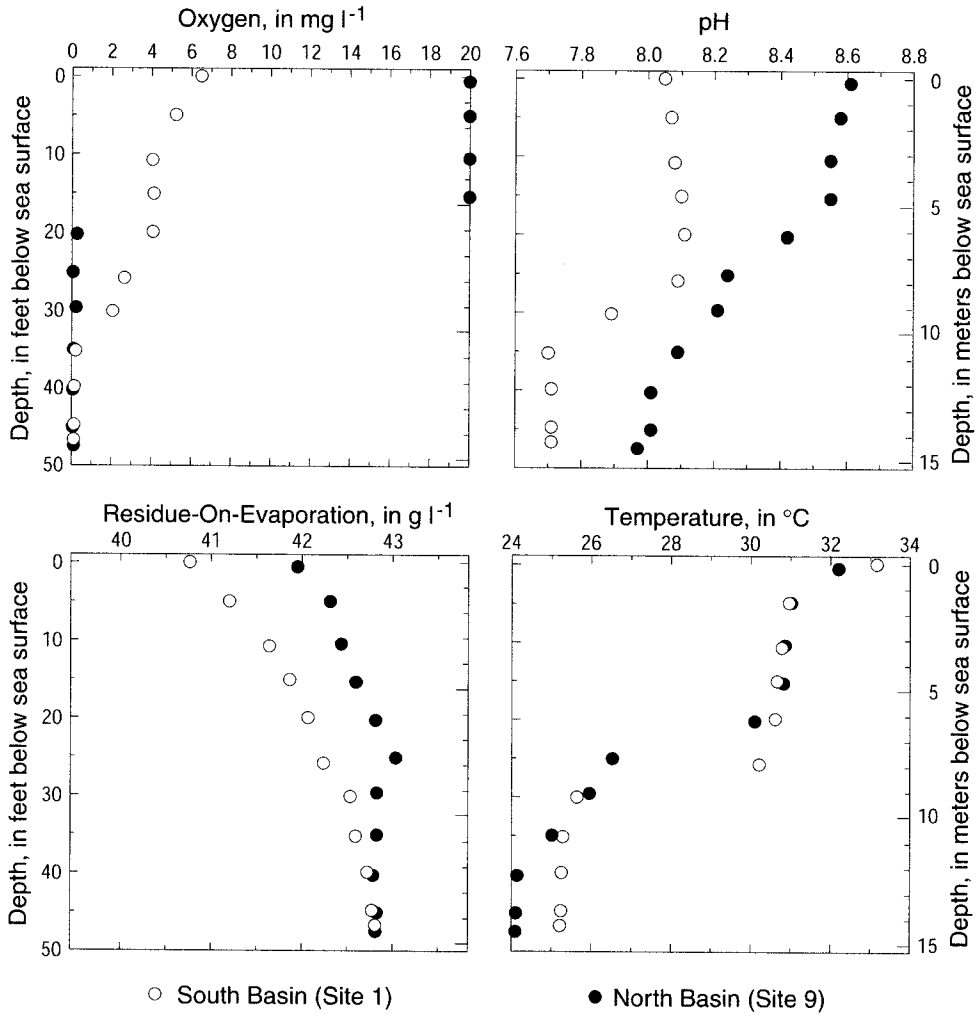


Figure 3. Selected water-quality profiles in the Salton Sea, July 1998.

Table 1. Physical characteristics of bottom sediment from the Salton Sea. Initial 13 digits in ID are site latitude and longitude, grain size is in percent by weight and depth is in meters

Site no.	Station ID	Depth	Clay	Silt	Sand	Visual field observations
1	331600115453001	14.6	86	13	1	Olive-gray organic muck
2	331400115450001	13.1	62	18	15	Olive-gray organic muck
3	331400115380001	4.6	<1	1	99	Medium fine sand
4	331023115473701	4.6	20	27	53	Many barnacle shells
5	330835115434501	4.6	14	10	76	Some barnacle shells
6	331215115410001	9.1	33	33	34	Some worm tubes
7	331930115484001	13.1	64	19	17	Olive-gray organic muck
8	332637115512001	9.1	32	35	33	Abundant live barnacles and pileworms
9	332400115553001	15.2	81	13	6	Olive-gray organic muck
10	332908116011501	9.1	49	50	1	Dark gray clay + organic muck
11	332958116023501	4.6	29	68	3	Black clay

Table 2. Selected aqueous data from bottom water in the Salton Sea, July 1998. Concentrations in mg l^{-1}, SC in dS m^{-1}, and ROE in g l^{-1}

Constituent Site no.	1	2	7	9	6	10	3	4	5	8	11
		(Deep)			(Medium)				(Shallow)		
Temperature, °C	25.2	25.5	24.8	24.1	26.4	31.1	29.3	28.7	29	31.1	31.5
Dissolved oxygen	0.1	0.1	0.1	0.1	0.1	15	1.1	<0.1	<0.1	16	9.3
Ammonium-N	1.7	1.7	1.8	2.2	1.8	0.7	1.1	1.4	1.3	0.74	0.78
Organic-N	3.2	3.1	2.8	3.2	3.4	2.9	3.0	2.9	2.9	3.0	2.9
Nitrite-N	<0.01	<0.01	<0.01	<0.01	<0.01	0.03	0.02	<0.01	<0.01	0.04	0.03
Nitrate-N	0.05	<0.05	0.05	0.05	0.05	0.11	0.07	0.05	<0.05	0.08	0.09
Orthophosphate-P	0.044	0.054	0.043	0.04	0.044	0.028	0.029	<0.010	0.022	0.016	0.011
Silica	14	14	15	16	15	7.7	9.7	11	11	7.6	7.3
SC at 25 °C	54.7	54.8	54.3	54.8	54.7	54.5	54.4	54.6	54.7	54.8	54.6
ROE at 180 °C	43.1	43.1	42.6	42.0	41.3	43.2	43.2	40.8	42.5	41.2	43.1
DOC	44	-	42	42	40	42	43	42	43	43	44
Alkalinity as $CaCO_3$	210	210	210	210	210	210	210	200	220	190	190

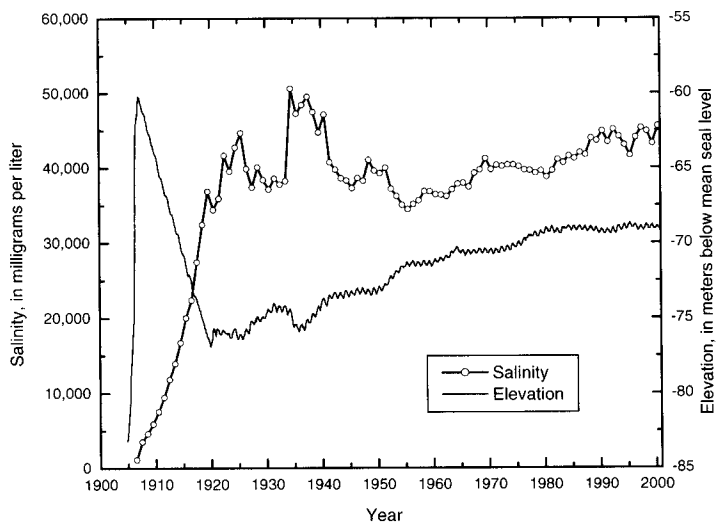


Figure 4. Historical averaged annual Salton Sea salinity and monthly surface water elevations (at Fig Tree John). Data before 1929 from Tostrud (1997), the rest from Imperial Irrigation District files.

tually absent in bottom water from the deep sites, and even from shallow sites in the south basin (Table 2). However, bottom water at Site 8, 10 and 11 is supersaturated (9–16 mg l^{-1}), creating conditions, especially at Site 8, near Salt Creek (Fig. 2), for numerous live pileworms and barnacles in bottom sediments. Just as DO decreases with increasing depth, so also does pH, reflecting the dominance of respiration and organic-matter degradation over primary biological production (Fig. 3).

Bottom water from the 11 sites was analyzed for the nutrients C, N and P. The results (Table 2) compare favorably with those from a single sample collected in the late 1980s (Schroeder, 1996). Virtually all of the aqueous nitrogen is in reduced forms. Ammonium concentration ranges from 0.74 to 2.2 mg N l^{-1} (highest at the deepwater sites) and organic nitrogen ranges from 2.8 to 3.3 mg N l^{-1}. Concentrations of both reduced species are far higher than are concentrations of nitrate, which ranges from <0.05 to only 0.11 mg N l^{-1}, and nitrite, which is detectable (>0.01

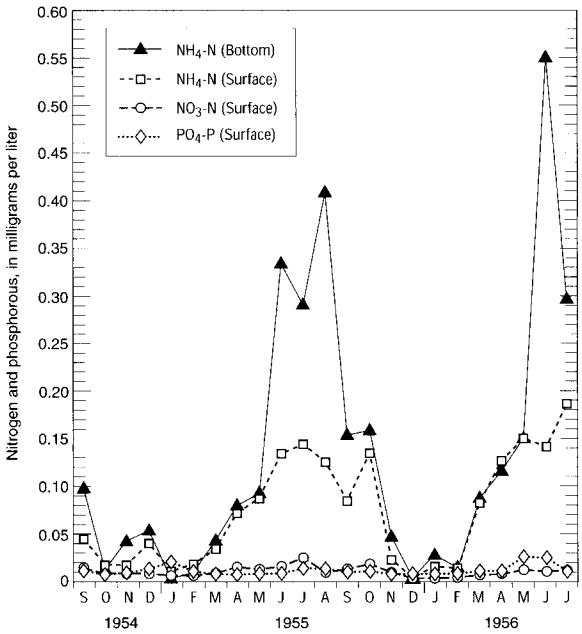


Figure 5. Historical nutrient concentrations in the Salton Sea (from Carpelan, 1961). (Compare to current concentrations given in Table 2).

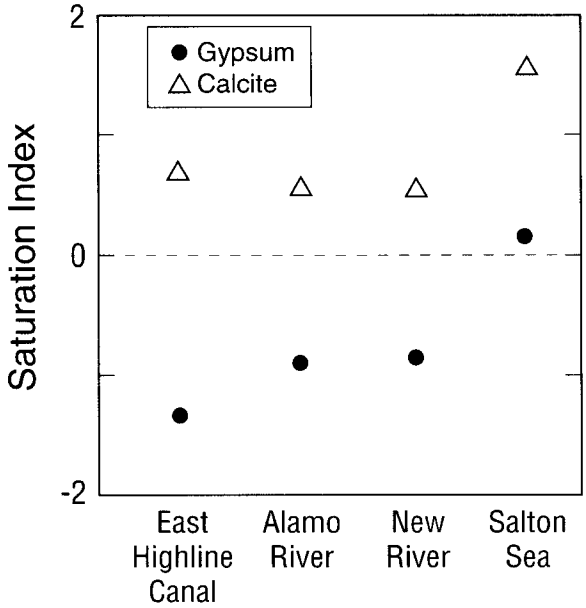


Figure 6. Saturation indices (departure from equilibrium) for calcite and gypsum in the Salton Sea and its source waters.

mg N l^{-1}) only at those sites where nitrate also is present (Table 2) .

Orthophosphate and dissolved hydrolyzable P concentrations were found to be low (0.01–0.05 mg P l^{-1}) and so near the MRL that results are subject to large uncertainties (Table 2). Comparison of these nutrient concentrations with levels that existed in the mid-1950s (Fig. 6, reproduced from Carpelan, 1961), only a few years after the heavy use of chemical fertilizers began, indicates a several-fold increase in NH_4, and little or no change in P. Possible explanations for the low P are discussed later in the section, 'Phosphorus Removal'.

Dissolved organic carbon (DOC) concentration in bottom water ranges from 40 to 44 mg C l^{-1}, which is within the analytical precision. This yields a C:N:P atom ratio of about 4000:400:1 for water in the Salton Sea, which can be compared to 800:15:1 in the ocean and 80:15:1 in soft biological tissue (Broecker, 1974). The classical interpretation of this nutrient concentration and ratio data is that the Salton Sea is highly eutrophic and that P is by far the limiting nutrient relative to N, although the possible role of micro-organisms and detritus on light attenuation and mixing within the water column as limiting factors also is recognized. The fact that the aqueous C/N ratio is somewhat higher in the Salton Sea (~10) compared to biological tissues (5–6) suggests that a large fraction of the high DOC is derived from biological production within the lake (is autochthonous), but that external (allochthonous) loading also is substantial.

Bottom sediment

Visual observations and grain-size data from the sampling in 1998 (Table 1) show an increase in the fine-particle content at sites more distant from shore, especially away from the large rivers located at the south end of the lake. Concentrations of organic carbon, selected trace elements, nutrients, and xenobiotic (synthetic) organic compounds are positively correlated with clay plus silt content, and hence, generally increase with distance from shore.

Organic compound data for which concentrations exceed the MRL ($\approx$5 μg kg^{-1} for aromatic hydrocarbons and $\approx$1 μg kg^{-1} for organochlorines) are summarized in Table 3. The sites are listed from deep to shallow across the table and the relation to distance from shore and with grain size is evident. Combustion of hydrocarbons and other organic matter from large urban centers, such as Mexicali, are commonly sources of PAHs; however, their concentrations are low in the Salton Sea (Table 3), because of dilution by relatively clean suspended sediment in irrigation runoff (R. Schroeder, 1995–6, unpublished data). The

Table 3. Selected organochlorine and aromatic hydrocarbon concentrations in surface sediment grab samples from the Salton Sea. Concentrations are in $\mu g\ kg^{-1}$ dry weight; E = estimated value, close to the detection limit

Constituent Site no.	1	2	7	9	6	10	3	4	5	8	11
		(Deep)			(Medium)				(Shallow)		
					Monocyclic and Polycyclic Aromatic Hydrocarbons						
Phenol	140	38	98	69	8.7	11	E3.8	8.1	5.3	30	16
p-Cresol	35	19	110	34	7	E8.2	<5	6.6	E3.1	15	9.3
2,6-Dimethylnaphthalene	630	300	1,100	460	43	66	E4.4	38	25	90	58
1,6-Dimethylnaphthalene	51	22	110	36	E3.9	E5.6	<5	E3.1	E2.5	6.4	E4.7
Phenanthrene	46	<10	<10	<10	<5	<10	<5	<5	<5	<5	E2.1
Anthracene	47	<10	<10	<10	13	<10	<5	<5	<5	<5	E2.3
Fluoranthene	E4.0	E2.7	12	E6.2	E1.6	E2.3	<5	<5	<5	E1.1	E3.8
Pyrene	E3.4	E2.5	16	E5.2	E1.3	E2.0	<5	<5	<5	E1.1	E3.5
					Organochlorine Compounds						
Dieldrin	<1.5	<1.5	<1.5	<1.5	0.55	<1.0	<0.5	0.47	<0.5	0.59	0.7
DDE	14	10	39	24	4.1	6.0	0.24	1.5	0.67	3.0	4.4
DDD	E0.92	<1.5	<1.5	1.9	<0.5	<1.0	<0.5	<0.5	<0.5	<0.5	E0.46
DDT	<1.5	<1.5	<1.5	<1.5	<0.5	<1.0	<0.5	<0.5	<0.5	<0.5	<0.5
PCBs	<15	<45	<45	<15	<15	<5	<15	<15	<15	<15	<15

higher values for 2,6-dimethylnapthalene may reflect petroleum combustion sources (boats) within the lake or in the basin.

DDE (the predominant DDT metabolite), though of an agricultural rather than urban origin, also follows the aforementioned spatial pattern, with enrichment in the fine-grained organic-rich sediments from central parts of the Salton Sea (Table 3). Organochlorine concentrations are comparable to those reported in bottom sediment from drainage channels and rivers in the Salton Basin (Setmire et al., 1990) and, therefore, do not indicate any unusual enrichment within bottom sediment of the Sea. PCBs were not detected in any of the samples from the Salton Sea.

Concentrations of C, N and P, were determined in the <850-μm fraction of surface sediment from the 11 sites sampled in 1998 to evaluate the spatial distribution of these nutrients. Results on dry weight basis (Table 4), display the same spatial pattern already described, with highest concentrations found in the finest sediment far from shore. Inorganic carbon (IC) concentration ranges from about 1% in the Alamo River delta (Site 3) to about 5% in the center of the north basin (Site 9); these values indicate 10–40% calcite, since abundant calcite but no dolomite or magnesite were detected in x-ray diffraction analysis of bottom sediment (B. Jones, 2001, written communication). Organic carbon (OC) concentration at these two sites yields the full range of 0.08 and 6.3%, respectively.

Total N concentration exhibits a spatial pattern similar to that of OC and ranges from 0.06 to 0.97%. Total nitrogen is almost entirely composed of ammonium plus organic nitrogen because nitrate and nitrite are negligible in the reducing sediment. The relatively low OC/TN ratios of 6–8 (Table 4) indicate that the dominant source of sedimentary organic matter in the Salton Sea probably is from algae that use N from agricultural runoff (Meyers & Ishiwatari, 1993). The very low OC/TN ratios, below even that in living tissue, at Sites 3, 5 and 8 near the Alamo River, New River, and Salt Creek outlets, respectively, all occur in coarse-grained sediment with very low organic content. These ratios could reflect a greater relative contribution of inorganic nitrogen (ammonium) at these particular sites, or errors inherent in the analysis at these low concentrations.

Atomic OC/total P ratios (Table 4) fall into two groups; those >120, which generally occur in deep sites, and those <60. The higher values are somewhat larger than is typical for living algae, the major source of organic matter in sediment, suggesting recycling of P-rich organic detritus in the water column before deposition (Summons, 1993). Atomic N/P ratios also fall into two groups, with the deep sites having ratios >20

Table 4. Selected element concentrations in surface sediment grab samples from the Salton Sea. C, N and S concentrations are in percent dry weight; others are in mg kg^{-1}

Constituent											
Site no.	1	2	7	9	6	10	3	4	5	8	11
		(Deep)			(Medium)				(Shallow)		
Inorganic carbon	3.5	3.8	4.2	5.1	2.4	3.7	1.2	1.4	1.3	3.7	1.3
Organic carbon	5.2	4.7	3.8	6.3	1.30	3.4	0.08	0.65	0.39	0.68	1.6
Nitrogen	0.90	0.79	0.66	0.97	0.26	0.51	0.06	0.10	0.11	0.26	0.27
Phosphorus	790	850	670	660	580	690	180	530	330	560	700
Sulfur	3.6	3.5	4.3	4.6	1.5	2.2	1.4	2.5	2.1	5.6	1.4
Organic C/Total N	6.7	7.0	6.7	7.6	5.8	7.9	1.5	7.2	4.3	3.1	6.8
Organic C/Total P	170	190	150	250	58	130	12	32	30	31	58
Total N/Total P	25	27	22	32	10	16	8.0	4.4	7.1	10	8.5
Molybdenum	36	34	31	75	2.0	27	0.73	1.4	1.4	2.8	6.2
Selenium	8.8	5.8	8.0	9.7	1.5	11	0.58	0.90	1.0	1.8	2.7
Uranium	14	14	14	20	3.0	14	2.4	2.7	2.5	5.0	5.3

and the near-shore sites having ratios <10. Ratios that are higher than in soft tissue indicate N enrichment relative to P in the Salton Sea, as was noted earlier in the discussion on aqueous concentrations. In fact, the solid-phase data actually 'understate' the N/P ratio of sedimentary organic matter because a large proportion of the total P is natural input from soils, as discussed in later sections.

Sulfur (S) data (Table 4), exhibit a spatial pattern that is only partially similar to that of OC and various trace elements for which higher concentrations are generally associated with finer material. Site 8, near Salt Creek, is the most obvious exception in that it has the highest reported S concentration (Table 4) despite a relatively high coarse content (Table 1). As noted earlier, the bottom sediment at this site contained numerous live barnacles and calcareous concretions, together with gypsum. The S/Se ratios (Table 4) in near-shore sites are generally higher (S is enriched relative to Se) compared to deep sites. Apparently, Se-depleted gypsum makes a greater contribution within the coarse sediment closer to shore.

The earliest Se concentrations in bottom sediment collected by the USGS from the Salton Sea was from a grab sample obtained in 1986 along an arc between the center of the south basin and the outlets of the Alamo and New River (Schroeder et al., 1988). The Se concentration on the sieved silt + clay fraction was 3 mg kg^{-1}, which is about 10 times higher than average Se concentrations in soil from the Imperial Valley (Schroeder et al., 1993). Sixteen samples taken closer to shore in the Alamo River delta had Se concentrations of 0.2–2.9 mg kg^{-1} (Schroeder et al., 1993; Setmire et al., 1993). On the basis of the apparent relation to distance from shore, a single grab sample was collected from near the center of the lake in May 1996 that yielded the highest Se concentration of 9 mg kg^{-1} (Setmire & Schroeder, 1998). Data from the 11 sites sampled in 1998 (Table 4) confirm the anticipated spatial pattern of lower concentrations for Se and other trace elements in the coarser sediment near the riverine sources, and higher concentrations in the finer sediment from interior parts of the Sea.

Nitrogen and selenium mass balance

Understanding the fate and cycling of Se in the Salton Sea Basin is of special importance because: (1) Se is present in relatively high concentrations (2.5 $\mu g\ l^{-1}$), essentially all as selenate, in irrigation water delivered from Colorado River (Engberg, 1999; Kharaka et al., 2001); (2) Se concentrations in subsurface drainwater, present mainly as selenate, are much higher (generally 10–100, and up to 300 $\mu g\ l^{-1}$) than in irrigation water, primarily due to high evapotranspiration in the desert conditions (Setmire & Schroeder, 1998; Kharaka et al., 2000); and (3) the present USEPA chronic water-quality criterion that is protective of wildlife and aquatic life is only 5 $\mu g\ l^{-1}$; furthermore, many aquatic biologists believe the criterion value should be lowered to 2 $\mu g\ l^{-1}$, because Se is rendered more toxic by bioaccumulation in the food

chain of fish and avian populations (Presser et al., 1994; Engberg et al., 1998).

Selenium occurs in four oxidation states, at the redox conditions that exist in the Salton Basin, that determine Se partitioning between water, sediment and air and thus determine its bioavailibility and toxicity (Schroeder et al., 1993; Setmire & Schroeder, 1998). Irrigation drainwater is aerobic in nearly all parts of the Salton Basin: hence, Se occurs dominantly as the highly soluble selenate (+VI) in both irrigation water and subsurface drainwater (Kharaka et al., 2000). The concentration of Se in the imported Colorado River water is high ($\sim$2.5 μg l^{-1}) and Se values are further concentrated in subsurface drainwater, with a median value of $\sim$30 μg l^{-1}, and ranging up to 300 μg l^{-1}. Stable water isotopes (Michel & Schroeder, 1994) and the ratio of conservative chemical components, Se/Cl and Se/B, indicate that the high Se concentrations in drainwater as well as water salinities that average 5000 mg l^{-1} total dissolved solids, result primarily from the extremely high evapotranspiration rates ($\sim$1.8 m yr^{-1}) in the desert environment of the Salton Basin (Setmire & Schroeder, 1998; Kharaka et al., 2000).

The biogeochemical cycle of Se in anoxic environments such as those encountered in the deeper water and bottom sediment of the Salton Sea result in the reduction of selenate to selenite (+IV), Se° (0) and ultimately to metal and organically bound selenide (-II) (Cooke & Bruland, 1987; Oremland, 1994; Setmire & Schroeder, 1998). Dissolved Se concentrations in anoxic environments are low because selenite and Se° have a high affinity for sorption onto sediments, especially organic matter, clay minerals and iron oxyhydroxides and the solubility of metal selenides, including $FeSe_2$ and $CuFeSe_2$, is extremely low (White & Dobrovsky, 1996; Kharaka et al., 2001). Also, some of the end products of Se reduction, such as the hydrogen and alkyl selenides, are gases and could potentially be volatilized to the atmosphere (Cooke & Bruland, 1987). The environmental geochemistry of Se is detailed in a recent volume edited by Frankenberger & Engberg (1998).

Dissolved Se concentrations in Salton Sea water are low (0.5–2 μg l^{-1}) and Cl values are about 17 000 mg l^{-1}, resulting in Se/Cl ratios (about 0.006×10^{-5}) that are much lower than those of the drainage water in Salton Basin or the roughly equivalent value for the Colorado River water (2.2×10^{-5}), indicating that Salton Sea is a major sink for Se (Cooke & Bruland, 1987; Setmire & Schroeder, 1998; Kharaka et al., 2001). Were Se to continue accumulating in the water, as has the conservative Cl, the Se concentration in the Salton Sea would have risen to about 400 μg l^{-1} (Schroeder & Orem, 2000). This analysis shows that more than 99% of Se that has entered the Salton Sea is no longer present in the water column. The missing Se may be sequestered in bottom sediment, in biota, and (or) may be lost by volatilization. Results discussed below strongly suggest that virtually all of the Se in the Salton Sea is present in the bottom sediment.

The amount of Se in the lake's biota can be estimated from the concentration of Se in different organisms that reside in the water column reported in Schroeder et al. (1993). It is estimated that the lake contains 10^8 fish (Riedel et al., 2001). Using an average weight of 1 kg per fish and a Se concentration of 2 μg g^{-1} (wet weight) (Setmire & Schroeder, 1998), yields 200 kg of Se in fish tissue. This compares with about 10 000 kg of Se in the water column, estimated by multiplying the lake's volume of 10^{13} l (7.6 million acre-ft), calculated from the dimensions of the Salton Sea given in the introduction) times an aqueous Se concentration of 1 μg l^{-1}. Thus, the Se in fish tissue is only 2% of Se in solution. Additional Se is present in organisms from lower trophic levels, but the exact amount of this Se is not known at this time. The total Se from lower organisms probably is not likely to significantly exceed the total Se in fish, even though the mass of these likely is an order of magnitude or more greater than the mass of fish, but the Se content of these organisms is lower than that of fish, by a factor of 10 for algae (Setmire & Schroeder, 1998; Fig. 5, p. 219).

The loss of Se from the water column by volatilization can be studied by examining its speciation data, which show no selenate, even in the oxygenated surface waters of Salton Sea, and show that selenite comprised 33% of total Se in the upper 4 m, but selenite was not detected in deeper water. The bulk of Se (58–81%) is in the form of nonvolatile organic selenides, but the volatile dimethyl selenide (DMSe) comprised 2–11% and showed increased percentages with depth, possibly indicating degassing at the lake surface (Cooke & Bruland, 1987; Setmire & Schroeder, 1998).

Estimation of Se and N loss from the Salton Sea water by volatilization to the atmosphere or sequestration within bottom sediment can be made through a comparison of Se and N concentrations with those of two other elements, (molybdenum) Mo and (uranium) U. These four elements (though to a lesser extent for N) exhibit similar geochemical behavior; they occur

as highly soluble species in aerobic environment, such as the rivers that deliver them to the Salton Sea, and as insoluble species in anaerobic conditions, such as the bottom sediments, where they are sequestered (Calvert, 1976; Setmire et al., 1993). Because Mo and U, unlike Se and N, do not occur as gases during reduction, they can be used to 'normalize' for the possible loss by volatilization of Se and N. Therefore, any decrease in the ratio of Se and N to Mo and U between rivers that discharge to the Salton Sea and bottom sediment within the Sea itself is a measure of net removal from the system. Because of the environmental importance of Se and N, it is important to know whether the Se and N discharged to the Salton Sea are removed as a result of volatilization, or whether they are retained within its bottom sediment.

In order for the conclusions from the simple calculations that follow to be valid, the amount of each element contained within the Salton Sea's water must be negligible compared to that element's total input. It has already been noted that less than 1% of the total Se ever discharged to the Sea now resides in its water. Concentrations of Mo and U in the Salton Sea are only a few micrograms per liter and also represent less than 1% of the total amount in surface water discharged to the Sea (Schroeder et al., 1993; Schroeder, 1996). If N discharge has remained about the same for the past 50 years (the period during which use of chemical fertilizers has been widespread), aqueous N concentration in the Salton Sea would be about 20 times higher (Schroeder & Orem, 2000) than the approximately 5 mg l^{-1} now present. The DOC contained in the Salton Sea equals about 20% of total input from surface-water discharges, based on current DOC concentrations in the Alamo and New Rivers – an amount that is still minor, but not negligible.

Validity of this calculation is also dependent on condition that the data must be representative of conditions over at least the previous 10–15 years – a period that matches the top 2–3 cm of deposition for the sediment grab samples collected in 1998. River concentrations are obtained from monthly monitoring (single sample from each river for U) for one year (1988–89) from the two major rivers that convey irrigation runoff, the Alamo and the New, at their outlets to the Salton Sea (Schroeder et al., 1993). The two rivers represent almost 80% of total water discharge to the Sea. About half of the remaining water discharged to the Salton Sea is from surface drainage channels, which have chemical concentrations similar to those of the two major rivers, and from the Whitewater River, which also carries substantial irrigation drainage (Michel & Schroeder, 1994). The remaining sources have little additional influence on element ratios of surface water discharged to the Sea.

Although the aqueous data used in the subsequent calculation are from monitoring for one year (1988–89) only, long-term monitoring values reported for salinity and Se (Iwatsubo, 1993), and compiled for N (Fig. 7), the element that exhibits the highest variability in the rivers, can be used to establish the fact that mean annual chemical concentration in surface water discharged to Salton Sea has not changed significantly during the last 30 years. The N data are from the Alamo River at Drop 3 (Fig. 1), about 10 km upstream from the river's outlet to the Salton Sea. Nearly all of the water in the Alamo River is from agricultural runoff in the Imperial Valley and its chemical composition changes little between Drop 3 and the river's outlet.

Calculations for 5 elements, using 1988-89 river data in Schroeder et al (1993) and apportioning 60% to the Alamo and 40% to the New River, yields the following mean input concentrations:

Element	Weighted concentration
Nitrogen	9.3 mg l^{-1}
Selenium	6.3 μg l^{-1}
Uranium	15.8 μg l^{-1}
Molybdenum	12.3 μg l^{-1}
Organic carbon	10.4 mg l^{-1}

The RSD on these values is about 20% (ranges from 17% for Mo to 23% for N). Note that for U the value is based only one sample from each river. Because of the small number of samples, U data are used only to substantiate results calculated using Mo.

The mean mass ratios of Se:Mo:U:N:C are 1:2.0:2.5:1500:1700 in river input. The analogous ratios are 1:3.0:2.3:1100:5400 in surface sediment from the Salton Sea (data in Table 4). The RSD values for element ratios from bottom sediment are lower when normalized for U than for Mo; the values, as expected are higher (about 50%, with a range from 32% for Se/U to 74% for OC/Mo) for bottom sediment than for river inputs. Using the above elemental ratios, the calculated values obtained by normalizing for Mo yield the following results: 33% loss for Se, 51% loss for N and 112% gain for OC. The calculated values obtained by normalizing for U are: 10% gain for Se, 20% loss for N and 247% gain for OC. Results obtained with

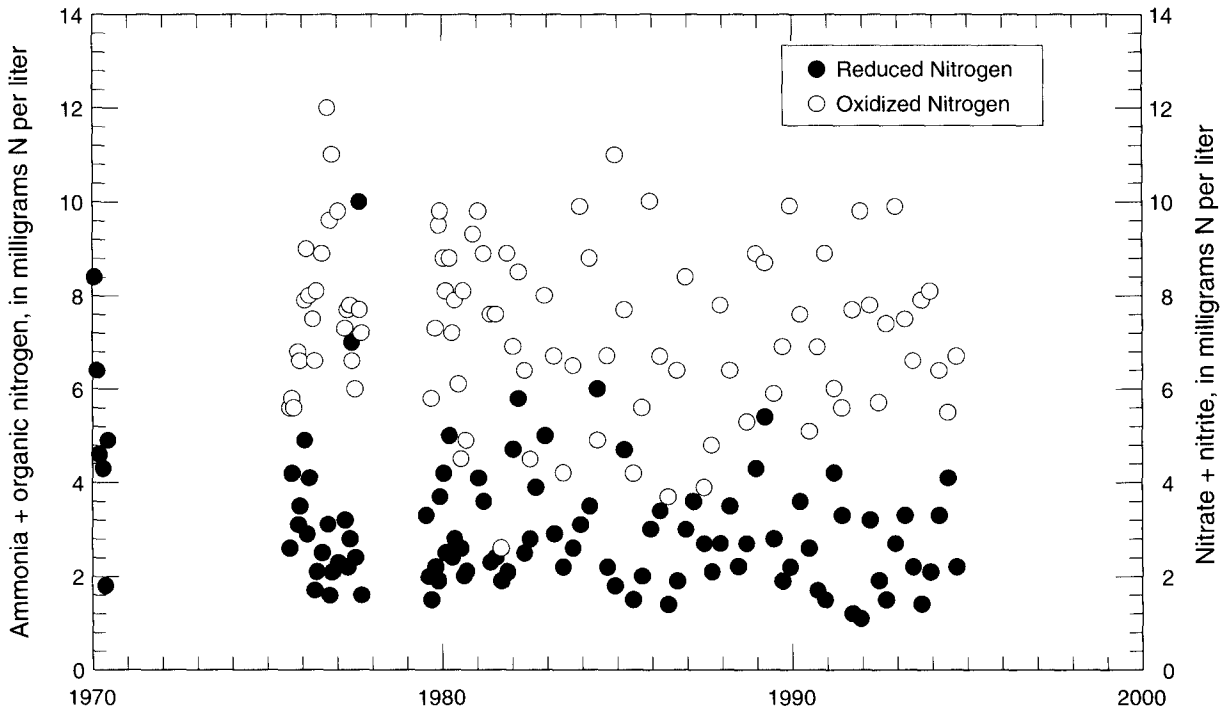


Figure 7. Nitrogen concentrations in the Alamo River at Drop 3 (shown in Fig. 1) since 1970.

Mo and U are comparable within data limitation, and indicate major net production of OC, some loss of N and possibly minor loss of Se within the Sea itself. The calculated gain for OC is a 'net' value; and hence, does not account for any recycling of carbon within the water column or at the water–sediment interface, which could be quite extensive in this eutrophic lake. Significant production of OC within the Salton Sea also was inferred (and discussed elsewhere in this paper) on the basis of low C/N ratios in water and sediment. The losses calculated for Se and N carry large uncertainties as a result of slight differences in the geochemical behavior of these elements, data limitations and spatial differences, but imply that most, if not all, the Se and N discharged to the Salton Sea remains within the Sea's sediment where the elements are potentially available to the benthic biota, or for remobilization into the overlying water. Detailed measurements of mass balances and fluxes for all compartments of the geochemical cycle, including all biota and wind deposition, for each element has the potential to yield improved estimates for net fluxes of Se and N.

Nutrient profiles in cores

Vertical profiles of C, N and P in cores from Site 9 in the north basin and from Site 10 in water of medium depth between the north basin and Whitewater River delta are shown in Figure 8. Nutrient and inorganic element profiles suggest that the depositional history recorded from Site 10 may not be continuous (slumping or episodic redistribution), and therefore results from this core are discussed in less detail than are those from Site 9.

Concentrations of OC and N decrease by almost an order of magnitude with increasing core depth in the center of the north basin (Site 9) and reach a relatively constant concentration a little below 20 cm (Fig. 8). These OC and N profiles are used to delineate the horizon that represents formation of the Salton Sea and implies an average sediment accumulation rate of 2.3 mm yr^{-1}. Additional element data (Ca, S, Al, Se and Mo) that support this sedimentation rate are discussed later in the section, "Historical Record from Cores". Analysis of a single Ekman dredge sample collected in 1996 had indicated low activities for ^{137}Cs and for excess ^{210}Pb, probably because of inefficient scavenging from the atmosphere in this extremely arid environment. Radiometric analyses on cores collected in 1999

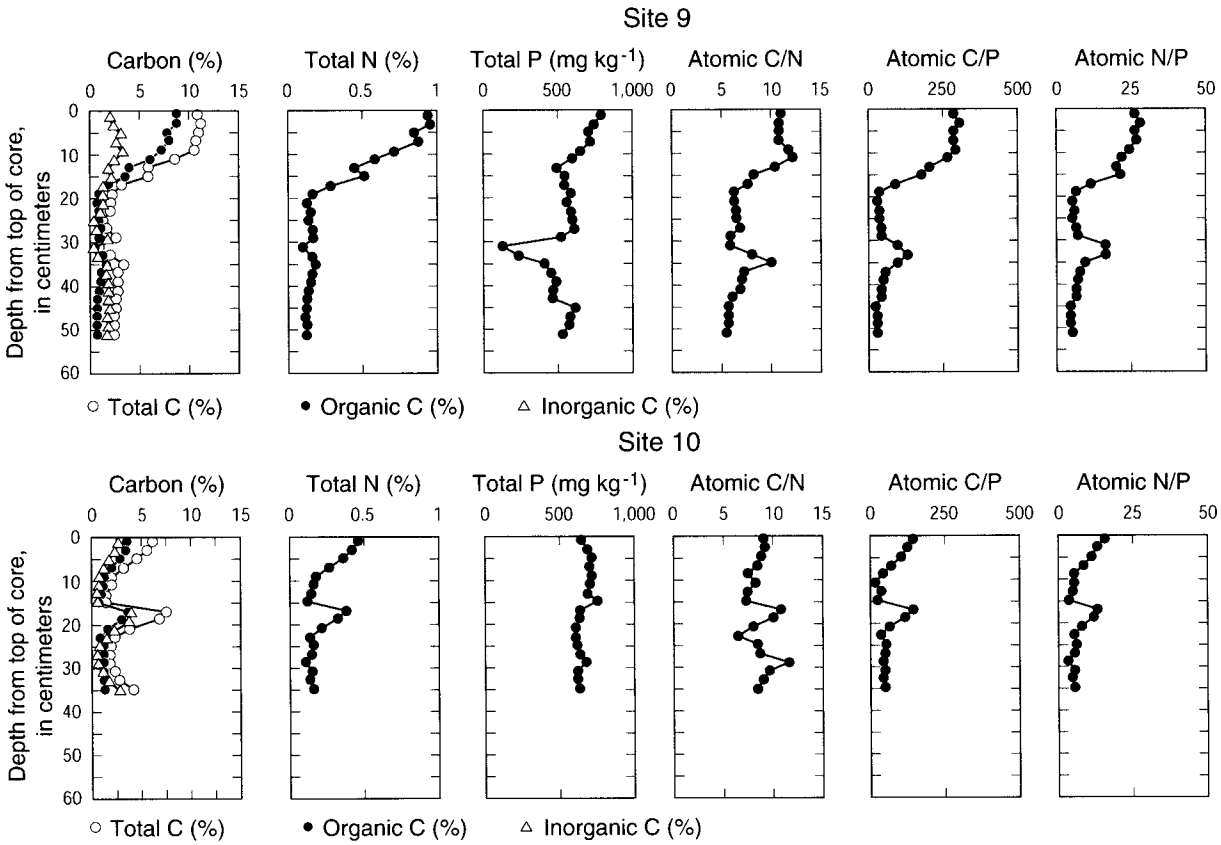


Figure 8. Nutrient profiles in core sediment from the Salton Sea.

confirmed the earlier result (J. Holmes, pers. comm.) and indicate that this method of dating will require larger diameter cores (more material) to be used. An alternative method to determine sediment ages is to match DDE profiles to the historical pattern of agricultural DDT use. Data on DDE in Table 3 indicate that this method would likely be successful in the Salton Sea, and could be used to date cores in the future.

The shapes of the OC and N profiles (Fig. 8) in the upper 20 cm do not approximate theoretical curves of diagenesis (Berner, 1980) and, therefore, suggest an increasing load of both OC and N over time. The slope of both curves declines above about 8 cm, suggesting a rapid increase in the load of both elements prior to about 1965 and only a modest increase since then. Inorganic carbon (IC) concentration varies much less than that of OC, presumably because calcite deposition has been occurring in the Salton Sea throughout its history. As a result, IC gradually increases as a proportion of total carbon (TC) from 19% at the surface to 77% near the bottom of the core from Site 9.

Phosphorus profiles, discussed in more detail later, show that P concentration decreases from about 800 mg kg^{-1} at the surface to 500–600 in depths that predate formation of the Salton Sea. The decrease in concentration, which is much less than for OC and N, implies that about two-thirds of the total P at the sediment surface derives from a natural (eroded soil) as opposed to an anthropogenic source and, therefore, may be in a refractory form.

Dry bulk density (DBD) information is needed to calculate element accumulation rates from concentrations and, as expected, DBD values increase with increasing core depth as water is expelled by the weight of the overlying sediment (Fig. 9). Current accumulation rates for C, N and P are calculated using the estimated sedimentation rate of 0.23 cm yr^{-1}, DBD data, and element concentrations from the 0 to 2-cm interval for the cores shown in Figure 8. The calculated accumulation rates likely represent minimum values, since the sedimentation rate is an average throughout the history of the Salton Sea and recent

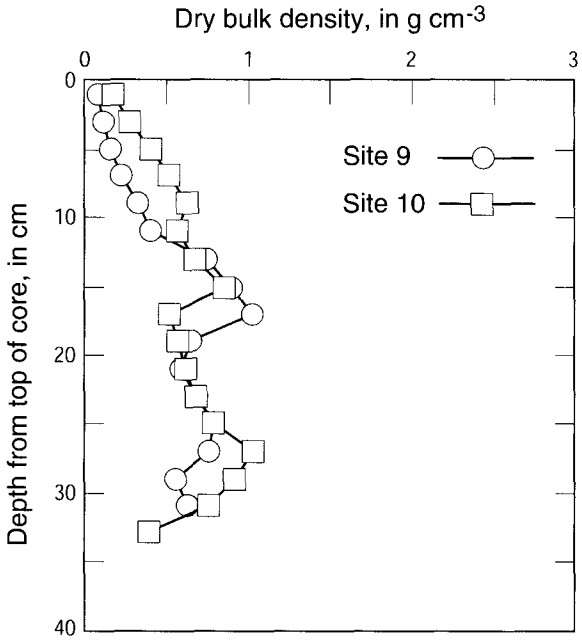


Figure 9. Density profiles in cores from the Salton Sea.

sedimentation rates may be higher because of eutrophication. Estimated minimum accumulation rates are as follows:

Element	Site 9	Site 10
Total C (g C cm^{-2} yr^{-1})	2.2×10^{-3}	2.3×10^{-3}
Organic C (g C cm^{-2} yr^{-1})	1.7×10^{-3}	1.3×10^{-3}
Inorganic C (g C cm^{-2} yr^{-1})	4.2×10^{-4}	9.8×10^{-4}
Total N (g N cm^{-2} yr^{-1})	1.9×10^{-4}	1.7×10^{-4}
Total P (g P cm^{-2} yr^{-1})	1.6×10^{-5}	2.4×10^{-5}

The estimated accumulation rates from the two sites are about the same for TC, OC and N and are reasonably comparable for IC and P.

Nutrient fluxes

The concentration of ammonium and dissolved reactive phosphorus (DRP) in overlying water and in porewater at Sites 9 and 10 are shown in Figure 10. Concentrations of both ammonium and DRP are much higher in porewater than in the overlying water, reflecting the recycling of labile sedimentary N and P (Berner, 1980). Higher concentrations of ammonium and DRP in porewater relative to the overlying water indicate a flux of these nutrients out of the porewater. The flux of ammonium and DRP from the porewater into the overlying water at Sites 9 and 10 was calculated from Fick's Law of Diffusion:

$$F_i = -\phi D_i \theta^{-2} (dc/dz),$$

where F_i is the diffusion flux of species i, ϕ is sediment porosity, D_i is the diffusion coefficient for species i, θ is tortuosity of the sediment, and dc/dz is the linear slope of the concentration *versus* depth curve of the species of interest in porewater. Porosity is approximated from a water content of 90% by volume, and an average dry bulk density (DBD) of 0.493 g cm^{-3} for sediment from the upper 24 cm at Site 9 and 0.554 g cm^{-3} for the upper 26 cm at Site 10 (Fig. 9). Tortuosity is assumed to be 1. Diffusion coefficients for ammonium and DRP in the Salton Sea are taken from Krom & Berner (1981). Calculated fluxes are then:

	Site 9	Site 10
Ammonium	2.5×10^{-6} $\mu g\ cm^{-2}\ s^{-1}$	1.4×10^{-6} $\mu g\ cm^{-2}\ s^{-1}$
DRP	3.2×10^{-7} $\mu g\ cm^{-2}\ s^{-1}$	1.2×10^{-7} $\mu g\ cm^{-2}\ s^{-1}$

Estimated flux of both ammonium and DRP is higher at Site 9 than at Site 10. This reflects the steeper increase (higher gradient) in porewater concentrations with depth at Site 9. The estimated fluxes are comparable to those reported for near-shore marine sediments (McCaffrey et al., 1980; Klump & Martens, 1981).

Nutrient flux from the bottom sediment, derived from these two cores, can be compared with discharge from surface water to determine relative contribution from each. Using an average value for fluxes listed above and a lake area of 1000 km^2 yields annual loads by diffusion out of the bottom sediment of about 6 $\times 10^5$ kg yr^{-1} for N and about 7 $\times 10^4$ kg yr^{-1} for P. Annual discharge from rivers and surface drains carrying mostly irrigation drainage is computed from a water discharge of about 1 km^3 and average N and P concentrations at the outlet to the Salton Sea of approximately 10 and 1 mg l^{-1} yielding 10^7 and 10^6 kg yr^{-1}, respectively. The conclusion is that nutrient loading from surface water discharged to the Salton Sea exceeds that from diffusion out of its bottom sediment by about an order of magnitude.

A second mechanism, in addition to diffusive flux, whereby N can potentially be reintroduced into the water column is by oxidation of sedimentary ammonium and organic nitrogen in parts of the Salton Sea where high-DO bottom water is in contact with the sediment surface. To test this hypothesis, a covered and continuously stirred mixture of sediment from the

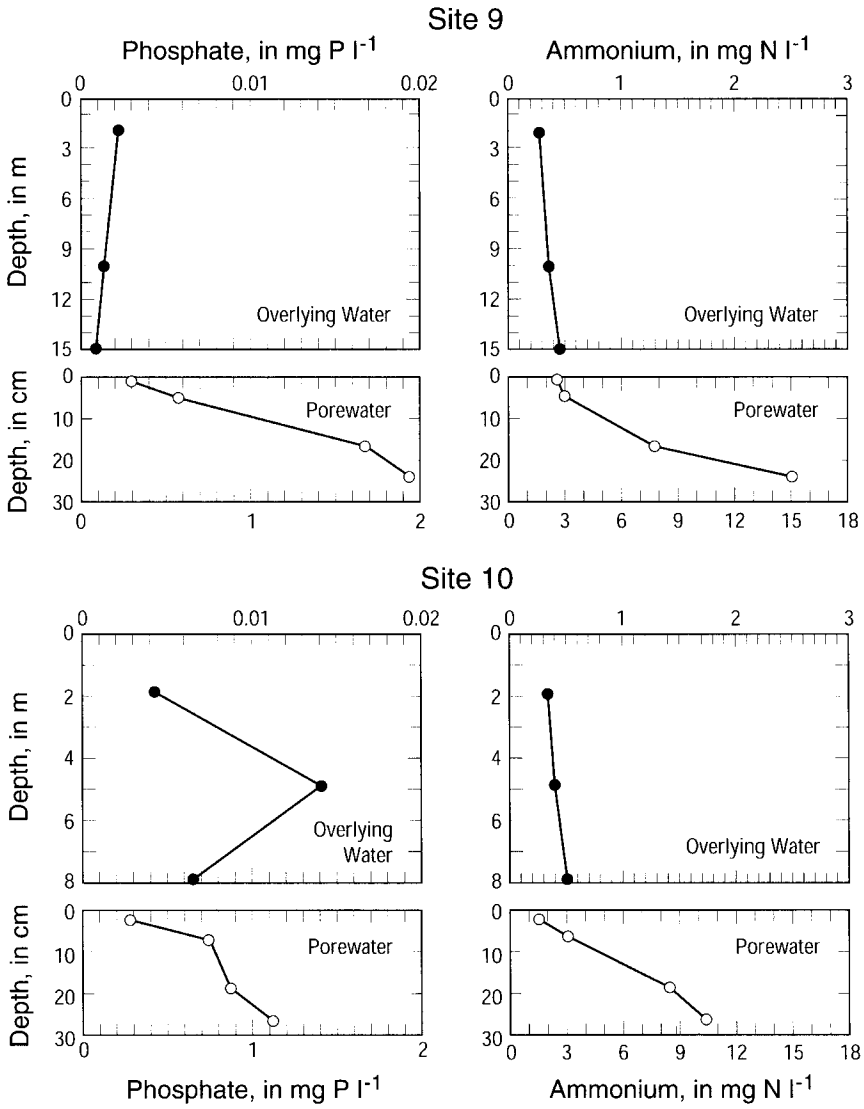


Figure 10. Nutrient profiles across the sediment–water interface in the Salton Sea. (Note changes in scale.)

center of the north basin (Site 9) plus filtered surface water (four parts water added to one part wet sediment by volume) was infused with oxygen by bubbling with filtered air. Aliquots were periodically withdrawn for filtration and chemical analysis and results are shown in Figure 11. The sediment changed color from olive gray to reddish brown, indicating oxidation of iron sulfides, within a few days. Soon thereafter, nitrite, an intermediate species in N oxidation, appears, followed by nitrate that then continues to increase, reaching a value of 35 mg -N l^{-1} and becoming the dominant N species, for the remainder of the 70-day experiment. These results clearly show oxidation and mobilization of N from bottom sediment under aerobic conditions.

Selenium determinations were not attempted on these samples because Se concentrations were expected to be below detection limit after the dilution required (1:100) to lower the high salt content of water to values acceptable for the ICP-MS analysis. A modified ICP-MS method (Gil Ambats, pers. comm., 2001), involving lowering water salinity by ionic exchange and precipitation of AgCl and AgBr, made it possible to determine Se in a water sample kept in contact with sediment in sealed container after completion of laboratory experiment. The high concentration of

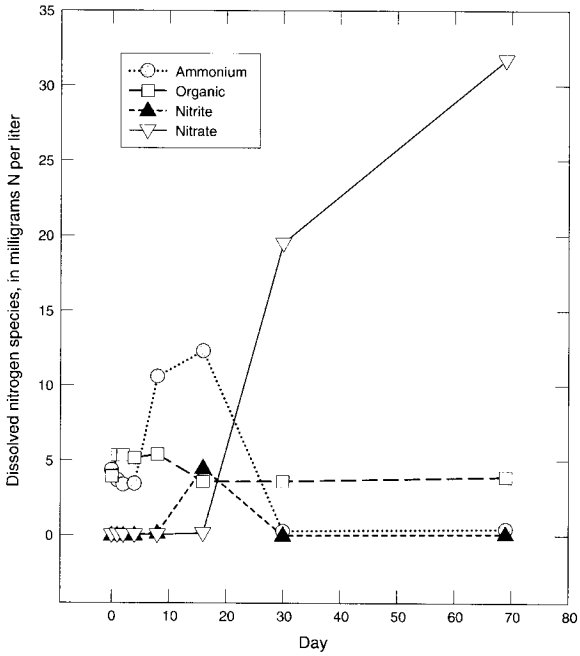


Figure 11. Nitrogen transfer from Salton Sea sediment to water in a laboratory simulation.

Se (15±4 μg l^{-1}, compared to ~1 μg l^{-1} in Salton Sea water) obtained in oxygenated water reacted with sediment, also suggest the possibility for oxidation and mobilization of Se from bottom sediment, as observed in many field investigations and column experiments (Presser et al., 1994; Kharaka et al., 2001).

It is noted that only the sites from shallow and medium depths shown in Figure 2 contain detectable, albeit very low, nitrate and nitrite concentrations in the bottom water (Table 2), where oxygen is generally present at higher concentrations than in deeper parts of the Salton Sea. This pattern could result from some minor oxidation of bottom sediment at these sites, oxidation of dissolved and particulate material within the water column itself, or both.

Phosphorus removal

A detailed understanding of the factors that control P concentration is important because of this element's role as a limiting nutrient in the Salton Sea. Aqueous N concentration appears to have increased by almost an order of magnitude since the early 1950s, but there seems to have been little change in aqueous P concentration. A similar historical trend is revealed by the concentration profiles in sediment cores (Fig. 8). The aqueous N:P atom ratio of 400 in the Salton Sea is nearly 10 times higher than the ratio in the Alamo River (N from Fig. 7 and P from Fig. 12). The New River at its outlet to the Salton Sea will likely have a little lower N:P ratio than the Alamo River because several percent of its flow consists of domestic and municipal wastewater from Mexico (Setmire, 1984). Clearly, aqueous and sediment data indicate P is being effectively scavenged from the water in the Salton Sea when compared to N.

One possible explanation for the apparent lack of a temporal increase in P is that most of the P that arrives at the Salton Sea is sorbed to sediment so strongly that it is not biologically available. Information on the physical and chemical forms of P on solid-phase material, which could be used to infer biological availability, is not currently available, and clearly is needed. In contrast to N, most of the P that is present in the Salton Sea is of natural, as opposed to anthropogenic, origin. In fact, the P concentration in core material beneath the 1905–07 boundary that marks formation of the Salton Sea at about 600 mg kg^{-1}, is about the same as the P concentration in Imperial Valley soil (Schroeder et al., 1993).

Lakes undergoing increasing eutrophication commonly owe the trend to recycling of P from anaerobic, organic-rich bottom sediment into the overlying water column. Yet, this does not seem to be occurring as rapidly in the Salton Sea, possibly because a substantial proportion of the P may be irreversibly sequestered within the bottom sediment as highly insoluble apatites (Schroeder & Orem, 2000). Apatite minerals form the skeletal material of vertebrates and the frequent die-off of as many as 10^6 fish during single epizootics in the Salton Sea (Riedel et al., 2001) might be providing an efficient mechanism for removal of P from the water into the sediment. Sorption and incorporation in sedimentary calcite is another possible mechanism for sequestration of P. Estimates of the fish population and their skeletal P content along with mineral composition of the sediment are needed to ascertain the relative importance of each mechanism.

Historical record from cores

Analysis of cores from receiving water bodies can be a useful method to reconstruct historical changes (trends) in water quality where long-term monitoring data are scant or nonexistent (Schroeder, 1985; Callender & Van Metre, 1997; Van Metre et al., 1997). Selected major-element (Ca, S, and Al) concentrations from a core depicted in Figure 13 are used to

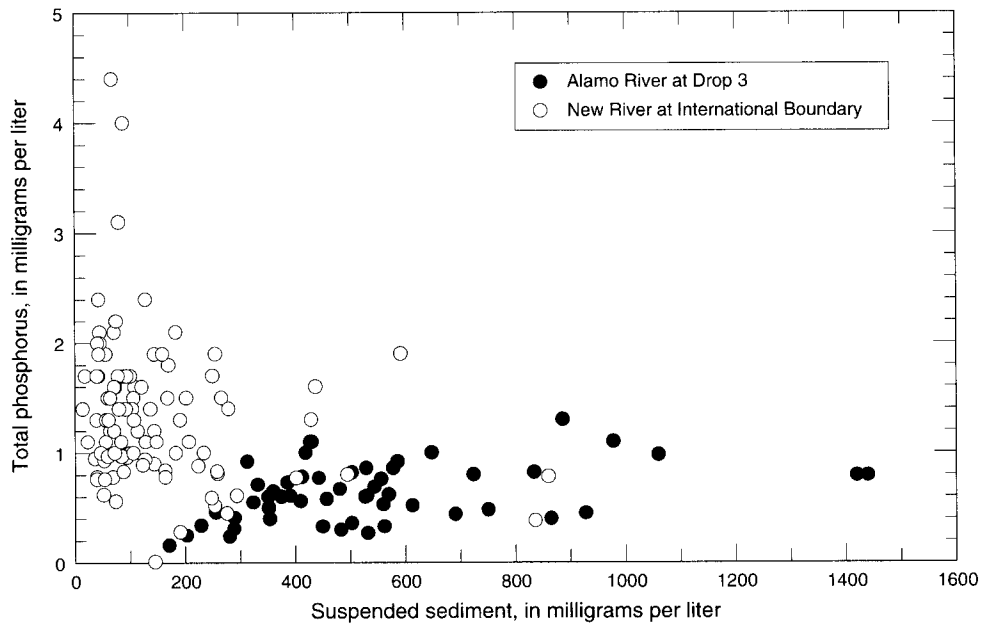


Figure 12. Relation between total-phosphorus and suspended-sediment concentrations in the New and Alamo Rivers since 1970.

infer the 1905–07 boundary that marks formation of the Salton Sea. The profiles show a distinct discontinuity at 22–24 cm, with high Ca and S and low Al relative to concentrations in sediment above and below this interval. (We observed that P concentration also drops markedly in this same interval.) These results likely are due to accumulation of efflorescent minerals, including gypsum, on the dry lakebed that preceded massive flooding which formed the Salton Sea. The gypsum, in effect, dilutes Al in this interval because it replaced much of the aluminosilicate material that composes the local soil. This 'gypsum dilution' also results in much lower concentrations for about 20 other elements (but increases for Mo and As) that typically are associated with the aluminosilicate phase.

Since the Colorado River is the source of irrigation water and Se that reach the Salton Sea, it is possible that chemical profiles in cores obtained for this study might reveal historical trends in the level of Se in the Colorado River itself. Measurements of concentration and discharge in the Colorado River and its tributaries indicate that Se behaves like a conservative ion as it moves downstream (Engberg, 1999). Selenium is transported to the Colorado River from weathering of seleniferous deposits in the Upper Colorado River Basin. Presently about 80% of dissolved Se load and 53% of total salinity are attributable to anthropogenic (mostly agricultural development) activities (Mueller & Osen, 1988; Trueman, 1999; Kharaka et al., 2001), but Se concentrations also may have been higher in the past from initial leaching as extensive undeveloped areas came under cultivation. Hamilton (1999) presents evidence for such higher historical exposures to Se locally within the Colorado River. The Se profile (Fig. 14) wherein concentration increases from about 9 mg kg^{-1} at the surface to about 15 at 10–12 cm, could indicate that Se in Lower Colorado River water diverted to the Salton Basin might have reached 4 $\mu g\ l^{-1}$ in the past, compared to 2.5 $\mu g\ l^{-1}$ today. The Se maximum at 10–12 cm (Fig. 14) could result from other geochemical processes, but its location in the core corresponds to a date of about 1950 in the Salton Sea, and allowing for the residence time of Se in the Colorado River system, translates to 1930–1940 in the Upper Colorado River basin (Michel & Schroeder, 1994).

Long-term implications for the Salton Sea

Protection of the ecological resources and enhancement of the economic value of the Salton Sea has recently stimulated a restoration effort. A part of that effort has produced an environmental impact report that evaluates the effect proposed remediation or 'no-action' will have on the Sea (Cohen et al., 1999). In

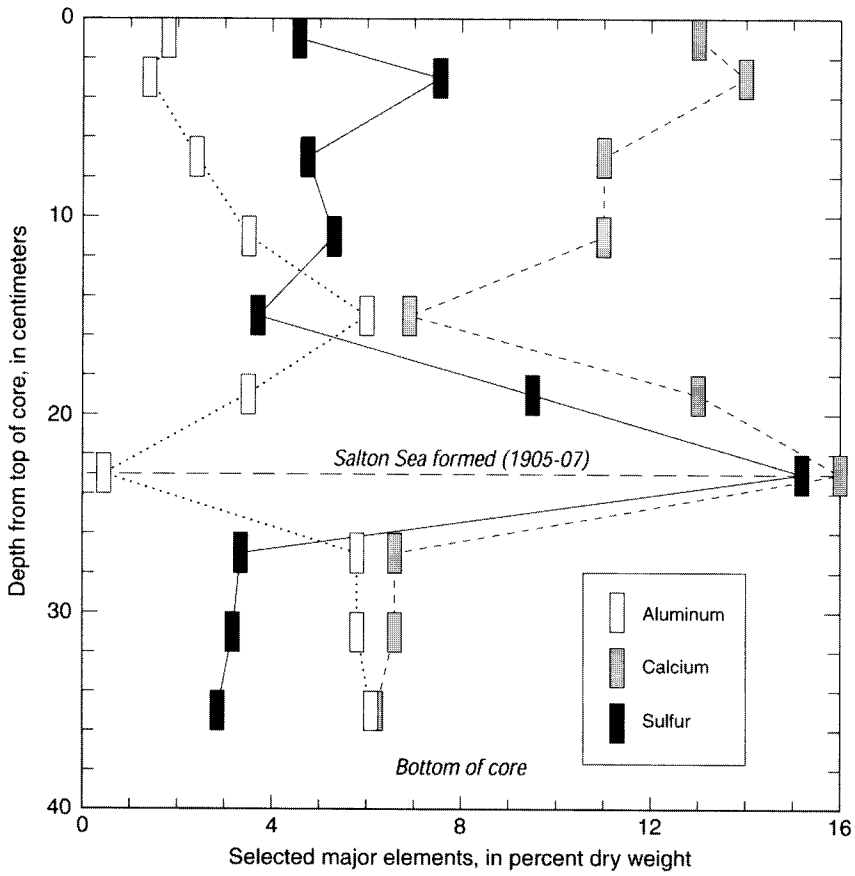


Figure 13. Selected major-element profiles in a core from Site 9 in the Salton Sea.

making predictions, it is wise to recognize how different current conditions are from what might have been anticipated 100, or even 50 years ago. The effects of intentional alteration (restoration) are even more difficult to predict. Therefore, we make only limited projections herein, and they apply to what might happen with no intervention.

The most obvious projection is that increasing salinity will eventually eliminate saltwater fish from the Salton Sea. The major-ion chemistry of the Sea will evolve by increased salinity and the precipitation of calcite, gypsum, sepiolite, and magnesite and/or dolomite, toward a relative increase in Na, Mg, Cl, and, SO_4, and a decrease in the proportion of Ca and HCO_3. In arid environments, as salinity increases pH also typically increases, but, this trend will not occur in the Salton Sea as long as water from Colorado River, with low HCO_3 and higher Ca and Mg, continues to be supplied to the basin.

Transfer of water currently used for irrigation in the Imperial Valley to the urban areas of southern California will convert submerged parts of the Sea to shoreline. If the decrease in lake elevation is about 4.6 m, texture and contaminant concentrations of the newly exposed sediment will not differ greatly from the current near-shore environment. However, bottom sediment from medium water depths (about 9 m) is higher in N and Se than from shallower depths, and this sediment would be exposed to more oxic conditions that generally prevail at shallower depths, increasing the possible remineralization (solubilization by oxidation) of these elements. Whether or not this causes an increase in concentration of these constituents within the water column will then depend on whether reducing conditions remain effective at transferring these elements to the bottom sediment in deeper parts of the Sea, as they appear to do now.

Removal of fish from the Salton Sea may have the most significant effect on aqueous P concentra-

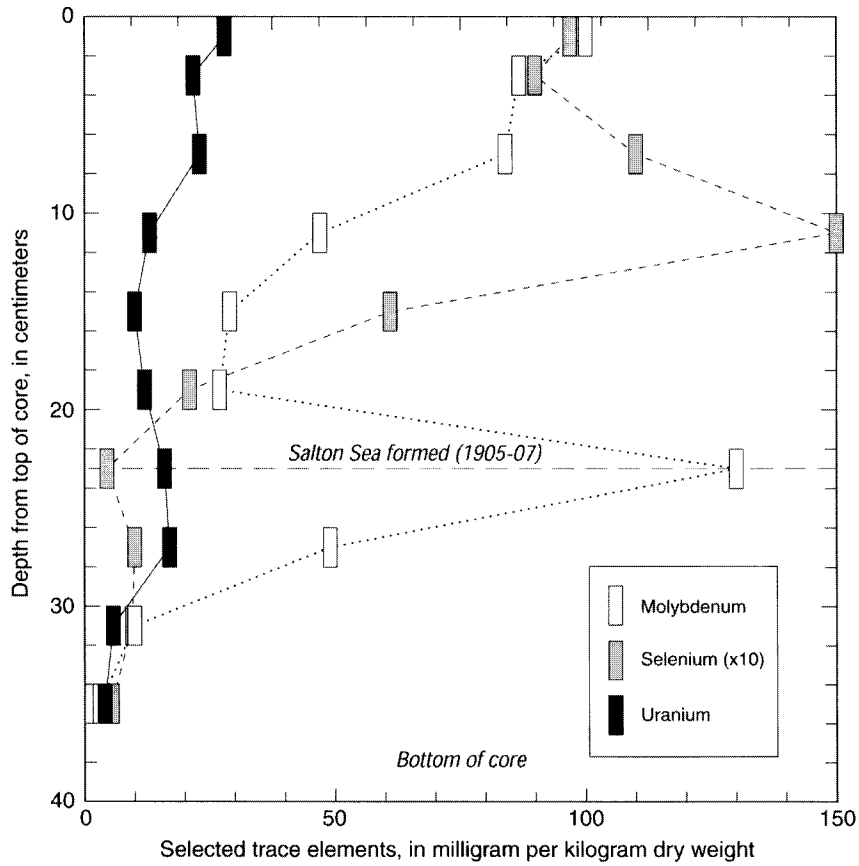


Figure 14. Selected trace-element profiles in a core from Site 9 in the Salton Sea.

tions. Since frequent fish die-offs are a significant mechanism for transfer of P into insoluble apatite minerals from water into bottom sediment, removal of fish will decrease the rate of this transfer. Furthermore, if fish become entirely absent, it is possible that greater recycling of P from anaerobic sediment into the overlying water may accelerate the Salton Sea's rate of eutrophication.

Finally, monitoring by the USGS on the New River at the international border has confirmed the transboundary transport of contaminants typical of urban centers, and their substantial dilution at the river's outlet to the Salton Sea. Long-lived DDT degradation products present on both sides of the border also are transported to and accumulate in the Salton Sea's bottom sediment. However, any of the anticipated changes at the Salton Sea are unlikely to have a significant effect on these contaminants, either because their concentrations are low or because there exists no extraordinarily effective mechanism for their enrichment in sediment and biota.

Summary and conclusions

The Salton Sea has been accumulating chemical constituents delivered by its tributary streams for nearly 100 years because it has no outlet. The buildup of soluble and unreactive chemicals, such as Cl, has resulted in the development of a quasi-marine lake. In contrast, chemicals that react to form insoluble phases ultimately enter the sediments that accumulate on the floor of the Sea. Solubility and sorption properties are especially relevant for two important contaminants, Se and N. The Se is contained in Colorado River water used for irrigation, and N is derived mostly from chemical fertilizer. Both are delivered to the Salton Sea as highly soluble oxyanions by the aerobic Alamo and New Rivers, but are removed as reduced species in anoxic sediment on the Sea's floor. Without this removal mechanism, Se values would be about 400 μg l^{-1} and N would be about 100 mg l^{-1} in the Salton Sea's water, rather than the observed concentrations of only about 1 μg l^{-1} and 5 mg l^{-1}, respectively.

Ironically, anoxic conditions responsible for producing the noxious odors and leading to periodic die-offs of large numbers of fish in the Salton Sea have prevented aqueous Se and N from reaching levels that could indeed pose an extreme environmental hazard. Thus, it is important that any engineering changes made to the Salton Sea do not change the circulation pattern or alter the food chain in such a way as to cause rapid reintroduction of these contaminants from sediment into the overlying water.

It is known that bacteria are capable of converting Se and N into gases that can then be volatilized to the atmosphere (Cooke & Bruland, 1987; Oremland, 1994). By comparing concentrations of Se and N with those of Mo and U that are not effected by volatilization, we estimate that loss from this process may have been about 10% for Se and a one-third loss for N, but this estimation has large uncertainties, especially for results obtained by normalizing to U.

Dissolved-N concentration in the Salton Sea is several times higher today than it was in the mid-1950s; yet dissolved phosphorus (P) concentration has changed little; P is by far the limiting nutrient, based on N:P ratios in the Salton Sea. One possible explanation for minor changes in P is that phosphate is efficiently removed from the water column by incorporation with calcium as apatite minerals – the material that composes fish bone. If so, attempts to slow or reverse excessive biological productivity (eutrophication) through large-scale harvesting of fish may not result in lowering the dissolved P concentration that would thereby improve the trophic status of the Salton Sea. An alternative explanation is that the geochemical cycle for P remains primarily controlled by the same water–sediment 'equilibrium' relations over time because P is predominantly of natural origin, and most of it may be recalcitrant.

Bottom sediment from 11 locations distributed throughout the Salton Sea is dominated by sand near the mouths of large rivers and by organic-rich clay in deeper parts of the Sea. The high organic content results from burial of organic matter produced by biological activity under eutrophic conditions. Calcium carbonate content increases with distance from shore to about 40% in surface sediment from the center of the Sea. The sediment in most locations was highly anaerobic and devoid of macroinvertebrates, but these were abundant at places such as near the mouth of Salt Creek, where DO in bottom water was high. The presence of DDE, a degradation product of DDT, at concentration as high as those reported for bottom material from agricultural drains is noteworthy. The presence of DDE suggests its potential value for dating event horizons in future cores from the Salton Sea.

Acknowledgements

Funds for this study were provided by the Department of the Interior's National Irrigation Water Quality Program (partly matched with cooperative funds from the USGS) and by the U.S. Geological Survey's Eastern Energy Resources Team. We thank John Elder, Peter Glenn, Frank Rinella, John Turk, Theresa Presser, Mark Sylvester, David Piper, Bob Michel, Tom Bullen, Doug Barnum and an anonymous reviewer for technical comments; Jerry Woodcox for editorial assistance; and Larry Schneider and James Thordsen for graphics.

References

Aspila, K. I., H. Agemian & A. S. Y. Chau, 1976. A semi-automated method for the determination of inorganic, organic, and total phosphate in sediments. The Analyst 101: 187–197.

Broecker, W. S., 1974. Chemical Oceanography: Harcourt Brace Javanovich, Inc. 214 pp.

Berner, R. A., 1980. Early Diagenesis, a Theoretical Approach: Princeton University Press, Princeton, New Jersey: 250 pp.

Callender, E. & P. C. Van Metre, 1997. Reservoir sediment cores show U.S. lead declines: Envir. Sci. Technol. 31: 424–428.

Calvert, S. E., 1976. The mineralogy and geochemistry of near-shore sediments. In Riley, J. P. & R. Chester (eds), Chemical Oceanography, Vol. 6., 2nd edn. Academic Press, New York: 187–280.

Carpelan, L. H., 1961. Physical and chemical characteristics. In Walker, B. W. (ed.), The Ecology of the Salton Sea, in Relation to the Sportfishery. Calif. Game and Fish Bull. No. 113: 17–32

Cohen, M. J., J. I. Morrison & E. P. Glenn, 1999. Hazard or haven: the ecology and future of the Salton Sea. Pacific Inst. for Studies in Develop., Environ., and Ecology, Oakland, Calif.: 63 pp.

Cooke, T. D. & K. W. Bruland, 1987. Aquatic chemistry of selenium: evidence of biomethylation. Envir. Sci. Technol. 21: 1214–1219.

Dowd, M. J., 1956. History of Imperial Irrigation District and the development of Imperial Valley: Imperial Irrigation District Dowd Memorial Library, El Centro, Calif.: 94 pp.

Engberg, R. E., 1999. Selenium budgets for Lake Powell and the Upper Colorado River Basin: J. am. Water Res. Ass. 35: 771–786.

Engberg, R. A., D. W. Westcot, D. Delamore & D. D. Holz, 1998. Federal and state perspectives on regulation and remediation of irrigation-induced selenium problems. In Frankenberger, W. T. & R. A. Engberg (eds), Environmental Chemistry of Selenium. Marcel Dekker, Inc, New York, Chapter 1: 1–26.

EPA, 1979. Methods for Chemical Analysis of Water and Waste: Environmental Monitoring and Support Laboratory, Office of Research and Development, U.S. Environmental Protection Agency, Cincinnati, Ohio.

Federal Water Quality Administration, 1970, Salton Sea California. Water Quality and Ecological Management Considerations: U.S. Department of the Interior, Federal Water Quality Administration, Pacific Southwest Region: 54 pp.

Frankenberger, W. T. & R. A. Engberg (eds), 1998. Environmental Chemistry of Selenium. Marcel Dekker, Inc., New York: 713 pp.

Guy, H. P., 1969. Laboratory theory and methods for sediment analysis: U.S. Geol. Survey Techniques of Water-Res. Invest. Book 5, Chapter C1: 58 pp.

Hamilton, S. J., 1999. Hypothesis of historical effects from selenium on endangered fish in the Colorado River Basin. Human and Ecol. Risk Assess. 5: 1153–1180.

Hely, A. G., G. H. Hughes & B. Ireland, 1966. Hydrologic Regime of the Salton Sea, California: U. S. Geol. Survey Prof. Paper 486–C: 32 pp.

Iwatsubo, R. T., 1993. Stream water quality: California In Paulson, R. W., E. B. Chase, J. S. Williams & D. W. Moody (eds), National Water Summary 1990–91: Hydrologic events and stream water quality. U.S. Geol. Survey Water-Supply Paper 2400: 187–196.

Jehl, J., Jr., 1996. Mass mortality events of eared grebes in North America. Am. J. Field Ornith. 67: 471–476.

Kaiser, J., 1999. Battle over a dying sea: Science 284: 28–30.

Kharaka, Y. K., J. J. Thordsen, R. A. Schroeder & J. G. Setmire, 2000. Nanofiltration used to remove selenium and other minor elements from wastewater. In Courtney, Y. (ed.), Minor Elements 2000. Soc. Mining, Metal. Explor: 371–380.

Kharaka, Y. K., E. G. Kakouros & J. B. Miller, 2001. Natural and anthropogenic loading of dissolved selenium in Colorado River Basin. In Cidu, R. (ed.), Proc. 10th Internat. Symp. on Water–Rock Interaction, A. A. Balkema Publishers 2: 1107–1110.

Klump, J. V. & C. S. Martens, 1981. Biogeochemical cycling in an organic rich coastal marine basin – II. Nutrient sediment–water exchange processes. Geochimica et Cosmochim. Acta 45: 101–121.

Krom, M. D. & R. A. Berner, 1981. The diagenesis of phosphorus in a nearshore marine sediment: Geochimica et Cosmochim. Acta 45: 207–216.

McCaffrey, R. J., A. C. Myers, E. Davey, R. Morrison, M. Bender, N. Luedtke, D. Cullen, P. Froelich & G. Klinkhammer, 1980. The relation between pore water chemistry and benthic fluxes of nutrients and manganese in Narragansett Bay, Rhode Island. Limnol. Oceanogr. 25: 31–44.

Meyers, P. A. & R. Ishiwatari, 1993. The early diagenesis of organic matter in lacustrine sediments. In Engel, M. H. & S. A. Macko (eds), Organic Geochemistry, Principles and Applications. Plenum Press, NY: 185–209.

Michel, R. L. & R. A. Schroeder, 1994. Use of long-term tritium records from the Colorado River to determine timescales for hydrologic processes associated with irrigation in the Imperial Valley, California. Appl. Geochem. 9:387–401.

Mueller, D. K. & L. L. Osen, 1988. Estimation of natural dissolved solids discharge in the Upper Colorado River Basin: U.S. Geol. Survey Water-Supply Paper 87-4069: 63 pp.

NWIS web address is at http://water.usgs.gov/ca/nwis/qwdata/. (The interested reader can access the data from this web site using the station ID numbers listed in Table 1, or obtain the data directly from the senior author at the address listed in this report).

Orem, W. H., H. E. Lerch & P. Rawlik, 1997. Geochemistry of surface and pore water at USGS coring sites in wetlands of south Florida: 1994 and 1995: U.S. Geol. Survey Open-File Rep. 97–454: 55 pp.

Orem, W. H., C. W. Holmes, C. Kendall, H. E. Lerch, A. L. Bates, S. R. Silva, A. Boylan, M. Corum, M. Marot & C. Hedgman, 1999. Geochemistry of Florida Bay sediments: nutrient history at five sites in eastern and central Florida Bay. J. Coastal Res. 15: 1055–1071.

Oremland, R. S., 1994. Biogeochemical transformations of selenium in anoxic environments. In Frankenburger, W. T. Jr. & Benson, Sally (eds), Selenium in the Environment. Marcel Dekker, Inc., New York, Chapter 8: 389–420.

Parkhurst, D. L., 1995. User's guide to PHREEQC – a computer program for speciation, reaction-path, advective-transport, and inverse geochemical calculations: U.S. Geol. Survey Water-Res. Invest. Rep. 95-4227: 143 pp.

Pacific Institute, 2001. A proposal to preserve and enhance habitat at the Salton Sea: Pacific Institute for Studies in Development, Environment, and Security, 654 13th Street, Oakland, Calif.: 7 pp.

Presser, T. S., M. A. Sylvester & W. H. Low, 1994. Bioaccumulation of selenium from natural geologic sources in Western States and its potential consequences. Envir. Manag. 18: 423–436.

Riedel, R., L. Helvenston & B. Costa–Pierce, 2001. Fish biology and fisheries ecology of the Salton Sea. Final Report to the Salton Sea Authority under EPA grant Report # R826552-01-0.

Schroeder, R. A., 1985. Sediment accumulation rates in Irondequoit Bay, New York based on lead-210 and cesium-137 geochronology: Northeastern Environ. Sci. 4: 23–29.

Schroeder, R. A., 1996. Transferability of environmental assessments in the Salton Sea Basin, California, and other irrigated areas in the Western United States to the Aral Sea Basin, Uzbekistan. In Micklin, P. P. & W. D. Williams (eds), The Aral Sea Basin. Proc. of the NATO Advanced Research Workshop "Critical Scientific Issues of the Aral Sea Basin: State of Knowledge and Future Research Needs". Tashkent, Uzbekistan, May 2–5, 1994. NATO ASI Series, Partnership Sub-Series, 2. Environment–v. 12, Springer-Verlag: 121–137.

Schroeder, R. A. & W. H. Orem, 2000. Nutrient dynamics in the Salton Basin – implications from calcium, uranium, molybdenum, and selenium. Am. Geophys. U. Spring Meeting, Washington, D.C., May 30–June 3, 2000, EOS Trans. Suppl. 81, no. 19, Abstract no. H31B-02: p. S196.

Schroeder, R. A., J. G. Setmire & J. C. Wolfe, 1988. Trace elements and pesticides in the Salton Sea area, California. In Proc. on Planning Now for Irrigation and Drainage. Irrigation Division, Am. Soc. Civil Eng., Lincoln, Nebraska, July 19–21, 1988. 700–707.

Schroeder, R. A., M. Rivera, B. J. Redfield, J. N. Densmore, R. L. Michel, D. R. Norton, D. J. Audet, J. G. Setmire & S. L. Goodbred, 1993. Physical, chemical, and biological data for detailed study of irrigation drainage in the Salton Sea area, California, 1988–90. U.S. Geol. Survey Open-File Rep. 93–83: 179 pp.

Setmire, J. G., 1984. Water quality in the New River from Calexico to the Salton Sea, Imperial County, California: U.S. Geol. Survey Water-Supply Paper 2212: 42 pp.

Setmire, J. G. & R. A. Schroeder. 1998. Selenium and salinity concerns in the Salton Sea area of California. In Frankenberger, W. T., Jr & R. A. Engberg (eds), Environmental Chemistry of Selenium. Marcel Dekkar, Inc., New York, Chapter 12: 205–221.

Setmire, J. G., J. C. Wolfe & R. K. Stroud, 1990. Reconnaissance investigation of water quality, bottom sediment, and biota associated with irrigation drainage in the Salton Sea area, California, 1986–87: U.S. Geol. Survey Water-Res. Invest. Rep. 89–4102: 68 pp.

Setmire, J. G., S. L. Goodbred, D. J. Audet, R. A. Schroeder, W. R. Radke & J. N. Densmore, 1993. Detailed study of water quality, bottom sediment, and biota associated with irrigation drainage in the Salton Sea area, Imperial County, California, 1988–90: U.S. Geol. Survey Water-Res. Invest. Rep. 93-4014: 102 pp.

Summons, R. E., 1993. Biogeochemical cycles, a review of fundamental aspects of organic matter formation, preservation, and composition. In Engel, M. H. & S. A. Macko (eds), Organic Geochemistry, Principles and Applications. Plenum Press, New York: 3–21.

Strickland, J. D. H. & T. R. Parsons, 1973. A Practical Handbook of Seawater Analysis: Fisheries Research Board of Canada, Ottawa, Ontario: 310 pp.

Trueman, D., 1999. Quality of water Colorado River Basin: U.S. Department of the Interior Progress Report No. 19, 93 pp. + appendix A.

Tostrud, M. B., 1997. The Salton Sea, 1906–1996, computed and measured salinities and water levels: Colorado River Board of California. November 1997: 72 pp.

Van Metre, P. C., E. Callender & C. C. Fuller, 1997. Historical trends in organochlorine compounds in river basins identified using sediment cores from reservoirs: Envir. Sci. Technol. 31: 2339–2344.

White, A. F. & N. M. Dubrovsky, 1996. Chemical oxidation-reduction controls on selenium mobility in groundwater systems. In Frankenburger, W. T. Jr. & Benson, Sally (eds), Selenium in the Environment. Marcel Dekker, Inc., New York, Chapter 8: 185–221.

Hydrobiologia **473:** 47–54, 2002.
D.A. Barnum, J.F. Elder, D. Stephens & M. Friend (eds), The Salton Sea.
© 2002 *Kluwer Academic Publishers. Printed in the Netherlands.*

Characteristics and contaminants of the Salton Sea sediments

Richard A. Vogl[1] & Ryan N. Henry[2]
[1]*HydroGeo Consultants, 3151 Airway Avenue, Suite H1, Costa Mesa, CA 92626, U.S.A.*
[2]*PCR, One Venture, Suite 150, Irvine, CA 92618, U.S.A.*

Abstract

This was the first comprehensive study to evaluate the distribution of sediment types and sediment contaminants throughout the Salton Sea. The sampling effort encompassed the entire Sea plus its three main tributaries, and included collection of sediment samples from 73 locations. The agricultural runoff that keeps the Sea alive is loaded with salts, pesticides, selenium, and other metals. Metals and metalloids found at elevated concentrations and of potential ecological concern were cadmium, copper, molybdenum, nickel, zinc, and selenium. The most significant metalloid of concern was selenium, which was limited to the upper 30 cm of sediment. There did not appear to be any strong correlation between the sand, silt, or clay content with the areas of elevated metals and metalloids. Acetone, 2-butanone, and carbon disulfide were also widespread but appeared to be associated with natural biological processes within the sediments. One of the most significant findings of this study was the absence of elevated concentrations of organic chemicals commonly used in agriculture earlier this century, such as dichlorodiphenyltrichloroethane (DDT).

Introduction

The Salton Sea is the largest lake in California, with a current length of 56 kilometers (km), width of 24 km, and maximum depth of approximately 15 m. It is approximately 85 m below mean sea level and its salinity is 44 parts per thousand. The Sea is a closed drainage system that receives 5.8 cm of rain a year, with air temperatures reaching 50 °C. Agricultural wastewater keeps the Sea alive and carries contaminants such as pesticides, selenium, and other elements, as well as salt leached from the agricultural fields.

Previous studies on Salton Sea bottom sediments have identified a variety of elements and organic chemicals including organochlorine pesticide residues of banned DDT (1,1,1-trichloro-2,2-bis[p-chlorophenyl]-ethane) and its derivatives, DDD (1,1-dichloro-2,2-bis[p-chlorophenyl]-ethane) and DDE (1,1-dichloro-2,2-bis[p-chlorophenyl]-ethylene). Many chemicals, including DDT, DDD, DDE, dichloromethane, polychlorinated biphenyls, polynuclear aromatic hydrocarbons, pesticides, selenium, and boron, have been identified in the riverbeds feeding into the Sea (Hogg, 1973; Eccles, 1979; Setmire & Stroud, 1990; Setmire et al., 1993; Bechtel, 1997). Prior to the current study, however, little was known about the current concentrations and distribution of these contaminants within the sediments of the Salton Sea. This is the first comprehensive study to evaluate the overall distribution of sediment types and contaminants throughout the Sea and its three major tributaries. A major objective of the study was to provide information that would be useful for development of effective management actions to save this valuable ecosystem.

Description of site studies

This investigation of the physical and chemical characterization of sediments in and around the Salton Sea, Imperial and Riverside Counties, California, was undertaken in the winter of 1998–1999. The study was implemented in two phases. In the first phase, sediments were sampled from December 15 through 22, 1998. The samples were analyzed for contaminant concentrations and particle size distribution in the bottom sediment of the Sea plus approximately 1.6 km up each of three of its main tributaries: the Whitewater, the Alamo, and the New rivers. Phase I sediment samples were collected from 42 grab sampling sites and six core sampling sites.

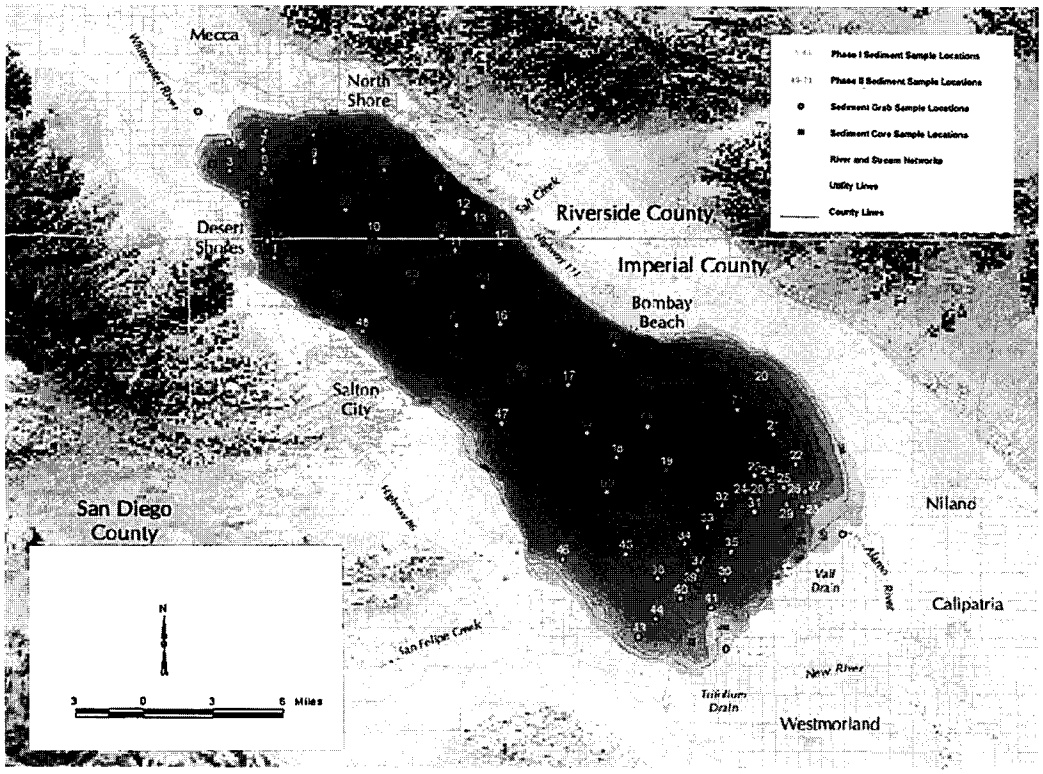


Figure 1. Phase I and II sampling locations.

Based on the results of the first phase of investigation, a second phase of sediment sampling was conducted from January 19 through 22, 1999, to further assess and measure contaminant concentrations and evaluate particle-size distribution in the bottom sediment. This second sampling phase focused on the significant areas of interest identified during Phase I and included sediment sampling at 15 grab sites and 10 core sites. The locations of Phase I and Phase II sampling sites are shown on Figure 1 above.

Materials and methods

A stainless-steel modified Birge-Ekman-style box sediment sampler, 15.24 centimeters (cm) by 15.24 cm by 15.24 cm in size, was used to collect samples at the 57 grab sample locations of the 73 sampling sites. For each grab sample, up to 710 cubic centimeters of material was retained for inorganic and organic chemical analyses, depending on sample recovery. Sediment samples were transferred directly from the sampling equipment into clean, laboratory-grade glass jars using a stainless-steel trowel.

The core samples were collected using an AMS stainless-steel soft sediment sampler that can produce a 5-cm square by 182-cm long core. The corer can take up to 182 cm of undisturbed samples from soft sediment, provided that rocks or dense materials are not encountered. The AMS soft sediment sampler consists of two stainless steel, 182-cm long, right-angle-shaped sampler halves, each with a pointed lower end, that create a 5.08-cm square when locked together. One half contains a riveted sediment trap that engages when the sampler is pulled from the sediment. Sediment samples obtained using the stainless steel corer were collected from a boring advanced down to a maximum of 182 cm below ground surface (bgs), with samples for laboratory analyses taken at 30-cm intervals. The cores were carefully measured for total length and different layers of sediment without disturbing the sediment-water interface. Cored samples were lithologically described and classified using the Unified Soil Classification System. As with the grab samples, these samples were transferred to clean, laboratory-grade glass jars using a stainless steel trowel that was cleaned between samples.

Each sediment sample was analyzed for particle size, total metals and metalloids consisting of the California Code of Regulations 17 metals series (antimony, arsenic, barium, beryllium, cadmium, chromium, cobalt, copper, lead, mercury, molybdenum, nickel, selenium, silver, thallium, vanadium, and zinc) using EPA Method 7000S, volatile organic compounds using EPA Method 8260, semi-volatile organic compounds using EPA Method 8270, chlorinated pesticides and polychlorinated biphenyls (PCBs) using EPA Method 8081, organophosphate and nitrogen pesticides using EPA Method 8141, and chlorinated herbicides using EPA Method 8151. A number of sediment samples were also analyzed for chlorinated pesticides using EPA Method 8270 as a confirmatory measure (EPA, 1980).

Results and discussion

Sediments sampled on the bottom of the Salton Sea consisted of silt, clay, and finer grained sands. The shallow sediment also included abundant barnacle shells and occasional fish bones. The surface sediment composition included a high percentage of sand outside Salton City and extending into the central, deeper parts of the Sea. Sand percentages near the mouths of the New and Alamo rivers were also high, as expected, from deposition of these heavier particles from higher velocity inflows into the Sea. The lower velocity Whitewater River delta, on the other hand, was predominantly silt. Silt was also abundant along the southwest near-shore area and along the shallow water bays near the New and Alamo rivers. A shallow layer of clay blankets the southwestern corner of the Sea and extends toward the center, near the deepest part of the Sea. Clay is also abundant near shore and offshore just north of Desert Shores. The majority of the deeper sediment sampled consisted predominantly of varied amounts of silt and clay, with lesser amounts of fine sand. The distribution of sand, silt, and clay determined from this study are depicted in Figures 2, 3 and 4, respectively.

Concentrations of metals and metalloids in the sediments were found to be higher in the northern part of the Sea. Concentrations were generally higher in the upper 30 cm of sediment. The chemical concentrations were compared against background and available sediment quality screening criteria commonly used in sediment assessment studies of saline environments: maximum 'baseline value' for soils of the western United States (Severson et al., 1987; modified from Shacklette & Boerngen, 1984) and National Oceanic and Atmospheric Administration (NOAA, 1991) effects range low (ERL) and effects range medium (ERM). For selenium, California Regional Water Quality Control Board, San Francisco Region, criteria for wetlands creation (Wolfenden & Carlin, 1992) were used because no ERLs or ERMs exist. NOAA ERL and ERM levels were used as a preliminary screening tool to define apparent elevated concentrations within the Sea. Based on these screening criteria, the following metals and metalloids were determined to be elevated and of potential ecological concern: cadmium, copper, molybdenum, nickel, zinc, and selenium, with the most elevated inorganic constituent being selenium.

Concentrations of cadmium ranged from 0.67 to 5.8 milligrams per kilogram (mg/kg). The highest reported concentrations of cadmium were found in the north-central part of the Sea. Concentrations of copper ranged from 8.1 to 53 mg/kg. The highest concentrations of copper were found near the mouth of the Whitewater River. Concentrations of molybdenum detected in the north and central part of the Sea ranged from approximately 11 to 194 mg/kg. The range of reported concentrations for nickel was from 3.3 to 33 mg/kg. The highest concentrations of nickel were detected at the mouth of the Whitewater River and in the deeper portion of the Sea. The range of concentrations for zinc was from 5.4 to 190 mg/kg. The highest concentrations of zinc were found at the mouths of the Whitewater River and Salt Creek. Concentrations of selenium detected at the Sea ranged from 0.086 to 8.5 mg/kg. The highest concentrations of selenium were found just offshore of Desert Shores. In general, metal and metalloid concentrations were elevated over much of the northern half of the Sea. The distribution of detected concentrations of cadmium, molybdenum, nickel, and selenium are depicted in Figures 5, 6, 7 and 8, respectively.

Elevated concentrations of organic chemicals in sediment were detected predominately in the northern part of the Sea. Of the 118 sediment samples analyzed for volatile organic compounds, 114 samples contained detectable concentration of acetone, carbon disulfide, and/or 2-butanone. These three detected chemicals are believed to be present as a result of natural biological anaerobic degradation processes occurring within Salton Sea sediment. Acetone concentrations ranged from 32 to 840 micrograms per kilogram (μg/kg). The highest concentrations of acetone were located near the mouth of the New River.

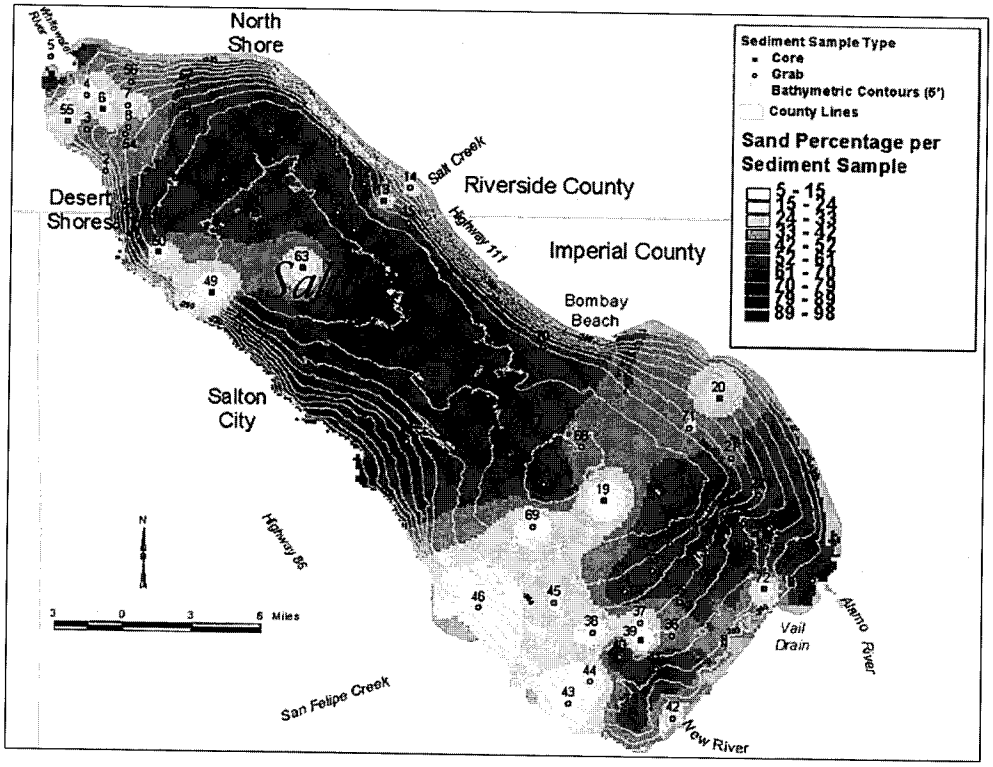


Figure 2. Sand percentage per sediment sample.

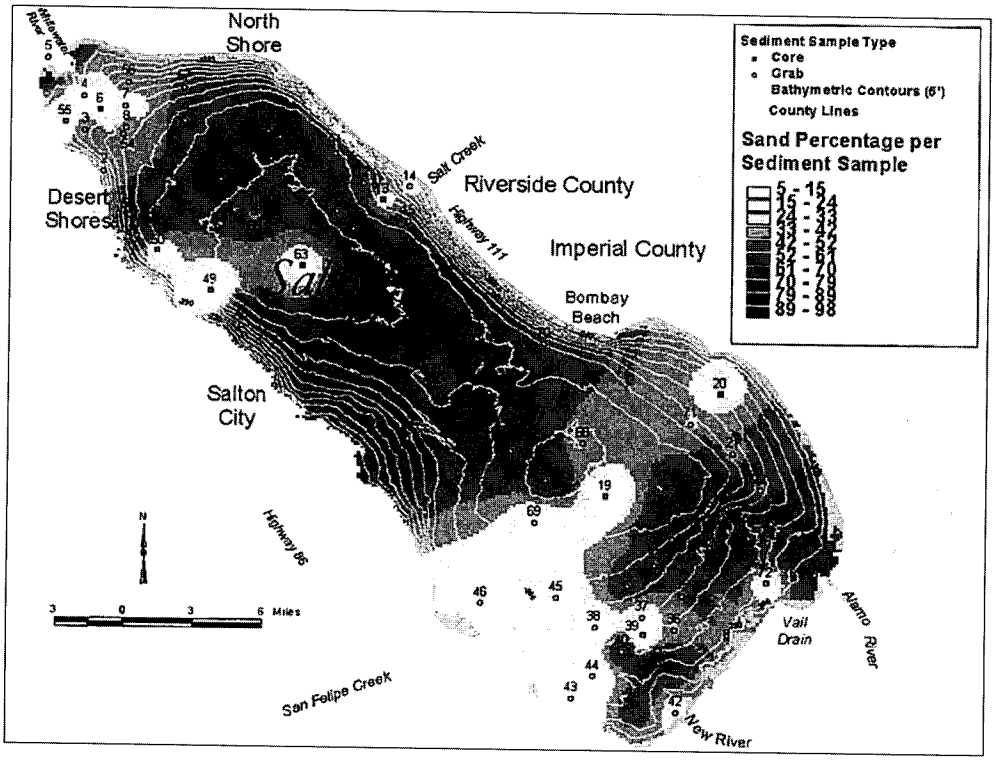


Figure 3. Silt percentage per sediment sample.

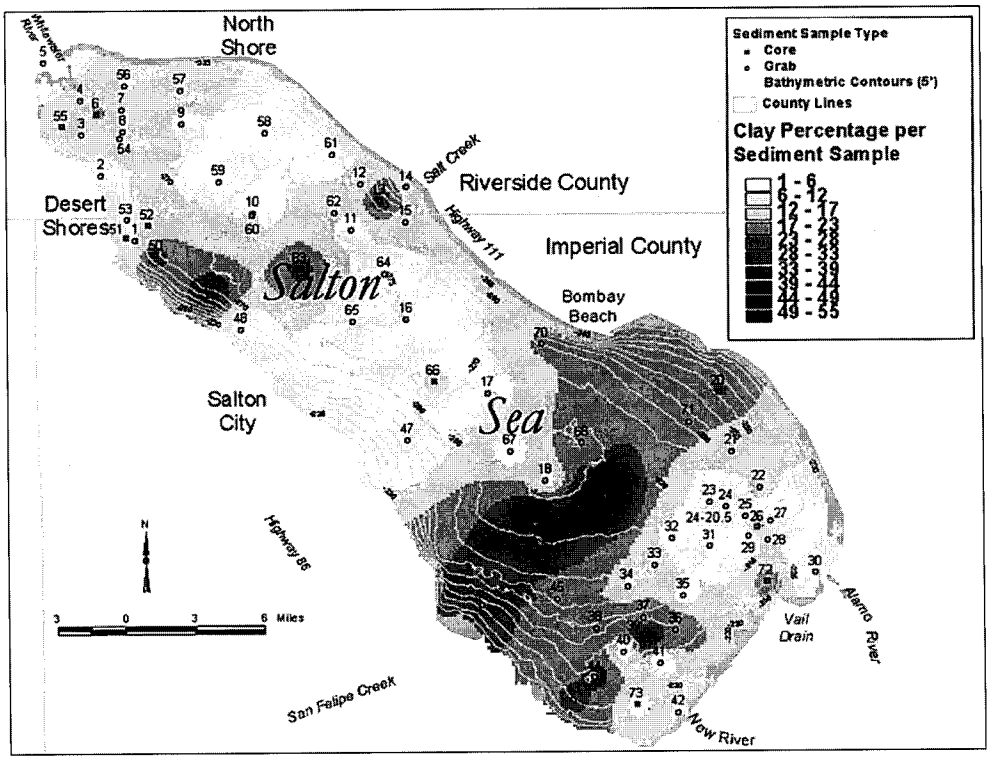


Figure 4. Clay percentage per sediment sample.

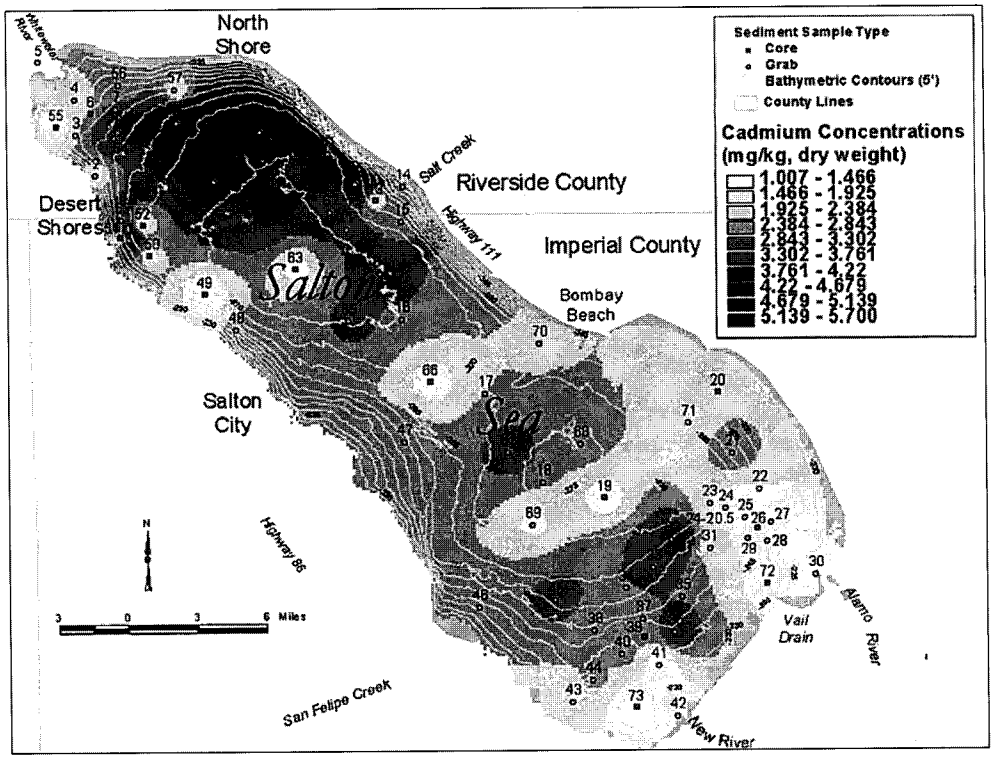


Figure 5. Cadmium concentrations.

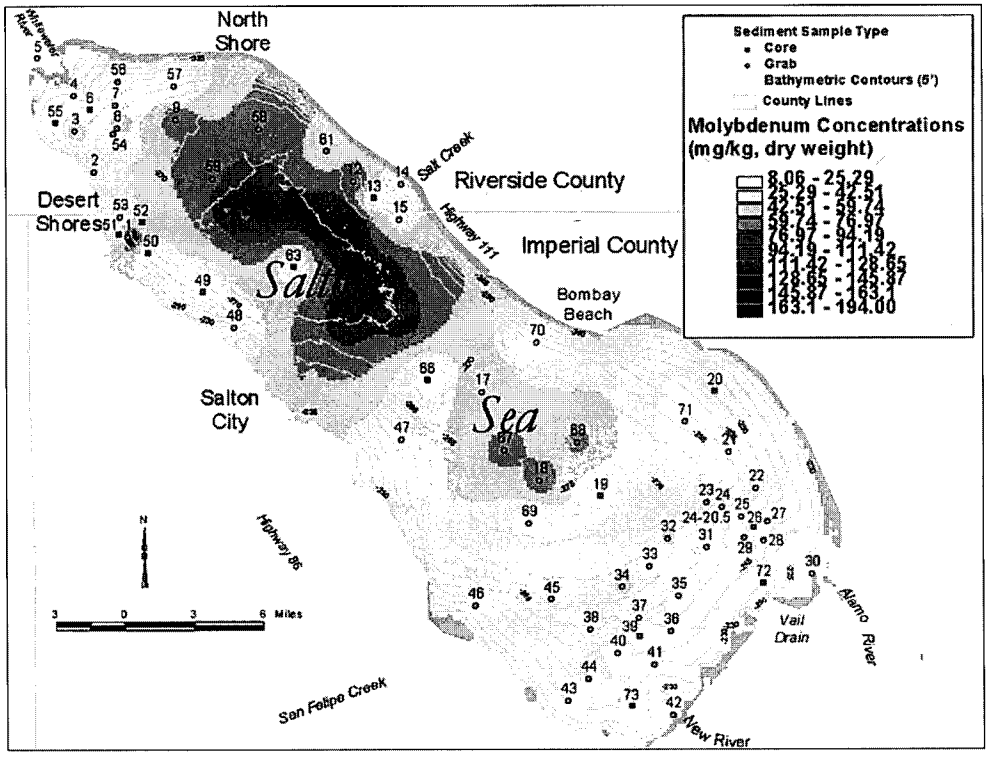


Figure 6. Molybdenum concentrations.

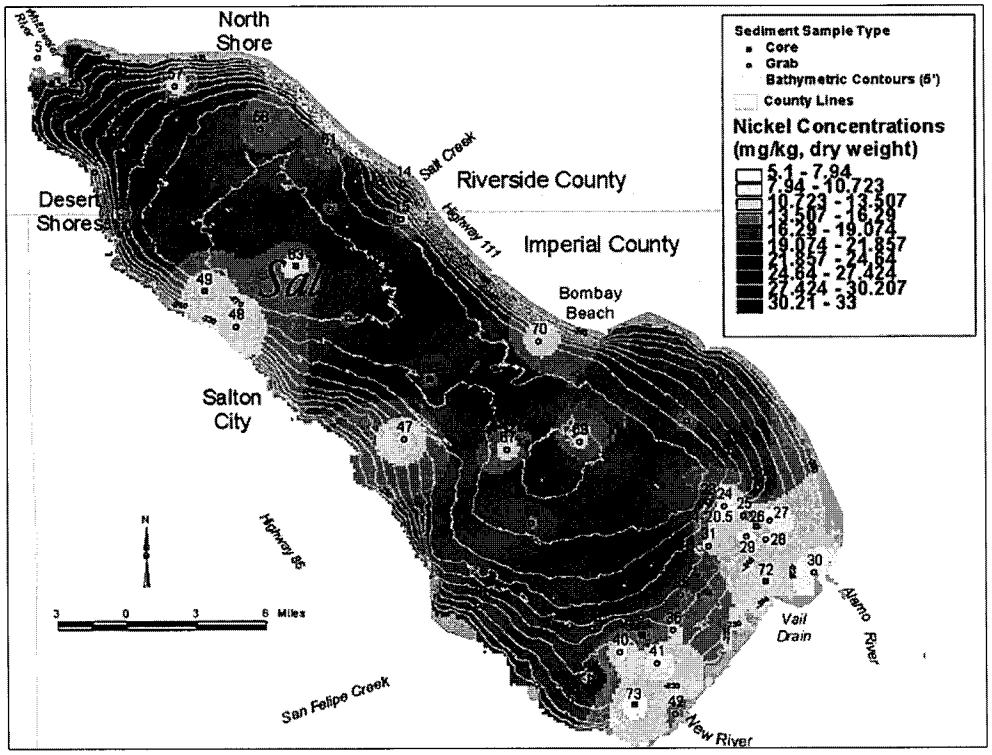


Figure 7. Nickel concentrations.

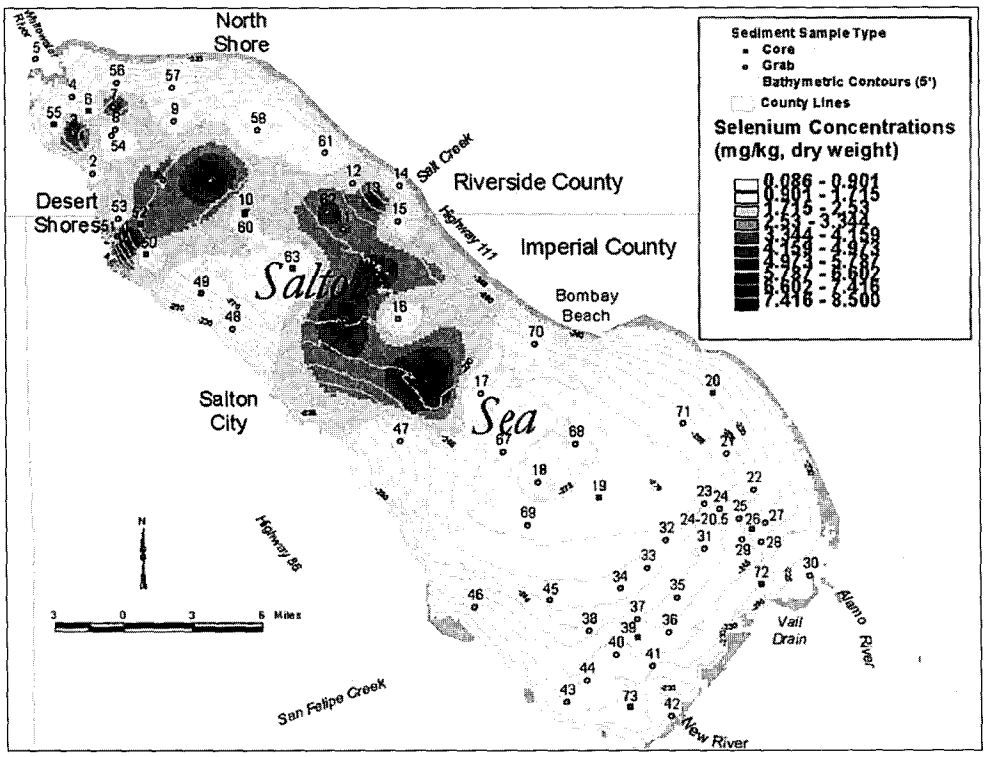


Figure 8. Selenium concentrations.

Carbon disulfide concentrations ranged from 15 to 1800 μg/kg. The highest concentrations of carbon disulfide were near the mouth of the Whitewater River. Concentrations of 2-butanone ranged from 11 to 150 μg/kg. The highest concentration of 2-butanone was detected in the northern portion of the Sea, offshore from Salton Sea State Park.

Only two other sediment samples contained detectable concentrations of other volatile organic compounds, including o-xylenes, 1,3,5-trimethylbenzene, 1,2,4-trimethylbenzene, naphthalene, and n-propylbenzene. These chemicals appeared to be very localized and non-pervasive.

One of the most significant findings of this study was that semi-volatile organic compounds, chlorinated pesticides, PCBs, organophosphate and nitrogen pesticides, and chlorinated herbicides were not detected in the sediment samples analyzed. Low concentrations of organochlorine pesticides may not have been detected in this study because of elevated reporting detection limits; however, a number of previously detected concentrations for these pesticides were above the laboratory detection limits for this study, yet nothing was detected even from our much larger data set. The detection limit problem resulted from the characteristics of Salton Sea sediments, which contain very high levels of organic carbon and sulfur. For each analysis, the laboratory attempted to achieve the lowest detection limit possible based on the available sample size and the matrix sampled.

Conclusions

The results of this study indicate that a number of metals and metalloids including cadmium, copper, molybdenum, nickel, zinc, and most notably selenium, are present at elevated concentrations in Salton Sea sediment at concentrations that could be of potential ecological concern. These elements were found in higher concentrations in the northern part of the Sea and appear to be generally limited to the upper 30 cm of sediment. There did not appear to be any strong correlation between the sand, silt, or clay content with the areas of elevated metals and metalloids. Relatively low concentrations of volatile organic compounds including acetone, 2-butanone, and carbon disulfide were widespread in the sediments throughout

the Sea, and have therefore been interpreted to be associated with natural anaerobic biologic decomposition processes within the sediments rather than an anthropogenic source. One of the most significant findings of this study was that semi-volatile organic compounds, chlorinated pesticides, PCBs, organophosphate and nitrogen pesticides, and chlorinated herbicides were not detected at elevated concentrations in the sediment samples analyzed indicating that the Sea was much healthier with respect to contamination than originally suspected.

References

Bechtel National, Inc., 1997. Final Addendum to the Removal Site Evaluation Report, Salton Sea Test Base Report, Salton Sea Test Base, Imperial County, CA.

Eccles, L. A., 1979. Pesticide residues in agricultural drains, southeastern desert area, California. U.S. Geological Survey Water Resources Investigation Report 79-16: 60.

Environmental Protection Agency, 1980. Publication SW-846, Test Methods for Evaluating Solid Waste, Physical/Chemical Methods.

Hogg, N. D., 1973. Chlorinated Hydrocarbon Pesticide Residues, Salton Sea, California. M.S. Thesis, California Polytechnic University, Pomona: 47.

National Oceanic and Atmospheric Administration, 1991. The Potential for Biological Effects of Sediment-Sorbed Contaminants Tested in the National Status and Trends Program. Office of Oceanography and Marine Assessment, Seattle, WA. Technical Memorandum NOS OMA 52. (Also cited as Long & Morgan, 1990.)

Setmire, J. et al., 1993. Detailed study of water quality, bottom sediment, and biota associated with irrigation drainage in the Salton Sea area, California, 1988–1990. Prepared in cooperation with the California Regional Water Quality Control Board, Colorado River Basin Region. Sacramento, CA. U.S. Geological Survey 93-4014: 102.

Setmire, J. & R. Stroud, 1990. Reconnaissance investigation of water quality, bottom sediment, and biota associated with irrigation drainage in the Salton Sea area, California, 1986–1987. [Sacramento, Calif.] Dept. of the Interior, U.S. Geological Survey, 89-4102: 68.

Severson, R. C., S. A. Wilson & J. M. McNeal, 1987. Analyses of bottom material collected at nine areas in the Western United States for the DOI irrigation drainage task group. U.S. Geological Survey, Open-File Report 87-490: 24.

Shacklette, H. & J. Boerngen, 1984. Element concentrations in soils and other surficial materials of the conterminous United States. U.S. Geological Survey Professional Paper 1270: 105.

Walker, J., 1996. Fresh-Water Inflow and Distribution of Laminated Sediments in the Salton Sea, California. Loma Linda University.

Wolfenden, J. & M. Carlin, 1992. Interim Screening Criteria and Testing Requirements for Wetland Creation and Upland Beneficial Reuse Projects. California Regional Water Quality Control Board, San Francisco Region.

Hydrobiologia **473:** 55–57, 2002.
D.A. Barnum, J.F. Elder, D. Stephens & M. Friend (eds), The Salton Sea.
© 2002 *Kluwer Academic Publishers. Printed in the Netherlands.*

Reconstruction of prehistoric Lake Cahuilla in the Salton Sea Basin using GIS and GPS

Joseph E. Buckles, Kazuyuki Kashiwase & Timothy Krantz
Salton Sea Database Program, University of Redlands, 1200 East Colton Avenue, P.O. Box 3030, Redlands, CA 92373-0999, U.S.A.

Key words: hydrology, Salton Sea, Lake Cahuilla, GPS, GIS, archaeology

Abstract

During prehistoric times, the Colorado River occasionally meandered into and filled the Salton Sea Basin, creating several huge inland lakes, variously called Lake LeConte and Lake Cahuilla. Previous researchers have identified high stands of these ancient lakes using standard survey methods. The objective of this investigation was to further delineate the prehistoric shorelines using satellite imagery, global positioning system (GPS) and geographic information system (GIS) technologies. Using one-meter digital orthophotographs, points were selected in the laboratory and were located in the field using a GPS. Point data were integrated with a digital elevation model (DEM) and elevation contours were plotted on Landsat-TM images, generating a range of prehistoric shorelines. Contours were then correlated with archaeological site data, geomorphic features, and other factors to reconstruct Early American settlement patterns for Lake Cahuilla. The combined GIS coverages of ancient Lake Cahuilla and cultural resources may be used together as a model for cultural resource constraints, identifying areas of high cultural resource sensitivity for evaluation of potential impacts as a result of implementation of Salton Sea restoration project alternatives.

Introduction

The Salton Trough is a northwestern landward continuation of the Gulf of California rift, formed by gradual subsidence coincident with the uplift of the surrounding mountains during the Miocene, Pliocene, and Pleistocene eras (Dibblee, 1954; Hamilton, 1961). During mid-Pleistocene time, sediments eroded from the Colorado Plateau were deposited in the Colorado River Delta to form a natural sediment dam across the trough (Downs & Woodward, 1961). Over time, the same actions that formed the dam also altered the course of the Colorado River to flow north, creating periodic stands of water in the Salton Basin.

Based upon travertine deposits, lake-related cultural resources and other geomorphic evidence, Waters (1981) and Wilke (1978) estimated there were three or four possible lacustral intervals in Salton Basin. The highest stand obtained an elevation of 12 m (39 ft) above sea level (asl) between 100 B.C. and 1580 A.D. (Wilke, 1978; Waters, 1981). At its climax, Lake Cahuilla encompassed over 5700 km^2 and reached depths of 95 m. Wilke identified three lacustral intervals for Lake Cahuilla, but Waters concluded that there were four lacustral intervals from 695 A.D. to 1580 A.D. (Waters, 1981).

Wilke reported that Lake Cahuilla could reach a maximum height of 12 m asl. For this to occur, flows from the Colorado River would have to continually fill the Salton Basin for a period of 12–20 years (Wilke op. cit.). At a height of 12 m asl, Lake Cahuilla would begin to spill over the drainage divide at Cerro Prieto, Mexico, draining to the Sea of Cortez. When the Colorado River would resume its course directly to the Gulf of California, it would take approximately 53 years for the basin to dry at an evaporation rate of 1.8 m per year.

Materials and methods

The fieldwork and research were primarily used to search for undeniable evidence of shoreline features. Up against time and limited resources, Remote Sens-

ing was the most valuable tool in discerning possible shorelines observable from LANDSAT-TM images. Global Positioning Units were then needed to store possible locations of features and used to navigate within close proximity of the features. The collected data is expected to be within the previous calculations made by Wilke & Waters as to the maximum elevation of the ancient lake.

The Lake Cahuilla shoreline reconstruction project has brought forth a model of ancient hydrology of the Salton Basin. The first phase of the reconstruction has identified the maximum elevation that Lake Cahuilla could have occupied during the past 2000 years. This was accomplished through the research of literature, interviews with authors, image analysis using one-meter resolution Digital Orthographic Quarter Quads (DOQQs), 30-m resolution LANDSAT TM Images, field surveys accompanied by global positioning system receivers (GPS), and finally post processing the data within a Geographic Information System (GIS).

Fourteen control points were identified on one-meter digital orthophoto quarter quadrangles (DOQQs) in the laboratory. Many of these points were clearly visible on the DOQQs, as evidenced by tufa deposits, differences in lake sediments, or other geomorphic features. One of the most clearly visible areas of the lakeshore can be viewed from Highway 86 along the northwest shore of present day Salton Sea at Travertine Rock, where the Lake Cahuilla shoreline is clearly visible nearly 30 m above the highway.

Geographic location data for the control points were programmed into global positioning system (GPS) receivers. These data were used to navigate as closely as possible to the control points in the field. Upon arriving at the approximate location, shoreline field evidence was used to precisely locate a field-verified control point. Using the GPS receiver, clusters of 180 geographic positions were collected for post-processing in the laboratory.

Post-processing was performed in the laboratory by differential correction and determination of a centroid within the point cluster. The control points were then plotted on 7.5-min digital raster graphics (DRGs). Elevations of the control points were correlated with a digital elevation model (DEM) to produce a shoreline delineation at 11.9 m asl.

Results

Of the 14 control points taken, three were eliminated due to inconsistencies with GPS satellite telemetry. By differential correction, the remaining 11 control points achieved 95% locational accuracy. This process eliminates 95% of the error introduced by the Department of Defense on the GPS system and distortion from the ionosphere.

The 11.9 m-contour was plotted on a LANDSAT-TM base image. The shoreline delineation for Mexico was not obtainable due to pending acquisition of digital elevation data for this region. To supplement this a 10 m contour was interpolated with the 11.9 m contour used for the California side of Lake Cahuilla (Fig. 1). The 11.9 m-contour is consistent with the approximated shoreline elevation of Wilke & Waters (op. cit.).

Discussion

Wilke identified lake-related cultural resources along the northwest shore of Lake Cahuilla. These include rock fish weirs, shell middens, fish remains, and other cultural artifacts. Wilke, Waters, and others obtained carbon dates for Lake Cahuilla from tufa and organic cultural remains. Based upon these carbon dates, four possible high stands of Lake Cahuilla were determined to exist approximately between 100 B.C. and 1580 A.D.

Lake related cultural resources are not yet catalogued separately from non-lake related sites. Therefore, a more empirical correlation between the Lake Cahuilla contour and cultural resources was not possible.

Conclusion

Although a direct correlation between Lake Cahuilla contours and cultural resources is not yet possible, there is abundant archaeological evidence of a relationship to early American settlements and the prehistoric lake. For this reason, the Lake Cahuilla contour may be used as an indicator of cultural resource potential. In this way, the Lake Cahuilla model may be used to identify cultural resource areas potentially affected by Salton Sea restoration alternatives.

Development of a cultural resources database of lake-related sites would greatly enhance our understanding of early American settlement patterns around

the ancient Lake Cahuilla and further refine the cultural resource constraints model.

References

Dibblee, T. W., Jr., 1954. Geology of the Imperial Valley region, California. In Jahns, R. H. (ed), Geology of Southern California. California Division of Mines and Geol. Bull. 170: 21–28.

Downs, T. & G. D. Woodward, 1961. Middle Pleistocene extension of the Gulf of California into the Imperial Valley (abstract). Geol. Soc. Am. Special Paper 68: 21.

Waters, Michael R., 1981. Holocene lacustrine chronology and archaeology of ancient Lake Cahuilla, California. Department of Geosciences, University of Arizona.

Wilke, J. P., 1978. Late prehistoric human ecology at Lake Cahuilla, Coachella Valley, California. Contr. of the Univ. of Calif. Arch. Res. Facility, Berkeley, California: Number 38, May.

Hydrobiologia **473:** 59–75, 2002.
D.A. Barnum, J.F. Elder, D. Stephens & M. Friend (eds), The Salton Sea.
© 2002 *Kluwer Academic Publishers. Printed in the Netherlands.*

Simulation of wind-driven circulation in the Salton Sea: implications for indigenous ecosystems

Christopher B. Cook[1], Gerald T. Orlob[2] & David W. Huston[3]
[1]*Pacific Northwest National Laboratory, P.O. Box 999 (K9-33), Richland, WA 99352, U.S.A.*
[2]*Department of Civil and Environmental Engineering, University of California-Davis, Davis, CA 95616, U.S.A.*
[3]*Department of Water Resources, Central District, 3251 S Street, Room E-25, Sacramento, CA 95816, U.S.A.*

Key words: transient CFD modeling, finite element method, acoustic Doppler current profiler, terminal basin lake, RMA10, thermohaline stratification

Abstract

The Salton Sea, the largest 'man-made' water body wholly within California, was formed in 1904 as the result of a levee failure along the Colorado River. Initially, flow into the Salton 'Sink' created a fresh water lake about 24 m deep with a water surface about 85 m below the level of the ocean. Salinity of the water body, at first roughly the same as the river, rose rapidly due to solution of previously accumulated residual salt, then following levee repair, adjusted to the combined influence of agricultural drainage accretions and evaporative losses. Water levels adjusted accordingly, at first declining then rising slowly until the mid 1930s when a level about 75 m below ocean level was reached. Thereafter, both water levels and salinity gradually rose, so that at present the surface elevation of the Sea stands near −69.5 m and salinity is approaching 45 g l^{-1}, about 30% above ocean salinity. The Salton Sea Authority is seeking practical methods for reducing water levels and controlling salinity within ranges that will protect beneficial uses of the Sea, its adjacent lands, and its indigenous ecosystems, both aquatic and avian. Proposed solutions include various physical changes in the bathymetry and configuration of the Sea, especially its southern basin. Because circulation in the Sea is driven primarily by wind stresses imposed on the water surface, and circulation changes are likely to affect the Sea's quality and ecology, a methodology for quantifying the effects of specific alternatives is required. For this purpose a mathematical model for simulation of the hydrodynamic behavior of the Sea has been developed, calibrated to data gathered by a field investigation conducted in 1997, and applied to alternative schemes that will isolate sections of the southern basin, thus changing the natural wind induced circulation in areas that are ecologically sensitive. The Salton Sea Hydrodynamic/Water Quality Model is constructed using the finite element method to represent the bathymetry of the Sea as it currently exists, or may subsequently be modified, in a three-dimensional grid. Given certain boundary conditions, for example wind stresses imposed on the surface, the model solves the three dimensional equations of motion and continuity, the advection–dispersion equation, and an equation of state dependent upon temperature and salinity, to obtain temporal and spatial descriptions of velocities and temperatures over a specified period of time. Using data derived from 1997 field measurements of velocities using acoustic Doppler current profilers and temperature sensors, the model was calibrated to reproduce mathematically the historic experience of field observation. The model successfully replicated principal features of the Sea's behavior, especially the persistence of a counterclockwise gyre in the southern basin and seasonal stratification. Once calibrated, the model was applied to evaluate the possible effects of changing water surface elevations in the Sea and altering its configuration to isolate sections for evaporative concentration of salts. These effects, evident in changes in velocity, were quantified with regard to their possible impacts on the aquatic habitat and the health of the Salton Sea ecology. A comparative evaluation of alternatives is presented.

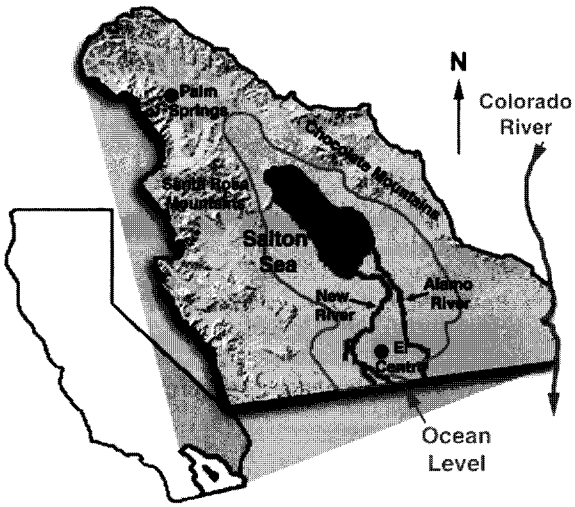


Figure 1. Location map of the Salton Sea Basin.

Introduction

The Salton Sea, often referred to as the largest 'man-made' water body in California (Fig. 1) was formed in late 1904 as the result of a break in a temporary levee along the Colorado River. For a period of about 16 months thereafter floodwaters flowed into the below-sea level depression, filling it to a depth of more than 24 m above its lowest elevation, approximately 84.7 m below mean sea level (msl). Since that time the water level in the Sea has been seeking a balance between the harsh desert forces that extract water by evaporation, the only mechanism for removal of water from this landlocked depression, and inflows from surface and subsurface sources. For a time following repair of the levee break in 1907, water levels declined rapidly at about 1.4 m per year, as water loss by evaporation greatly exceeded inflow. A minimum elevation of −76.5 m msl was reached in the 1920s, after which for about 15 years the level of the Sea fluctuated between −74 and −76 m msl. In 1934, the Sea began a slow rise, due in major part to a steady increase in agricultural drainage accretions attendant to importation of Colorado River water for a growing agricultural economy. By 1979 the Sea's level had risen about 7 m to −69.5 m msl, about that of its present (1999) condition, with a surface area of approximately 96 800 ha. The historic pattern of water level change is depicted in Figure 2.

During the course of historical changes in the Sea's water balance, its salinity also changed, due in major part to the continuous supply of salts delivered to the expanding irrigated areas surrounding the Sea and ultimately transferred to the Sea as agricultural drainage. The salinity record is rather fragmented but sufficient data are available to construct a fair representation of changes occurring over most of the Sea's life, as illustrated in Figure 2. During the period of levee repair, 1904–1907, the salinity of impounded water was virtually a composite of Colorado River flows delivered through the break, i.e. in the range of 700–800 mg l^{-1} total dissolved solids (TDS). However, because previous flooding-drying episodes in the hydro-geological history of the Salton depression had resulted in the incorporation of residual salts into bottom sediments, these were soon dissolved into the newly formed water body. Salinity rose dramatically during the first two decades following the levee break, achieving a concentration of about 42 g l^{-1} in 1924. For about 35 years, from 1945 to 1980, the salinity of the Salton Sea fluctuated from about 34 to 41 g l^{-1} (average of 38 g l^{-1}), almost the same as that of the ocean. However, as the volume of the Sea stabilized just above −69.5 m msl, the continued importation of salt forced a further rise in salinity, soon surpassing that of the ocean and threatening the delicate ecosystem that had been established artificially with the introduction in the 1950s of the sport fish, orange-mouth corvina (*Cynoscion xanthius*), and its principal prey, the gulf croaker (*Bairdiella icistia*). Today salinity is near its highest concentration, between 44 and 45 g l^{-1}, about 30% greater than that of the ocean, and well above the tolerance for sustained reproduction of most sport fish.

Current problems

Rising water levels and unchecked salinity increases have combined in recent years to threaten the future health of the Salton Sea, triggering actions on the part of various agencies, federal, state and local, to seek practical and implementable solutions. In 1993, the Imperial Irritation District, the Coachella Valley Water District, and the counties of Imperial and Riverside formed the joint powers Salton Sea Authority with a charter to improve water quality, stabilize water levels and enhance recreational and economic values of the Sea. In 1994, the Authority, the United States Bureau of Reclamation, and the California Department of Water Resources affirmed a joint agreement to identify and investigate potential solutions of the Sea's problems. Currently, the Authority is in the process of evaluating alternative strategies to restore the Sea to

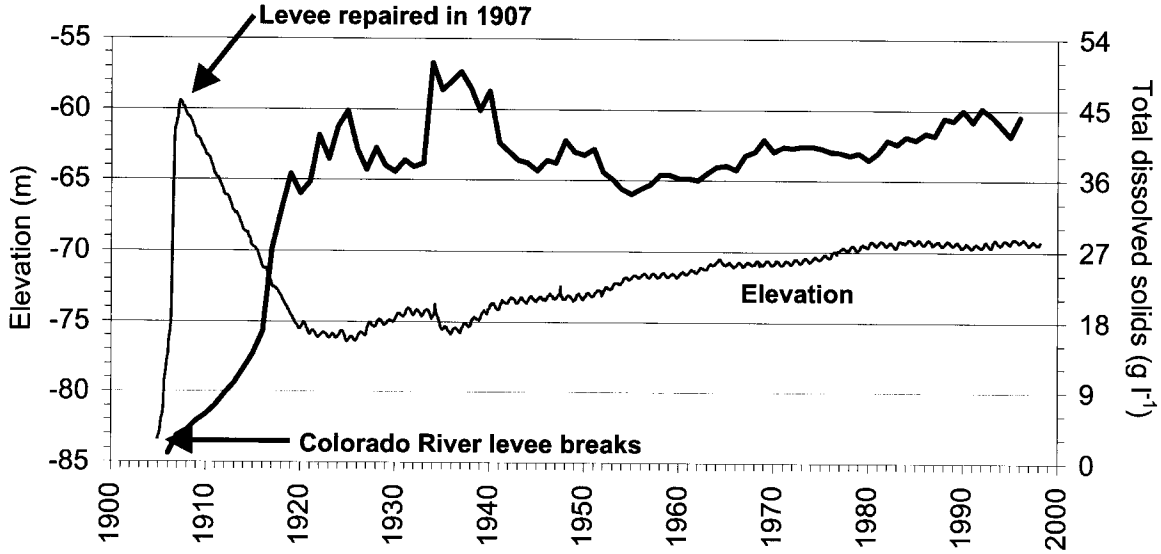


Figure 2. Historical water levels and salinity (data from Tostrud, 1997).

a sustainable viable state. Among alternatives being investigated are schemes that would modify the bathymetry and physical configuration of the Sea in order to restore desirable water levels and salinity. Implicit in achieving such objectives are possible impacts on ecosystems extant in the Sea that would result from changing or controlling water levels, modifying the Sea's water balance by regulating inflow and outflow, and redirecting the natural wind driven circulation in the Sea. In each instance, there are implications that the Sea's ecological health might be adversely (or beneficially) affected. This paper addresses a fundamental approach to evaluation of changes that might be anticipated if any of several alternatives now being considered are actually implemented in the future. The foundation for such evaluation is an explicit quantitative description of the present behavior of the water body, i.e. its circulation and thermal stratification under the impetus of prevailing meteorological and hydrological conditions. This was accomplished by constructing, calibrating and implementing a three-dimensional mathematical model of the Salton Sea.

Field monitoring program

Prior to this research, no temporal histories of water velocities or water temperatures had been recorded for the Salton Sea. Several university groups and governmental agencies had made spot samplings of the Sea, usually of its water quality, but these were sporadic, with gaps of weeks, even months, between observations. To calibrate accurately the proposed hydrodynamic model, time series of vertical profiles of both water temperatures and velocities had to be developed by *in situ* observations. This was accomplished for the first time during a field survey conducted by the UC Davis modeling team during 1997. The program entailed location of five fixed (by GPS) monitoring sites (Fig. 3) at which continuous recordings of water velocities were obtained using acoustic Doppler current profilers (ADCPs) and where thermistor strings were deployed to obtain data on the thermal structure of the Sea. These observations were supplemented at intervals throughout the field study period by spot observations of velocities, temperatures, and specific conductance.

The database assembled from these observations provided a unique history of circulation in the Sea, ranging from conditions of virtual homogeneity to strong stratification. It enabled identification of a persistent large counterclockwise gyre in the southern basin while documenting much lesser, even uncertain, circulation in the northern basin. Additionally, information required to define boundary conditions for the model were obtained at six CIMIS (California Irrigation Management Information System) stations around the periphery of the Sea (Fig. 3). These stations reported hourly averaged meteorological conditions, e.g. wind velocity and direction, air temperature, and relative humidity, providing information necessary for calculation of the heat budget for the Sea (Cook, 2000)

Name	Latitude	Longitude
Site 1	33°17'28" N	115°42'14" W
Site 2	33°12'35" N	115°41'20" W
Site 3	33°12'48" N	115°47'21" W
Site 4	33°20'14" N	115°51'02" W
Site 5	33°26'14" N	115°58'03" W

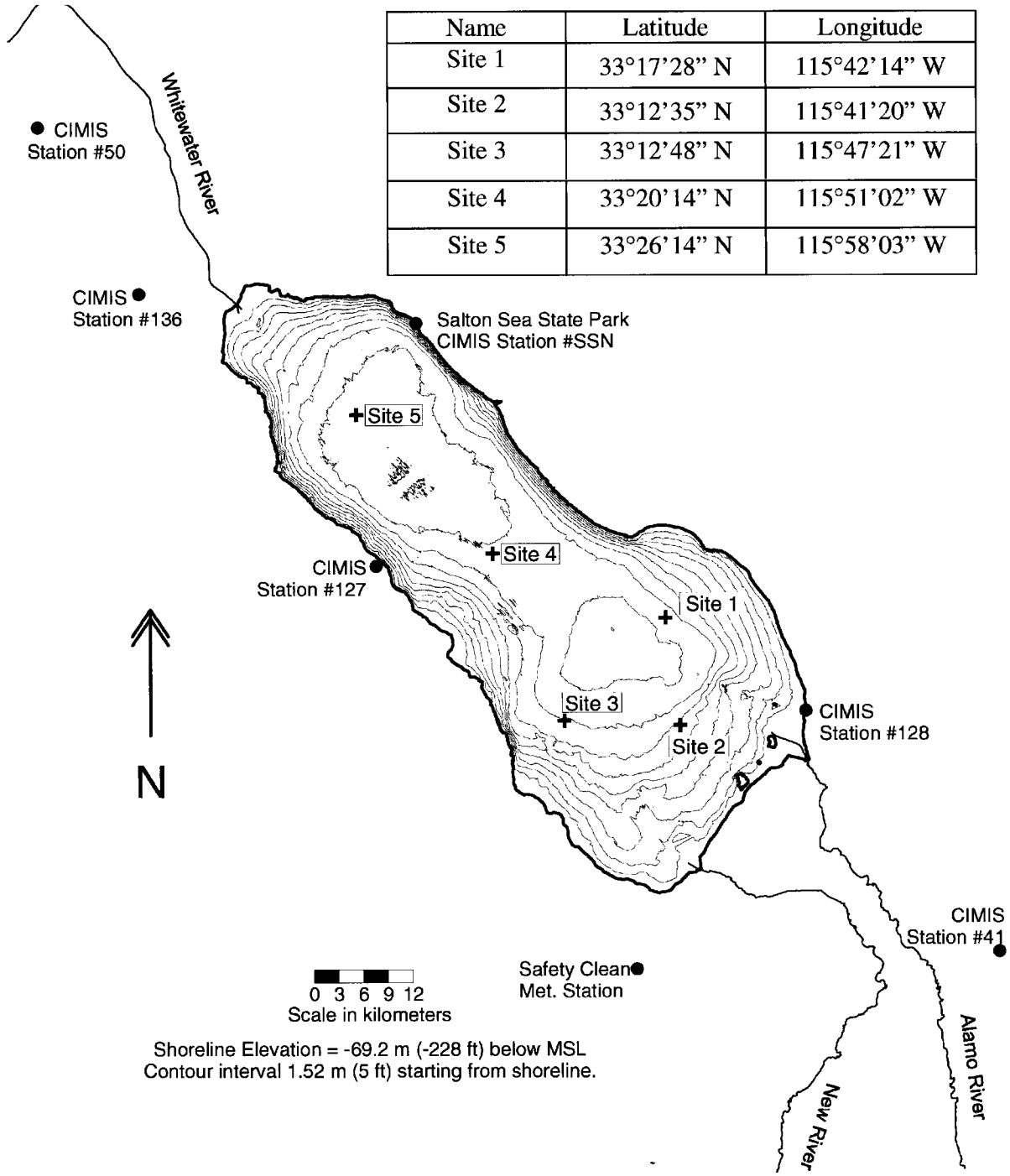


Figure 3. Locations of primary monitoring sites.

and to produce wind fields over the Sea's surface (Huston, 2000). An interpolation scheme developed by Barnes (1964), which interpolates observed wind values to a planimetric grid e.g. a finite element network, using an exponential distance weighting function was applied by Huston (2000) to produce a wind field to drive the hydrodynamic model.

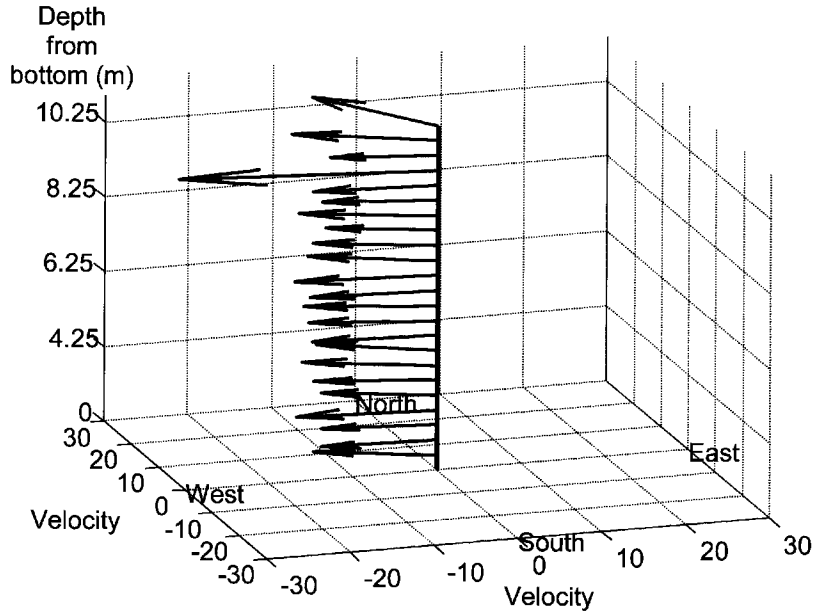


Figure 4. Typical ADCP velocity profile. Data gathered at 4 a.m. on October 24, 1997 at Site 1.

The US Geological Survey (USGS) continuously monitored the water surface elevation of the Sea. Data was gathered in the southern basin and was reported as daily averages in 0.3 cm (0.1 ft) increments. Although this data was sufficient for the initial stage boundary condition in the numerical model, it was not of fine enough detail to verify numerically predicted free-surface seiche.

Five primary monitoring sites were located in the Sea (Fig. 3) where water velocities and temperatures were monitored for extended periods during the 1997 field campaign. These sites were chosen to provide spatial characterizations of water circulation, temperatures and specific conductance (a surrogate for salinity) over selected monitoring periods. Because most of the management alternatives being considered by the Salton Sea Authority are likely to involve physical changes in the configuration of the southern basin, monitoring activity was most intense in this region.

To obtain necessary observations of water velocities for model calibration, ADCPs were deployed on the Sea bottom for long-term data acquisition at Sites 1 and 5 from March 24, 1997 to January 5, 1998. The ADCPs provided three-dimensional descriptions of water movement, i.e. velocity magnitudes and directions, in the water column above the instrument, and were programmed to collect data every 15–20 min at vertical resolutions between 0.40 and 0.25 m. Each velocity profile reported by the ADCP was an ensemble of between 160 and 300 individual readings (i.e. pings) sufficient to lower the theoretical standard deviation of the velocity measurements to approximately 1.0 cm s^{-1}. Figure 4 illustrates a typical output from an ADCP located at Site 1. Velocities are seen to vary in magnitude and direction depending on elevation in the water column.

In addition to the ADCPs, continuous recording temperature loggers (Onset Optical StowAway and Richard Brancker Research Fast Response) were deployed at all primary sites. During the spring and summer of 1997, loggers were suspended from anchored surface buoys and positioned at spacings corresponding roughly to the surface, upper quarter, mid-depth and bottom elevations in the water column. During the fall and winter, additional loggers were added to the strings at 2 m spacings along support cables. All loggers were set to record local temperatures at 15-min intervals or less, and pre/post-deployment verification ensured measured data were within the manufacturer's accuracy limits of ±0.2 °C. Also, portable conductivity sensors were deployed during occasional boat surveys to obtain spot vertical profiles at both fixed and temporary stations. Data derived from these profiles were used to quantify vertical and longitudinal salinity gradients along transects from the shoreline into the open Sea and changes in salinity in the vicinity of fresh water discharges from the New and Alamo Rivers (Fig. 1).

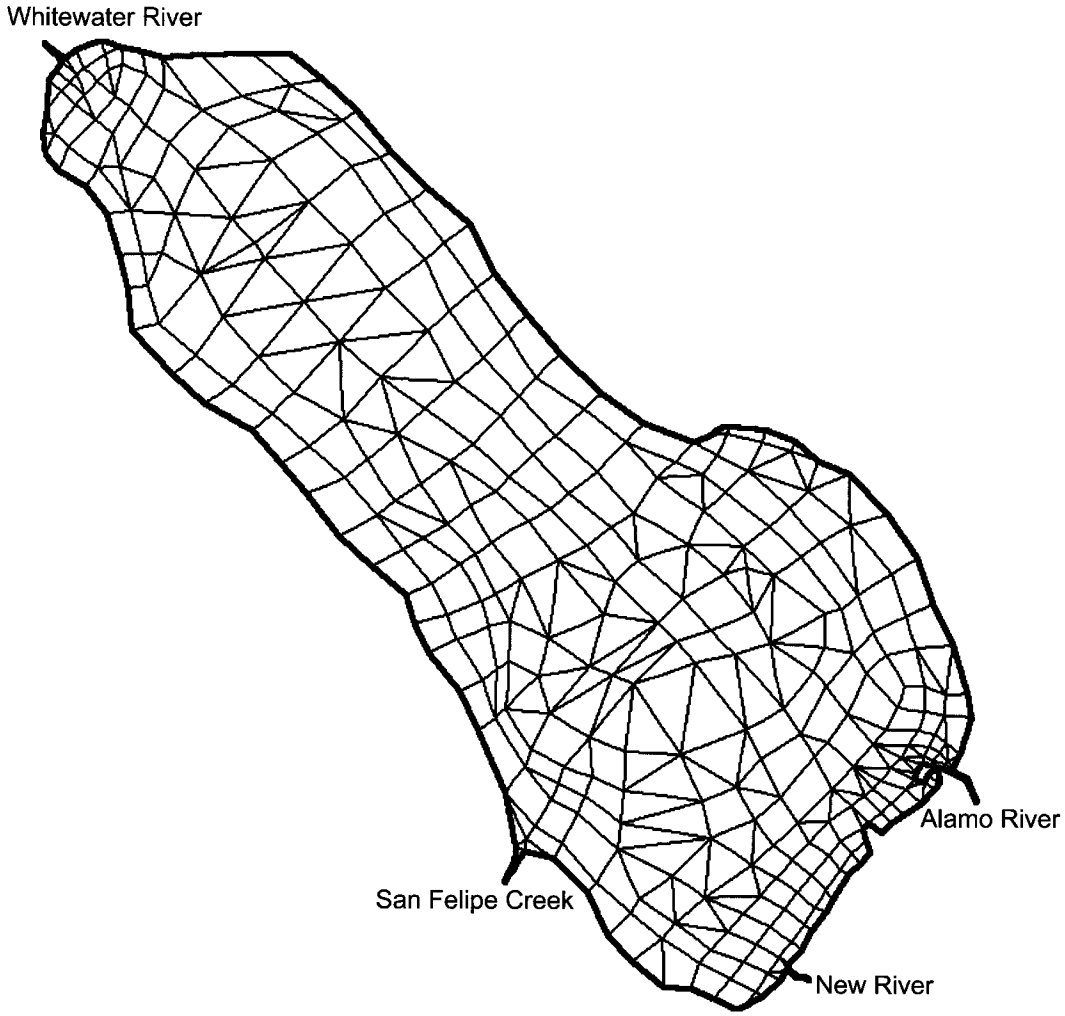


Figure 5. Typical finite element grid.

Model selection and development

A preliminary investigation of hydrologic and bathymetric properties of the Salton Sea and its setting in the Salton Basin indicated that circulation in the water body is largely dominated by wind shear stresses applied to the Sea's surface. The investigation discovered that seasonal thermal stratification might play an important role in distribution of energy imparted to the Sea, especially during spring and summer months. Coriolis forces may also contribute significantly to larger scale motions and must therefore be included in model formulation. On the other hand, momentum imparted to the Sea by its few small tributary streams is of such low order that these minor contributions to circulation may be neglected. These tentative conclusions were later reinforced by both preliminary model testing and field observations. An important additional consideration in model development was the need for flexibility in adapting the model to proposed alternative physical solutions to problems of water balance, water quality, and ecology.

These considerations dictated adoption of the three-dimensional finite element numerical model RMA10 as the most suitable for simulation of the Salton Sea's response to alternative management options. RMA10 is well documented (King, 1985, 1993) and has been tested in applications to a wide variety of one-, two- and three-dimensional hydrodynamic/water quality problems. The model solves numerically a set of partial differential equations describing changes

in state variables continuously over space and time, under dynamic boundary conditions. The governing equations for the hydrodynamic model of the Salton Sea are the three-dimensional momentum, volume continuity, and advection–dispersion equations, and an equation of state. The momentum equations include terms representing temporal and advective accelerations in the three principal directions, tractive forces due to wind and boundary friction, pressure forces due to variations in water surface elevation, Coriolis acceleration, and momentum loss due to turbulence. The equation of state is used to relate water density to changes in temperature, salinity and suspended solids. Thermal energy exchanges through the air-water interface are calculated within the model to estimate water temperatures, using the methodology developed originally by the Tennessee Valley Authority (1972).

To implement solution of the governing equations in the model, appropriate boundary conditions, e.g. wind field velocities, inflows, water levels, air temperatures, etc., must be supplied. Solution also requires estimation of vertical turbulent stresses and dispersion coefficients that for this case may be approximated by the methods of Mellor & Yamada (1974, 1982), with the stratification correction proposed by Henderson-Sellers (1982). A horizontal turbulence closure scheme attributed to Smagorinski (Lesieur & Metais, 1996) was adopted for this application of the model.

Model structure and boundary conditions

The Salton Sea Hydrodynamic/Water Quality Model represents the Sea's bathymetric characteristics as an assemblage of discrete three-dimensional elements, usually of polyhedral form. These are arranged to conform to the physical configuration of the Sea in numbers, sizes, and shapes that best describe its important features, e.g. inlets, islands, shorelines, etc., and as may be necessary to describe variations in state variables, e.g. velocities, temperatures, and salinities throughout three-dimensional space. Elements in the assemblage are interconnected at 'nodes' where properties of the system are to be simulated and where boundary conditions may be imposed. A typical finite element grid for the Salton Sea is illustrated in plan view in Figure 5.

Boundary conditions for the model are specified at nodal locations for the period of simulation. For example, because the Salton Sea's circulation is primarily wind driven, wind velocity fields must be created from meteorological observations at stations surrounding the Sea and interpolated to surface nodes in the model grid at intervals corresponding to time steps in the dynamic simulation. A representative wind field over the Salton Sea is shown in Figure 6.

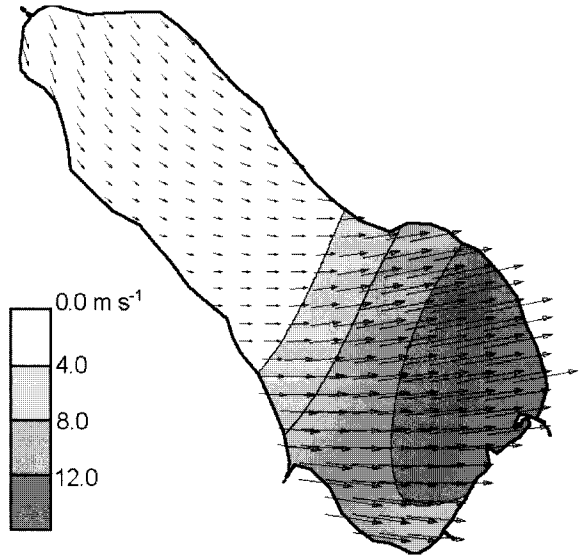


Figure 6. Representative wind field. October 23 at 6 p.m. (near peak of the storm event).

In a like manner, data for calculation of heat exchange, e.g. solar radiation, air temperature, relative humidity, and atmospheric pressure, are supplied to the model for simulation of water temperature changes. Hydrologic fluxes are introduced to account for the Alamo, New, and Clearwater Rivers. For the present study, flow rates were obtained from USGS gages near the river outlets, and characteristic water quality attributes were assigned based upon field observed values (Huston et al., 1999).

Model calibration

Calibration of the model is an iterative process, involving an organized adjustment of model parameters, such as roughness coefficients, diffusivities, and heat exchange coefficients, until agreement is achieved between the model's primary state variables and field observations. Because of the complexity of the Sea's hydrodynamic responses and the dynamic forces driving circulation – both highly variable over the field season – it was necessary to select representative time series of field conditions, both within the water body

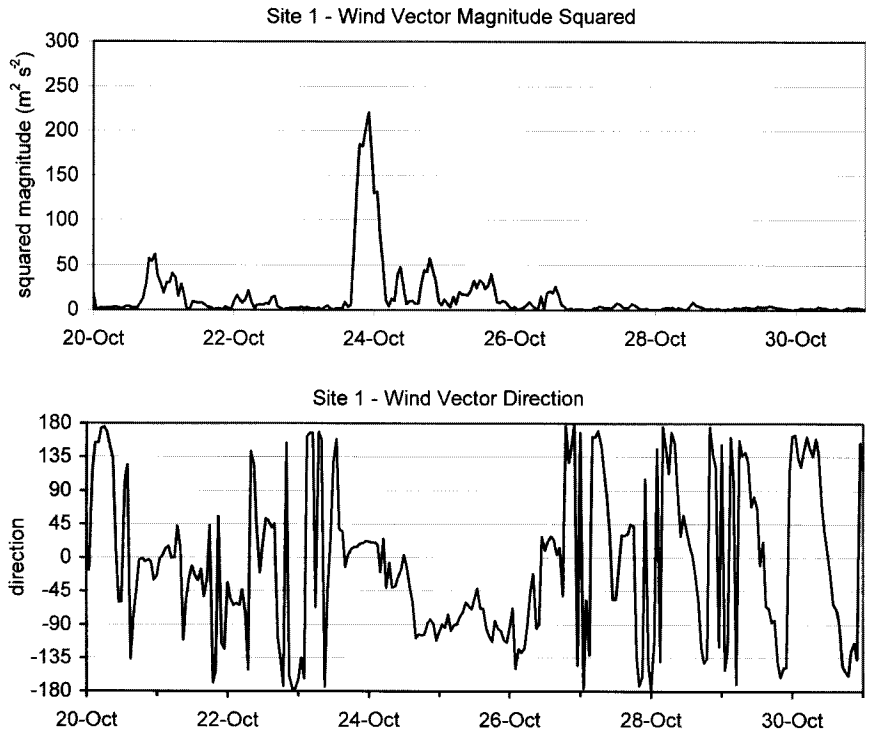


Figure 7. Time series of wind speed squared (proportional to the wind shear stress on the watersurface) and direction, Site 1. October simulation period. (Note: trigonometric sign convention is used, with zero degrees oriented due east.)

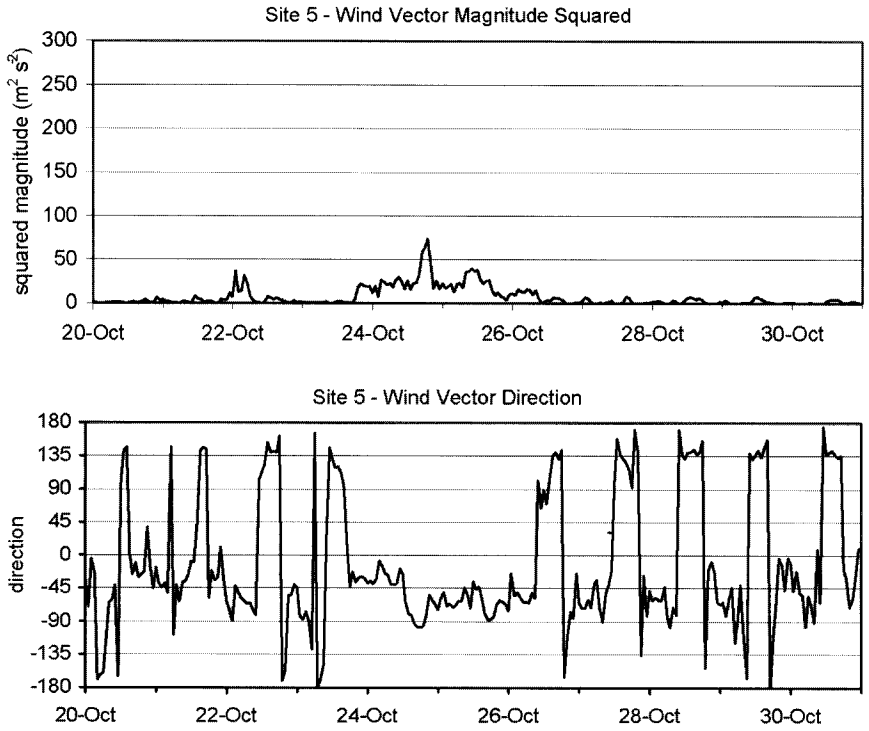


Figure 8. Time series of wind speed squared and direction, Site 5. October simulation period.

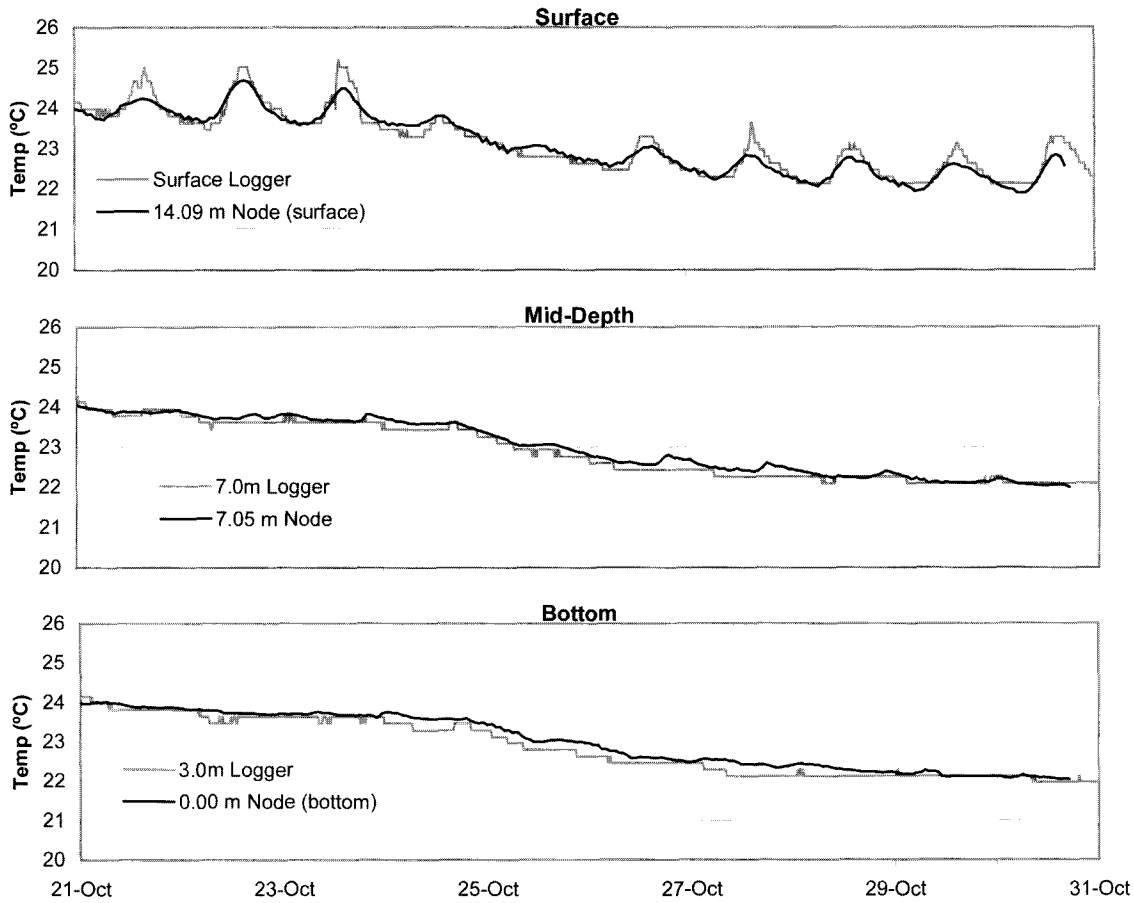


Figure 9. Simulated vs. observed water temperatures, Site 5. Surface, mid-depth and bottom, October simulation period (tick placed at midnight).

and the overlying atmosphere that were of sufficient duration and detail to assure a reasonable calibration. Two hydrodynamic conditions were selected: a case of 'minimal stratification' corresponding to a nearly homogeneous, well mixed state of the water column, and a case of 'strong stratification' when a distinct thermocline persisted in the water column. For the case of minimal stratification, the month of October was selected as representative. It provided the largest body of data on velocities, temperatures, and conductivities of any period of similar length during the 1997 campaign. For the strong stratification case, the period of May 20–31 was selected. At the beginning of this period the Sea was strongly stratified at most locations. Despite a series of strong wind events occurring in the southern basin, the remainder of the Sea remained stratified during the 11-day period.

October simulation period

To initiate calibration, it was necessary first to 'warm-up' the model to an initial state closely corresponding to the actual conditions of the Sea at the beginning of the chosen calibration period. The model was started 11 days before the selected calibration period October 20–31, in order to include the influence of an earlier storm event that occurred on October 11 and that could have affected circulation throughout the Sea. This event persisted for approximately two days, with peak wind speeds in the southern and northern basins of similar magnitude to those observed on the evening of October 23 (Figs 7 and 8).

During this period, calibration parameters, primarily boundary roughness (Manning n) and heat exchange coefficients, were systematically adjusted over a range of values to minimize differences between model and prototype (Cook, 2000). Results of simu-

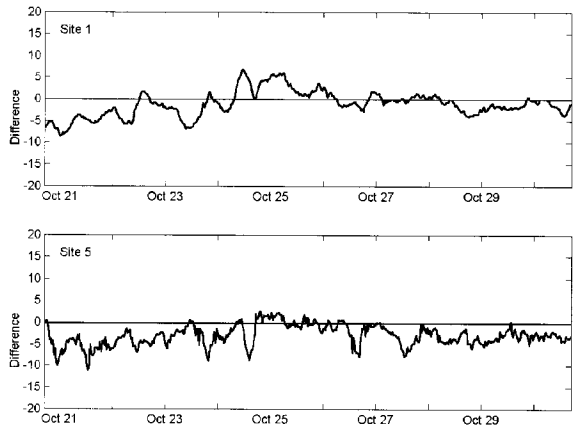


Figure 10. Differences (simulated minus observed) in water velocity at approximately mid-depth. (Site 1 at 6.6 m, and Site 5 at 6.5 m below the water surface).

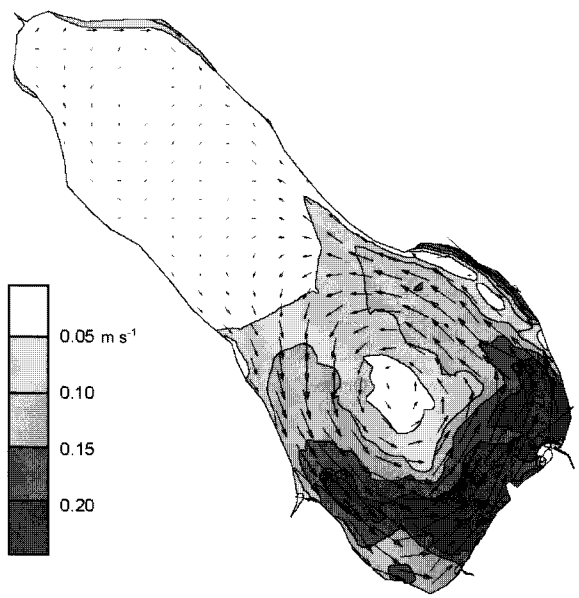


Figure 11. Circulations at mid-depth, October simulation period (October 24 at 9 p.m.).

lation with the adjusted model are illustrated in Figure 9, showing time series of temperature at Site 5 in the northern basin over the 10-day simulation period. Simulated temperature histories at several levels in the water column are seen to track the observed temperature profiles closely throughout the October 20–31 period, even including major features of observed diurnal temperature fluctuations in the near-surface zone. Average errors throughout the period are less than 0.35 °C.

Water velocity differences (simulated minus observed) using the final calibration parameters are shown in Figure 10. In this figure, differences vary over the transient solution, and at Sites 1 and 5 the RMS of the differences over the period are 3.29 and 3.22 cm s^{-1}, respectively. During the October 20–31 period, water velocities were generally much higher in the southern basin than in the northern basin, due largely to much higher surface winds observed in the south. Water velocities near Site 1, for example, reached 21 cm s^{-1} during the October 24 storm event, while in the northern basin they rarely exceeded 6 cm s^{-1}, as shown in Figure 11.

The simulations also illustrate the strong wind-induced counterclockwise gyre and the increased intensity of local velocities in near-shore areas of the basin, factors of special significance from the ecological viewpoint. It is worthy of note also that circulation in the northern basin is generally weak, less structured, and somewhat chaotic, factors that suggest a lesser rate of exchange with the rest of the Sea.

May simulation period

Time series of velocities and temperatures were also developed for a period of May 20–31 during which the northern basin was strongly stratified. Analysis of velocities measured during the May 20–31 period, especially for Sites 1 and 5, indicated a distinctly different behavior of the Sea from that noted in the October data. This was evidenced most strongly by dramatic variations in velocity magnitudes and directions, both above and below the thermocline. Gradual deepening of the upper comparatively well-mixed layer suggested the existence of internal wave motions, evident in ADCP records at Site 5, and illustrated in Figure 12. The graphical display of velocity magnitudes and directions on a depth-time field provided additional insight to phenomena perhaps unique to Salton Sea hydrodynamics, but likely of broader scientific import. Information on the magnitude and direction of velocity vectors through the depth of the water column highlights progressive deepening of the well-mixed upper layer and the changing orientation of circulation between the upper and lower strata. There is some evidence in the ADCP record, illustrated in the plots of Figure 12, of a double thermocline, intermediate quiescent zones, and possible internal waves (e.g. see 1.0 m logger, Fig. 14). These are phenomena that are subjects for additional investigations (Cook, 2000).

Initially, model warm-up and dynamic simulation were attempted for the May 20–31 period using the grid of Figure 5. This grid had previously been

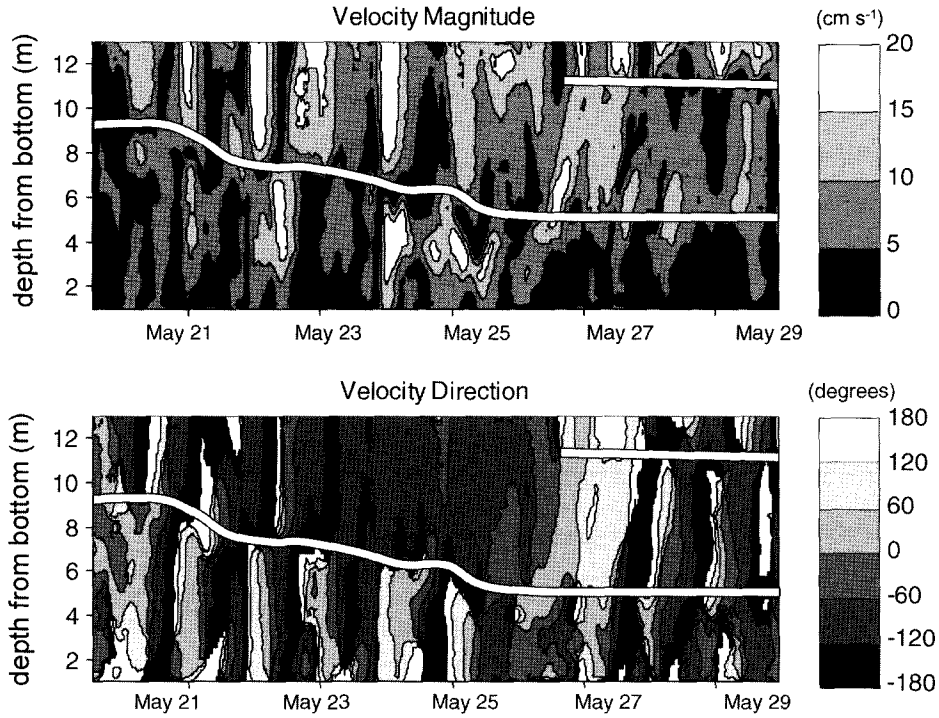


Figure 12. Observed water velocities at Site 5. Lines indicate estimated position of the thermocline(s) from thermistor and ADCP records.

found satisfactory for the non-stratified case and for simulation of alternative management scenarios under nonstratified conditions. However, because simulation of the stratified case required additional vertical resolution – at least doubling the number of layers in the grid and extending simulation times – the model was accordingly modified for multiple runs by eliminating elements along the shoreline.

Application of the modified grid with its greater vertical resolution allowed assessment of circulation under conditions of a well-developed and persistent thermal structure. As in the case of non-stratified conditions, the model was first 'warmed-up' by simulating circulation induced by storm events occurring in the initial 4 days of the simulation period (Fig. 13). Differences between observed and simulated water velocities were calculated, as in the non-stratified case, although RMS differences were larger at 6.19 and 6.81 cm s^{-1} for Sites 1 and 5, respectively. The largest differences occurred at the peaks of the observed velocity spikes in the epilimnion and hypolimnion (Fig. 12). Generally the model under-predicted these peaks of velocity magnitude, although the underlying residual circulation patterns observed by the ADCP are present in the simulation results (Cook, 2000).

Simulated water temperatures derived from the adjusted model demonstrate its ability to replicate observed patterns of thermal stratification and destratification and the accompanying changes in circulation. As for the case of the non-stratified water column, the development of thermal stratification through the selected period, May 20–31, is illustrated by comparing time series of temperatures at Sites 1 and 5 (southern and northern basins, respectively) at selected levels in the water column. In this case, simulated and observed temperature histories for Sites 1 and 5 compare favorably against logger observations at one-quarter depth and near the bottom of the water column, as depicted in Figures 14 and 15.

In the southern basin at one-quarter depth in the water column, the model is seen to track the general pattern of temperature through the 11-day simulation period quite closely. Near the bottom of the water column, where the logger record corresponds to a position 1 m above the bottom, model results for a node at the bottom and a node 1.3 m above the bottom bracket the field sensor record fairly well. A similar comparison is made for Site 5 in the northern basin. At one-quarter depth, the general trend of the temperature history is fairly well followed, although the details of temperature fluctuations captured in the temperature

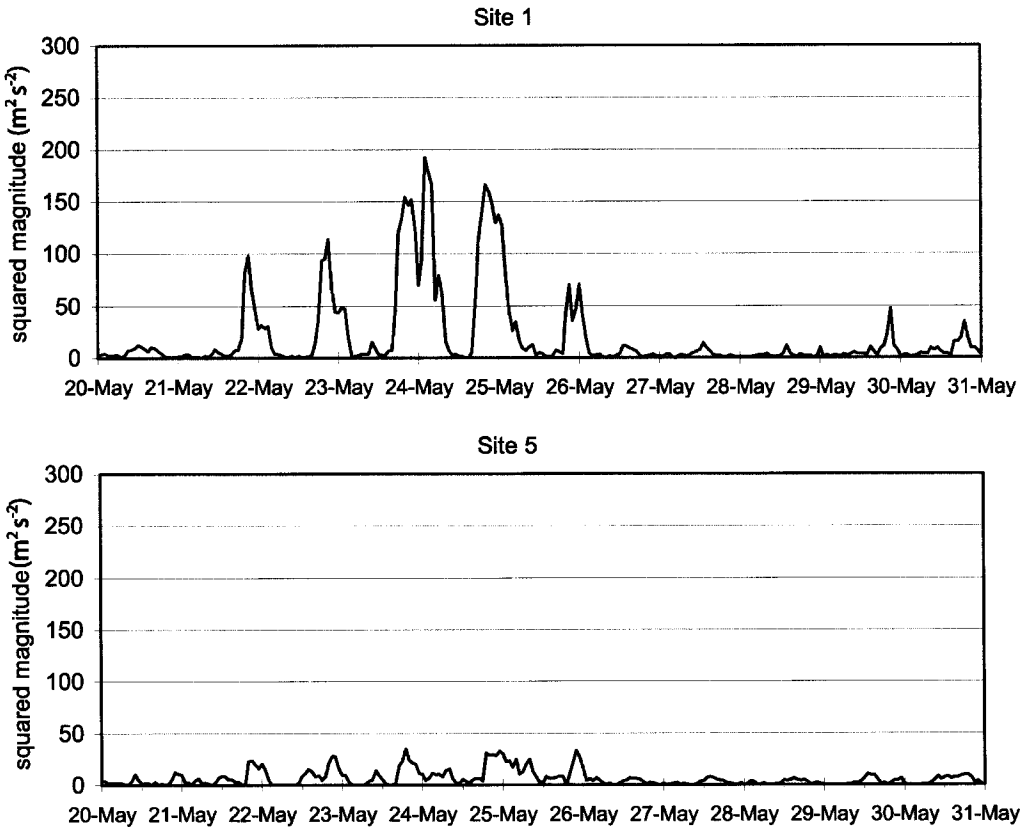


Figure 13. Time series of wind energies. May simulation period.

sensor record are not well simulated. Near the bottom of the water column at Site 5, the historic observation time series at one meter off the bottom is bracketed by the model results at the bottom and 1.4 m above the bottom.

Comparison of October and May periods

The general nature of stratification in the Salton Sea may be described further by comparing temperature histories at Sites 1 and 5 during the October and May simulation periods. Figure 16 displays patterns of isotherms on a depth-time field for the water columns at both Sties 1 and 5, confirming the general state of thermal stratification, or lack thereof, during the October simulation period. The plot is supportive of the general conclusion that both Salton Sea basins are nearly homogenous during most of the month. The effects of convective mixing are evidenced by a 2 °C cooling of the water column through its full depth during the simulation period.

In the May simulation, a condition of strong stratification is well characterized by depth-time plots of isotherms developed in the 11-day period of simulation. As illustrated earlier, strong thermal stratification developed during the spring in the northern basin, while the southern basin was only weakly stratified. The creation of a thermocline in the northern basin is a prominent process identified in the May simulation, one that results in the capture and retention of cooler water near the bottom of the water column as long as the thermal structure remains undisturbed by storm events. Intense mixing throughout the water column of the southern basin during the May simulation period is further illustrated in Figure 17.

Management alternatives

The simulation capability of the Salton Sea Hydrodynamic/Water Quality Model has been demonstrated in the foregoing descriptions of its implementation for two characteristic scenarios of wind-driven circulation, an October case of weak stratification and a May case of comparatively strong stratification. The model was calibrated for these cases to give credible descrip-

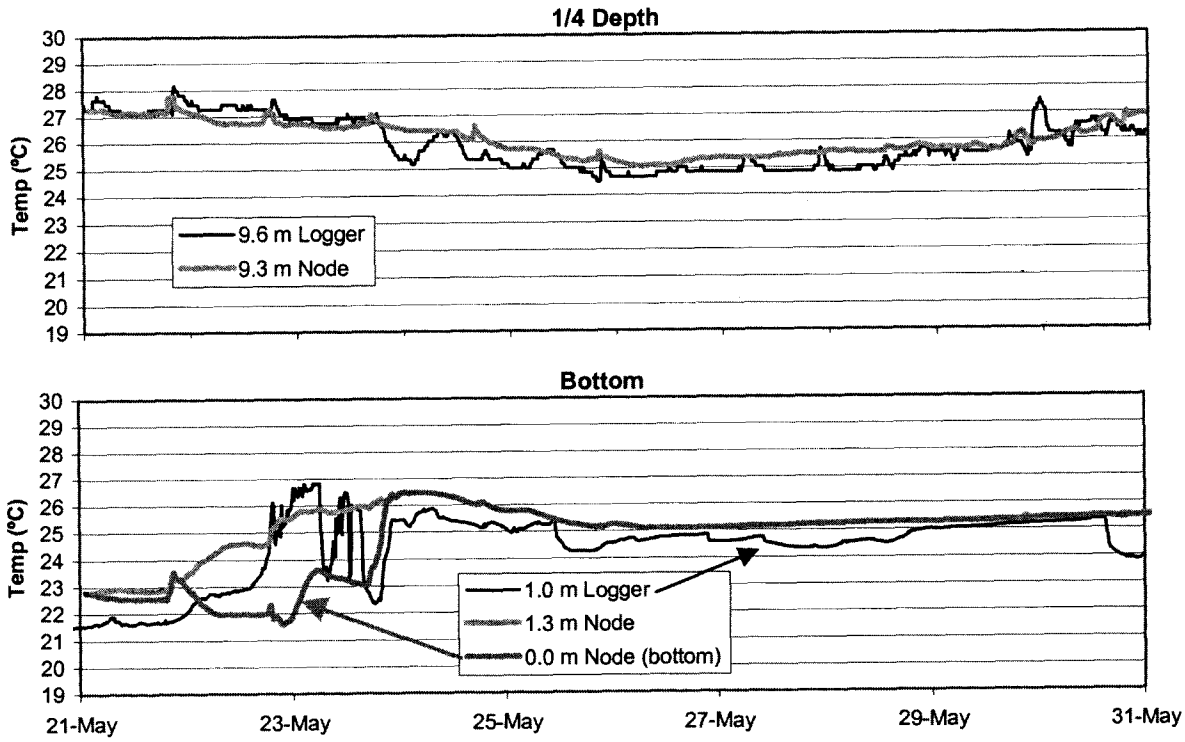


Figure 14. Simulated vs. observed water temperatures, Site 1. One-quarter depth and near bottom, May simulation period.

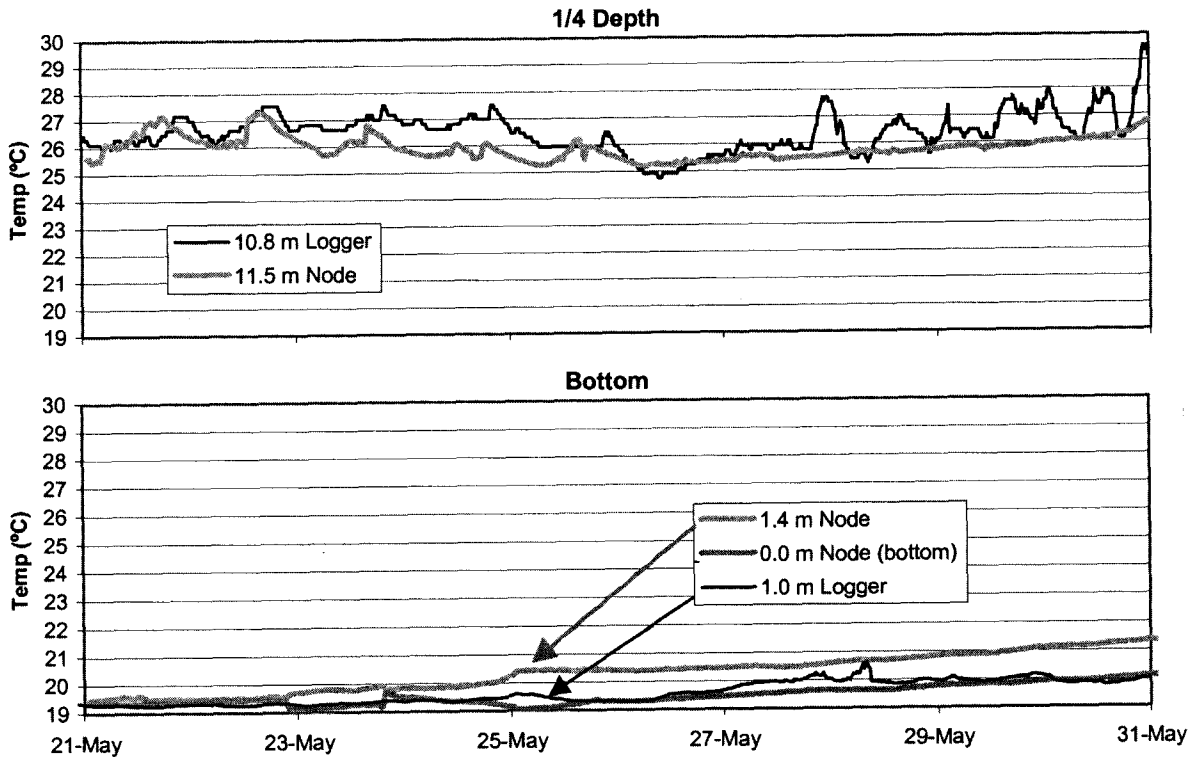


Figure 15. Simulated vs. observed water temperatures, Site 5 One-quarter depth and near bottom, May simulated period.

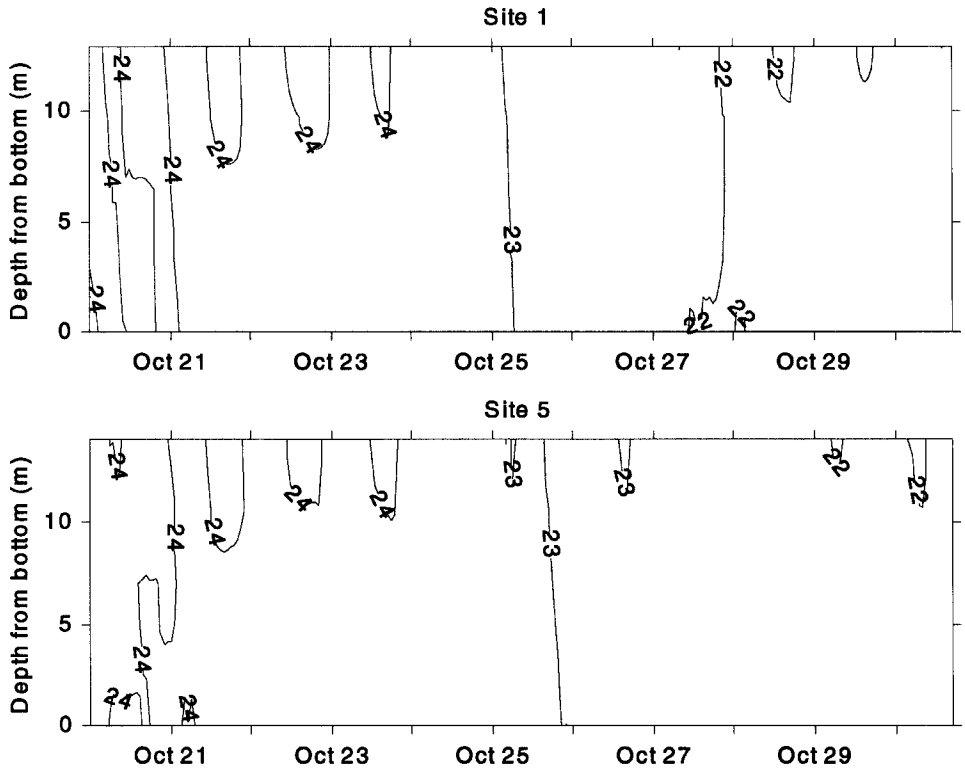


Figure 16. Simulated temperature isotherms, Sites 1 and 5 October simulation period.

tions of circulation and thermal conditions in the Sea as actually observed in the field. It is considered at this point a useful tool for assessment of the impacts of alternative management options that may entail major changes in the physical boundaries and bathymetry of the Sea. Its application is demonstrated by simulation of some proposed alternatives as illustrated in Figure 18.

Following the conventional approach, the model is used to assess quantitatively the incremental changes in circulation patterns that would result from implementation of a particular alternative as compared to a so called 'base case.' At this point, four alternatives are being considered, each representing different configurations of diked impoundments proposed for evaporative concentration of salts for eventual export. These options are illustrated in Figure 18, showing the configuration of three basin ponds. These ponds separately, or in combination, would isolate portions of the southern basin of the Salton Sea sufficient in areal extent to facilitate evaporative losses and to restore water levels and salinities in the un-diked main body of the Sea to acceptable levels.

In each case, the configuration of the Sea would be changed significantly in area and along its southern boundaries. Accordingly, it may be expected that circulation in the un-diked water body will be affected in ways not easily predicted. The model described in this paper was designed to aid in predicting possible consequences of these alternatives, especially those that may be of water quality or ecological importance.

Application of the model begins with establishing the base case. This first requires construction of a finite element grid for the Sea that represents the baseline bathymetry and allows easy adjustment to any of the several alternative configurations. For present purposes, the baseline grid adopted is that used for the previously described calibration process, as shown in Figure 5. All grids included stubs for tributaries with the appropriate inflows specified. Second, the water surface elevation was fixed at an elevation of −69.2 m, corresponding to the current elevation of the Sea. Third, a specific wind scenario was adopted. For this case study, the wind field scenario for the non-stratified calibration exercise (October 9–30) was adopted. All other conditions affecting model performance remained as determined in the previous calibration exercises.

Five simulations were carried out in the study, a base case and four alternative diking schemes. Two

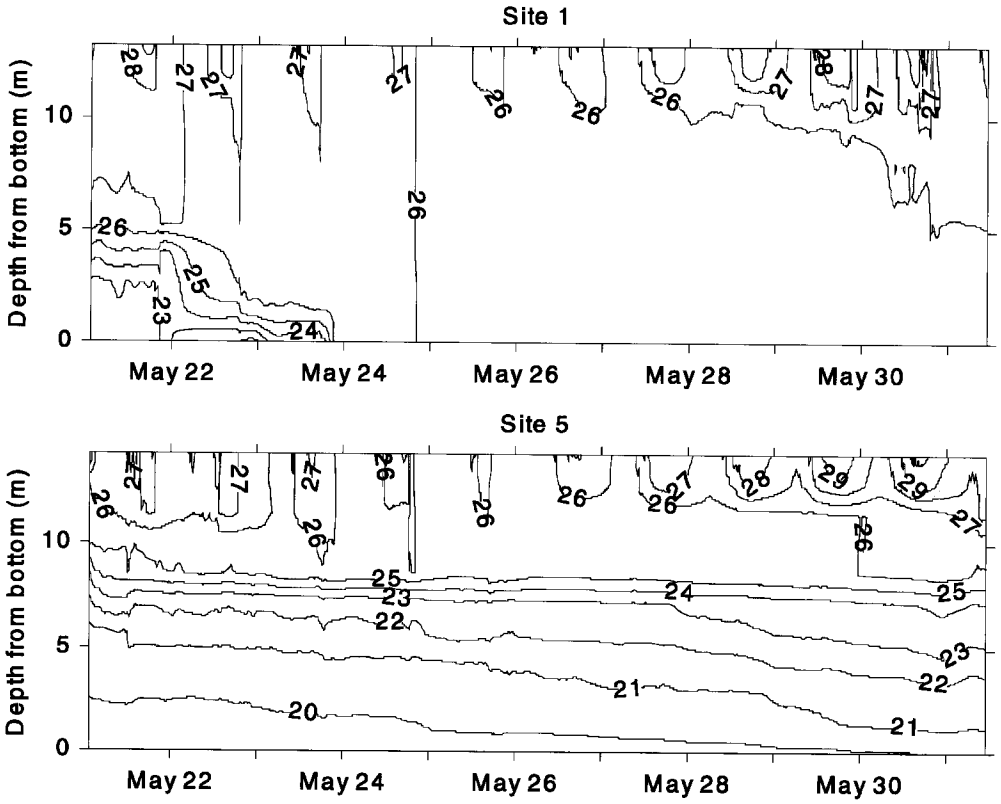


Figure 17. Simulated temperature isotherms, Sites 1 and 5. May simulation period.

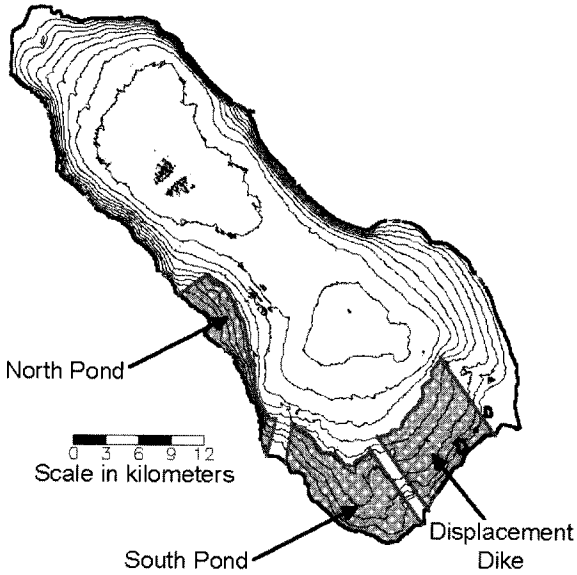


Figure 18. Diked impoundment management alternatives.

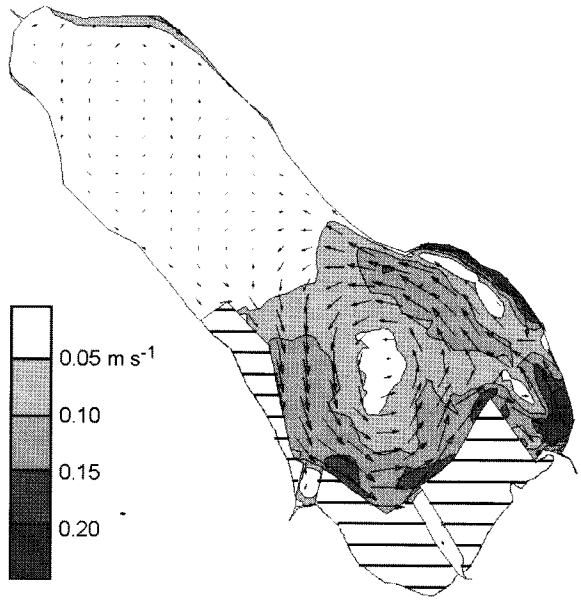


Figure 19. Management scenario results with north and south ponds and displacement dike. Mid-depth water velocities.

alternatives considered the north and south ponds separately, a third considered a combination of the two ponds, and the fourth, a combination of all ponds, including that identified with the 'displacement dike.' The circulation patterns in Figure 19 corresponds to velocities generated by the model at mid-depth in the water column at the peak of the storm event, about 9 p.m. on October 24, 1997. Velocities at this time, indicated by vectors in the figure are considered to be near maximum. These may be compared to the base case circulation results shown in Figure 11. The former configuration, with the north and south ponds and the displacement dike area, was selected to demonstrate application of the model.

To quantify the incremental effects of alternatives with respect to the base case, differences were determined by subtracting alternative simulation results from those of the base case. Results of this step are shown in Figure 20. Negative differences indicate that velocities were reduced by the alternatives and positive differences indicate increases. Circulation pattern differences are generally greatest near the boundaries of the impoundments. With only the northern pond in place, differences are very slight; velocity changes occur only downstream (following the streamlines) of the pond. For the south pond, water velocities drop dramatically upstream and downstream, the largest negative differences occurring in the region east of the New River discharge. Here velocities could be as much as 10 cm s^{-1} smaller than those of the base case, an indication of a potential sediment deposition zone. The greatest differences occurred in the case where all three ponds were combined (Fig. 20). In some localities, velocities were reduced by more than 10 cm s^{-1}. The displacement dike greatly affects circulation, causing two large stagnation zones, one between the south pond and the displacement diked area and another downstream of the displacement dike. Delta areas of the New and Alamo Rivers could also be significantly affected by this configuration, since flow stagnation could impede mixing of river inflows with the Sea. Increased detention times in these areas might be expected to affect all time-dependent processes, e.g. dissolved oxygen, nutrient balances, bio-uptake, benthic interaction, and biodegradation.

Summary and conclusions

The Salton Sea, created in 1904 by an inadvertent breach of a Colorado River levee, has since experienced changes in water levels and quality that threaten its aquatic and avian ecosystems. Alternative measures are currently under consideration to control water levels and salinity, and to restore the Sea to its previous health. Among these are proposals to construct artificial impoundments constrained within earthen dikes for the purpose of evaporative concentration of salts preparatory to export. These structures, encompassing sections of the Sea to form evaporation ponds, will intrude on the present configuration of the water body, thus altering its volume, water surface area, and affecting its exposure to wind and other atmospheric conditions. Because circulation in the Sea is primarily driven by the wind in the Salton Basin, the properties of which are measurable at surrounding meteorological stations, it is expected that water velocities and temperatures will change under the conditions of diking alternatives.

To assess quantitatively possible changes in the Sea's hydrodynamic and water quality behavior, as well as its ecological response, a three-dimensional hydrodynamic/water quality model has been developed, calibrated, and applied preliminarily to the Sea. A field monitoring program was implemented in 1997 to gather data for construction of the model and to provide the necessary database for calibration. The field program included deployment of acoustic Doppler current profilers and strings of temperature loggers suspended from anchored buoys at fixed locations in the Sea. At the same time as monitoring of the Sea was being conducted, data on atmospheric conditions, especially wind velocity vectors and observations needed for heat budget calculations by the model, were assembled from local meteorological stations and analyzed to provide wind fields to drive the model.

Calibration and adjustment of the model to initial conditions required simulation of the Sea's response to time series of wind events sufficient in length to include occasional storm episodes that were discovered to play important roles in inducing persistent circulation in the water body. Two simulation periods were selected for calibration and 'warm-up' of the model, one during the month of October when the Sea was more or less homogeneous and another in May when strong stratification was experienced, especially in the southern basin. Calibration of the model was successfully carried out, first for the October simulation period by adjustment of boundary roughness and heat exchange coefficients and later for a period in May when the Sea tended to be strongly stratified. The

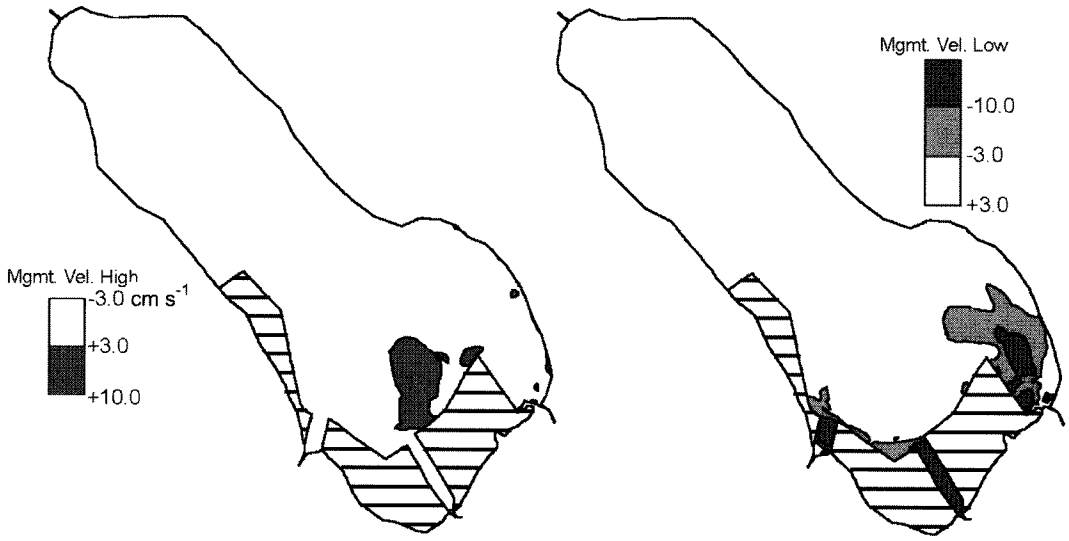


Figure 20. Contours of water velocity differences (management alternative minus base case results).

model provided credible three-dimensional dynamic histories of water velocities and temperatures for the 11-day test period in October.

The second calibration was carried out for a 10-day period in May during which strong stratification was observed, especially in the northern basin. During this exercise, the model grid was adjusted to improve its run time while preserving good representation of the state of the water body as identified by velocities and temperatures. A successful calibration demonstrated the model's capability to simulate dynamically the main features of the southern basin's circulation and the persistent strong stratification in the northern basin. The model emerging from this process was considered suitable for application in evaluation of alternative measures to control water levels and salinity.

The Salton Sea Hydrodynamic/Water Quality Model was then applied to simulate circulation under conditions defined by four proposed diking alternatives. The alternatives included physical features, such as earthen dikes that isolated portions of the Sea and constrained circulation in directions and magnitudes previously not predictable, except by the model. Results of the four alternatives were compared to a base case, i.e. to present conditions of velocities and temperatures. The model demonstrated that local velocities could be substantially increased in some areas where resuspension of sediments could occur and decreased in other areas where stagnation might adversely impact water quality and ecological values. The model is presently available for additional investigation of the Salton Sea and its future.

References

Barnes, S., 1964. A technique for maximizing details in numerical weather map analysis. J. appl. Meteorol. 3: 396–409.

Cook, C. B., 2000. Internal dynamics of a terminal basin lake: a numerical model for management of the Salton Sea. Ph.D. Dissertation, Dept. of Civil & Env. Engr., Univ. of Ca.-Davis.

Henderson-Sellers, B., 1982. A simple formula for vertical eddy diffusion coefficients under conditions of nonneutral stability. J. Geophys. Res. 87(C8): 5860–5864.

Huston, D. W., 2000. Application of a wind field analysis to a three-dimensional hydrodynamic model of the Salton Sea, California. M.S. Thesis, Dept. of Civil & Env. Engr., Univ. of Ca.-Davis.

Huston D. W., C. B. Cook & G. T. Orlob, 1999. New and Alamo Rivers Project: Preliminary Data Collection and Analysis for Development of Hydrodynamic and Water Quality River Models, Report 99–3, Water Res. & Env. Modeling Group, Ctr. for Env. & Water Res. Engr., Univ. of Ca.-Davis.

King, I. P., 1985. Strategies for finite element modelling of three dimensional hydrodynamic systems. Adv. Wat. Res. 8: 69–76.

King, I. P., 1993. A finite element model for three-dimensional density stratified flow. Australian Water and Coastal Studies Report, April.

Lesieur, M. & O. Metais, 1996. New trends in large-eddy simulations of turbulence. Ann. Rev. Fluid Mech. 28: 45–82.

Mellor, G. & T. Yamada, 1974. A hierarchy of turbulence closure models for planetary boundary layers. J. Atmosph. Sci. 31: 1791–1482.

Mellor, G. & T. Yamada, 1982. Development of a turbulence closure model for geophysical fluid problems. Rev. Geophy. Space Phys. 20(4): 851–875.

Tennessee Valley Authority, 1972. Heat and Mass Transfer Between A Water Surface and the Atmosphere, Water Res. Research, Engr. Lab., Rep. No. 14, April.

Tostrud, M., 1997. The Salton Sea 1906–1996 Computed and Measured Salinities and Water Levels, Colorado River Board of California, California Resources Agency.

Hydrobiologia **473:** 77–92, 2002.
D.A. Barnum, J.F. Elder, D. Stephens & M. Friend (eds), The Salton Sea.
© 2002 *Kluwer Academic Publishers. Printed in the Netherlands.*

Preliminary studies of cyanobacteria, picoplankton, and virioplankton in the Salton Sea with special attention to phylogenetic diversity among eight strains of filamentous cyanobacteria

A. Michelle Wood[1], Scott R. Miller[1,3], W.K.W. Li[2] & Richard W. Castenholz[1]
[1]*Department of Biology, University of Oregon, Eugene, OR 97403, U.S.A.*
[2]*Biological Oceanography Section, Bedford Inst. of Oceanography, P.O. Box 1006, Dartmouth, Nova Scotia, Canada B2Y 4A2*
[3]*Present address: Department of Genetics, North Carolina State University, Raleigh, NC 27695, U.S.A.*

Key words: cyanobacteria, picoplankton, phylogeny, *Geitlerinema*, *Oscillatoria*, *Beggiatoa*, molecular systematics, ultraplankton, viruses, saline lake, microbial mats, flow cytometry

Abstract

Cyanobacterial diversity in the Salton Sea, a high-salinity, eutrophic lake in Southern California, was investigated using a combination of molecular and morphological approaches. Representatives of a total of 10 described genera (*Oscillatoria*, *Spirulina*, *Arthrospira*, *Geitlerinema*, *Lyngbya*, *Leptolyngbya*, *Calothrix*, *Rivularia*, *Synechococcus*, *Synechocystis*) were identified in the samples; additionally, the morphology of two cultured strains do not conform to any genus recognized at present by the bacteriological system. Genetic analysis, based on partial 16S rRNA sequences suggested considerable cryptic genetic variability among filamentous strains of similar or identical morphology and showed members of the form-genus *Geitlerinema* to be distributed among three major phylogenetic clades of cyanobacteria. Cyanobacterial mats, previously described from the Sea were, in fact, composed of both filamentous cyanobacteria and a roughly equivalent biomass of the sulfur-oxidizing bacterium *Beggiatoa*, indicating their formation in sulfide rich regions of the lake. Flow cytometric analysis of the water samples showed three striking differences between samples from the Salton Sea and representative marine waters: (1) phycoerythrin-containing unicells, while abundant, were much less abundant in the Salton Sea than they were in typical continental shelf waters, (2) *Prochlorococcus* appears to be completely absent, and (3) small (3–5 μm) eukaryotic algae were more abundant in the Salton Sea than in typical neritic waters by one-to-two orders-of-magnitude. Based on flow cytometric analysis, heterotrophic bacteria were more than an order of magnitude more abundant in the Salton Sea than in seawater collected from continental shelf environments. Virus particles were more abundant in the Salton Sea than in typical neritic waters, but did not show increases proportionate with the increase in bacteria, picocyanobacteria, or eukaryotic algae.

Introduction

The Salton Sea is a large, eutrophic, saline lake located in the Southern California desert. The basin is more than 200 feet below sea level and the Sea was formed by an accidental and temporary diversion of the Colorado River to the Salton Sink in the early 1900s (Walker, 1961). While originally a freshwater lake, the Sea has changed dramatically in size, salinity, and biology during its 100-year history. Agricultural and municipal wastewaters now supply 88% of the inflow to the lake, the present salinity is greater than that of seawater (41–45 g l^{-1} increasing at 0.3–0.4 g l^{-1}), and summer conditions are characterized by periodic deoxygenation events during which surface sulfide levels can exceed 0.5 mg l^{-1} (Tostrud, 1997; Watts et al., 2001).

The Sea has a long history of use for sport fisheries and its fish stocks are also important to numerous migrating and breeding bird species. However, recent fish kills and avian deaths, combined with the pattern of increasing salinity, have increased concern over

the long-term future of the Sea. Salinity levels, which could reach 91 g l^{-1} by 2010 (Imperial Irrigation District, 1989), may already place stress on key elements of the food chain and could exceed the physiological tolerance of many organisms.

It is difficult to evaluate the ecological condition of the Sea because of the relative paucity of information about the biotic composition of the ecosystem. Only two studies provide information about primary producers in the Sea (Carpelan, 1961; USDI, 1970). Both of these studies were completed before widespread recognition that the 'microbial loop' community consisting of heterotrophic bacteria, protistan grazers, viruses, and ultraphytoplankton constitutes a dynamic food web that can be responsible for a large percentage of material and energy flow in aquatic ecosystems (Pomeroy, 1974; Fuhrman, 1997; Azam, 1998). The dominant primary producers in the microbial loop of the open ocean are two forms of picocyanobacteria, *Synechococous* and *Prochlorooccus*, both of which could have been introduced to the Sea multiple times as ocean water was added to the sea with fish stocks. Carpelan (1961) noted the presence of visible massed growths of 'bluegreen algae' on the bottom of shallow regions of the main body of the lake and on pilings and buoys, but his work was completed long before the role of picocyanobacteria in the microbial loop was recognized. Thus, it does not include any consideration of the possible role of picocyanobacteria in the plankton.

The need for further information regarding cyanobacterial diversity and dynamics in the Salton Sea extends beyond the importance of considering the role of cyanobacteria in the microbial loop of the Sea. As noted previously, Carpelan (1961) describes several forms of filamentous cyanobacteria in benthic mats; he also mentions that pieces of the mats are occasionally seen floating in the water column, a phenomenon that frequently occurs in the summer under current conditions (Hurlbert, pers. comm.). This is not surprising since cyanobacteria are widely recognized for their ability to grow and flourish in extreme conditions, particularly in the presence of sulfide, high temerpature, or high salinity. Blooms of cyanobacteria occur in many lacustrine environments and are often associated with anthropogenic pollution (Edmondson & Lehman, 1981; Thornton, 1982) and/or fatal poisonings in mammals, fish, and birds (Carmichael, 1992, 1994, 1997; Dow & Swoboda, 2000). Thus, sulfide levels and high nutrient concentrations in the Sea may promote the growth of cyanobacterial mats, and these mats may be sources of toxins that affect the many birds and fish that depend on the Sea.

In this study, we report the results of a preliminary survey of cyanobacteria and associated organisms in the Salton Sea. The study is based on material collected in 1999 and includes consideration of the overall composition of 'cyanobacterial mats' as well as the first flow cytometric characterization of the microbial loop community of the Salton Sea. Taxonomic identification of field and cultured material conforms to modern bacteriological standards as published in Bergey's Manual of Systematic Bacteriology (2nd edn., Boone et al., 2001). We also used molecular genetic approaches to reveal some of the morphologically cryptic phylogenetic diversity associated with forms of that were common in the Sea.

Methods

Field sampling and examination of field material

Water samples containing planktonic organisms and samples of benthic algae scraped from rocks or pilings and/or embedded in salt crusts were collected from the shore in January and June, 1999. Sites sampled in January were located along the southern and eastern shores of the lake (dikes along the shoreline between New and Alamo Rivers, Garst Road, Red Hill Marina, Bombay Beach, Varner Harbor and the open beach at the State Recreation Area Headquarters; see Fig. 1 in Lange & Tiffany, 2002). In June, samples were collected at these locations as well as six additional sites on the western and southern shores (Desert Shores, Salton Sea Beach, Riviera Keys, and Obsidian Butte; cf. Fig. 1, Lange & Tiffany, 2002). Samples for flow cytometry were immediately preserved with 1% (final concentration) paraformaldehyde and frozen in liquid nitrogen. The remaining material was stored, refrigerated, until it was examined microscopically and used for strain isolation.

Isolation of cultured strains

Pure cultures were obtained from samples collected in January. Nutrient composition of the culture medium corresponded to that of the standard cyanobacterial medium BG11 (Castenholz, 1988) prepared with 24 g l^{-1} 'Instant Ocean'™. In order to increase the chances of isolating a physiologically diverse range of strains, media were also prepared at two higher salinity levels (43.5 and 70 g l^{-1}) by adding NaCl.

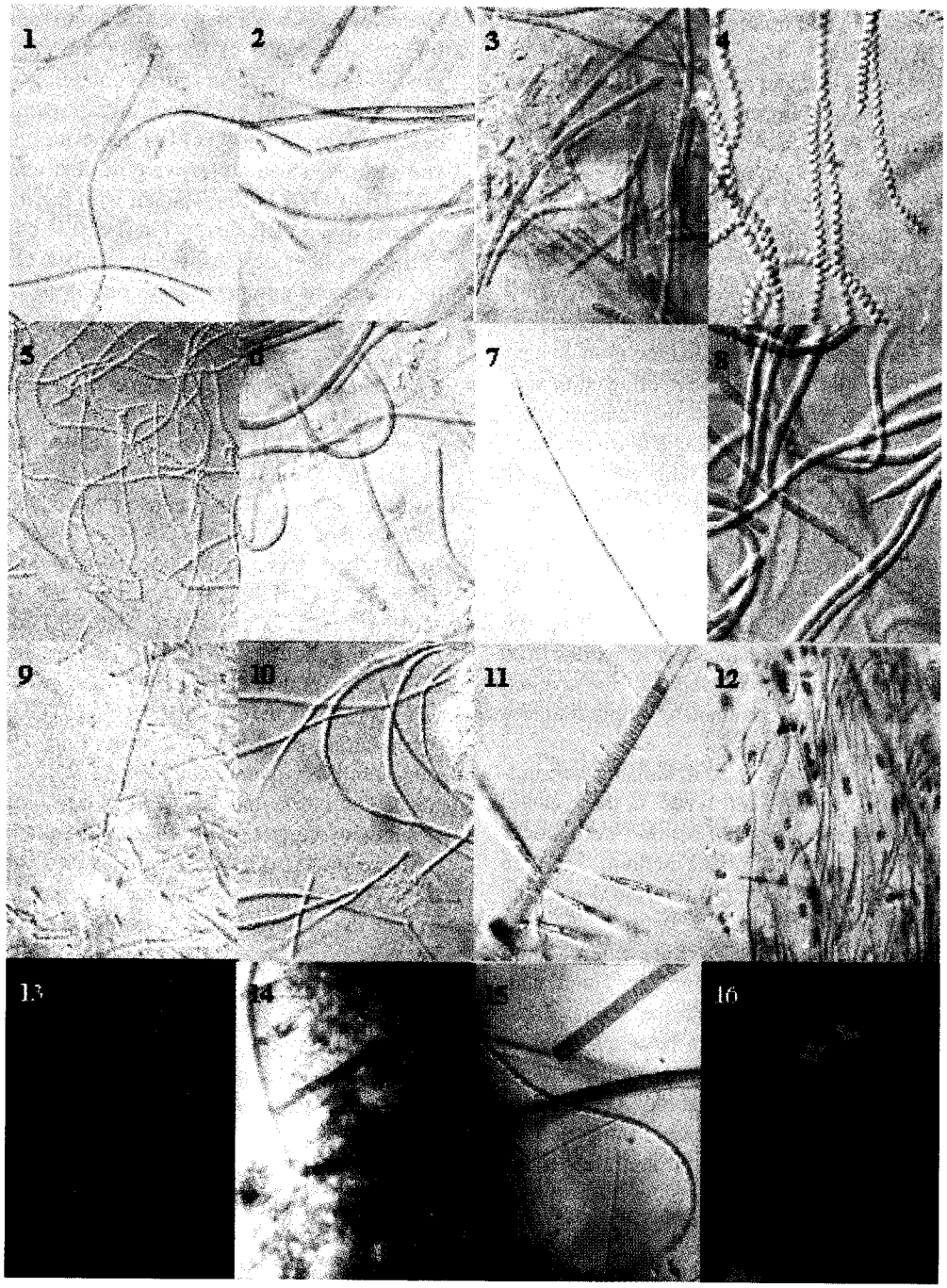


Figure 1. Field Samples and selected clonal isolates of cyanobacteria from the Salton Sea viewed by Nomarski Differential Interference Contrast (Panels 1–12, 14, 15) or epifluorescence microscopy (Panels 13, 15). Strain identifications are CCMEE 5439 (Panel 1); 5438 (Panel 2); 5433 (Panel 3); 5419 (Panels 4, 5); 5403 (Panel 6); 5446 (Panel 7, 8); 5407 (Panel 9); and 5435 (Panel 10). Panels 11 and 12 show the close association of pennate diatoms with epilithic *Lyngbya* (Panel 11) and multi-species mat material (12). Panels 13 and 14 show the same mat sample illuminated by transmitted light (14) and green light with epifluorescence illumination (13); the brightly red fluorescing cells and filaments are cyanobacteria with phycocyanin as the dominant light harvesting pigment; the filaments that are prominent in Panel 14, but which do not show any autofluorescence in Panel 13 are filaments of the sulfide oxidizing bacterium *Beggiatoa*; *Beggiatoa* was common in essentially all samples of mat material we examined by microscopy (see text). Panel 15 shows filaments of *Oscillatoria, Leptolyngbya*, and several thin filaments of *Geitlerinema* in a mat sample. Panel 16 shows autofluorescence from tetrads of planktonic unicells identified as *Synechocystis* sp; individual cells are ~1.5 μm in diameter. All images were obtained using 1000× magnification except those in Panels 5 and 7 which were obtained using 400× magnification.

Thus, cells were isolated into media reflecting current conditions in the lake (~43.5 g l^{-1}), as well as conditions considerably less and considerably more saline than the current lake environment (24 and 70 g l^{-1}). At the beginning of the isolation process, media for enrichment cultures also contained cyclohexamide (final concentration 400 mg l^{-1}) to inhibit the growth of eukaryotic algae. Media was solidified for plating using 3% Difco™ agar.

Several approaches were used to obtain isolates. Benthic samples consisting mainly of filamentous cyanobacteria were used as non-spread inoculum on agar plates, and motile gliding forms were allowed to separate from the mass. After filaments had radiated from the original point of inoculation, single filaments were picked off on small agar blocks with watchmaker's forceps and transferred to liquid medium. This enrichment was allowed to grow, examined by microscopy for uniformity of morphotypes in the culture, and replated on an agar plate (see Castenholz, 1988). A single filament from the population growing on the second plate was re-isolated into liquid media. The culture was considered a clonal isolate of the original morphotype after these two rounds of single filament isolation.

Dilution series were also used to isolate representatives of the most abundant cell types. In these cases, water samples or homogenates of benthic were inoculated into a dilution series of liquid medium, and then the community that grew up into the liquid medium used to inoculate an agar plate.

Water samples from the Sea were filtered onto polycarbonate filters (0.2 μm pore size) and agar plates were inoculated by dragging the filters across the agar surface. Colonies of unicells which grew on the plates were used to isolate clonal cultures using standard techniques of streak dilution. Additionally, unicellular forms isolated from benthic samples were inoculated onto plates using material that grew in the dilution series, general enrichments, or raw sample material and clonal cultures established from serial transfers of individual colonies that grew up on the plates.

Flow cytometry

Samples for flow cytometry were preserved and frozen in liquid nitrogen immediately after collection as described above; samples were stored at −80 °C until shipped to Bedford Institute of Oceanography on dry ice where they were again stored at −80 °C until analyzed. Samples were analyzed unstained and undiluted for the abundance of the major ultraphytoplankton groups (small phycoerythrin-containing cells, *Prochlorococcus*, and eukaryotic ultraphytoplankton) as described in Li (1995). For heterotrophic bacteria and viruses, the samples were diluted ten-fold in 10 mM Tris-EDTA buffer, stained with the nucleic acid-specific dye SYBR Green-I at 5×10^{-5} concentration of the supplier stock (Molecular Probes, Oregon), and the organisms enumerated according to Marie et al. (1999).

DNA isolation, amplification and sequencing

Genomic DNA of clones was isolated as described by Pitcher et al. (1989). Fragments of the 16S ribosomal RNA (rRNA) gene spanning *Escherichia coli* nucleotide positions 360–1326 were amplified in 50 μl reactions containing 10 mM Tris–HCl, pH 8.3, 50 mM KCl, 200 μM of each dNTP, 1.12 mM $MgCl_2$, 1.25 U *Taq* polymerase (Perkin Elmer), ~10 ng genomic DNA, 0.2 μM each of primer CYA359F (Nübel et al., 1997) and primer PLG2.3 (5′CTTCA(C/T)G(C/T)AGGCGAGTTGCAGC3′), a modification of PLG2.1 (Urbach et al., 1992). Reaction conditions were 40 cycles of 94 °C for 1 min, 58 °C for 1 min and 72 °C for 2 min. Amplification products were purified with the QIAquick-spin PCR purification kit (Qiagen), and cleaned amplification products were directly sequenced with an ABI Prism 377 at the University of Oregon's DNA Sequencing Facility.

Sequence alignment and phylogeny reconstruction

16S rRNA gene sequences were aligned as described in Miller & Castenholz (2000). Briefly, this entailed encoding secondary structure information for the mature 16S rRNA into a preliminary alignment prior to final pairwise alignment using Malign 2.7 (Wheeler & Gladstein, 1994) with pairwise addition of taxa and a gap cost to substitution cost of 3. Missing data were treated as unknown nucleotides.

Neighbor-joining, maximum parsimony and maximum likelihood phylogenies were inferred with PHYLIP 3.5c (Felsenstein, 1993). The neighbor-joining phylogeny was constructed with the NEIGHBOR program using a distance matrix calculated with DNADIST assuming Kimura's two parameter model (Kimura, 1980) with a transition to transversion ratio of 2. Maximum parsimony reconstructions were

Table 1. Cyanobcteria reported from the Salton Sea. (B-benthic samples; P-plankton samples) or among clonal isolates (C). Species reported by Carpelan (1962), which represents the only other survey of cyanobacteria from the Salton Sea, are included here for completeness

Taxon	This study		Carpelan[a]
	January	June	
Filamentous Forms			
Oscillatoria	B,C	B	B[g]
Spirulina	B,P,C	B	B
Arthrospira	B	B	
Geitlerinema	B,C	B	
Lyngbya	B,C	B	P
Leptolygnbya	B,C	B	
Calothrix	B	B	
c.f. Rivularia	B	B	
Phormidium tenue[a]			B
Plectonema calotrichoides[a]			B
Hydrocoleum sp.[a]			B
Undescribed	C		
Unicellular or Aggregates			
Synechococcus[b]	B,P,C	B,P	
c.f. *Synechocystis*[c]	P,C	P	
c.f. *Chroococcidiopsis*[d]	B,P		
c.f. '*Acaryochloris*'[e]	C		
Pleurococcus turgidus[a,f]			B
Pleurocapsa crepidinum[a]			B
Gomphosphaera lacustris[a]			P

[a] Used botanical classification system.
[b] Phycoerythrin and phycocyanin-dominant forms.
[c] 2 μm cells in tetrads.
[d] No baeocytes observed.
[e] See Miyashita et al. (1996); nomen nudem.
[f] Probable misspelling of *Chroococcus*; see text.
[g] Described as 'near *O. laetevirens*'.

obtained with DNAPARS, and a majority rule consensus diagram of equally parsimonious trees was found using CONSENSE. The maximum likelihood tree was inferred using DNAML with a transition to transversion ratio of 2 and sequential addition of sequences. The neighbor-joining and parsimony trees were bootstrap pseudoreplicated 1000 times, while the maximum likelihood phylogeny was bootstrapped 100 times. All trees were rooted with *Aquifex pyrophilus*, a hyperthermophile on an early branch of the Bacterial 16S RNA phylogenetic tree (see Madigan et al., 2000).

Results

Field samples

Microscopic examination of field samples revealed cell types that conformed to basic morphological features of eight genera of filamentous cyanobacteria and three genera of cyanobacteria that occur as unicells or aggregates (Table 1). Common genera referred to below are two genera of filamentous cyanobacteria which lack sheaths (*Oscillatoria* and *Geitlerinema*), both of which are motile, and which differ primarily in the cell dimensions. *Oscillatoria* (as currently defined) has disc-shaped cells that are wider than they are long and *Geitlerinema* has cells that are longer than they are wide, length being measured along the long axis of the filament (cf. Castenholz et al., 2001). *Lyngbya*, which was common in samples collected from rocks along the shore, has disc-shaped cells similar to those of *Oscillatoria*, but the trichome is encased in a distinct, persistent and firm sheath. Often the filaments appear brownish-colored because of the presence of an extracellular UV-protective pigment (scytonemin) bound in the sheath (see Garcia-Pichel & Castenholz, 1991).

Plankton samples, examined under epifluorescence microscopy, revealed a diversity of unicellular forms, the most common of which were representatives of the genera *Synechococcus* and *Synechocystis*. Individuals in both genera are short rods or coccoid cells ~1–2 μm in diameter; members of the two genera are distinguished by the number of planes of cell division: in *Synechococcus* cell division occurs along a single plane, producing pairs of dividing cells and, in *Synechocystis*, cell division occurs in two orthogonal division planes, occasionally producing characteristic tetrads of individual cells (e.g. Fig. 1.16). When excited with green light by epifluorescence microscopy, some of these small cells fluoresced orange, revealing the presence of phycoerythrin as the predominant light harvesting pigment and others fluoresced red under the same conditions. Since the red fluorescence disappeared when the cells were excited with blue light, it conformed to that expected from phycocyanin-dominant cells (see Wood et al., 1985). Single trichomes of filamentous cyanobacteria were observed in most water samples prepared for epifluorescence microscopy. Some of these trichomes were clearly members of the genus *Spirulina* based on their tightly coiled trichomes; others were not classified to genus but appeared to be members of Subsection III of the

Cyanobacteria (formerly Oscillatoriales, see Castenholz et al., 2001). Based on morphology, genera represented were *Oscillatoria*, *Geitlerinema*, *Leptolyngbya* and possibly others. Among the oscillatorian trichomes observed in the plankton, some had phycoerythrin and some had phycocyanin as the predominant photosynthetic pigment. Extremely small particles ($\ll$0.5 μm) that fluoresced orange when illuminated by green light were also common in the plankton samples; these particles, presumably containing phycoerythrin because of the golden-orange fluorescence, occurred in aggregates of many ($\sim$30–100) individually fluorescing cells or particles; we never observed any material like this in the enrichment cultures.

Great diversity of form was found among the filaments associated with floating mats and benthic samples collected from pilings and rocks. For example, a single subsample of mat material collected from a Varner Harbor piling in January revealed five different forms of oscillatorian cyanobacteria; these differed in the presence or absence and rate of motility, trichome width, presence or absence of phycoerythrin, presence or absence of a sheath, appearance of cross-walls, and presence or absence of constrictions at cross-walls. Mat samples collected at different locations were similar in color and consistency when examined macroscopically, but often contained different morphotypes of cyanobacteria that were easily distinguished from one another when samples were examined microscopically. Typical floating mat material was a mixture of one or two dominant morphotypes of filamentous cyanobacteria intertwined with filaments of the sulfide or sulfur-oxidizing chemolithotroph *Beggiatoa*. (Figs 1.13,1.14). For example, the dominant cyanobacterial morphotype in a *Beggiatoa*-rich sample of floating mat material collected from Salton Sea Beach in June was highly motile, with a trichome diameter of 4–5 μm and a curved, novel tip on terminal cells in the filaments; this morphotype was assigned to the genus *Geitlerinema* based on cell dimensions, lack of a sheath, and motility. This mat also included filaments of *Spirulina*, two morphotypes of *Beggiatoa* (4 and 8 μm wide), filaments of the green alga *Chaetomorpha*, and a large *Oscillatoria* (trichome width 8–10 μm). This motile filament was dark green, particularly at the cross-walls, and had a slight curve at the tip; while much less common than the *Geitlerinema* morphotype that dominated the mat sample from Salton Sea Beach, it was the dominant filamentous cyanobacterium in a sample collected the same day from Varner Harbor. Other morphotypes in the mat from Varner Harbor included a morphotype of *Geitlerinema*, a large *Spirulina*, a very large *Oscillatoria* (20 μm trichome width), and a smaller *Oscillatoria* (5μm trichome width) which was distinguished from another *Oscillatoria* of similar dimensions by the consistent granular appearance of the cross walls in one of the two morphotypes.

In most mat samples, the biomass of *Beggiatoa* was greater than, or comparable to, that of the filamentous cyanobacteria. Unicellular cyanobacteria, diatoms, and some other small photosynthetic eukaryotes were also apparent in the mat samples when they were examined with epifluorescence microscopy.

In January, 1999, we were interested in the possible winter refugia for organisms that formed benthic mats in the summertime. Samples of consolidated hard substrate, composed largely of barnacles, were collected in shallow water from the bottom of the lake off the beach near the State Recreation Area. Small ($\sim$10 mm^2) areas of bluegreen discoloration were observed in some places on the barnacle shells. Subsequent microscopic of a single sample scraped from one of these bluegreen areas revealed the presence of *Calothrix* (with phycoerythrin and heterocysts), *Spirulina*, a large morphotype (18 μm trichome width) of *Oscillatoria* containing phycoerythrin, two other smaller morphotypes of phycoerythrin-containing *Oscillatoria* that differed in trichome width, and at least one morphotype of phycocyanin-dominant *Oscillatoria*.

Lyngbya was especially common on rocks along the waterline at Desert Shore; most of these filaments were covered with pennate diatoms (Fig. 1.11). *Lyngbya* was found growing epilithically in both January and June, although diatom growth on the filaments was more luxuriant in the samples collected in June. The most common diatom found growing on Lyngbya was *Tabularia parva*, although *Achnanthes brevipes* and *Licomorpha* sp. are also found as occasional epiphytes on *Lyngbya* in the Sea (Mary Ann Tiffany, pers. comm.).

Flow cytometry

The results of flow cytometric analysis of water samples from three locations sampled in the Salton Sea in January, 1999 and two locations in the northern Gulf of Mexico sampled in October, 1998, are presented in Table 2. All samples were analyzed together, and the data from the Gulf of Mexico are presented as representative of ultra/picoplankton community structure in a marine community typical of neritic waters at

Table 2. Results of flow cytometric analysis of surface samples from the Salton Sea, with comparative data from samples collected at 2 m on the inner (I) and outer (II) West Florida continental shelf (Gulf of Mexico). Values $\times 10^3$ ml^{-1}; ND=Not detected

	Dike Road	Bombay Beach	Refuge Hdqtrs. Beach	Gulf Mexico-I	Gulf Mexico-II
Phycoerythrin-containing unicells	2.45	2.91	3.57	263.03	11.53
Prochlorococcus	ND	ND	ND	15.76	29.25
Small Eukaryotic Algae	128.89	91.41	111.55	4.02	0.79
Heterotrophic Bacteria	4366.02	4714.75	3972.41	886.93	219.68
Viruses-Type II	69 338.42	46 524.28	68 480.04	12 062.66	3901.02
Viruses-Type I	2698.34	4961.23	5353.38	1846.8	321.97
Total Viruses	72 036.76	51 485.51	73 833.78	13 909.46	4223.17

warm, temperate latitudes. Three dramatic differences between the Salton Sea picophytoplankton community and the neritic picophytoplankton community are apparent: (1) phycoerythrin-containing unicells, while abundant, were much less abundant in the Salton Sea than they were in typical continental shelf waters, (2) the very small divinyl-chlorophyll *a*-containing picocyanobacterial taxon *Prochlorococcus* appears to be completely absent from the samples we collected in the Salton Sea, and (3) small eukaryotic algae (typically cells ~3–5 μm effective spherical diameter; see Li & Wood, 1988) were more abundant in the Salton Sea than in typical neritic waters by one-to-two orders-of-magnitude. Not unexpectedly, because of the highly eutrophic conditions, heterotrophic bacteria were also more than an order of magnitude more abundant in the Salton Sea than in seawater collected from continental shelf environments. Interestingly, virus particles, while more abundant in the Salton Sea than in water samples from the continental shelf, did not show increases proportionate with the increase in bacteria or eukaryotic algae. Viruses were considerably more abundant, but roughly the same order of magnitude in the Sea as on the inner continental shelf. This trend was true for both Type I and Type II virus particles which, on the basis of nucleic acid staining intensity and apparent size, are thought to be possibly cyanophage and bacteriophage (Type II) or viruses of eukaryotic algae (Type I) (see Marie et al., 1999).

Cultured strains

Eighty-four clonal strains of cyanobacteria were isolated from the Salton Sea samples collected in January, 1999; all have been accessed into the NASA/University of Oregon Culture Collection of Microorganisms from Extreme Environments (UO-CCMEE; http://cultures.uoregon.edu). Because this project was of limited duration, isolates that grew quickly are disproportionately represented in the collection; most of these were isolated in medium of either low (24.5 g l^{-1}) or Salton Sea salinity (43.5 g l^{-1}). Only three clonal cultures were established in high salinity medium although the appearance of additional morphotypes in the enrichments during the project period indicates that many more could have been isolated if time had permitted; among the morphotypes that grew in high salinity enrichments, but which were not purified as clonal cultures, were several morphotypes of *Spirulina* and *Oscillatoria*, at least one morphotype of *Pseudanabaena*, and a number of unicellular forms (probably *Synechococcus* and/or *Synechocystis*). All three high-salinity isolates in the collection are filamentous forms (CCMEE Strains 5471, 5478, 5479).

The complete set of 84 strains isolated from the Salton Sea includes isolates from all sites sampled in January, and from samples of planktonic and benthic material. Filamentous and unicellular morphotypes were isolated from both water samples and benthic samples. The collection includes strains with phycoerythrin as the dominant light harvesting pigment, strains with phycocyanin as the dominant light harvesting pigment, and an unusual strain that appears to produce chlorophyll *d* as the predominant light harvesting pigment (A. M. Wood et al., in prep.).

While the collection does include several representatives of strains forming tightly coiled trichomes (*Spirulina* spp. sensu Castenholz, 2001) and several with thick persistent sheaths (*Lyngbya* spp. sensu Castenholz, 2001), the majority of the isolates are filamentous strains, most of which lack a sheath. Many of these are of morphotypes which were common in

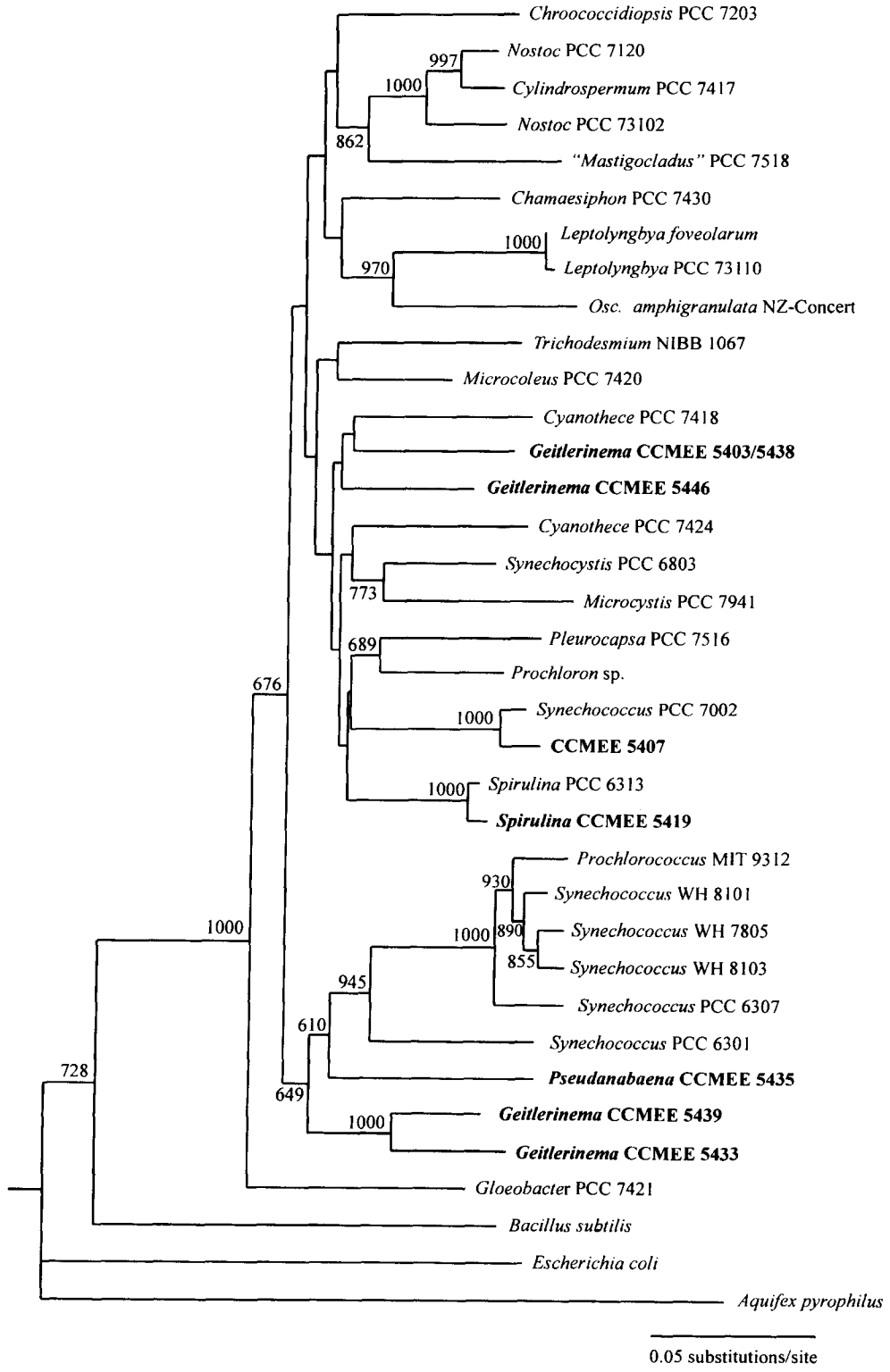


Figure 2. Cyanobacterial phylogeny inferred from ~960 bp of 16S rRNA sequence data using the Neighbor Joining method. A value at a node indicates the percentage of the time that the taxa to the right of the node formed a clade for 1000 bootstrap pseudoreplicates. Bootstrap values <50% are not shown.

Table 3. Cultured stains selected for phylogenetic analysis

Strain	Form-genus[a]	Width (μm)	Motility	Source
CCMEE5435	*Pseudanabaena*	1.2–3.0	Slow	Varner Harbor mat
CCMEE5439	*Geitlerinema*	1.0–2.0	Slow	Barnacle[b]
CCMEE5433	*Geitlerinema*	2.0	Very slow	Varner Harbor mat
CCMEE5438	*Geitlerinema*	2.0	Slow	Barnacle[b]
CCMEE5403	*Geitlerinema*	2.0	Rapid	Scraped off dike rip rap
CCMEE5419	*Spirulina*	1.2–1.3	Rapid	Sediment in boat harbor, Bombay Beach
CCMEE5446	*Geitlerinema*	3.0	Slow	Plankton sample collected from dikes
CCMEE5407	*Undescribed*	1.2	Nonmotile	Scraped off dike rip rap

[a]Taxonomic authority: Bergey's Manual of Systematic Bacteriology, 2nd Edn. (Boone & Castenholz, 2001).
[b]Barnacles collected in shallow water off the State Recreation Area headquarters.

mat material and which are very difficult to distinguish form one another based on morphology (cf. Fig. 1). Since several of the strains would key to the same species using the botanical system of classification commonly used in applied limnology, we were particularly interested in determining how much cryptic genetic diversity might exist among morphologically similar strains found in mats and attached to rocks and pilings. Thus, of the eight strains selected for further phylogenetic and morphological characterization, five would be placed in the same form-genus (*Geitlerinema*) and two (CCMEE 5403 and CCMEE 5419) were completely indistinguishable from one another morphologically (Table 3). Of the eight strains included in the phylogenetic analysis, all but strain CCMEE 5446 were isolated into low salinity medium (24 g l^{-1}); strain CCMEE 5446 was isolated into medium of intermediate salinity (43.5 g l^{-1}).

Phylogenetic analysis

Neighbor-joining (Fig. 2), maximum parsimony (Fig. 3), and maximum likelihood (Fig. 4) methods were employed to infer the position of eight clones isolated in this study within the cyanobacterial 16S rRNA gene phylogeny. All eight are classified taxonomically as members of Subgroup III of the cyanobacteria (formerly Oscillatoriales) under the current system (Castenholz et al., 2001). The maximum parsimony phylogeny shown (Fig. 3) is a consensus diagram of the three equally most parsimonious trees (2064 steps). The maximum likelihood phylogeny (Fig. 4) had a ln likelihood = −11389. These trees are similar to published cyanobacterial phylogenies (e.g. Wilmotte, 1994) in that they do not resolve many of the internal nodes. However, in most cases they provide consistent, robust information about the phylogenetic affinities of the Salton Sea clones included in the analysis. Each is discussed in detail below.

In trees produced by all three analyses, CCMEE 5435 (Fig. 1.10) was the basal lineage in a clade including marine *Synechococcus* and *Prochlorococcus* isolates, although this association was only robust for the neighbor-joining phylogeny (Fig. 2). The sequence is ~98% similar to that for *Leptolyngbya* PCC7375 (not shown), a phycoerythrin-containing filamentous cyanobacterium isolated from a marine plankton sample (Rippka et al., 1979).

Strains CCMEE 5439 (Fig. 1.1) and CCMEE 5433 (Fig. 1.3) are sister taxa in all three phylogenies with extremely strong bootstrap support (Figs 2–4). They are also a sister group to a large clade including strain CCMEE 5435 (discussed above), although this association is only supported by bootstrap analysis for the neighbor-joining phylogeny. In addition to having slightly wider trichomes, cross-walls at the cell junctions are more distinct in CCMEE 5439 than CCMEE 5433.

With the exception of showing faster motility, Strains CCMEE 5438 (Fig. 1.2) CCMEE 5403 (Fig.

1.6) are essentially identical to CCMEE 5433 morphologically. However, they show little sequence homology with CCMEE 5433, as reflected by the lack of a close phylogenetic relationship between these two strains and CCMEE 5433 in any analysis (Figs 2–4). The two strains, one isolated from scrapings off the rip rap along the dikes between the New River and Alamo river (CCMEE 5403) and the other isolated from a mat sample collected at Varner Harbor (CCMEE 5438), share identical 16S rDNA sequences but their phylogenetic status was unclear. They were the sister taxa of *Cyanothece* PCC 7418 in the neighbor-joining and maximum likelihood phylogenies (Figs 2 and 4), but this association was not supported by bootstrap analysis in these trees, nor was it obtained in the maximum parsimony reconstruction (Fig. 3). However, subsequent analysis indicated that their sequence is >99% similar to that of *Geitlerinema* PCC7105, a marine isolate of Subgroup III (formerly Oscillatoriales; see Castenholz et al., 2001) (data not shown).

According to all three phylogenetic analyses, Strain CCMEE 5419 (Figs 1.4–1.5) groups with *Spirulina* PCC6313, an isolate from brackish water, with 100% bootstrap support (Figs 2–4). The position of this clade within the phylogeny as a whole was not resolved. Grouping of CCMEE 5419 with PCC6313 in our analysis was expected; cyanobacteria forming tightly coiled trichomes with regular helical coils appear to be a monophyletic group (Nübel et al., 2000).

The phylogenetic status of Strain CCMEE 5446 (Figs 1.8–9) is unclear, as its position is variable across phylogenetic reconstruction methods (Figs 2–4). A BLAST search of the GenBank database found it to be most closely matched with *Cyanothece* ATCC 51142, but their similarity was only ~93% (data not shown). Microscopically, this strain looks very similar to the other strains of *Geitlerinema* described above (compare Fig. 1.8 with 1.2 and 1.6), but the trichomes are slightly wider (~3 μm) and distinguished by a novel twisted and tapered pointed tip (Fig. 1.7).

Strain CCMEE 5407 (Fig. 1.9) consistently showed a robust phylogenetic association with *Synechococcus* PCC7002 (Figs 2–4). Overall the strain exhibits a combination of features that do not allow it to be placed in any genus under the current system (see Castenholz et al., 2001) indicating that no cultured representative of this taxon has been described before. The strain is brownish yellow in culture and the constrictions at the cross-walls of adjoining cells are pronounced. Cells are nearly isodiametric but slightly longer than wide; the strain appears to be nonmotile. In the botanical tradition of cyanobacterial taxonomy, the morphology of the strain corresponds to *Phormidium foveolarum* Gomont (Frémy, 1930).

Discussion

We found a variety of morphological cyanobacteria in all habitats and samples we examined. Differences between the list of cyanobacterial genera identified in this study and those identified by Carpelan (1961) largely arise from differences in the systematic standards utilized at the time of his study. At least two of the strains identified as *Geitlerinema* by us would have been described as *Phormidium* in his study; *Plectonema calotrichoides* is unknown in the polyphasic system as no cultured material conforms to the morphotype of this botanical species. We also believe that the organism he described as *Pleurococcus turgidus* was actually *Chroococcus turgidus* (Kütz) Näg. since we cannot find the genus *Pleurococcus* in any taxonomic treatment of the cyanobacteria or blue-green algae. Carpelan's omission of several genera of picoplanktonic cyanobacteria that we found to be common in the Sea almost certainly results from the fact that these organisms were largely overlooked in all aquatic environments before the introduction of epifluorescence microscopy and flow cytometry. We consider it likely that these organisms were present in the Sea at the time of Carpelan's study.

Our study, and Carpelan's before it, identified cyanobacterial mats as a common feature in the Sea. However, our epifluorescence analysis showed clearly that the mat material is not solely composed of cyanobacteria, but also includes *Beggiatoa*, a sulfur oxidizing bacterium as a major structural and biomass component. This means that most mats are formed in association with sulfide layers in the water column or sediment and raises the possibility that some of the cyanobacteria in the sea may be among those which are capable of utilizing H_2S as an electron donor for photosynthesis instead of water (Cohen et al., 1986; Castenholz et al., 1991). Additionally, mat material collected in different parts of the Sea, while superficially similar in color and consistency, varied considerably in composition. As noted previously, some mat samples were dominated by a single morphotype of filamentous cyanobacteria and others contained two or more dominant morphotypes of filamentous cyanobac-

Figure
indicat
<50%

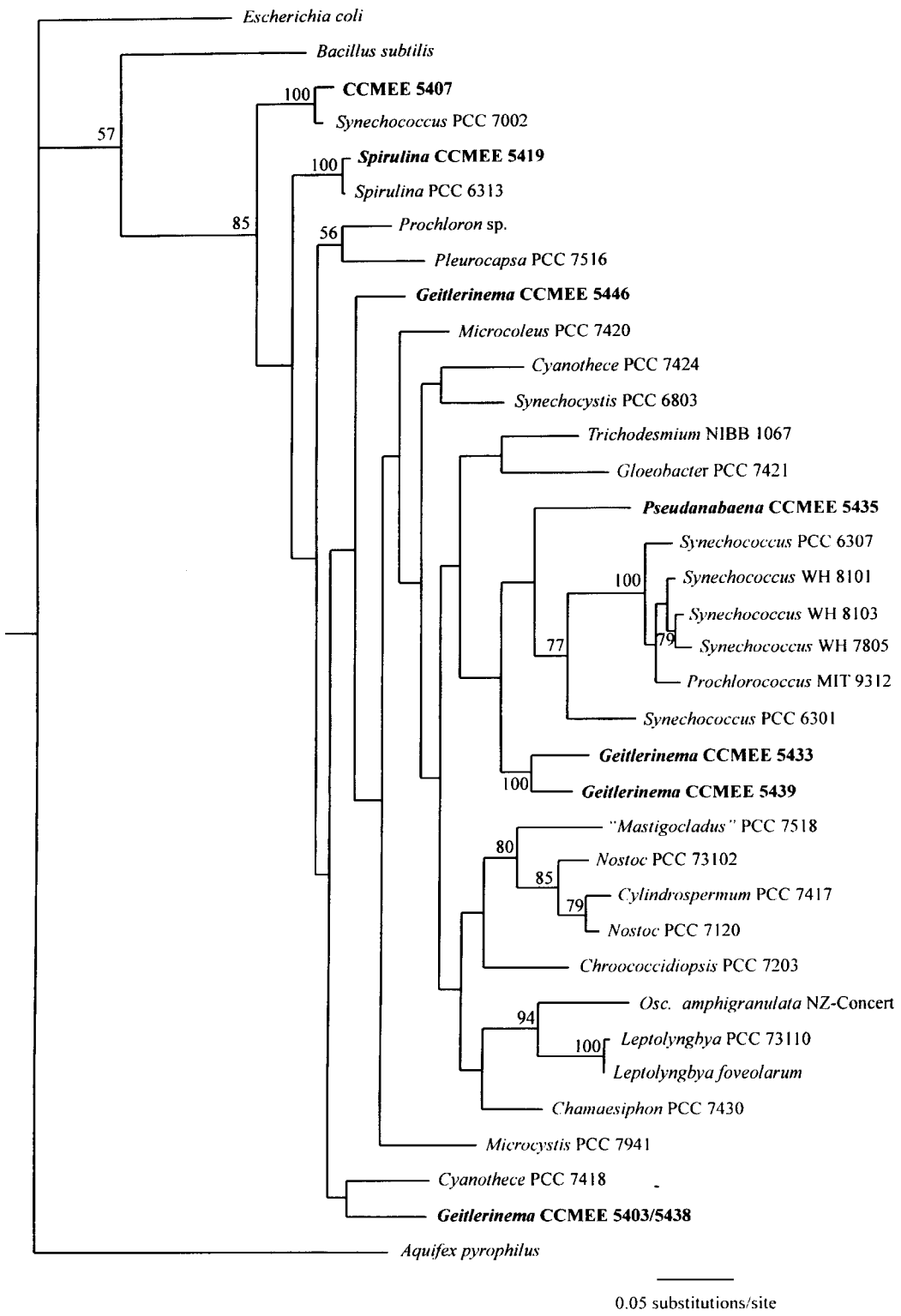


Figure 3. Cyanobacterial phylogeny inferred from ~950 bp of 16S rRNA sequence data using Maximum Likelihood method. A value at a node indicates the percentage of the time that the taxa to the right of the node formed a clade for 100 bootstrap pseudoreplicates. Bootstrap values <50% are not shown.

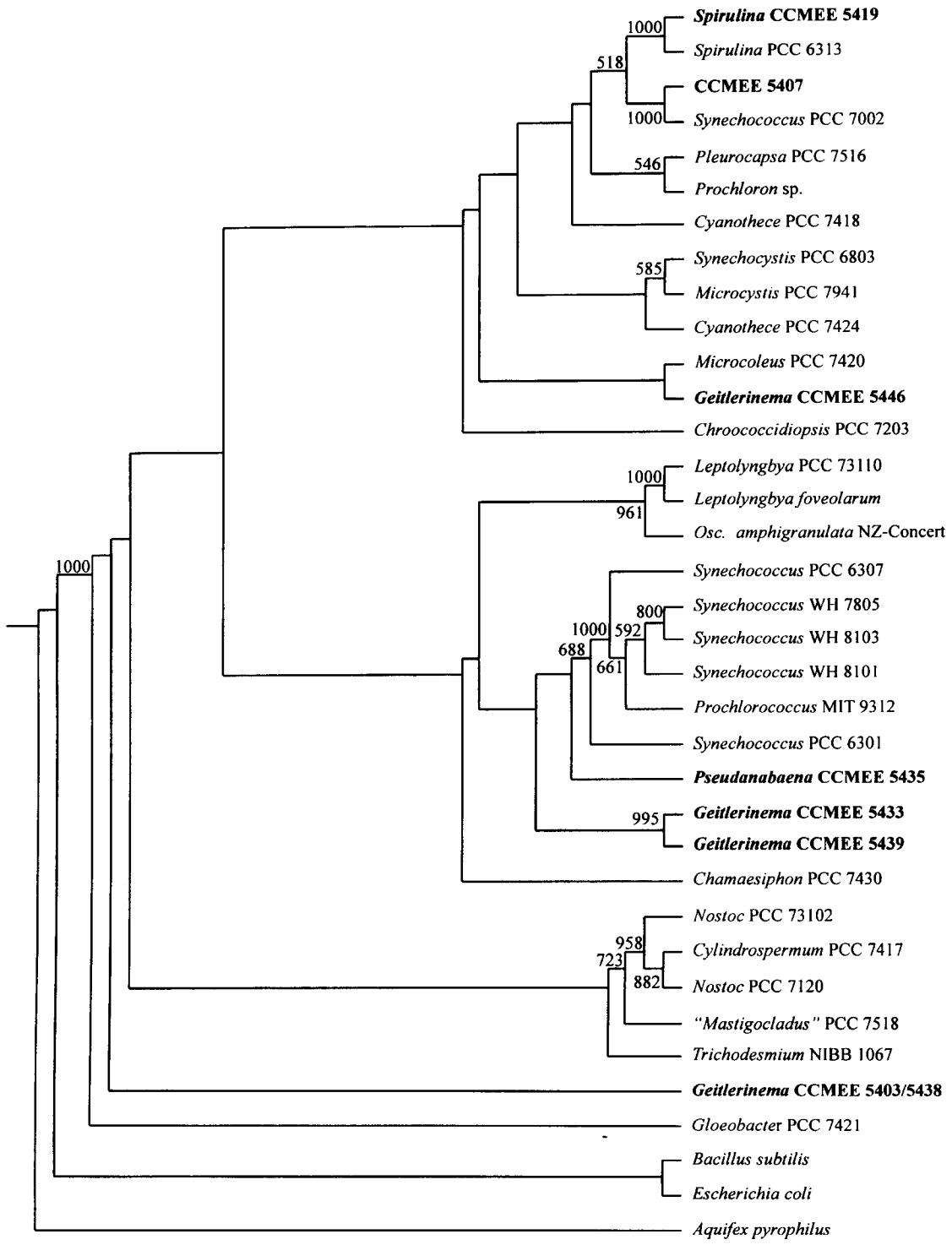


Figure 4. Cyanobacterial phylogeny inferred from ~950 bp of 16S rRNA sequence data using Maximum Parsimony. A value at a node indicates the percentage of the time that the taxa to the right of the node formed a clade for 1000 bootstrap pseudoreplicates. Bootstrap values <50% are not shown.

teria, as well as numerous less abundant morphotypes of filamentous cyanobacteria and many small diatoms and unicellular cyanobacteria. Even the small patch of blue-green material scraped off a barnacle colony revealed five morphotypes from four genera when examined by microscopy, and yielded two additional morphotypes from another genus when used as the inocculum for an enrichment culture. Thus, each mat community may have slightly different biogeochemical properties, possibly reflected in differences in productive capacity under different conditions of oxygen availability, level of irradiance, and/or sulfide concentration; these differences may, in turn, be reflected in differences in palatability to grazers.

In the plankton, the communities described by flow cytometry differ from those of neritic marine waters in ways that might be predicted by the difference in trophic status. For example, the high abundance of small eukaryotic algae is common in eutrophic estuaries and, while we do not know the taxonomic identity of these organisms, it is likely that the community includes a number of small flagellates that are difficult, sometimes impossible, to identify in preserved samples.

As noted before, *Prochlorococcus marinus* is widely regarded as an oceanic phytoplankter that succeeds primarily under conditions of extreme oligotrophy (Partensky et al., 1999). Thus, we interpret its absence from our samples as reflective of its general exclusion from the Sea due to its presumed intolerance of eutrophic conditions. The relatively low concentration of phycoerythrin-containing unicells was unexpected since these organisms reach very high abundance in warm, nutrient-rich water. The value of 10^5 cells ml^{-1} observed at one of our Gulf of Mexico stations is representative of values found in the Gulf of California in upwelling-influenced areas (Wood et al., unpublished data). Our culture collection and evaluation of the field samples by epifluorescence microscopy revealed the presence of small unicellular cyanobacteria which utilize phycocyanin as the primary light harvesting pigment as well as phycoerythrin-containing unicells in the Salton Sea. In the open ocean, these organisms are selected against because the red wavelengths of light they require for photosynthesis are rapidly absorbed by seawater (Wood, 1985). In the Salton Sea, these organisms are not under any particular disadvantage when competing with phycoerythrin-dominant strains. Because the euphotic depth is always very shallow, the spectral composition of available light should be relatively unaffected by the differential absorption of red and blue light by water. Thus, it is possible that the total abundance of picocyanobacteria in the plankton of the Salton Sea may be comparable to that of marine waters, but that it is composed of a greater range of pigment types. Ideally, methods for routine application of flow cytometry to the analysis of samples from the Salton Sea will be modified from those used for analysis of marine samples to take the presence of phycocyanin-dominant picocyanobacteria into account.

The high numbers of bacteria and viral particles observed in the flow cytometry study suggest that there is a very dynamic microbial loop operating in the Sea. The concentration of Type I viruses, thought to represent bacteriophage and cyanophage combined (Marie et al., 1999), exceeds the highest abundance of total viral particles observed during a spring bloom period in a Norwegian estuary by about an order of magnitude and exceed peak abundance of strain-specific cyanophage occurring in Woods Hole Harbor by several orders of magnitude (Bratbak et al., 1990; Waterbury & Valois, 1993). These high numbers may explain the fact that viral abundance, while higher in the Sea than in coastal marine waters, is not proportional to the even higher bacterial abundance. It is possible that the complex host-phage dynamics involved with infection and growth of viral particles has a maximum upper limit that is partially determined by the overall diversity of hosts (Cottrell & Suttle, 1991; Waterbury & Valois, 1993; Suttle & Chan, 1994; Paul & Kellogg, 2000). It is also possible that the lifetime of viral particles is shorter than that of the hosts (Noble & Fuhrman, 1999) and, thus, turnover accounts for the apparently 'low' relative increase in viruses relative to bacteria when we compare the Salton Sea values with other marine ecoystems. Regardless, viruses clearly play a role in termination of algal blooms in other marine environments (Bratbak et al., 1993; Paul & Kellog, 2000) and have a significant influence on particle flux (Proctor & Fuhrman, 1990; Fuhrman & Noble, 1995; Proctor, 1997). Given the values for viral particles and hosts in the Sea, it is clear that study of the details of the microbial loop will be a fruitful area for further research on the Salton Sea ecosystem.

Overall, our impression is that the Salton Sea contains a very diverse cyanobacterial flora. As is typical for this group of organisms, a considerable amount of morphological similarity masks a tremendous amount of genetic diversity; sequence data from only eight strains of generally similar morphology spans nearly the entire genetic distance encompassed by the cy-

anobacterial 16S rRNA tree (Figs 2–4). Our study is the first molecular characterization of genetic diversity within the form-genus *Geitlerinema*, but other investigators have obtained similar results in other large cyanobacterial genera (Wilmotte et al., 1997; Wilmotte & Herdman, 2001, Nadeau et al., 2001). These data highlight the difficulty any investigator encounters when trying to identify nominal species groups of cyanobacteria in field samples. Of the eight strains included in our phylogenetic analysis, five would have been classified as species of *Oscillatoria* using the botanical system or *Geitlerinema* under the current bacterial system, but they fall into at least two, and possibly three major clades of cyanobacteria based on their 16S rRNA sequences (Figs 2–4). Most notably, three strains included in our phylogenetic study (CCMEE 5433, CCMEE 5438, and CCMEE 5403) were nearly identifical morphologically and would all key to *Oscillatoria amphibia* Ag. (Frémy, 1929) in the botanical tradition of cyanobacterial systematics; these strains fell into two widely divergent clades based on 16S rRNA sequence (Figs 2–4). In culture, these strains differed slightly in their apparent rate of motility but this would not be apparent if one were examining preserved material. Overall, we conclude that the conservative approach of using form-genera and description of morphological types in field material without assigning species names is preferred for description of community structure. Without genetic characterization, assignment of the same species names to organisms of similar morphology suggests a level of common ancestry that cannot be assumed for many cyanobacteria of the forms that are common in the Salton Sea.

The close genetic association of Strain CCMEE 5435 with the marine unicellular strains *Prochlorococcus* MIT9312, *Synechococcus* WH8101, WH7805, and WH8103 suggests that this strain is of oceanic origin. Other authors in this volume (see Lange & Tiffany, Rogerson & Hauer) have discussed the many ways in which marine organisms have been introduced to the Sea during its short lifespan so that the presence of truly marine strains in the plankton or benthic community would be expected. Continuous introduction of freshwater forms of cyanobacteria via migratory birds and inputs from the New River and Alamo River can also be expected. Combined with our success at culturing strains of cyanobacteria from the Salton Sea at a wide range of salinities, this suggests that cyanobacteria will be a major component of the autotrophic community under nearly any management scenario.

Most proposed management scenarios for the Salton Sea project reduction of salinity, but only to conditions more typical of the open ocean environments. However, the Sea differs dramatically from marine environments by having very high nutrient concentrations, frequent occurrence of low oxygen and high sulfide levels in the water column, and high concentrations of dissolved organic carbon (Watts et al., this volume). Taken together, these conditions suggest that cyanobacteria, particularly the forms in mat communities with the sulfur-utilizing *Beggiatoa* may play an important role in carbon fixation and biogeochemical processes in the Sea because of their tolerance of H_2S and low dissolved oxygen levels.

Many cyanobacteria produce toxins that are particularly lethal to mammals, birds, and fish. Among taxa we have identified in our study, there is overlap at the generic level with five known toxin producing species (*Lynbgya, Oscillatoria, Pseudanabaena, Synechococcus, Synechocystis*). Since cyanobacteria do not have to occur as blooms to produce toxic effects in mammals and birds, especially when cyanobacteria can be concentrated in mat material that may be ingested by herbivores, the possibility that cyanobacteria are involved in bird and fish kills needs further evaluation.

Acknowledgements

We want to thank the many people who contributed to this study, particularly Michael Waters and William Yeoung who spent many hours assisting in the isolation of the clonal cultures, to S. Garbush and L. Wingard for maintenance of the cultures, and to C. Everroad for assistance with graphics. We also thank Stuart Hurlbert for his continuous and enthusiastic encouragement and the SDSU Salton Sea research group, particularly Mary Ann Tiffany, B. Kuperman, Victoria Matey, and Joan Daimler for their assistance at the lake. Special thanks are offered to B.J. Wood and W.W. Wood for inspiration and encouragement and to C. Trees and K. Steidinger for introducing us to this fascinating ecosystem. Financial support was provided in part by the United States Environmental Protection Agency through grant #R86552-01-0 to the Salton Sea Authority, and from the Office of Naval Research through grant N0014-99-1-0177. The research results have not been subjected to the EPA's required peer review and therefore do not necessarily reflect the view of the Agency. Therefore no official endorsement should be inferred.

References

Azam, F., 1998. Microbial control of oceanic carbon flux: the plot thickens. Science 280: 694–696.

Boone, D. R., R. W. Castenholz & G. M. Garrity (eds), 2001. Bergey's Manual of Systematic Bacteriology, 2nd edn. Vol. 1. The Archaea and the Deeply Branching and Phototrophic Bacteria. Springer Verlag, NY (ISBN 0-387-98771-1).

Bratbak, G., M. Heldal, S. Norland & T. F. Thingstad, 1993. Viruses as partners in srping bloom microbial dynamics. Appl. Envir. Microbiol. 56: 1400–1405.

Carmichael, W. W., 1992. Cyanobacteria secondary metabolites – the cyanotoxins. J. appl. Bacteriol. 72: 445–459.

Carmichael, W. W., 1994. Toxins of cyanobacteria. Sci. am. 1992, 274: 64–70.

Carmichael, W. W., 1997. The cyanotoxins. Adv. Bot. Res. 27: 211–256.

Carpelan, L. H., 1961. Phytoplankton and plant productivity. In Walker, E. D. (ed.), The Ecology of the Salton Sea, in Relation to the Sportfishery. Fish Bul. 113, Calif. Dept. Fish and Game: 33–42.

Castenholz, R. W., 1988. Culturing methods for cyanobacteria. Methods Enzymol. 167: 68–93.

Castenholz, R. W., 2001. Phylum BX. Cyanobacteria, Oxygenic Photosynthetic Bacteria. In Castenholz, R. W. & D. Boone (eds), Bergey's Manual of Systematic Bacteriology, 2nd edn. Vol. III: 473–599.

Castenholz, R. W., B. B. Jørgensen, E. D. D'Amelio & J. Bauld, 1991. Photosynthetic and behavioral versatility of the cyanobacterium *Oscillatoria boryana* in a sulfide-rich microbial mat. FEMS Microbiol. Ecol. 86: 43–58.

Castenholz, R. W., R. Rippka, M. Herdman & A. Wilmotte, 2001. Subsection III. (Formerly Oscillatoriales Elenkin 1934). In Castenholz, R. W. & D. Boone (eds), Bergey's Manual of Systematic Bacteriology, 2nd edn. Vol. I: 539–562.

Cohen, Y., B. B. Jørgensen, N. P. Revsbech & R. Poplawski, 1986. Adaptation to hydrogen sulfide of oxygenic and anoxygenic photosynthesis among cyanobacteria. Appl. Envir. Microbiol. 51: 398–407.

Cottrell, M. T. & C. A. Suttle, 1991. Widespread occurrence and clonal variation in viruses which cause lysis of a cosmopolitan, eukaryotic, marine phytoplankter, *Micromonas pusilla*. Mar. Ecol. Prog. Ser. 78: 1–9.

Dow, C. S. & U. K. Swoboda, 2000. Cyanotoxins. In Whitton, B. A. & M. Potts (eds), The Ecology of Cyanobacteria: Their Diversity in Time and Space. Kluwer Academic Publishers, Dordrecht: 613–632.

Edmondson, W. T. & J. Lehman, 1981. The effect of changes in the nutrient income on the condition of Lake Washington. Limnol. Oceanogr. 26: 1–29.

Felsenstein, J., 1993. PHYLIP (Phylogeny Inference Package) version 3.5c., Distributed by the author. Dept. of Genetics, University of Washington, Seattle.

Frémy, P., 1929–1933. Cyanophycées des Côtes d'Europe. Mém. Soc. Nationale des Sciences Naturelles et Mathématiques de Cherbourg, Tome XLI (reprinted by A. Asher & Co. B.V., Amsterdam, 1972).

Frémy, P., 1930. Les Myxophycées de l'Afrique équatoriale francaise. Archives de Botanique, Tome III, Memoire No. 2.

Fuhrman, J. A., 1999. Marine viruses and their biogeochemical and ecological effects. Nature 399: 548.

Fuhrman, J. A. & R. T. Noble, 1995. Viruses and protists cause similar bacterial mortality in coastal waters: evaluation and field results. Mar. Biol. 66: 109–120.

Garcia–Pichel, F. & R. W. Castenholz, 1991. Characterization and biological implications of scytonemin, a cyanobacterial sheath pigment. J. Phycol. 27: 395–409.

Imperial Irrigation District, 1989. Environmental impact report for proposed water conservation program and initial water transfer. California State Clearinghouse #86012903.

Kimura, M., 1980. A simple method for estimating evolutionary rate of base substitution through comparative studies of nucleotide sequences. J. Mol. Evol. 16: 111–120.

Lange, C. B. & M. A. Tiffany, 2002. The diatom flora of the Salton Sea, California. Hydrobiologia 473/Dev. Hydrobiol. 161: 179–200.

Li, W. K. W., 1995. Composition of ultraphytoplankton in the North Atlantic. Mar. Ecol. Prog. Ser. 122: 1–8.

Li, W. K. W. & A. M. Wood, 1988. Vertical distribution of North Atlantic ultraphytoplankton: analysis by flow cytometry and epifluorescence microscopy. Deep-Sea Res. 35: 1615–1638.

Madigan, M. T., J. M. Martinko & J. Parker, 2000. Brock Biology of Microorganisms, 9th edn. Prentice Hall, Upper Saddle River, NJ.

Marie, D. E., C. P. D. Brussard, R. Thyrhaug, G. Bratbak & D. Vaulot, 1999. Enumeration of marine viruses in culture and natural samples by flow cytometry. Appl. Envir. Microbiol. 65: 45–52.

Miller, S. R. & R. W. Castenholz, 2000. Evoluiton of thermotolerance in hot spring cyanobacteria of the genus *Synechococcus*. Appl. Envir. Microbiol. 66: 4222–4229.

Miyashita, H., K. Adachi, N. Kurano, H. Ikemoto, M. Chihara & S. Miyachi, 1997. Pigment composition of a novel photosynthetic prokaryote containing chlorophyll *d* as the major chlorophyll. Plant Cell Physiol. 38: 274–281.

Nadeau, T.-L., E. C. Milbrandt & R. W. Castenholz, 2001. Evolutionary relationships of cultivated Antarctic oscillatorians (Cyanobacteria). J. Phycol. 37: 650–654.

Nübel, U., F. Garcia–Pichel & G. Muyzer, 2000. The halotolerance and phylogeny of cyanobacteria with tightly coiled trichomes (*Spirulina* spp. Turpin). Int. J. Syst. Evol. Microbiol. 50: 1265–1277.

Noble, R. T. & J. A. Fuhrman, 1999. Breakdown and microbial uptake of marine viruses and other lysis products. Aquat. Microl. Ecol. 20: 1–11.

Partensky, F., W. R. Hess & D. Vaulot, 1999. *Prochlorococcus*: a marine photosynthetic prokaryote of global significance. Micro. Mol. Biol. Rev. 63: 106–127.

Paul, J. H. & C. A. Kellogg, 2000. Ecology of bacteriophages in nature. Viral Ecol. 211–246.

Pitcher, D. G., N. A. Saunders & R. J. Owen, 1989. Rapid extraction of bacterial genomic DNA with guanidium thiocyanate. Lett. Appl. Microbiol. 8: 151–156.

Pomeroy, L. R., 1974. The ocean's food web: a changing paradigm. Bioscience 24: 499–504.

Proctor, L. M., 1997. Advances in the study of marine viruses. Microscop. Res. Tech. 37: 136–161.

Proctor, L. M. & J. A. Fuhrman, 1991. Roles of viral infection in organic particle flux. Mar. Ecol. Prog. Ser. 69: 133–142.

Rippka, R., J. B. Deruelles, J. B. Waterbury, M. Herdman & R. Y. Stanier, 1979. Generic assignments, strain histories and properties of pure cultures of cyanobacteria. J. gen. Microbiol. 111: 1–61.

Rogerson, A. & G. Hauer, 2002. Naked amoebae (Protozoa) of the Salton Sea, California. Hydrobiologia 473/Dev. Hydrobiol. 161: 161–177.

Suttle, C. A. & A. M. Chan, 1994. Dynamics and distribution of cyanophages and their effect on marine *Synechococcus*. Appl. Envir. Microbiol. 60: 3167–3174.

Thornton, J. A., 1982. Lake McIlwaine; the eutrophication and recovery of a tropical African man-made lake. Dr W. Junk. Publishers, The Hague: 251 pp.

Tostrud, M. B., 1997. The Salton Sea 1906–1996: computed and measured salinities and water levels. Colorado River Board of California, California.

Urbach, E., D. Robertson & S. W. Chisholm, 1992. Multiple evolutionary origins o prochlorophytes within the cyanobacterial radiation. Nature 355: 267–269.

USDI, 1970. Salton Sea, California: water quality and ecological management considerations. U.S. Dept. Interior, Federal Water Quality Administration, Pacific Southwest Region: 53 pp.

Walker, B., 1961. The ecology of the Salton Sea, California, in relation to the sportfishery. State of California, Dept. of Fish and Game, Fish Bulletin No. 113: 204 pp.

Waterbury, J. B. & F. W. Valois, 1993. Resistance to co-occurring phages enables marine *Synechococcus* communities to coexist with cyanophages abundant in seawater. Appl. Envir. Microbiol. 59: 3393–3399.

Watts, J. M., B. K. Swan, M. A. Tiffany & S. H. Hurlbert, 2001. Thermal, mixing, and oxygen regimes of the Salton Sea, California, 1997–1999. Hydrobiologia 466/Dev. Hydrobiol. 162: 159–176.

Wheeler, W. & D. Gladstein, 1994. MALIGN, 1.99 Ed.

Whitton, B. A. & M. Potts, 2000. Introduction to the Cyanobacteria. In Whitton, B. A. & M. Potts (eds), The Ecology of Cyanobacteria. Kluwer Academic Publishers, Dordrecht: 1–12.

Wilmotte, A., 1994. Molecular evolution and taxonomy of the cyanobacteria. In Bryant, D. A. (ed.), The Molecular Biology of the Cyanobacteria. Kluwer Academic Publishers, Dordrecht: 1–25.

Wilmotte, A. & M. Herdman, 2001. Phylogenetic relationships amongst the cyanobacteria based on 16S rRNA sequences. In Boone, D. R. et al. (eds), Bergey's Manual of Systematic Bacteriology, 2nd edn. Vol. I. The Archaea and the Deeply Branching and Phototrophic Bacteria. Springer-Verlag, NY.

Wilmotte, A., W. Stam & V. Demoulin, 1997. Taxonomic study of marine oscillatoriacean strains (Cyanophyceae, Cyanobacteria) with narrow trichomes. III. DNA–DNA hybridization studies and taxonomic conclusions. Algol. Stud. 87: 11–28.

Wood, A. M., 1985. Adaptation of the photosynthetic apparatus of marine ultraphytoplankton to natural light fields. Nature 316: 253–255.

Wood, A. M., P. K. Horan, K. Muirhead, D. A. Phinney, C. M. Yentsch & J. B. Waterbury, 1985. Discrimination between pigment types of marine *Synechococcus* spp. by scanning spectroscopy, epifluorescence microscopy, and flow cytometry. Limnol. Oceanogr. 30: 1303–1315.

Hydrobiologia **473:** 93–102, 2002.
D.A. Barnum, J.F. Elder, D. Stephens & M. Friend (eds), The Salton Sea.
© 2002 *Kluwer Academic Publishers. Printed in the Netherlands.*

Flagellate *Cryptobia branchialis* (Bodonida: Kinetoplastida), ectoparasite of tilapia from the Salton Sea

Boris I. Kuperman, Victoria E. Matey & Steven B. Barlow
Department of Biology and Center for Inland Waters, San Diego State University San Diego, CA 92182, U.S.A.

Key words: Salton Sea, *Oreochromis mossambicus*, ectoparasites, *Cryptobia branchialis*, ultrastructure, flagella, attachment, gills, infestation, pathogenicity

Abstract

An infestation of young tilapia, *Oreochromis mossambicus* Peters, by the flagellate *Cryptobia branchialis* was observed at the Salton Sea, California, in September, 1997. This is the first report of *C. branchialis* in a highly saline water-body (43 g l^{-1}). Ultrastructure of *C. branchialis* as well as its effect on the gills of tilapia were studied using the scanning and transmission electron microscopy. No direct effect of *C. branchialis* on the epithelial cells of fish gills was observed. However, alterations of gill general structure, such as deposition of copious mucus on the gill surface, swelling of filaments, reduction of respiratory lamellae and their transformation into short club-shaped structures were found in infected fish. This suggests mortality of young tilapia may arise from decreased gill function in response to *Cryptobia* infestation.

Introduction

Flagellates of the genus *Cryptobia* Leidy (Bodonidae: Kinetoplastida) are parasites of freshwater and marine fish around the world. The genus includes 52 nominal species (Woo & Poynton, 1995). Of these, 47 species are endoparasites that live in either the blood or the digestive tract, and five species are ectoparasites that attach to fish skin and especially gills. Ectoparasitic *Cryptobia* enter into the gill chamber via the mouth and attach to the gill epithelium. They have a direct life cycle and multiply by longitudinal fission. Newly -formed parasites detach from the gills and become free-living in water.

Among ectoparasitic *Cryptobia*, the most widely spread species is *Cryptobia branchialis* Nie (Chen, 1956). For decades, *C. branchialis* has been recorded in Europe, Asia, North America, and the Philippines as a parasite of cultured freshwater fish (Chen, 1956; Bauer et al., 1969; Lom, 1980; Natividad et al., 1986; Alvarez–Pellitero et al., 1993; Woo & Poynton, 1995; Plumb, 1997). The effect of this parasite on aquaculture is very harmful, and *C. branchialis* had been implicated in mortality of carp, goldfish and catfish in many parts of the world (Chen, 1956; Bauer et al., 1969; Naumova, 1969; Hoffman, 1978).

By the 1980s, it was known that cryptobiids tolerate a wide range of salinity and can infect not only freshwater but also marine fish. The first record on marine fish infestation by *Cryptobia* was from the Chesapeake Bay and its tributaries (salinity from 11 to 22 g l^{-1}), USA. Six species of marine and estuarine fish were found heavily infected by an ectoparasitic *Cryptobia* sp. morphologically very close *C. branchialis* (Burreson & Sypek, 1981). In 1989, *Cryptobia* sp. was found on the gills of sea bream, *Sparus aurata*, in full strength sea water in southern France (Blanc et al., 1989). Lastly, Diamant (1990) identified and described in detail a new species, *Cryptobia eilatica*, from two species of fish from the highly saline (39–41 g l^{-1}) Red Sea, Israel.

This report describes the heavy infestation of young tilapia, *Oreochromis mossambicus* Peters, by *C. branchialis* in the Salton Sea, an inland salt lake in Southern California. We documented the prevalence, intensity and foci of fish infestation as well as the ultrastructure of the parasite and its effect on fish gills.

Materials and methods

The Salton Sea

The Salton Sea (33° 25′ N, 115° 50′ W) is the largest lake in California with surface area of 980 km^2 and a 153 km shoreline. Its location and form, as well as sampling locations are shown in a number of maps (Kuperman & Matey, 1999; Watts et al., 2001). Current salinity of the Salton Sea is 43 g l^{-1}, and shallow water temperature fluctuates from 12.5 °C in winter to 40 °C in summer. Oxygen tension varies spatially and temporally from 0 to >20 mg l^{-1} (Watts et al., 2001).

Sampling and preparation

Eighty specimens of young tilapia *Oreochromis mossambicus* Peters, the dominant fish species in the Salton Sea, were collected on 17 September, 1997, at Bombay Beach (33° 20′ 50.6″ N, 115° 43′ 59.8″ E) from a school of fish swimming in the shallows along the shoreline. That day, water temperature at 20–30 cm depth at the shoreline was 30 °C. Fish were caught with dip nets and transported to a field laboratory on the lakeshore. Size range of fish was measured to the nearest millimeter. Body length of 65 fish was 1.0–1.2 cm, and 2.5–4 cm for 15 fish.

After measuring the fish, we examined their bodies, gills and fins under dissecting and compound microscopes for the presence of ectoparasites. Prevalence and intensity of fish infestation by *C. branchialis* were determined in fresh unfixed samples. Prevalence of infestation was defined as percentage of fish infected, and intensity was defined as a number of parasites per fish and was recorded as high (+++, thousands of parasites per fish), medium (++, hundreds of parasites per fish), and low (+, dozens of parasites). Gills of 20 fish infected by *C. branchialis* were selected for studies by electron microscopy (SEM and TEM) and light microscopy (LM).

For comparison, during September, 1997, from fish collected in Varner Harbor we selected 20 specimens of young tilapia (1.0–4.0 cm) that were not infected by any ectoparasites. Their gills were also examined by SEM.

Electron microscopy and light microscopy

Gill arches of fish infected and not infected by *C. branchialis* were quickly dissected from gill chambers on both sides of the head, fixed in cold Karnovsky fixative for 2 h, postfixed in 1% osmium tetraoxide for 1 h, and dehydrated using a graded ethanol with the final change in absolute ethanol. After that, specimens for LM and TEM studies were embedded in Epon resin blocks. Semithin sections (1 μm) were stained with 0.5% methylene blue and azure II, then examined with a Nikon Microphot microscope. Ultrathin sections were double stained with uranyl acetate and lead citrate, and examined in a Philips 410 transmission electron microscope.

Mean dimensions of 50 specimens of fixed parasites on the ultrathin sections of infected gills were measured with an ocular micrometer.

Samples for SEM studies were fixed as above, critical- point-dried with liquid CO_2, mounted on the stubs, sputter-coated with gold-palladium, and examined with a Hitachi S-2700 scanning electron microscope at an accelerating voltage of 10 kV.

Results

Examination of young tilapia collected at Bombay Beach in September 1997, showed heavy infestation of fish gills by *Cryptobia.* General morphology and ultrastructure of this organism allowed us to identify it as *Cryptobia branchialis.*

General morphology and ultrastructure of C. branchialis *from the Salton Sea*

C. branchialis found on tilapia gills is a pear-shaped or elongated unicellular organism, rounded at the anterior end and tapered posteriorly (Figs 1A, B and 2A). Mean body length of fixed parasites is 10.5 μm (range 7.5–11.6 μm), and mean width is 4.1 μm (range 2.8–4.6 μm). Two flagella of *C. branchialis* arise from 2 kinetosomes lying on the bottom of the flagellar pocket (Figs 1C and 2A, 2D). These flagella have different lengths and positions. The short anterior flagellum, length 8.7 μm (range 6.1–10.2 μm) is curved, directed freely out from the cell, and bears fine filaments (Fig. 1B, C). The long recurrent flagellum, 19.5 μm (range 13.8–28.2 μm) extends posteriorly and ends as a free flagellum that attaches the parasite to the gill epithelium (Figs 1B–D and 2A, 2C, D).

There are two modes of attachment of *C. branchialis* to fish gill epithelium. In the most common case, the membrane of the free portion of the recurrent flagellum is expanded (Fig. 2A, C) and forms a ledged ridge, in close contact to the host cell membrane (Fig. 3A, B). It provides multiple interfaces with

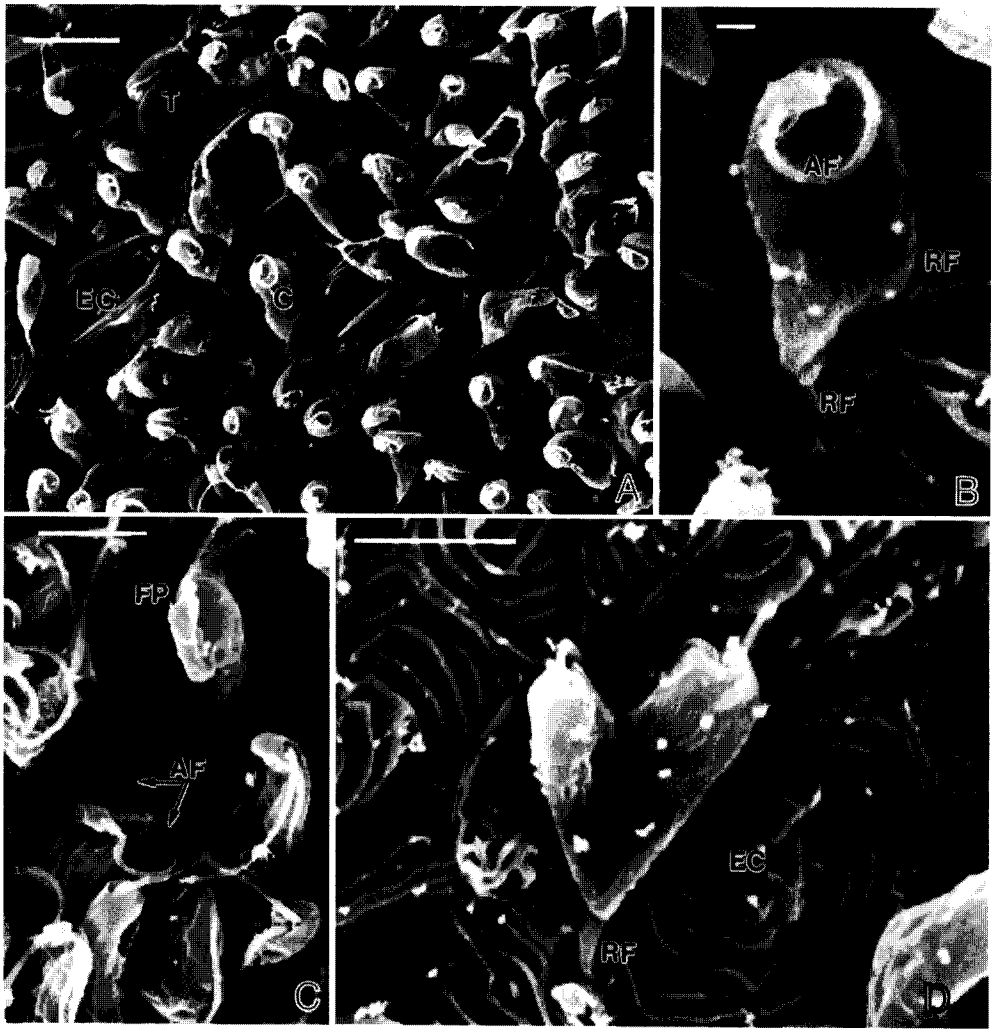


Figure 1. Cryptobia branchialis on the gills of tilapia, SEM. (A) Numerous *C. branchialis* on the gill filaments; (B) General view of *C. branchialis* attached to epithelial cell; (C) group of *C. branchialis* – note anterior flagella with fine fibrills (arrow); (D) Longitudinal fission of *C. branchialis.* AF – anterior flagellum, C – cryptobia, EC – epithelial cell of fish gills, FP – flagellar pocket, RF – recurrent flagellum, T – trophont of *Amyloodinium ocellatum.* Scale bars: A= 10 μm, B= 1 μm, C & D= 5 μm.

the host's cell along most of the free recurrent flagellum. In a second case, only the tip of the recurrent flagellum contacts the host's epithelial cell (Figs 2D and 3D). In both modes, the flagellum does not pierce the membrane of the epithelial cell but is positioned into an intercellular invagination like a sword in its sheath. These attachment sites are usually located above intracellular junctions between adjacent cells of gill epithelium (Figs 2A, D and 3A–C). Electron dense structures that resemble gap junctions are found at the points of interaction between membranes of the recurrent flagellum and gill epithelial cells (Fig. 2C).

As is typical for these flagellates, *C. branchialis* is surrounded by a membrane covered with fuzzy coat and strengthened by sub-pellicular microtubules (Fig. 2B). A round cytostome and a contractile vacuole are placed in the anterior part of the cell near the flagellar pocket (Fig. 2D). A spherical or oval nucleus with large endosome and patches of peripheral chromatin is located in the posterior part of the cell (Fig. 2A, B, D). A single mitochondrion extends through the cell but does not encompass the nucleus (Fig. 2C). The mitochondrion consists of a prominent elongated kinetoplast (mean size 3.2×1.6 μm) that is composed of a net of fine microfibrils (Fig. 2B). The kineto-

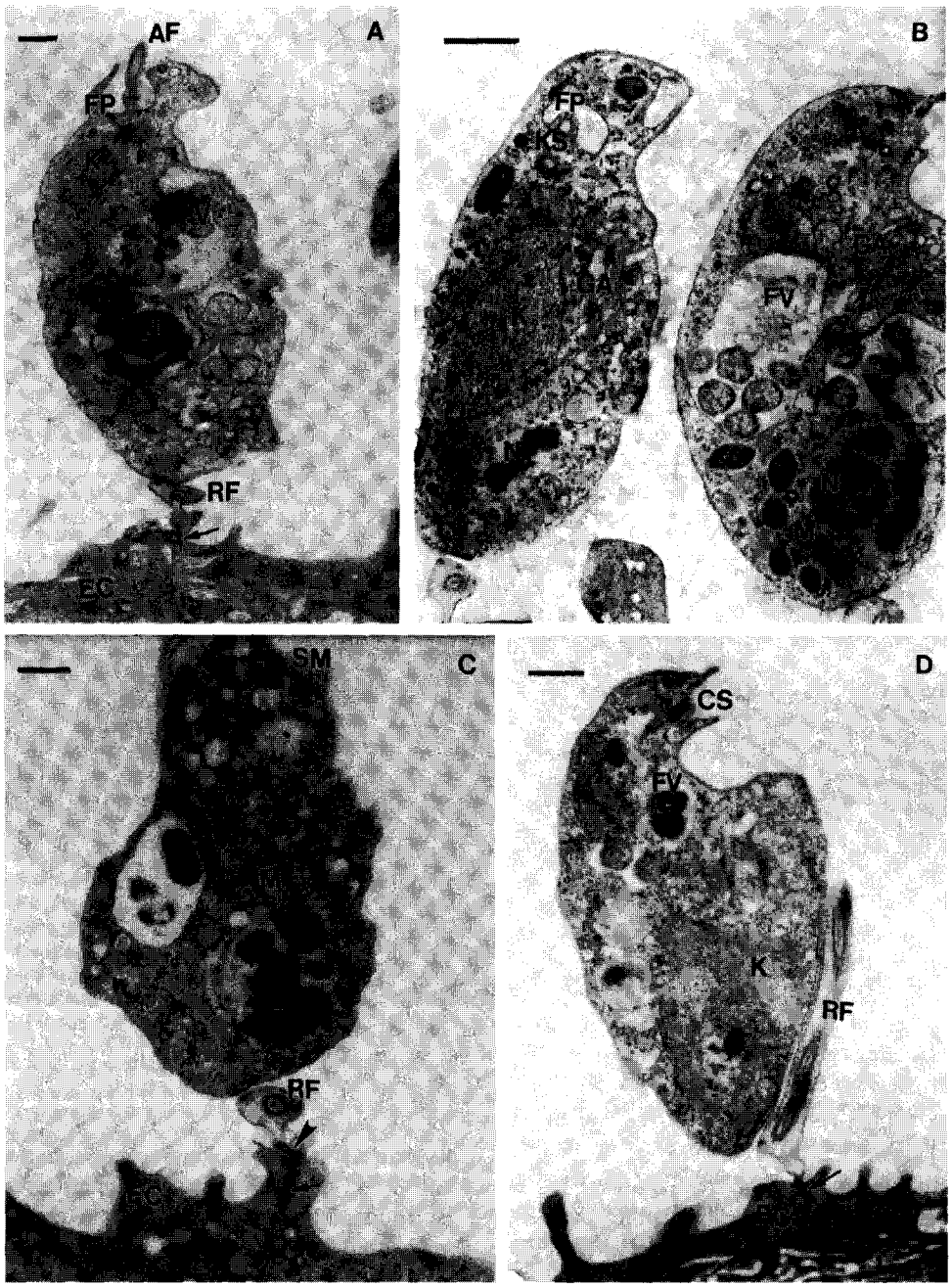


Figure 2. Ultrastructure of *C. branchialis*, TEM. (A) general view; (B–D) sections showing details of the ultrastructure. FV – food vacuoles, GA – Golgi apparatus, K – kinetoplast, KS – kinetosome, M – mitochondrion, N – nucleus, SM – subpellicular microtubules. Arrow – intercellular junctions between adjacent cells of fish gill epithelium, arrowhead – gap junction between recurrent flagellum and host's cell membrane. Scale bars: A–C = 1 μm.

plast is always located close to the kinetosome but does not show any connections with it (Fig. 2B). A well - developed Golgi apparatus is also situated near the kinetoplast (Fig. 2B). Numerous food vacuoles filled with electron-dense degraded content or ingested bacteria are distributed randomly throughout the cytoplasm (Fig. 2A – D).

Figure 3. Modes of attachment of recurrent flagellum to cell membrane of gill epithelium. (A, B) ledged ridge of recurrent flagellum adhered to epithelial cell; (C) contact with a tip of recurrent flagellum. Arrow – intercellular junction between gill epithelial cells. Scale bars: A–C = 0.2 μm.

C. branchialis reproduces by binary fission , and numerous dividing organisms may be found on the gill surface of infected tilapia (Fig. 1D).

Prevalence, intensity and foci of infestation

Young tilapia that was collected at Bombay Beach demonstrated 100% prevalence and high intensity of infestation by *C. branchialis.* Flagellates were found only on the fish gills. Thousands of *C. branchialis* have carpeted gill filaments and respiratory lamellae (Figs 4A, B and 6B). Numerous parasites were located between respiratory lamellae, covered gill arches and concentrated between gill rakers (Figs 4 A, C and 5A, B). As parasites can be easily detached from the cells of host's epithelial tissues, the real extent of infestation may be determined only on the fresh wet samples.

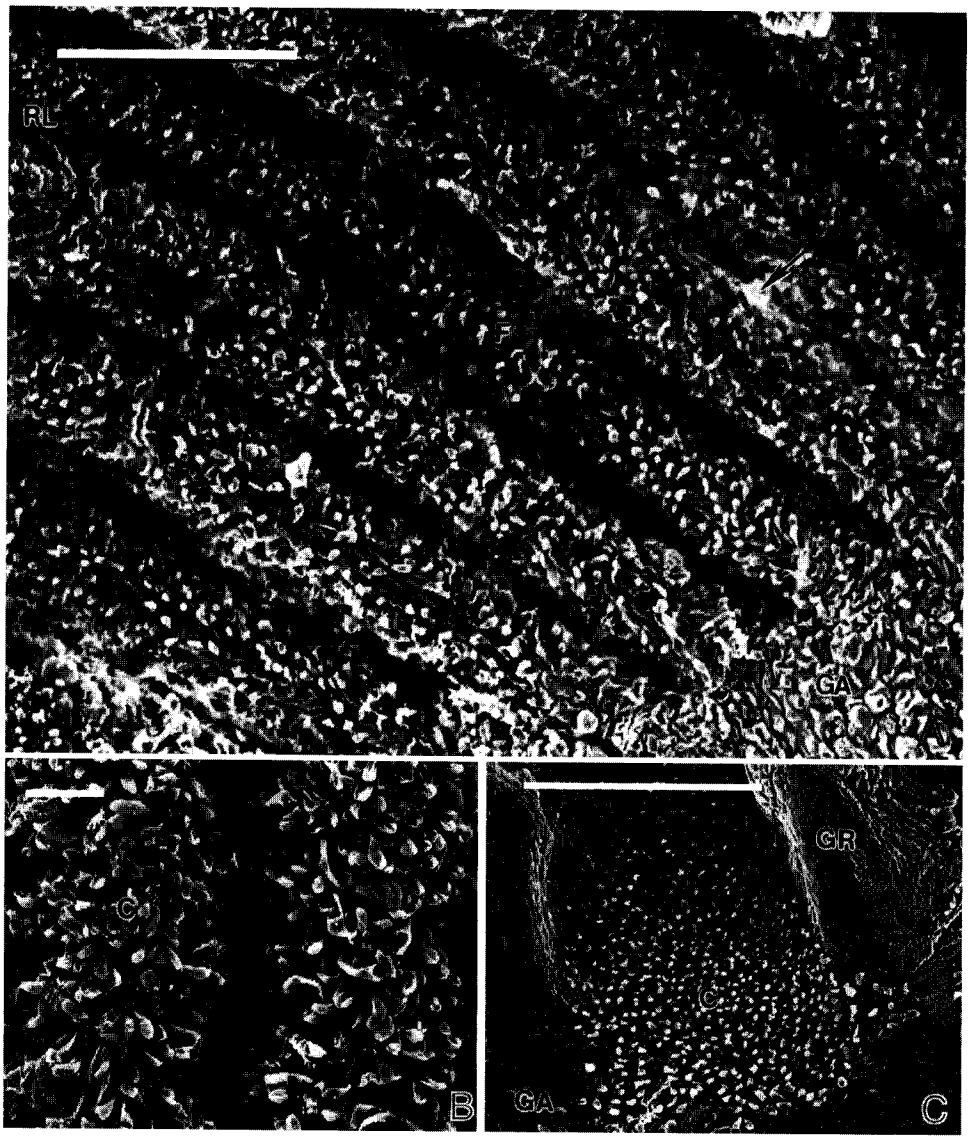


Figure 4. Distribution of *C. branchialis* on fish gill surface, SEM. (A) Gill filaments with parasites and copious mucus deposition (arrow), (B) median part of filaments carpeted with parasites, (C) parasites between gill rakers. (F) gill filament, GA – gill arch, GR – gill raker, RL – respiratory lamella. Scale bars: A, C= 100 μm, B= 20 μm.

Single trophonts of the dinoflagellate, *Amyloodinium ocellatum,* were rarely found amongst cryptobia on the gill filaments (Fig. 1A).

Pathogenicity

Gills of tilapia infected by *C. branchialis* were abnormally red and covered with a thick film of mucus. Both SEM and LM studies demonstrated dramatic changes of the general structure of the gills of these fish.

Gills of young tilapia that were not infected by *C. branchialis* exhibit strait and slim filaments bearing well developed respiratory lamellae separated by wide interlamellar spaces (Fig. 6A). In infected fish, both gills filaments and lamellae were very swollen (Fig. 6B). The latter become partially reduced and transformed into short club-like structures separated by very narrow interlamellar spaces filled with mucus. In especially heavily infected fish, gill filaments completely loose their wing-like structure and appear as thick rods tightly covered with cryptobia (Fig. 4A).

Figure 5. Fish gills infected by *C. branchialis*, LM. Ca – capillary, E – erythrocyte, FE – epithelium of filament, RE – respiratory epithelium. Scale bar= 10 μm.

Light microscopy shows that cells of gill epithelium are hypertrophied especially in respiratory lamellae (Fig. 5A–B). Enlargement of epithelial tissues is combined with expansion of blood vessels stuffed with erythrocytes.

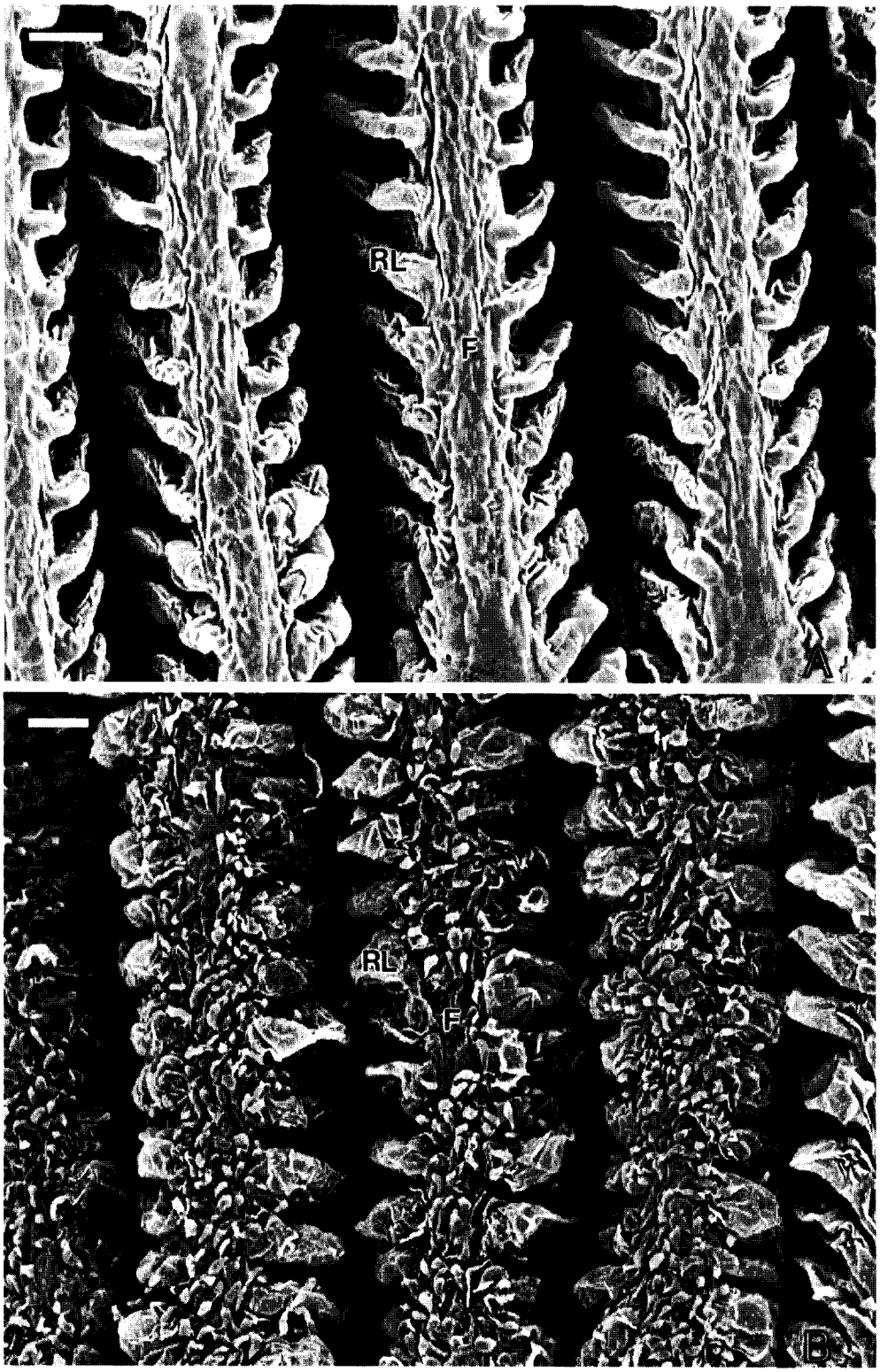


Figure 6. Structure of gills of young tilapia uninfected (A) and infected (B) by *C. branchialis* (A) slim filaments bearing thin lamellae separated with wide interlamellar spaces, (B) swollen filaments with short and thick respiratory lamellae separated with narrow interlamellar spaces. RL – respiratory lamellae. Scale bar: A & B= 20 μm.

On the other hand, we found no direct damage of fish gill epithelium at the points of recurrent flagellum contact with the cell membrane of the host. SEM studies did not show irritation, lesions or other types of disturbances of fish epithelial tissues. No special structures such as fibrils or vesicles were found in the cytoplasm of epithelial cells at the site of the attachment of *C. branchialis*.

Discussion

For the first time, fish from the Salton Sea were found highly infected by ectoparasitic *Cryptobia*. Parasites were smaller than previously reported cryptobiids, which ranged in size in fixed specimens from 10.7 to 22 μm (body length), and from 2.2 to 6.2 μm (body width) (Bauer et al., 1969; Lom, 1980; Diamant, 1990; Woo & Poynton, 1995). Because of the presence of a prominent kinetoplast, large mitochondrion, round cytostome and contractile vacuole, they have a great morphologic similarity with *C. branchialis* (Lom, 1980) and *Cryptobia* sp. (Burreson & Sypek, 1981), and differ from *C. eilatica* (Diamant, 1990). Based on general morphology and ultrastructure, we identified this flagellate as *C. branchialis*.

Cryptobia sp. from the Chesapeake Bay and *C. eilatica* from the Red Sea demonstrate strong resistance to high salinity, 22 g l^{-1} and 41 g l^{-1}, correspondingly (Burreson & Sypek, 1981; Diamant, 1990). However, *C. branchialis* that live and reproduce in the Salton Sea, currently 43 g l^{-1}, which is 10% saltier than the Red Sea, appears to be a more halotolerant species than even *C. eilatica* (Diamant, 1990). *C. branchialis* from the Salton Sea is also surprisingly resistant to high water temperature. Untill now, 25 °C was considered as the upper thermal limitation for *Cryptobia* spp. (Burreson & Sypek, 1981; Diamant, 1990). However, fish infected by *C. branchialis* were collected when the water temperature at the Sea was 30 °C. High temperature may induce rapid growth and reproduction of *C. branchialis* and massive infestation of fish gills. The extremely high level of parasitaemia found in tilapia from the Salton Sea is unusual for wild fish but common in aquaculture (Bauer et al., 1969; Hoffman, 1978).

We note that *C. branchialis* at the Salton Sea infect young tilapia fry. In aquaculture, fry are known to be more susceptible to *C. branchialis* than are adults (Chen, 1956; Bauer et al., 1969). An outbreak of infestation by *Cryptobia* spp. may kill all the young fish in a pond in a few days, but the disease has a lesser impact on older fish, which usually recover.

The pathogenicity of *Cryptobia* spp. for fish is debatable. Old studies based on light microscopy showed strong harmful effects of cryptobiids on fish gills (Chen, 1956; Bauer et al., 1969; Naumova, 1969; Hoffman, 1978). These include overproduction of mucus, destruction of gill epithelium, and formation of thrombi followed by death (Chen, 1956). In more recent electron microscopic studies focused on the direct interaction between flagellates and gill epithelium, no ultrastructural alterations were found at sites of *Cryptobia* attachment to epithelial cells (Lom, 1980; Diamant, 1990). It was concluded that *Cryptobia* is a harmless ectocommensal that could not affect fish gills. Mortality events registered in aquaculture during outbreaks of infestation by *Cryptobia* spp. were considered as being caused by other undetected pathogens. These data appear contradictory only at first glance. From our data it may be seen that the absence of damage on the ultrastructural level does not mean that general gill structure is normal. Gills of young tilapia infected by *C. branchialis* with no visible alterations of epithelial cells showed reduced lamellae and swollen filaments, and a thick film of mucus covering both structures. Such types of gill abnormalities were not found in tilapia uninfected by cryptobia in other sites of the Salton Sea (Varner Harbor, Red Hill, and Salton City) at the same months. Different alterations were developed in tilapia fry from the Salton Sea infected by other parasitic protozoans, such as *Amyloodinium ocellatum* and *Ambiphrya ameiuri* (Kuperman & Matey, 1999, Kuperman et al., 2001).

What we have concluded is that *C. branchialis* is an ectoparasite affecting fish gills. Significant reduction of respiratory lamellae, hypertrophy of respiratory epithelium, and deposition of copious mucus on the gill surface caused by *C. branchialis* may depress oxygen consumption. On the other hand, respiratory failure may be reinforced by low oxygen tension registered at the Salton Sea during summer–early autumn months (Carpelan, 1961; Watts et al., 2001).

Whether *C. branchialis* affect gills by releasing some chemical factors or by other mechanisms is be a good topic for future investigations.

Acknowledgements

Our sincere thanks to Dr V. D. Kalinnikova (Moscow State University, Russia) for useful discussion and

consultations. We are grateful to our colleagues M.A. Tiffany and J. Watts for their invaluable help in the field, and J. Dainer for her skilled assistance with computer wrestling and figure preparations. We gratefully acknowledge Dr S. Hurlbert for his permanent attention to our work, good advice and useful comments on the manuscripts. We are especially thankful to Dr Lois Tiffany and the Salton Sea Research Management Committee and Salton Sea Science Subcommittee for financial support.

References

Alvarez-Pellitero, P., A. Sitja-Bobadilla & A. Franco–Sierra, 1993. Protozoan parasites of wild and cultured sea bass, *Dicentrarchus labrax* (L.), from the Mediterranean area. Aquacult. Fish. Manage 24: 101–108.

Bauer, O. N., V. A. Musselius & Y. A. Strelkov, 1969. Diseases of pond fishes. Izdatelstvo Kolos, Moscow. Israel Program for Scientific Translations, Jerusalem, 1973.

Blanc, E., A. Marques, G. Bouix, G. Brugerolle & G. Breuil, 1989. *Cryptobia* sp. from the gills of the gilt head sea bream *Spagus aurata*. Bull. Europ. Assoc. Fish Pathol. 9: 81–82.

Burreson, E. M. & J. R. Sypek, 1981. *Cryptobia* sp. (Mastigophora: Kinetoplastida) from the gills of marine fishes in the Chesapeake Bay. J. Fish Dis. 4: 519–522.

Chen, C. L., 1956. The protozoan parasites from four species of Chinese pond fishes: *Ctenopharyngodon idellus, Mylopharyngodon picteus, Aristhichthys nobilis* and *Hypophthalmichthys molithrix*. Acta hydrobiol. sinica 1: 19–42.

Diamant, A., 1990. Morphology and ultrastructure of *Cryptobia eilatica* n. sp. (Bodonidae: Kinetoplastida), an ectoparasite from the gills of marine fish. J. Protozool. 37: 482–489.

Hoffman, G. L., 1978. *Bodomonas concava,* a cryptoc cryptogram for crippling *Cryptobia branchialis*. Am. Fish. Soc., Fish Health Sect. Newsletter, 6: 9.

Kuperman, B. I. & V. E. Matey, 1999. Massive infestation by *Amyloodinium ocellatum* (Dinoflagellida) of fish in a highly saline lake, Salton Sea, California, U.S.A. Dis. aquat. Org. 39: 65–73.

Kuperman, B. I., V. E. Matey & S. H. Hurlbert, 2001. Parasites of fish from the Salton Sea, California, U.S.A. Hydrobiologia 466: 195–208.

Lom, J., 1980. *Cryptobia branchialis* Nie from fish gills: ultrastructural evidence of ectocommensal function. J. Fish Disease 3: 427–436.

Naumova, A. M., 1969. Parasitism of *Cryptobia branchialis* on carp. Rybovodstvo i bolezni ryb.: Kolos, Moscow: 253–254 (in Russian).

Natividad, J. M., M. G. Bondad-Reantaso & J. R. Arthur, 1986. Parasites of Nile tilapia (*Oreochromis niloticus*) in the Philippines. In Maclean J. L., L. B. Dizon & L. V. Hosilos (eds), The First Asian Fisheries Forum. Asian Fisheries Society, Manila, Philippines: 255–259.

Plumb, J. A., 1997. Infectious diseases of tilapia. In Costa-Pierse B. A. & J. E. Rakocy (eds), Tilapia aquaculture in the Americas, vol. 1. World Aquaculture Society, Baton Rouge, Louisiana, United States: 212–228.

Watts, J. M., B. K. Swan, M. A. Tiffany & S. H. Hurlbert, 2001. Thermal, mixing and oxygen regimes of the Salton Sea, California, 1997–1999. Hydrobiologia 466/Dev. Hydrobiol. 162: 159–176.

Woo, P. T. K. & S. L. Poynton, 1995. Diplomonadida, Kinetoplastida and Amoebida (Phylum Sarcomastigophora). In Woo, P. T. K. (ed.), Fish Diseases and Disorders, Vol.1. Protozoan and Metazoan Infections. CAB International, Oxon, UK: 27–96.

Hydrobiologia **473:** 103–120, 2002.
D.A. Barnum, J.F. Elder, D. Stephens & M. Friend (eds), The Salton Sea.
© 2002 *Kluwer Academic Publishers. Printed in the Netherlands.*

Metazooplankton dynamics in the Salton Sea, California, 1997–1999

Mary A. Tiffany, Brandon K. Swan, James M. Watts & Stuart H. Hurlbert
Department of Biology and Center for Inland Waters, San Diego State University, San Diego, CA 92182, U.S.A.

Key words: zooplankton, *Balanus amphitrite*, *Neanthes succinea*, *Apocyclops dengizicus*, *Brachionus rotundiformis*, *Synchaeta* spp., tilapia, *Oreochromis mossambicus*, saline lakes, polymixis, sulfide, anoxia

Abstract

The dynamics of metazooplankton populations were studied over 3 years at the saline (43 g l^{-1}) Salton Sea, California's largest lake. Total abundance was highest in summer following late winter/early spring phytoplankton blooms. At this time, metazooplankton consisted mostly of the copepod, *Apocyclops dengizicus*, and the rotifer, *Brachionus rotundiformis*. In August or September, severe crashes in the metazooplankton populations occurred each year in mid-lake due to strong wind events which increased mixing and caused low oxygen and high sulfide concentrations throughout the water column. Larvae of the polychaete worm, *Neanthes succinea* and the barnacle, *Balanus amphitrite* were present mostly in late winter and spring. Their scarcity in summer is due in part to persistent anoxic bottom conditions that decrease adult populations and in part to predation by tilapia, an omnivorous fish that has become abundant in the lake since the 1960s. Two *Synchaeta* species, rotifers not previously reported from the Sea, were abundant in winter and spring and predation on these may have permitted the copepod to persist at low levels through the winter. There were two major changes in metazooplankton dynamics since 1954–1956 in addition to the appearance of the two synchaetid rotifers in the fauna. First, there are now much lower densities of barnacle and polychaete larvae in the fall, probably due to the invasion of the zooplanktivorous fish, tilapia. Second the precipitous crashes now seen in metazooplankton densities, especially the copepod, in late summer-early fall did not occur in the 1950s possibly because fall overturn events did not result in such high sulfide levels.

Introduction

The Salton Sea is a unique ecosystem, partly due to its history of marine fish and invertebrate introductions made for the purpose of establishing a sport fishery, and partly due to its unusual conditions of temperature range, nutrient loading, elevated salinity and polymixis. It is likely the Sea supported freshwater zooplankters in the earliest years of its existence. These would have been introduced with the Colorado River water that formed the original freshwater lake in 1905–1907. As the Salton Sea became more saline, many of these would not have survived. By the 1950s, the salinity of the Salton Sea was similar to that of the ocean, but with a different ionic composition. Calcium and sulfate were proportionately higher in the Salton Sea, chloride lower and sodium about the same as the ocean (Carpelan, 1961a).

The level of the Salton Sea is maintained by agricultural and municipal wastewaters which cause massive, more or less continuous algal blooms due to high nutrient input (Carpelan, 1961b; Bain et al., 1970; Reifel et al., 2002; M. Tiffany, unpublished data). The same waters bring salts to this closed basin lake which has caused an increase in salinity over the decades since its formation. Presently the salinity is about 43 g l^{-1}.

In 1954–1956, four species dominated the metazooplankton (Carpelan, 1961c). At that time, the salinity was approximately that of seawater. Maximum abundance of metazooplankton occurred in summer when one rotifer (*Brachionus plicatilis* Müller) and one copepod (*Cyclops dimorphus* Keifer) dominated, and lowest abundance was in midwinter. *B. plicatilis* was the most numerous zooplankter, though found almost exclusively in the summer months. Fu et al. (1991a, b) determined from morphological and genetic characters that a strain of *Brachionus* derived in 1978 from the Salton Sea (their clone 'a-sal') was the S-type, or small type, which is now considered to be *B. ro-*

tundiformis Tschugunoff (Segers, 1995). Carpelan did not mention any other rotifer species as being present in the Salton Sea. Hart et al. (1998) and Simpson et al. (1998) found two *Synchaeta* species, a *Colurella* species, and two unidentified rotifers in experimental microcosms established with Salton Sea water, the only other reports of rotifers from this system.

In 1954–1956, the copepod was most abundant from June to November or December and was undetected from January to May (Carpelan, 1961c). Carpelan stated that although some copepods were consumed by young fish, most of them died and simply added to the detritus of the sediments. Dexter (1993) later determined this copepod to be *Apocyclops dengizicus* Lepeschkin, which has been redescribed by Mirabdullayev & Stuge (1998). She observed it to be present in nearshore waters year round, although with lower densities in the winter. Her experiments demonstrated that reproduction in this species is impaired above 57 g l^{-1}.

The barnacle, *Balanus amphitrite* Darwin, was probably introduced to the Salton Sea in the 1940s by seaplanes or boats transported from the Pacific Ocean (Carpelan, 1961c). These barnacles occur on hard substrates around the periphery of the lake. Their empty calcareous shells, along with many fish bones, form many of the beaches of the lake. The immature barnacle has two planktonic forms, the nauplius larva followed in development by the cyprid larva. Carpelan (1961c) found that the barnacle larvae had two peaks of abundance, in spring and fall, with low densities in mid summer and mid winter. In all seasons, densities of barnacle larvae were higher at his nearshore station (100 m from shore) compared to his offshore station (ca. 3.8 km from shore), reflecting proximity to sessile adult populations along the shore. The abundance of the barnacle may begin to decline if and when the salinity reaches ~50 g l^{-1} due to weakening of its shells or decreased growth rates (Simpson & Hurlbert, 1998).

The polychaete, *Neanthes succinea* Frey & Leukart, was deliberately introduced to the Salton Sea by the California Department of Fish and Game in the 1930s to provide food for sport fish. This species is one of the most important members of the ecosystem, fed upon as adults by both birds and fish (Walker, 1961; Detwiler et al., 2002). *N.succinea* adults become reproductive when they change into a form called the heteronereid. Eggs turn into small, setigerous two-segmented larvae within ~36 h (Carpelan, 1961c). Larvae are planktonic until they reach the 9–12 segment stage when they begin to settle to the sediments to start a benthic existence. It has been suggested that the polychaete will not be able to reproduce in the Salton Sea once salinities exceed ~50 g l^{-1} (Hanson, 1972; Kuhl & Olgesby, 1979). Scanning electron microscope images of the rotifer *B. rotundiformis*, copepod, barnacle larvae, and adult and larval polychaetes are presented in Kuperman et al. (2002).

Zooplankton was studied during a 15 month microcosm experiment using Salton Sea organisms and water designed to assess the effects of salinity (30–65 g l^{-1}) and of a planktivorous fish, tilapia (*Oreochromis mossambicus* Peters), on the ecosystem (Simpson et al., 1998; Simpson & Hurlbert, 1998; Hart et al., 1998; González et al., 1998). Ciliates, brine shrimp (*Artemia franciscana* Kellog) and an amphipod (*Gammarus mucronatus* Say) dominated the water column at most salinities. Predation by *A. dengizicus* was thought to reduce populations of the rotifer *B. plicatilis* (probably actually *B. rotundiformis*) through predation. Two *Synchaeta* species were present early in the experiment. Fish dramatically decreased the abundance of the larger invertebrates. Ciliates, in both number and biovolume, comprised a large proportion of the zooplankton at all salinities.

Ciliate and amoeba faunas in the lake are very diverse (Small et al., 2002; Rogerson & Hauer, 2002). The abundant planktonic forms likely play a large role in linking microbes to larger members of the food web (Pierce & Turner, 1992; Rogerson & Hauer, 2002).

The present investigation was undertaken as the lake has experienced many recent fish kills and bird die-offs, salinity is increasing, and engineering projects to restore the Sea are under consideration. Since Carpelan's (1958, 1961a) study in 1954–1956 the salinity has risen from about 33 g l^{-1} to the present 43 g l^{-1}. Also the planktivorous, euryhaline fish, tilapia, has become very abundant in the Salton Sea since its introduction in the 1960s (Black, 1988; Costa-Pierce & Riedel, 2000; Riedel et al., 2002) and is likely to have had major effects on the plankton. The purpose of the present study was to determine the current composition and dynamics of the zooplankton of the Salton Sea and their environmental relations. This paper reports results for the metazoan zooplankters. Results for the protozoan zooplankters, which were sampled and counted with phytoplankton methodology, will be presented in a later report.

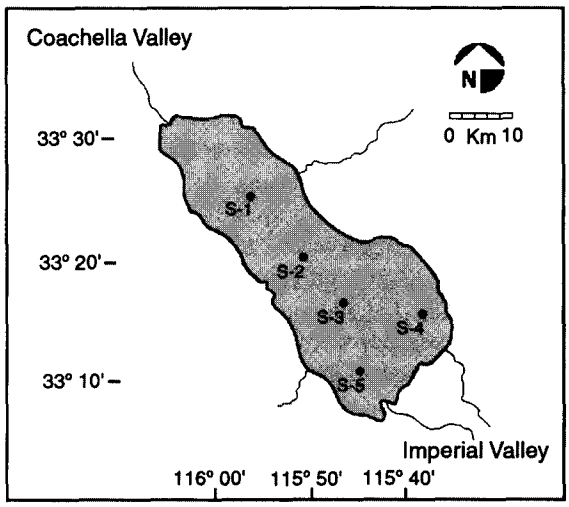


Figure 1. Map of the Salton Sea, showing location of zooplankton stations.

Materials and methods

Field sampling procedures

Zooplankton samples were taken at five mid-lake stations (see Watts et al., 2001 for the exact dates each station was sampled) at variable times mid-day (Fig. 1). Three stations (S-1, S-2, and S-3) along the mid-axis of the lake were sampled at 2–5 week intervals from January 1997 to January 2000. These three stations were chosen to represent the main water mass of the Sea. There are two main basins in the Salton Sea one in the north and one in the south with a slight lake bottom rise in between (Ferrari & Weghorst, 1997). These affect circulation patterns and currents. Station S-1 was in the center of the northern basin, S-3 at the northern edge of the southern basin and S-2 midway between. In 1997–1998, only one or two stations were sampled on some dates as a result of logistical problems or strong winds. In January 1999, two additional, shallower stations (S-4 and S-5) at the southern end of the lake were added to provide more information on spatial variation and in particular the influence of freshwater inflows. In 1999, all five stations were sampled on every sampling date.

At each station, one or two samples were taken at each depth with a 32-l Schindler trap equipped with a 55 μm mesh net, at 2 m intervals from lake surface, starting at 0.5 m, to near lake bottom (12.5 m at S-1, 10.5 m at S-2 and S-3, and 6.5 m at S-4 and S-5). In 1997–1998, station S-1 was sampled to a depth of 10.5 m only. Samples were placed in vials and preserved in 5% formaldehyde. For each sampling site and date, temperature and dissolved oxygen were measured, Secchi disk readings made, and samples taken for analysis of phytoplankton and nutrients.

Table 1. Estimated biovolumes for individual metazooplankters

Taxon and stage	Volume (10^3 μm^3)
Brachionus rotundiformis	1130
Synchaeta aff. *vorax*	219
Synchaeta sp.	835
Balanus amphitrite nauplii	13 100
*Balanus amphitrite*cyprids	19.6
Apocyclops dengizicus copepodids	8630
Apocyclops dengizicus nauplii	902
Neanthes succinea larvae	47 600

Plankton enumeration

In the laboratory, zooplankton samples were counted with standard procedures, using a compound microscope at 40× (or at 100× for extremely abundant taxa) and a modified, 40 mm × 50 mm Sedgwick–Rafter cell. The entire sample was placed in the chamber. In the case of scarce or moderately abundant forms, the contents of the whole chamber were enumerated. When a particular species was so abundant in a particular sample as to average more than 10–15 individuals per field of view or per strip transect, then for that sample that species was counted in only 4–10 fields or transects. This allowed the sample volume examined for less abundant species to be kept constant, a reduction of >80% in time required to count a sample, and only a trivial decrease in precision of the density estimates for the abundant species in that sample.

For 1999 only, the samples from 0.5 to 6.5 m for each station were composited. This was also done for the 8.5 and 10.5 m samples for each of the deeper stations (S-1, S-2 and S-3). The equivalent of 32 l of lake water was counted in each case. This compositing was done to accelerate counting of samples when it was decided that additional information on vertical distribution was not needed.

Biovolumes of zooplankters were calculated by measuring 40 individuals of each taxon or stage and using simple geometric shapes to approximate the more complex shapes of individuals (Table 1).

Data analysis

Geometric means were used as measures of central tendency. To deal with the presence of zero values in data sets, a constant was added to each datum prior to the taking of its log. This constant was the smallest non-zero value possible, given the sampling and counting protocols and reporting units used. For 32-l Schindler trap samples examined in their entirety (1997–1998), or the equivalent of 32-l from composited samples (1999), and for reporting of densities as number per liter, the constant was 0.031 (= 1/32).

Five general approaches were used to summarize the patterns of zooplankton abundance. First, for an overview of the general variation of numerical density of metazooplankton over the three-year interval 1997–1999, the mean density for each taxon for the three mid-lake stations was calculated for each date. For each station, the mean for the water column was calculated using the density data for the six sampling depths (0.5–10.5 m). Mean density over stations was determined over whatever number of stations were sampled on a particular date. Second, mean biovolume densities for the three mid-lake stations, S-1, S-2, and S-3, were calculated for each date for 1997–1999 for each taxon or stage and for total metazooplankton using the biovolume values in Table 1. Third, to examine horizontal variation we used density values obtained from the 1999 composited 0.5–6.5 m samples for all five stations. This depth range was used because the shallow stations (S-4 and S-5) could only be sampled to 6.5 m. Fourth, to assess variation with depth, the geometric mean density found at each depth over stations S-1, S-2 and S-3 was calculated for four dates during 1997–1998 when all taxa were present. Two-way ANOVAs were performed to assess evidence of variation with depth, with stations treated as a blocking factor.

Lastly, to assess historical change we compared the 1954–1956 metazooplankton densities at Carpelan's (1961c) deepwater station with the 1997–1999 densities at our station S-1. These stations were similarly situated, both in the northern basin in deep water. Carpelan's station was ~6 km west and 0.5 km north of S-1, 5.5 km from the western shore and with a water depth of 12 m. S-1 was ~8 km from either shore and had a water depth of 14 m. Since Carpelan presented the arithmetic mean densities from three depths (0.5, 6 and 12 m), for 1997–1998 we calculated arithmetic mean densities obtained for our sampling depths (0.5, 6.5 and 10.5 m) corresponding most closely to his. Since the samples at each station in 1999 were composited over all depths (0.5–10.5 m) and then enumerated, however, we had to use values for those composite samples for 1999. Some arithmetic means had a value of zero. In order to plot arithmetic mean numbers per liter on a log scale, we added a constant to all means. As the samples represented the zooplankton present in 3 l (Carpelan's samples) and 32 l of water (our samples), we used a constant of 0.33 (= 1 individual per 3 l) for Carpelan's data and 0.031 (=1 individual per 32 l) for our own. These numbers represent the lowest possible non-zero concentrations given the methods employed. Because Carpelan combined abundance data for the nauplii larvae and copepodids of *A. dengizicus*, for the two forms of *B. amphitrite* larvae, and for the eggs and larvae of *N. succinea*, these densities were also combined in our analysis.

Results

Six species dominated the metazooplankton during the period January 1997–January 2000: three rotifers, a copepod and the larvae from two benthic invertebrates (Fig. 2). Mean water column temperatures varied from 13–14 °C (January) to 31–34 °C (July–September) and dissolved oxygen from 0 to >20 mg l^{-1} (Watts et al., 2001).

Rotifers

Five rotifers were observed in the Salton Sea during 1997–1999 in the plankton, algal mats or sediments. These were *Brachionus rotundiformis*, *Synchaeta* aff. *vorax*, *Synchaeta* sp., *Colurella dicentra* Gosse and an unidentified benthic rotifer that may be in the genus *Proales*. *C. dicentra* and the unidentified rotifer were not found in the plankton.

B. rotundiformis was the dominant rotifer in the summer. The average length of lorica of the *Brachionus* was 154 μm (n=20) which puts it into the species*B. rotundiformis* (Segers, 1995; Gomez & Serra, 1995) rather than *B. plicatilis* sensu stricto. Also the anterior spines are pointed like those of *B. rotundiformis* rather than obtuse like those of *B. plicatilis*, another distinguishing taxonomic feature. It is likely, from the mean length (200 μm) given by Carpelan (1961c), that *B. rotundiformis* was also the species seen in 1954–1956. Fu et al. (1991a) also described a clone of *B. rotundiformis* derived from a 1978 collection at the Salton Sea that had a mean lorica length of 225 μm.

Figur
S-3) f

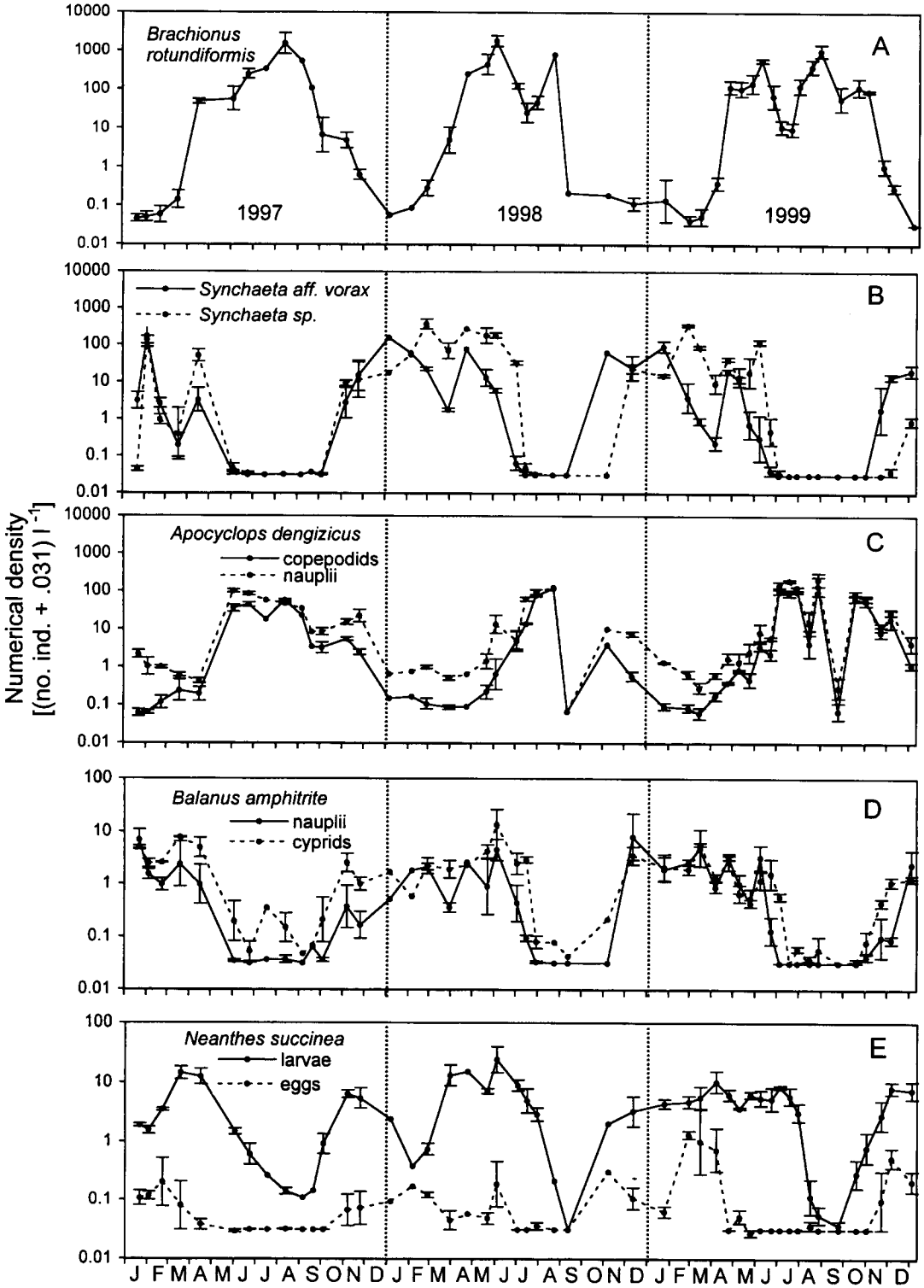


Figure 2. Numerical densities (geometric mean ±1 SE) of metazooplankton taxa during 1997–1999 for three mid-lake stations (S-1, S-2 and S-3) for the top 10.5 m of the water column.

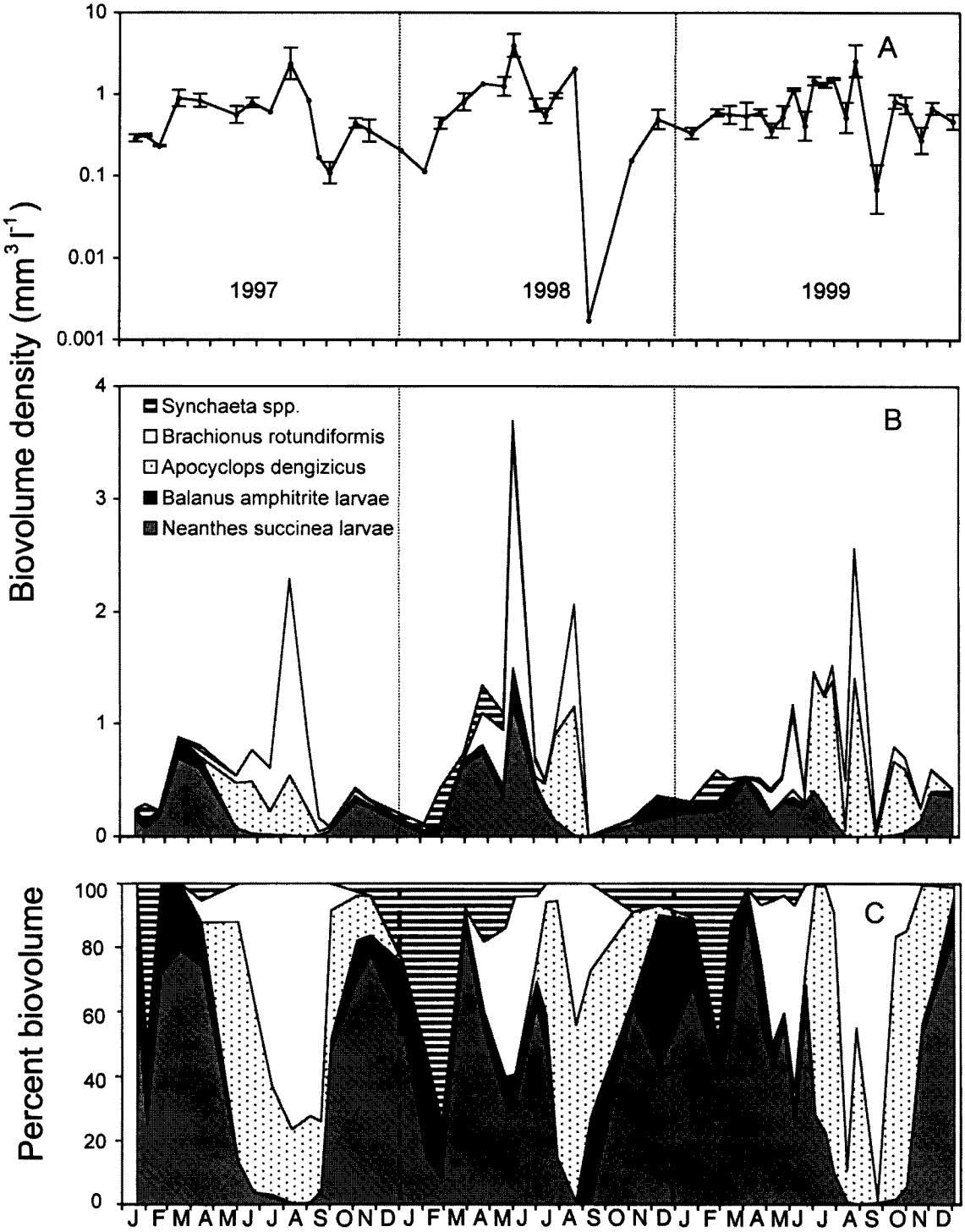


Figure 3. Zooplankton for three mid-lake stations, 1997–1999. (A) Total metazooplankton abundance (geometric mean biovolume density ± 1 SE). (B) Cumulative mean biovolume densities for individual metazooplankton taxa. (C) Relative mean biovolume densities for individual metazooplankton taxa.

B. rotundiformis abundance was low in winter, increased in spring, reached a maximum of >1000 ind. l^{-1} by mid-summer, and then tended to decrease through late summer (Figs 2A and 3A, B). Dramatic declines occurred on several occasions, usually in August and September. Densities were mostly < 0.1 ind. l^{-1} from December through March.

Males were not seen in most samples but were observed live in qualitative samples and found at densities up to 12 males l^{-1} (as much as 0.39% of total *B. rotundiformis* population) in some fixed samples. The maximum density of males occurred on the date and at the station (4 June 1998, S-3) where we also found a maximum of *B. rotundiformis* females (5490 ind. l^{-1}).

B. rotundiformis density generally decreased with depth, being 3–7 fold greater at the surface than at 12 m (Fig. 5). This tendency to decrease with depth was also observed in 1954–1956 (Carpelan, 1961c).

Two species of *Synchaeta* were observed. One of these, *Synchaeta* sp. (length, ~200 μm), was much larger than the other, *Synchaeta* aff. *vorax* (length, ~120 μm). *Synchaeta* sp. showed a temporal pattern almost the opposite of that of *B. rotundiformis* (Figs 2B and 3A, B). It was absent during summer, increased rapidly in late fall, achieved maximum densities of 300–400 ind. l^{-1} in February and crashed in late spring. Densities of *Synchaeta* sp. were generally lower in 1997 than in 1998–1999 and, in the latter two years, it disappeared from the spring plankton at least a month later than the smaller *Synchaeta* species. In 1999, the population was late reappearing in the fall, but our last sampling in January 2000 showed it had started to increase (ca. two months later than in 1997 and one month later than in 1998).

S. aff. *vorax* showed a similar pattern, but density in all three years showed a >99% decrease during late winter, then rebounded to a brief peak about May, before disappearing for the summer. Higher densities of this smaller *Synchaeta* species were seen in 1998 than in the other two years. Its abundance peaks tended to come ca. a month earlier than those of *Synchaeta* sp.

The two *Synchaeta* species were usually evenly distributed with depth (Fig. 5) although on two dates a significant difference with depth of *Synchaeta* aff. *vorax* was observed. These two rotifers are present mostly at times of year when the lake is nearly isothermal (Watts et al., 2001), and strong vertical mixing probably caused the densities to be more or less uniform.

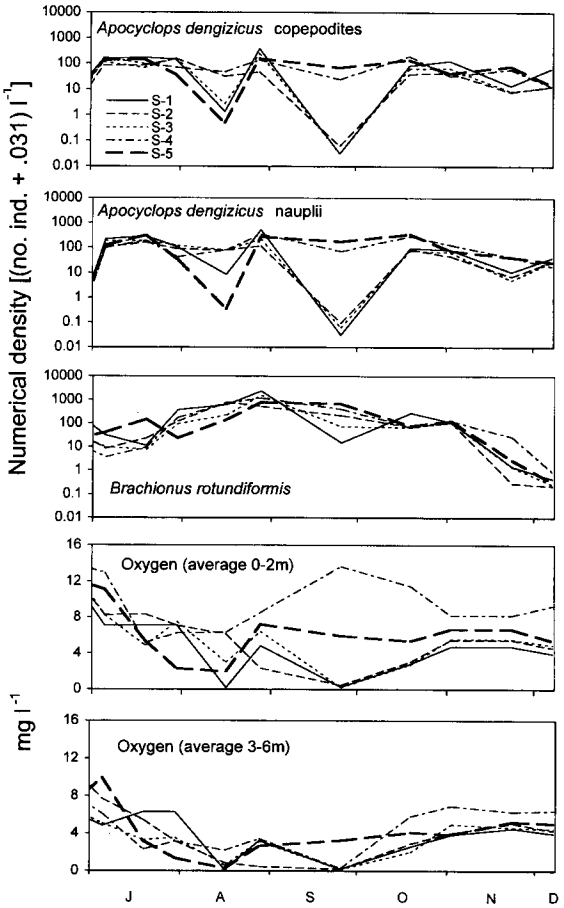


Figure 4. Horizontal (among station) variation in abundance of the copepod *A. dengizicus* (A, B), the rotifer *B. rotundiformis* (C), and oxygen concentration (D, E), during July–December 1999. Densities reported are means for samples from 0.5, 2.5, 4.5, and 6.5 m.

Apocyclops dengizicus

Although two harpacticoid copepods in addition to the cyclopoid copepod, *Apocyclops dengizicus*, have been reported from the Salton Sea (Dexter, 1995) only the cyclopoid was observed in the metazooplankton. Its density early in the year was low (ca. 0.1 ind. l^{-1}) but increased rapidly in late spring or early summer. In 1997, high densities were already attained by early June (36 ind. l^{-1}), whereas in 1998–1999 densities were still low at that time (0.6 and 7.1 ind. l^{-1}, respectively). The copepod was generally most abundant in July–August. Nauplii usually outnumbered the copepodids, especially during winter (Fig. 2C).

Mid-lake densities remained high all summer until abrupt declines, on one or more occasions, in late summer or early fall. Reductions of 90–99.9% were typical

(Fig. 4A, B). Many dead individuals were noted in fresh samples on one of these dates (12 September 1998). During the mid-lake crash in September 1999, however, copepod densities at the two nearshore stations declined little or not at all (Fig. 4A, B). This was correlated with surface water oxygen concentration which remained high at these shoreline stations while it plummeted at the mid-lake stations (Fig. 4D, E). Subsequent to these sudden decreases some recovery of the copepod population was observed in late fall-early winter, especially in 1999. Populations of *A. dengizicus* in winter months were very reduced, but even in winter at least a few nauplii were present in our samples and sometimes a few adults or copepodites as well. In summer and fall, an epizoic peritrich ciliate, *Rhabdostyla vernalis* Stokes often heavily covered the surface of copepodids and, more rarely, the larger nauplii (Kuperman et al., 1998). Kudo (1966) mentioned this ciliate as attaching to a species of *Cyclops*.

Both copepodids and nauplii showed variable patterns of depth distribution; however, they tended to vary in the same way on any one date (Fig. 5). On 7 November 1997 they decreased about 4-fold with depth whereas on 4 June 1998 they increased about 9-fold with depth. On 30 March 1998 nauplii increased with depth, but the few copepodids present on that date were more evenly distributed. On 12 December 1998 the distribution was relatively uniform; this was during a time when the lake was mixing freely. Carpelan (1961c) found that the density of copepods generally decreased with depth in his mid-day samples.

On several dates in 1999 metazooplankton abundance exhibited large declines at some stations while it was stable at other stations. On 16 August 1999 three stations (S-1, S-3 and S-5) showed extreme drops in the density of *A. dengizicus* and its nauplii (Fig. 4A, B). These were the three stations with lowest dissolved oxygen concentrations on that date (Fig. 4D, E). Two other stations (S-2 and S-4) showed lesser decreases (<90%) in copepod densities. By 28 August 1999 conditions had changed drastically: stratification had re-established, oxygen was present in the surface waters, and copepods had again become abundant at all five stations. On 25 September 1999 another zooplankton crash occurred. Stations S-1, S-2 and S-3 were the most affected, with almost complete disappearance of copepodids and nauplii there. Dissolved oxygen at these three stations was less than 0.6 mg l^{-1} at all depths, with most readings less than 0.3 mg l^{-1}. At stations S-4 and S-5 surface waters were well oxygenated and densities were high. By 17 October 1999 the populations of *A. dengizicus* at all five stations had returned to densities similar to those before the second crash (Figs 4A, B).

Balanus amphitrite *larvae*

Abundances of the two larval stages of *B.amphitrite* were assessed separately. In mid-lake, densities of cyprids were generally higher than those of the nauplii (Fig. 2D). This is probably due in part to the longer time spent in the cyprid stage and in part to the distance of mid-lake stations from the source of larvae, sessile adults along the shoreline. Many larvae likely had time to complete development past the naupliar stage by the time they reached mid-lake. Naupliar abundance each year was high (0.5–8 ind. l^{-1}) from January to May. It decreased by >90% by June 1997, and by somewhat later in 1998 and 1999. Densities stayed low all summer; often no nauplii were detected during this season. Naupliar density began to rise in November or December. Maximum densities occurred in January 1997, June and December 1998 and April 1999. The cyprid form followed a similar pattern with high densities in winter and much lower densities in summer. As with the nauplii, cyprid densities decreased earlier in 1997 than in the succeeding two years. In June1998 and 1999, abundance was >10-fold greater than in 1997. By August the density of cyprids was low in all three years. Both larval forms began to increase in fall earlier in 1997 than in 1998–1999.

Nauplii had a tendency to be scarcest at the surface with an apparent density maximum at about 6–8 m depth (Fig. 5). Cyprid densities decreased with depth, except on 12 December 1998 when an increase with depth was observed.

Neanthes succinea *larvae*

Larvae of *N. succinea* were detected on all sampling dates with the exception of 12 September 1998 (Fig. 2E). They were always scarce in summer and early fall and most abundant in spring to early summer, peaking usually at ~10 ind. l^{-1}. Density decreased earlier and more gradually in 1997 than in the other two years, showing a negative correlation with copepod density. As copepod densities increased, polychaete larval density decreased, and the earlier increase in copepod density in 1997 coincided with the earlier decrease in worm larvae in that year. In 1997 the polychaete larvae began to increase in abundance about a month sooner

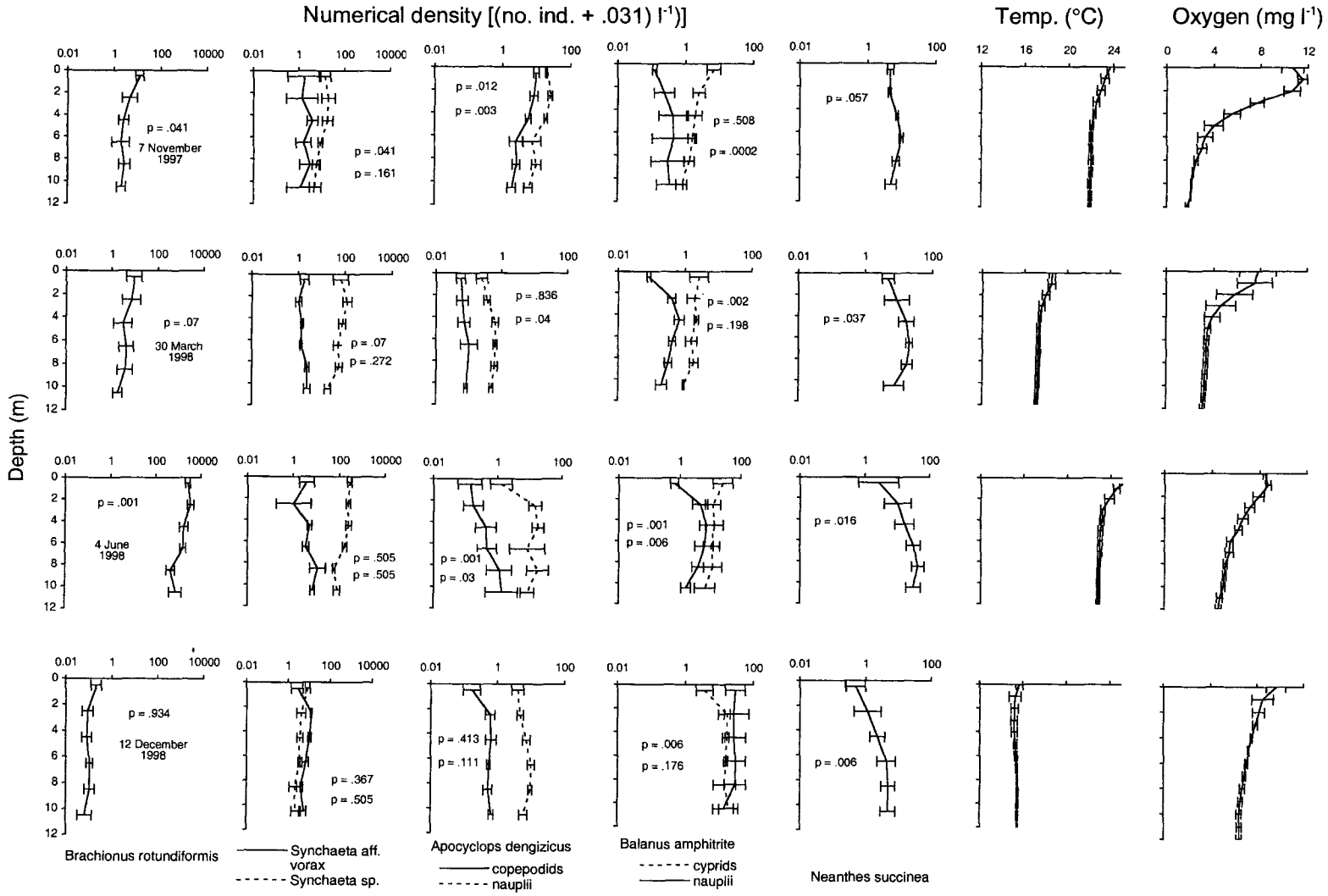


Figure 5. Variation with depth of metazooplankter densities (geometric mean ± 1 SE) and mean temperature and oxygen concentrations (arithmetic mean ± 1 SE), at three mid-lake stations (S-1, S-2 and S-3). P-values for forms represented by solid lines are given above those for forms represented by dashed lines.

in the fall than they did in 1998 or 1999. *Neanthes succinea* eggs, about 140 μm in diameter, were found in low numbers (generally <1 egg l^{-1}), mostly from November to April (Fig. 2E) and were undetected most of the summer.

Larvae of *N. succinea* typically had lowest densities in surface waters (Fig. 5). Their density was usually more than 10-fold higher at 10.5 m than at 0.5 m. This pattern was even observed on 12 December 1998 when the lake was isothermal and freely mixing and other taxa tended to be evenly distributed with depth. This tendency for worm larvae to congregate in deeper water may be related to larval settlement.

Ichthyoplankton

Fish eggs and larvae of an unidentified species were detected in small numbers in our 32-l samples. They were sporadically observed in the zooplankton from May to July 1997, from April to July in 1998 and 1999. These were found throughout the water column on the dates they were encountered.

Eggs and fry of bairdiella (*Bairdiella icistius* Jordan & Gilbert) were studied at the Salton Sea by Whitney (1961) in 1955–1957. He found that they were most abundant June through July with a few found in August, similar to our findings. Matsui et al. (1991) found larvae and eggs of this fish during March–September in 1987–1989.

The dates larval fish and fish eggs were seen in the zooplankton are generally in agreement with the seasons of spawning for bairdiella and corvina (*Cynoscion xanthulus* Jordan & Gilbert) in the Salton Sea (R. Riedel, pers. comm.). Bairdiella are by far the more common fish, and it is likely the species we observed in the plankton. The presence of this ichthyoplankton indicates some spawning is occurring even at the current elevated salinity of the Sea.

Zooplankton biovolume and composition

Total biovolume of the metazooplankton (TBM) was lowest in September following end of summer deoxygenation events when it dropped to <0.1 mm^3 l^{-1} (Fig. 3A). It recovered somewhat during winter and then typically increased rapidly during spring to peak at 2–4 mm^3 l^{-1} in summer.

In winter, the metazooplankton was dominated primarily by *N. succinea*, *B. amphitrite* and *Synchaeta* spp.; in summer *A. dengizicus* and *B. rotundiformis* dominated, especially during the biovolume maxima (Figs. 3B, C). In 1998, however, the biovolume maximum came in June, rather than in August as in 1997 and 1999, and *N. succinea* contributed significantly then. Spring and fall were transition periods during which, at times, all species were present.

Discussion

Results of this monitoring program suggest that metazooplankton populations are responsive to a number of specific factors. Our discussion will focus on the timing of summer metazooplankton density peaks, the dynamics of the planktonic larvae of benthic invertebrates, the sudden decrease in densities of copepods and rotifers in late summer, horizontal patterns of distribution, temporal succession of rotifer species, and the possible role of *Apocyclops dengizicus* predation. We will also compare the present metazooplankton populations with those observed in the 1950s and speculate on the future of the metazooplankton community if the salinity continues to rise.

Annual summer metazooplankton peaks

As secondary producers metazooplankton populations depend on algal primary production. Maximum biovolume of metazooplankton occurred each year in summer, following by a few months phytoplankton blooms that built up during winter and spring (M. Tiffany, unpublished data). Both bottom-up and top-down factors may have been involved. Nutrients were probably mixed into surface waters during the fall overturn period from material accumulated in anoxic bottom waters. These may be supplemented by nutrients released during August and September by decomposition of sulfide-killed metazooplankton, phytoplankton and fish. In these months, the concentration of particulate phosphorus, mostly in the form of phytoplankton and zooplankton, was about 8-fold that of orthophosphate (J. Watts, unpublished data). So decomposition of these organisms could make considerable amounts of dissolved phosphate available to phytoplankters surviving the overturn events. A reduction in grazing rate by *O. mossambicus*, a phyto- and zooplanktivorous fish, may also have favored the winter blooms of phytoplankton. This fish is reported to cease feeding at temperatures below about 16 °C (Kelly, 1956).

The timing of population increases and decreases were influenced by weather patterns, especially wind

conditions. These varied considerably from year to year producing corresponding variations in mixing, oxygenation and heating of the lake (Watts et al., 2001). They may account for maximum zooplankton densities being higher and occurring earlier in 1998 (early June) than in the other two years (mid or late August) (Fig. 3A). Greater mixing due to more wind in spring 1998 may have injected nutrients into the upper photic zone longer and increased phytoplankton availability for metazooplankters. It caused mean water column temperature in late June–early July to be about 8–9 °C warmer in 1998 than in 1997 and 1999 due to greater downward mixing of heat into lower strata. Higher temperatures may have increased primary production. And higher oxygen levels were maintained on the lake bottom until later in the spring in 1998 than in 1997 or 1999, a matter of special significance to the survival of benthic adults of *N. succinea* and *B. amphitrite*. One or all of these factors may have favored greater metazooplankton abundance in mid-1998. The greater abundance of *N. succinea* and *B. amphitrite* larvae in June–July 1998 relative to 1997 and 1999 may have been due especially to the last mentioned factor. Rotifers also seemed favored by spring windiness or rapid temperature increases. *Synchaeta* spp. densities were considerably higher in February–June 1998 than in the same period in 1997 or 1999. *B. rotundiformis* reached its maximum density in 1998 in early June, several months earlier than in 1997 or 1999.

Decline of barnacle and polychaete larvae in summer

The decreased abundance of *N. succinea* and *B. amphitrite* larvae in summer was probably due to seasonal factors causing mortality of both larvae and the adults that produce them. These include anoxic conditions over large portions of the lake bottom, drop in lake level, zooplanktivorous fish nearshore, and sulfide-laden water drifting to shore.

Populations of adult *N. succinea* were present at all depths in late winter–early spring, but in summer, areas >4 m were completely devoid of adults, presumably due to the periodic anoxic conditions there (Detwiler et al., 2002). These areas represent ~90 percent of the lake bottom (Ferrari & Weghorst, 1997). Thus, scarcity of mature polychaetes likely led to a lower production of larvae in the summer. Disappearance of larvae of *N. succinea* earlier in 1997 than in 1998 or 1999 may have been due to anoxia developing at depth sooner that year (Watts et al., 2001). Eggs of *N. succinea* were observed mid-lake only from October to May. As eggs develop into two segmented larvae rapidly (in ca. 36 h), it is likely these eggs were produced by adults from mid-lake sediments.

Most barnacle larval production is confined to a strip of shallow water around perimeter of the lake. Adults occur to depths of 2 m, but probably not much deeper, as the majority of the bottom of the lake is soft sediment (Detwiler et al., 2002). Carpelan (1961c) found densities of barnacle larvae were higher at his station 100 m from shore than at his station 4.8 km offshore, attributing this to proximity to adult barnacles.

Variable water levels could greatly affect barnacles. Lake level was highest about June of each year dropping 0.3–0.4 m to a low in October or November (Watts et al., 2001). This may have reduced larval production by leaving some adults dry above the waterline where they would not survive, let alone produce larvae.

Nearshore barnacle larvae and polychaete adults and larvae would be subject in summer to heavy predation by fish, especially tilapia (*O. mossambicus*) and bairdiella (*B. icistia* Jordan & Gilbert). Adults of these fish move to shoreline areas in summer where juvenile tilapia also become extremely abundant (Riedel et al., 2002). Thus there is a concentration of zooplanktivorous fish, precisely where most barnacle and polychaete larvae are being produced. Guts of tilapia fry often contain barnacle larvae (B. Kuperman, pers. comm.). Both larval and adult *N. succinea* are fed upon by tilapia. *B. icistia* probably feeds heavily on *N. succinea* adults, which are considered its main food in the Salton Sea (Whitney, 1961). This predation by fish thus could contribute greatly to reduced larval polychaete populations in summer.

Under certain wind and current conditions in summer, deoxygenated waters with high sulfide content – the Salton Sea's so-called 'green tides' – are pushed to shore. This phenomenon may occur to some extent in spring and early summer as well as during the major turnover events that we have documented in late summer. These local effects likely kill adult *B. amphitrite* and *N. succinea* along certain shorelines. Detwiler et al. (2002) found a 90% decline in *B. amphitrite* on algae-covered rocks at the south end of the Sea between July and September. Such a decline would lead to a lower production of planktonic larvae. Return of more favorable conditions in October allowed first the recovery of *B. amphitrite* and *N. succinea* adults and then their larvae.

Sulfide and late summer metazooplankton crashes

Strong wind events causing breakdown of thermal stratification and mixing of bottom and surface waters (Watts et al., 2001) apparently led to the metazooplankton crashes in late summer. For periods of a few days at a time the entire mid-lake water column became hypoxic with high concentrations of HS^-. On 16 August 1999, for example, sulfide concentration was 0.5–1 mg l^{-1} between the surface and 6 m depth and 3–5 mg l^{-1} below that (Watts et al., 2001). Many invertebrates are killed by levels of sulfide in this range, as low as 0.02–1.1 mg l^{-1} (Oseid & Smith, 1974). Both zooplankton and phytoplankton appear to have been decimated by these high sulfide concentrations. Of the metazooplankton species, *A. dengizicus* was most strongly affected by turnover events and *B. rotundiformis* to a lesser degree. Densities of other metazooplankton species were already at very low levels. Some benthic meiofauna have developed mechanisms to prevent toxic effects of sulfide (Vismann, 1991), but it is unlikely that zooplankters typical of aerobic environments have done so.

Ciliates, too, were affected by the deoxygenation events. Often during the year we found large ciliates (>55 μm) such as tintinnids, *Condylostoma* spp., *Fabrea salina* Henneguy or *Euplotes* spp. in the zooplankton (M. Tiffany, unpublished data). During the big turnover events in August or September, however, the protozooplankton in this size range consisted almost solely of *Sonderia* sp., a large ciliate ca. 150 μm long. *Sonderia* sp. is in a suborder, Plagiopylida, known for its members' ability to thrive in anoxic conditions (Small & Lynn, 1985). Probably it usually dwells at the sediment–water interface where low oxygen concentrations prevail. This species was seen in the zooplankton almost exclusively on dates during or shortly following these turnover events at times when metazooplankters were scarce.

These annual late summer crashes in plankton may be stressful to organisms in higher trophic levels. If fish are not directly killed by sulfide and anoxia, as about 7.6 million tilapia evidently were in August 1999 (Marcum, 1999; Watts et al., 2001), slower growth rates may be caused during this period by sudden extreme drops in plankton biomass.

Horizontal variation

Spatial heterogeneity of the metazooplankton of the Salton Sea was most apparent during the late summer overturn events. At these times, two species were dominant, *A. dengizicus* and *B. rotundiformis*. During the rest of the year, no consistent among-stations difference were exhibited by zooplankters.

During turnover events the central portions of the lake experienced the most severe crashes in metazooplankton densities (Fig. 4), probably because of the greater volume of anoxic, sulfide-rich bottom waters there prior to turnover (Watts et al., 2001). On 25 September 1999, for example, copepods would have been exposed to much higher sulfide levels at the mid-lake stations (S-1, S-2 and S-3) than at the shallower stations (S-4, S-5).

Rebound of copepod densities within a few weeks at mid-lake stations following a crash may have been facilitated by two factors. First, metazooplankters surviving in nearshore portions of the lake not subjected to crashes could have been redistributed by currents and repopulated the decimated mid-lake areas. Second, there was sufficient time for some local regeneration of populations, given their short generation times and late summer water temperatures of 30–32 °C (Watts et al., 2001).

We expected higher densities of planktonic larvae of *N. succinea* and *B. amphitrite* at our nearshore stations than at mid-lake ones, given the nearshore concentrations of adults of these species. The fact that this was not observed may have been due in part to greater predation by zooplanktivorous fish near shore, as discussed earlier, but also to long residence times in the plankton for these larvae and the fact that these 'nearshore' stations were actually several kilometers from shore. A polychaete related to*N. succinea*, *Nereis grubei* Kinberg, required 24 days to reach the 6–10 segment stage (Reish, 1954) and the larval phase of *B. amphitrite* has been reported to last 4–6 weeks (Egan & Anderson, 1986). These time frames appear ample for currents to distribute larvae throughout the lake.

Rotifer succession

The strong inverse relationship between densities of *Synchaeta* spp. and *Brachionus* may have been caused by seasonal variation in water temperature which may affect parthenogenic reproduction and formation or hatching of resting eggs. *Synchaeta* and *Brachionus* are common genera in marine coastal areas (Ridder, 1981). The Salton Sea is some ways resembles a eutrophic, highly productive marine environment, and so, although its salinity is about 25% higher than seawater, it is not surprising that these genera are found here. Both genera likely spend that portion of the year

they are not in the water column, as resting eggs in the sediment (Gilbert, 1974).

Temperature likely influences seasonal distribution of rotifers in the Salton Sea as it does in other aquatic ecosystems (Berzins & Pejler, 1989). For example, temperature has been shown to be correlated with the appearance and disappearance of *Synchaeta* and *Brachionus* in a freshwater system, with *Synchaeta pectinata* Ehrenberg dominating in cold seasons and *Brachionus calyciflorus* Pallas in the warm ones (Steltzer, 1998). *B. rotundiformis* is a thermophilic organism preferring a temperature range of 20–35 °C (Epp & Lewis, 1980; Yúfera et al., 1997), similar to water temperatures observed during the summer blooms of *B. rotundiformis* in the Salton Sea (Watts et al. 2001). In a brackish coastal pond in Florida (salinity 16–29 g l^{-1}), *B. rotundiformis* was absent in winter, became abundant in summer, and disappeared in October (annual temperature range 12–35 °C) (Snell & Serra, 1998), a pattern similar to that at the Salton Sea in 1997–1999.

The high population growth of *B. rotundiformis* in April of all three years coincided with blooms of phytoplankton (M. Tiffany, unpublished data), and may have been due, in part, to high food availability. Hatching of resting eggs in response to increasing water temperature in spring and formation of resting eggs in response to declining temperatures in fall may govern the dynamics of *B. rotundiformis*. Declining food supply in fall may also play a role in its disappearance then.

High densities of up to several hundred *Synchaeta* per liter in the winter plankton each year suggests these species do best at temperatures $<\sim 20$ °C. This is also a season when suitable prey such as the dinoflagellates *Heterocapsa niei* (Loeblich) Morrill & Loeblich III, ca. 25 μm in length, and *Gyrodinium uncatenum* Hulburt, ca. 50 μm in length, dominate the phytoplankton (M. Tiffany, unpublished data). *Heterocapsa* spp. have been found to be an excellent diet for *Synchaeta cecilia* Rousslet, especially in combination with cryptomonads (Egloff, 1988). This species is in the size range of *Synchaeta* aff. *vorax* (100–130 μm).

The sudden appearance of *Synchaeta* sp. about a month after blooms of *Synchaeta* aff. *vorax* in early winter and the ~90% decrease in *S.* aff. *vorax* abundance in March–April in 1998 and 1999 when *Synchaeta* sp. was achieving maximal densities (Fig. 2B) may reflect predation by the larger species on the smaller. Pourriot (1977) felt that *Synchaeta* species are obligate herbivores, and in culture they are usually fed algae. However, at least one *Synchaeta* species, *S. longipes-stylata* Gosse, which is about the same size as our *Synchaeta* sp. (ca. 200 μm length), has been described as a carnivore (Voigt & Koste, 1978) and our species may be carnivorous as well.

Apocyclops predation

A. dengizicus predation may cause some of the temporal patterns exhibited by other zooplankters. Adults of this species (to 1.3 mm) have been observed to ingest *Artemia* larvae larger than themselves (Hammer & Hurlbert, 1992) and the benthic harpacticoid copepod, *Cletocamptus deitersi* Richard (to 0.8 mm) (Dexter, 1995), and many cyclopoids are known to feed on rotifers (Fryer, 1957; Williamson, 1983). Hart et al. (1998) found indirect evidence that *B. rotundiformis* density in their microcosm experiment was reduced by *A. dengizicus* predation.

Indirect evidence of predation by *A. dengizicus* upon *B. rotundiformis* is seen in the rise in abundance of the copepod, with a lag period of 1–2 months, after the dramatic rise in *B. rotundiformis* in spring (Fig. 2A, C). The rate of growth of the *B. rotundiformis* population tapers off or declines after copepod become very abundant. This suggests that this rotifer may be a food source for the copepod during the summer.

Predation by *A. dengizicus* may also explain the strong inverse relationship between *Synchaeta* spp. and *A. dengizicus* densities. The soft-bodied, slow swimming illoricate *Synchaeta* spp. should be easy prey for the copepod. *Synchaeta* spp. may have been fed on by the copepod in late spring allowing the copepod to be present in low densities. Later, as *A. dengizicus* increased to high densities, *Synchaeta* densities declined until they were no longer detected by June or July. *Synchaeta* spp. were particularly vulnerable to predation by a similar cyclopoid *Cyclops vicinus* Ulianine in laboratory experiments (Plaßmann et al., 1997).

A. dengizicus can presumably feed on barnacle and polychaete larvae as well and may be a factor in keeping the level of these larvae low in summer. The barnacle and polychaete larvae range in length from ~225–670 μm and ~250–1600 μm, respectively, well within the known size range of prey for the copepod.

Changes since the 1950s

Marked changes appear to have taken place in the population dynamics of every Salton Sea metazooplankter species between 1954–1956 and 1997–1999 (Fig. 6).

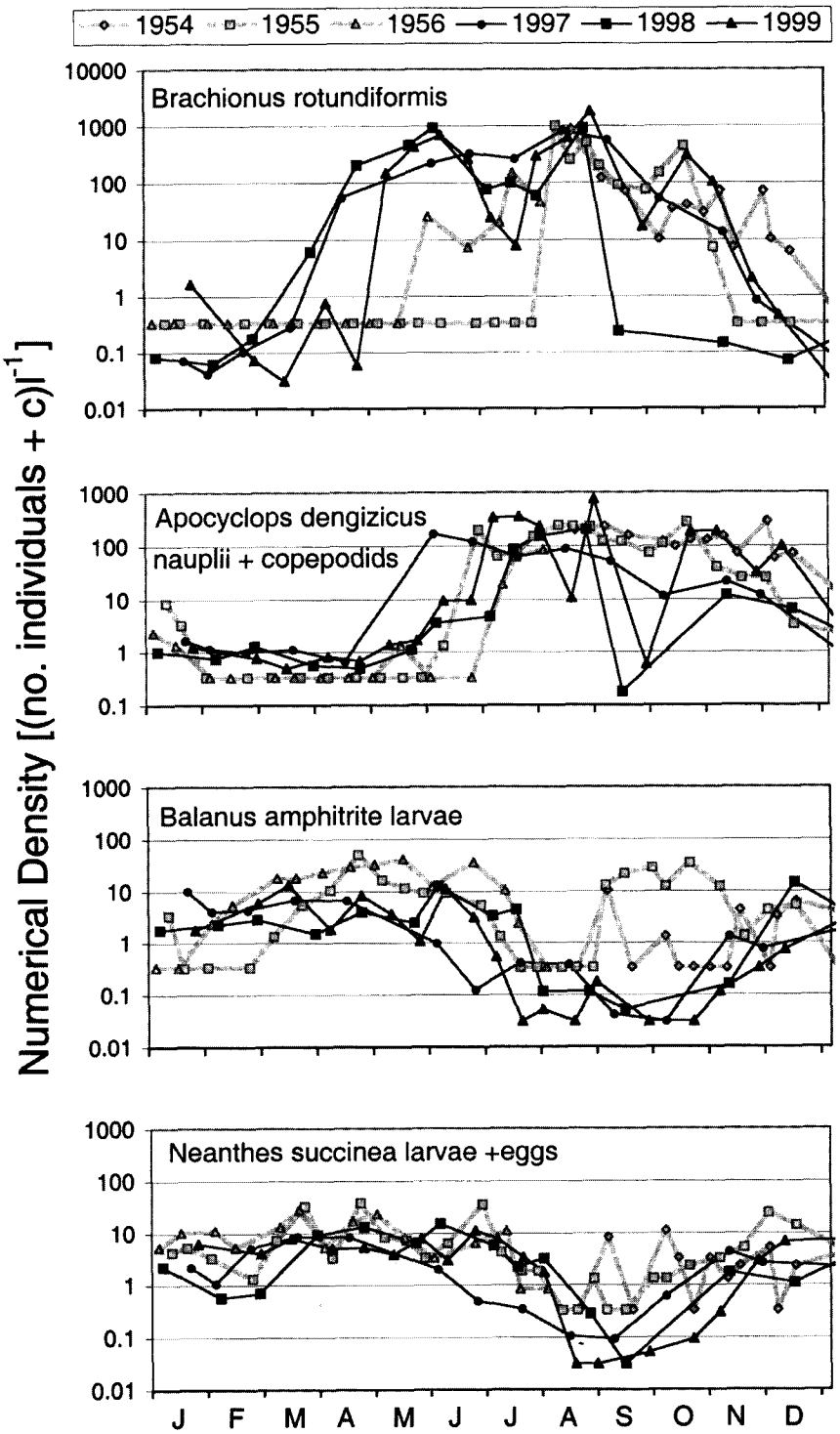


Figure 6. Comparison of metazooplankter densities, 1954–1956 *versus* 1997–1999. Values are arithmetic means for various depths at Carpelan's (1961c) deepwater station and one of our deepwater stations, S-1 (see 'Methods'). Value of the constant, c, in the label for the y-axis is the lowest possible non-zero density possible for the sampling protocol used. For Carpelan's data, c= 0.33 ind. l^{-1}; for our data c= 0.031 ind. l^{-1}.

Comparison cannot be exact in that our sampling stations and regime were not exactly the same (see 'Methods'), but many population differences were large and consistent. We believe most of these changes are a consequence of increased salinity and nutrient levels, higher sulfide concentrations, and establishment of tilapia. The separate effects of these factors are not easily distinguished. Differences cannot be attributed to temperature as water temperatures were similar in the 1950s and 1990s (Watts et al., 2001).

Two species of rotifers (*Synchaeta* spp.), now abundant in winter, were not observed in the earlier study. It is difficult to believe that Carpelan (1961c) would have missed collecting these rotifers even if they were present in densities lower than present ones (up to 400 ind. l^{-1}). In preserved form, however, these rotifers are contracted and difficult to recognize, so if live samples were not examined these may have been missed. Why they were present in 1997–1999 and not in the 1950s is uncertain. Possibly the rise in salinity favored these species physiologically or they simply colonized the lake late. If *Synchaeta* spp. were not present in the lake during Carpelan's study they likely became established before the early 1990s when they were present in tanks of a microcosm experiment established with Salton Sea water (Hart et al., 1998).

The dynamics of the *B. rotundiformis* population have changed considerably since the 1950s. Apparently in 1954–1956 *B. rotundiformis* was completely absent during January–April whereas, although it became scarce in winter, it was present year round during 1997–1999. Also, densities of >100 ind. l^{-1} were attained by April in 1997–1999 but not until July or August in 1954–1956. Similar mean densities (ca. 1000 ind. l^{-1}) were attained in mid-summer in both decades. Speculatively, the now higher salinity may favor hatching of resting eggs of this species at lower temperatures.

Abundance patterns of *A. dengizicus* showed two key differences between the 1950s and 1990s. First, the copepod was undetected during February–April in the 1950s but present at low densities throughout this period in the 1990s (Fig. 2C). Availability of rotifer prey might explain this change. In the 1950s, neither *Synchaeta* spp. nor *B. rotundiformis* was present February–April while in the 1990s the former were abundant and the latter at least present (Fig. 2A, B). Second, late summer crashes like those observed in 1997–1999 were not observed at all in 1954–1956. Densities of *A. dengizicus* declined only gradually from August to November in 1954–1956 whereas in 1997–1999 precipitous crashes occurred in late summer. The post-1950s increase in lake sulfide concentrations (Watts et al., 2001) and massive poisoning of zooplankters during late summer mixing events likely account for this new phenomenon.

Densities of barnacle larvae in 1997–1999 were about an order of magnitude lower in April–May and two orders lower in September–October, than in 1954–1956 (Fig. 6). Possible explanations include predation by *A. dengizicus* in spring, predation by tilapia in summer, increased macroalgae on substrates, and periodic high sulfide events.

The presence of *A. dengizicus* in spring 1997–1999, when it was apparently absent in 1954–1956 might explain the current lower densities of larvae of *B. amphitrite* in April–May. Barnacle larvae are in the size range for possible predation by this cyclopoid copepod, as indicated earlier.

Predation by tilapia may account for the major post-1950s decline in larval barnacle and polychaete densities. During 1954–1956, this fish was absent, but it is now extremely abundant in the lake. During April–October, this fish reproduces at a high rate and many shorelines are densely populated by its fry. Adult tilapia are also concentrated nearshore in summer (Riedel et al., 2002). Adult barnacles occur near shore where solid substrates are available and adult polychaetes are restricted in summer to shallow water substrates by anoxia (Detwiler et al., 2002). Their larvae are produced in the midst of this mass of juvenile and adult tilapia and may be rapidly consumed as the juvenile stage as well as the adult is zooplanktivorous (Mironova, 1969; Maitipe & De Silva, 1985). In 1954–1956, not only was this fish absent but the other fish present (e.g. bairdiella) may not have congregated nearshore, as conditions in mid-lake summer appear to have been better (Watts et al., 2001).

Competition for attachment space between macroalgae and barnacle cyprids attempting to settle may have been another factor. Filamentous green algae, *Chaetomorpha linum* Müller and *Enteromorpha intestinalis* (L.) Link, and *Cladophora* sp. appear to be much more abundant on hard shallow water substrates now than in 1954–1956 (Carpelan, 1961c; Detwiler et al., 2002). This may cause there to be fewer adult barnacles in the Sea now than in the 1950s and therefore fewer larvae produced.

Sulfide-laden surface waters formed in mid-lake and carried by currents to shore may kill adult barnacles and polychaetes in places, leading to reduced production of larvae as mentioned earlier. Given

the large increases in HS^- levels since the 1950s (Watts et al., 2001), the intensity of such shoreline kills likely has increased since the 1950s, just as have the mid-lake kills of plankton.

There are other possible explanations for changes in metazooplankton dynamics. The rise in salinity of approximately 8 g l^{-1} may have affected the metazooplankton in complex ways, via both the physiology of individual species and interactions of their populations (Simpson et al., 1998; Hart et al., 1998). There have also been changes in phytoplankton species composition and dynamics. For example, different dinoflagellates and diatoms now dominate (M. Tiffany, unpublished data) and *Chattonella marina*, a potentially toxic raphidophyte apparently absent in 1954–56, has become very abundant during the warmer half of the year (Tiffany et al. 2001). Thus, the quality of the food supply available has changed over time and possibly the amount as well.

Conclusions

The major changes in the dynamics of the metazooplankton of the Salton Sea since the 1950s have strong implications for the future of this lake. All of the dominant species present then are still in the Sea, with the addition of two rotifers, but there are late summer intervals now when the metazooplankton is decimated in large portions of the lake. These events could worsen or increase in frequency if sulfide concentrations continue to increase. Fish dependent on plankton may be affected by both poor water quality and a reduced food supply.

Continued salinity increase will change the metazooplankton community (Hart et al., 1998; Simpson et al., 1998). Some species, like the copepod, may remain in the Salton Sea for some time, given its high salinity tolerance (Dexter, 1993). Others may not be able to adjust to rising salinity. There are only six species in the metazooplankton and the loss of one or more of these may have major effects. For example, extirpation of the polychaete, an important part of the food web both as larvae and adults, inevitably would cause drastic changes in the entire system. Fish would decline from both a loss of the invertebrate food base and direct physiological effects of increased salinity. Fish-eating birds such as pelicans and cormorants would lose their food supply in the Sea. When most of the fish and predaceous copepods are gone, zooplankters vulnerable to predation such as *Artemia franciscana* may be able to invade the lake and become abundant. Total zooplankton production and standing crop would likely decline, however, as would also likely be the case for the benthos and phytoplankton.

Acknowledgements

We thank Steve Horvitz and Darrell Bennett and the staff of the Salton Sea State Recreation Area for offering their facilities and time during our study; Bob Harper and Jim Zimmer for logistical support; Joan Dainer for technical assistance; Kristen Reifel for field assistance; and Lois Tiffany and the Salton Sea Research Management Committee and Salton Sea Science Subcommittee for financial support. We are also grateful to Russ Shiel for advice on the rotifer taxonomy; and Dawn Bagley, Yvonne Pennebella and Darilyn Blancaflor for assistance with sample analysis. The research described in this article has been funded in part by the United States Environmental Protection Agency through grant #R826552-01-0 to the Salton Sea Authority. The research results have not been subjected, however, to the Agency's required peer review and therefore do not necessarily reflect the views of the Agency. Therefore, no official endorsement should be inferred.

References

Bain, R. C., A. M. Caldwell, R. H. Clawson, H. L. Scotten & R. G. Wills, 1970. Salton Sea, California: water quality and ecological management considerations. U.S. Dept. Interior, Fed. Wat. Qual. Administration, Pacific Southwest Region: 54 pp.

Balcer, M. D., N. L. Korda & S. I. Dodson, 1984. Zooplankton of the Great Lakes, a guide to the identification and zoology of the common crustacean species. Univ. of Wisconsin Press, Madison, Wisconsin.

Berzins, B. & B. Pejler, 1989. Rotifer occurrence in relation to temperature. Hydrobiologia 175: 223–231.

Black, G., 1988. Description of the Salton Sea sport fishery. 1982–83. Calif. Dept. Fish and Game, Inland Fisheries Admin. Rept. No. 88–9: 50 pp.

Carpelan, L. H., 1958. The Salton Sea. Physical and chemical characteristics. Limnol. Oceanogr. 3: 373–386.

Carpelan, L. H., 1961a. Physical and chemical characteristics. In Walker, B. W. (ed.), The Ecology of the Salton Sea, California in Relation to the Sportfishery. Calif. Fish and Game, Fish Bull. 113: 17–32.

Carpelan, L. H., 1961b. Phytoplankton and plant productivity. In Walker, B. W. (ed.), The Ecology of the Salton Sea, California in Relation to the Sportfishery. Calif. Fish and Game, Fish Bull. 113: 33–43.

Carpelan, L. H., 1961c. Zooplankton. In Walker, B. W. (ed.), The Ecology of the Salton Sea, California in Relation to the Sportfishery. Calif. Fish and Game, Fish Bull. 113: 49–62.

Costa-Pierce, B. A. & R. Riedel, 2000. Fisheries ecology of the tilapias in subtropical lakes of the United States. In Costa-Pierce, B. A. & J. E. Rakocy (eds), Tilapia Aquaculture in the Americas, Vol. 2. World Aquaculture Society, Baton Rouge.

Detwiler, P. M., M. F. Coe & D. M. Dexter, 2002. The benthic invertebrates of the Salton Sea: distribution and seasonal dynamics. Hydrobiologia 473/Dev. Hydrobiol. 161: 139–160.

Dexter, D. M., 1993. Salinity tolerance of the copepod, *Apocyclops dengizicus* (Lepeschkin, 1900), a key food chain organism in the Salton Sea, California. Hydrobiologia 267: 203–209.

Dexter, D. M., 1995. Salinity tolerance of *Cletocamptus deitersi* (Richard, 1897) and its presence in the Salton Sea. Bull. Southern California Acad. Sci. 94: 169–171.

Egan, E. & D. Anderson, 1986. Larval development of *Balanus amphitrite* Darwin and *Balanus variegatus* Darwin (Cirripedia, Balanidae) from New South Wales, Australia. Crustaceana 5: 188–207.

Egloff, D. A., 1988. Food and growth relations of the marine microzooplankter, Synchaeta cecelia (Rotifera). Hydrobiologia 157: 129–141.

Epp, R. W. & M. J. Lewis, 1980. Metabolic uniformity over the environmental temperature range in *Brachionus plicatilis*. Comp. Biochem. Physiol. 98C: 385–390.

Fryer, G., 1957. The food of some freshwater cyclopoid copepods and its ecological significance. J. anim. Ecol. 26: 263–286.

Fu, Y., K. Hirayama & Y. Natsukari, 1991a. Morphological differences between two types of the rotifer *Brachionus plicatilis* O. F. Müller. J. exp. mar. Biol. Ecol. 151: 29–41.

Fu, Y. K. Hirayama & Y. Natsukari, 1991b. Genetic divergence between S and L type strains of the rotifer *Brachionus plicatilis* O. F. Müller. J. exp. mar. Biol. Ecol. 151: 43–56.

Gilbert, J. J., 1974. Dormancy in rotifers. Trans. am. microsc. Soc. 93: 490–513.

Gomez, A. & M. Serra, 1995. Behavioral reproduction isolation among sympatric strains of *Brachionus plicatilis* Müller 1786: insights into the status of this taxonomic group. Hydrobiologia 313/314: 111–119.

González, M. R., C. M. Hart, J. R. Verfaillie & S. H. Hurlbert, 1998. Salinity and fish effects in Salton Sea microcosms: water chemistry and nutrient cycling. Hydrobiologia 381: 105–128.

Hammer, G. T. & S. H. Hurlbert, 1992. Is the absence of *Artemia* determined by the presence of predators or by lower salinity in some saline waters? In Robarts, R. D. & M. L. Bothwell (eds), Aquatic Ecosystems in Semi-arid regions: Implications for Resource Management. Nat. Hydrol. Res. Inst. Symposium Series 7, Environment Canada, Saskatoon: 91–102.

Hanson, J. A., 1972. Tolerance of high salinity by the pileworm, *Neanthes succinea*, from the Salton Sea, California. Calif. & Fish and Game 58: 152–154.

Hart, C. M., M. R. González, E. P. Simpson & S. H. Hurlbert. 1998. Salinity and fish effects on Salton Sea microecosystems: zooplankton and nekton. Hydrobiologia 381:129–152.

Kelly, H., 1956. Preliminary studies on *Tilapia mossambica* Peters relative to experimental pond culture. Proc. Ann. Conf. Southeast Game Fish Comm. 10: 139–149.

Kudo, R. R., 1966. Protozoology, 5th edn. Springfield, Ill., Thomas: 1174 pp.

Kuhl, D. L. & L. C. Oglesby, 1979. Reproduction and survival of the pileworm *Nereis succinea* in higher Salton Sea salinities. Biol. Bull. 157: 153–165.

Kuperman, B. I., V. E. Matey & S. B. Barlow, 1998. Ectocommensal and parasitic protozoans on fish, polychaetes, and crustaceans from the Salton Sea. J. Euk. Microbiol. 46: 6A (abstract).

Kuperman, B. I., V. E. Matey, D.M. Dexter & M. A. Tiffany, 2002. Invertebrates of the Salton Sea: a scanning electron microscopy portfolio. Hydrobiologia 473/Dev. Hydrobiol. 161: 203–216.

Maitipe, P. & S. DeSilva, 1985. Switches between zoophagy, phytophagy and detritivory of *Sarotherodon mossambicus* (Peters) populations in twelve man-made Sri Lankan lakes. J. Fish Biol. 26: 49–61.

Marcum, D., 1999. 7.6 million fish die in a day at the Salton Sea. Los Angeles Times, Thursday, August 12, 1999.

Matsui, M. L., A. Bond, G. Jordan, R. Moore, P. Garrahan, K. Iwanaga & S. Williams, 1991. Abundance and distribution of the ichthyoplankton in the Salton Sea in relation to water quality. Final Performance Report, Calif. Dept. of Fish and Game.

Mirabdullayev, I. M. & T. S. Stuge, 1998. Redescription of *Apocyclops dengizicus* (Lepeschkin, 1900) from central Asia. Spixiana 21: 173–178.

Mironova, N., 1969. The biology of *Tilapia mossambica* under natural and laboratory conditions. Ichthyology 9: 506–514.

Oseid, D. M. & L. L. Smith, 1974. Factors influencing acute toxicity estimates of hydrogen sulfide to freshwater invertebrates. Wat. Res. 8: 739–746.

Plaßmann, T., G. Maier & H. Stich, 1997. Predation impact of *Cyclops vicinus* on the rotifer community in Lake Constance in spring. J. Plankton Res. 19: 1069–1080.

Pierce, R. W. & J. T. Turner, 1992. Ecology of planktonic ciliates in marine food webs. Rev. aquat. Sci. 6: 139–181.

Pourriot, R., 1977. Food and feeding habits of Rotifera. Arch. Hydrobiol. Beih. Ergebn. Limnol. 8: 243–260.

Reifel, K. M., M. P. McCoy, M. A. Tiffany, S. H. Hurlbert & D. J. Faulkner, 2002. Possible importance of algal toxins in the Salton Sea, California. Hydrobiologia 473/Dev. Hydrobiol. 161: 275–292.

Reish, D. J., 1954. The life history and ecology of the polychaetous annelid *Nereis grubei* (Kinberg). Univ. Calif. Occasional Papers No. 14. 1–43.

Ridder, M., 1981. Some considerations on the geographical distribution of rotifers. Hydrobiologia 85: 209–225.

Riedel, R., L. Caskey & B.A. Costa-Pierce, 2002. Fish biology and fisheries ecology of the Salton Sea, California. Hydrobiologia 473/Dev. Hydrobiol. 161: 229–244.

Rogerson, A. & G. Hauer, 2002. Naked amoebae (Protozoa) of the Salton Sea, California. Hydrobiologia 473/Dev. Hydrobiol. 161: 161–177.

Segers. H., 1995. Nomenclatural consequences of some recent studies on *Brachionus plicatilis* (Rotifera, Brachionidae). Hydrobiologia 313/314: 121–122.

Simpson, E. P., M. R. González, C. M. Hart & S. H. Hurlbert, 1998. Salinity and fish effects on Salton Sea microecosystems: benthos. Hydrobiologia 381: 153–177.

Simpson, E. P. & S. H. Hurlbert, 1998. Salinity effects on the growth, mortality and shellõSS/SMALL/ŕ strength of Balanus amphitrite from the Salton Sea, California. Hydrobiologia 381: 179–190.

Small, E. & D. Lynn, 1985. Ciliates. In Lee, J. J., S. H. Hutner & E. C. Bovee (eds), Añ Illustrated Guide to the Protozoa. Society of Protozoologists, Lawrence, Kansas.

Small, E. B., G. F. Gebler & J. C. Cole, 2002. A survey of the ciliophora (protista) of the Salton Sea, California: preliminary results. Hydrobiologia (submitted).

Snell, T. W. & M. Serra, 1998. Dynamics of natural rotifer populations. Hydrobiologia 368: 29–35.

Steltzer, C.-P., 1998. Population growth in planktonic rotifers. Does temperature shift the competitive advantage for different species? Hydrobiologia 387/388: 349–353.

Tiffany, M. A., S. B. Barlow, V. E. Matey & S. H. Hurlbert, 2001. *Chattonella marina* (Raphidophyceae), a potentially toxic alga in the Salton Sea, California. Hydrobiologia 466: 187–194.

Vismann, B., 1991. Sulfide tolerance: physiological mechanisms and ecological implications. Ophelia 34: 1–27.

Voigt, M. & W. Koste, 1978. Rotatoria, die Rãdertiere Mitteleuropas. Gebrüder Borntraeger, Berlin: 673 pp.

Walker, B. W. (ed.), 1961. The Ecology of the Salton Sea, California in Relation to the Sportfishery. Calif. Fish and Game, Fish Bull. 113: 1–204.

Walker, K., 1983. A synopsis of ecological information on the saline lake rotifer *Brachionus plicatilis* Müller 1786. Hydrobiologia 81: 159–167.

Watts, J. M., B. K. Swan, M. A. Tiffany & S. H. Hurlbert, 2001. Thermal and mixing regimes and oxygen dynamics of the Salton Sea, California, 1997–1999. Hydrobiologia 466: 159–176.

Whitney, R. R., 1961. The Bairdiella. In Walker, B. W. (ed.), The Ecology of the Salton Sea, California in Relation to the Sportfishery. Calif. Fish and Game, Fish Bull. 113: 105–151.

Williamson, C. E., 1983. Invertebrate predation on planktonic rotifers. Hydrobiologia 104: 385–396.

Yúfera, M., G. Parra & E. Pascual, 1997. Energy content of rotifers (*Brachionus plicatilis* and *Brachionus rotundiformis*) in relation to temperature. Hydrobiologia 358: 83–87.

Hydrobiologia **473:** 121–128, 2002.
D.A. Barnum, J.F. Elder, D. Stephens & M. Friend (eds), The Salton Sea.
© 2002 *Kluwer Academic Publishers. Printed in the Netherlands.*

Freeliving nematodes from the Salton Sea

R. M. Warwick[1], D.M. Dexter[2] & B. Kuperman[2]
[1]*Plymouth Marine Laboratory, Prospect Place, West Hoe, Plymouth PL1 3DH, U.K.*
[2]*Department of Biology and Center for Inland Waters, San Diego State University, San Diego, CA 92182-4614, U.S.A.*

Key words: saline lakes, freeliving nematodes, *Daptonema*, *Dorylaimopsis*, *Leptolaimus*, *Oncholaimus*, *Paracyatholaimus pesavis*, *Ptycholaimellus*, *Sabatieria*, *Terschellingia*, *Theristus*, *Thalassomonhystera*, ?*Trefusia*

Abstract

Thirteen species, or putative species, of freeliving nematodes are recorded from a variety of habitats in the hypersaline Salton Sea, the largest inland lake in California. This doubles the number of species of multicellular invertebrates known to occur in the lake. All species are referable to known marine genera, and are regarded as having a marine coastal origin. The range of taxa present is representative of the full taxonomic spread found in marine coastal habitats, suggesting that a wide range of marine nematode taxa are capable of adapting to the hypersaline conditions. The broad spectrum of feeding types present suggests that nematodes play a variety of ecological roles within the lake.

Introduction

Nematodes occur in every conceivable habitat that can support life, and are the most numerous of all metazoans. In terms of numbers of species, although outnumbered on land by the arthropods, in the sea they are the most diverse metazoan taxon. The number of species present in samples of marine sediments is typically an order of magnitude greater than for any other major taxon. The key to their success is their physiological adaptability and ecological diversity. Freeliving (as opposed to parasitic) species partition the environment in various ways. Food partitioning seems to be the most crucial; most species are selective feeders, and many are highly selective. The feeding type for each marine species can be deduced from the physiognomic characters of its buccal cavity. The four feeding groups proposed by Wieser (1953) are:

1A. Species with no buccal cavity, or a narrow tubular one, regarded as 'selective deposit feeders' ingesting bacterial-sized particles.

1B. Species with a large buccal cavity, but unarmed with teeth: 'non-selective deposit feeders'.

2A. Species with a buccal cavity armed with small or moderately sized teeth: 'epigrowth' or diatom feeders.

2B. Species with large teeth or jaws: the 'predator/omnivore' group.

This classification has been elaborated on subsequently (see the recent review by Moens & Vincx, 1997) but largely remains valid in the absence of direct confirmatory observations on feeding behavior.

Freeliving nematodes play important functional roles in the ecosystem (Platt & Warwick, 1980). They are of major energetic importance in benthic systems, they form a significant part of the diet of many other animals, facilitate the mineralization of organic matter, influence the physical stability of sediments and the exchange of materials between the sediment and water column.

The objectives of this report are: (1) To compile an inventory of species of freeliving marine from a variety of habitats in the Salton Sea. (2) To determine their trophic composition as a way of assessing their ecological roles. (3) To examine the taxonomic spread of species in relation to the pool of potential colonizers of this extreme environment.

The Salton Sea is the largest inland lake in California. It was created between 1905 and 1907 by the accidental diversion of flood water from the Colorado River. The salinity gradually increased through time as did deliberate introductions of marine species into

the Sea. The known introductions began in 1930 and continued through 1957, and included sediments, algae, seagrass, invertebrates, and fish from the Gulf of California, the Gulf of Mexico, and San Diego Bay (Walker, 1961). The flora and fauna contains widely distributed species which flourish along the Atlantic, Pacific, and Gulf coasts of the United States (Detwiler et al., 2002). Certainly, nematodes would have been present in the introduced material.

The Sea is quite shallow (average 8 m, deepest 15 m), and currently has a salinity of 43 g l^{-1}. The temperature and oxygen levels are highly variable. Water temperature averages as low as 13 °C in winter and as high as 34 °C in summer (Watts et al., 2001). Oxygen is high in winter (up to 20 mg l^{-1}), but the Sea becomes anoxic, especially at depths >2 m, for long periods in the summer (Watts et al., 2001). Marine organisms have been deliberately introduced into the Sea on several occasions (Walker, 1961). The multicellular invertebrates so far recorded from the Salton Sea are the polychaetes *Neanthes succinea* Frey and Leuckart and *Streblospio benedicti* Webster, the oligochaetes *Thalassodrilides gurwitschi* Hrabe, *Thalassodrilides belli* Cook, and an enchytraeid, the amphipods *Gammarus mucronatus* Say and *Corophium louisianum* Shoemaker, and the barnacle *Balanus amphitrite* Darwin. Also present but not quantified in any benthic studies are the turbellarian *Macrostomum pusillum* Ax, the harpacticoid copepod *Cletocamptus deitersi* Richard, the ostracod *Cyprideis beaconensis* Le Roy, and the insect *Trichocorixa reticulata* Guérin-Menéville (Kuperman et al., 2001; Detwiler et al., 2002).

The benthic habitats include rocky substrates covered with barnacles (*B. amphitrite*) and two macroscopic species of chlorophytes (*Chaetomorpha linum* Müller *and Entermorpha intestinalis* (L.) Link), a heterogeneous shoreline substrate composed of barnacle shell remains, sand, and gravel (in various mixtures), rare 'muddy' shoreline substrates, usually only in bays or enclosed areas and which were not sampled quantitatively, and the major offshore sediments dominated by sandy silt.

Methods

The sites sampled for nematodes were mainly located along the eastern side of the Salton Sea. Overall, the shoreline barnacle shell substrates (sand gravel shell mixture) are dominated by *Neanthes* and oligochaetes, while *Balanus* and *Gammarus* were occasionally present. The offshore sediments were dominated by *Neanthes*, which is basically the only macroinvertebrate present at 4 m and deeper. *Streblospio* and *Thalassodrillides belli* occurred in very low densities, while *Gammarus* was rarely present in the offshore sediments (Detwiler et al., 2002).

Sample processing

The locations and types of substrata sampled for nematodes are shown in Table 1. Qualitative samples were collected from shoreline and offshore locations. Sediments collected from deeper water were collected using a petite Ponar grab (Detwiler et al., 2002), from which the top 3 cm were scraped and saved for nematode analysis. Sediment cores and trowels were used to scrape soft sediments at very shallow depths along the shoreline for nematodes. The barnacle and algal covered rock was scraped using a stainless steel box (Detwiler et al., 2002). No specific area or volume of material was collected. Nematodes were isolated from the qualitative samples, all of which were smaller than a litre, and no attempt was made to collect every nematode present in the sample. Most samples (nos. 1–14) were immediately fixed in 10% formalin before gross sorting, while samples 15–20 were examined live under dissecting microscope and gross sorted before fixation in 10% formalin). They were mailed in tubes to Plymouth (unfortunately sample 11 dried up in transit). The nematodes were prepared for microcopic examination by washing them into a glass cavity block with a mixture of 5% glycerol and 10% ethanol. These were placed on a warm (30 °C) hotplate for 24 h to allow the water and ethanol to evaporate off, leaving the worms in pure glycerol. Microscope slides were prepared with paraffin wax rings, and the worms in glycerol carefully transferred to the centers of the rings. A coverslip was then placed on the ring and the slide transferred to a warm hotplate (55–60 °C) to melt the wax. After cooling, the edges of the coverslip were sealed with Bioseal No. 2 (for more details see Somerfield & Warwick, 1996).

The nematodes on the slides were identified under the compound microscope. The density of each species in each sample has not been calculated, since the samples were not initially quantitative and sorting selectivity was variable. However, species that were markedly dominant in particular samples were noted. All the species were referable to known marine genera: only one has been positively identified to species level

Table 1. Location and attributes of Salton Sea nematode sampling stations

Substratum Type, sample no.	Location	Date	Depth	Other characteristics
Heterogeneous substrates				
1	Corvina Beach	Oct. 24, 1999	Shoreline	intermingled barnacle shell remains, coarse sand and some gravel (mixed substrate)
2	Red Hill Marina	Oct. 24, 1999	Shoreline	mixed substrate
15	Varner Harbor	Dec. 1, 1999	Shoreline	within attached barnacle community
16	Bombay Beach	Dec. 1, 1999	Shoreline	within algal mats
18	Obsidian Butte	Dec. 1, 1999	Shoreline	shoreline plankton tow
Muddy substrates				
17	Garst Road	Dec. 1, 1999	Shoreline	muddy anaerobic substrate
20	Crystal Cove, Salton City	Dec. 4, 1999	Shoreline	muddy anaerobic substrate
Sandy silt substrates				
3	Obsidian Butte	Dec. 4, 1999	Shoreline	anaerobic sandy silt with abundant detritus
9,12	Offshore	Sept. 28, 1999	2 m	Transect 2, 3, respectively [A]
8,10,13	Offshore	Sept. 28, 1999	4 m	Transect 1, 2,3, respectively[A]
11,14	Offshore	Sept. 28, 1999	6 m	Transect 2, 3, respectively[A]
Sandy substrates				
9	Offshore	Sept. 28, 1999	2 m	Transect 2[A]
Clayey substrates				
12	Offshore	Sept. 28, 1999	2 m	Transect 3[A]
Laboratory cultures				
4	Red Hill Marina	Oct. 24, 1999	Shoreline[B]	Laboratory cultures of *Gammarus mucronatus* at 45 g l^{-1}
5	Red Hill Marina	Oct. 24, 1999	Shoreline[B]	Laboratory cultures of *Gammarus mucronatus* at 50 g l^{-1}
6	Red Hill Marina	Oct. 24, 1999	Shoreline[B]	Laboratory cultures of *Gammarus mucronatus* at 55 g l^{-1}
7	Red Hill Marina	Oct. 24, 1999	Shoreline[B]	Laboratory cultures of *Gammarus mucronatus* at 60 g l^{-1}

[A] For specific locations along offshore transects see Detwiler et al. (2002). [B] Initiated with water and suspended sediments collected here.

and some have been given tentative species names, but more exact specific identifications must await further taxonomic work.

Measurement of biodiversity

Biodiversity indices

On a regional scale, species richness is sometimes difficult to measure: the harder one looks the more species one finds. Apart from this dependence on sampling effort, Harper & Hawsworth (1994) further argue that biodiversity cannot be regarded as just the number of species in an area, and advocate measures that reflect the phylogenetic divergence of the organisms present. The important question posed here is whether the species found in the Salton Sea can be regarded as a random selection from the range of taxa found in potential marine sources of colonization, or whether the subset of species is taxonomically restricted to a few specialized groups that can tolerate the stressful environmental conditions. To address this question, two measures of phylogenetic diversity have been determined, taxonomic distinctness (Warwick & Clarke, 1995) and variation in taxonomic distinctness (Clarke & Warwick, 2001), which can both utilize simple presence/absence data (species lists). Average taxonomic distinctness (Δ^+) is a measure of the degree to which the species are related taxonomically to each other, and is the average path length between every pair of species traced through a taxonomic tree. Ideally such a path should be traced through a cladogram of species relationships, but for the majority

of taxa these have not been resolved, and the use of a standard Linnaean classification is pragmatic. However, a comprehensive phylogenetic classification based on cladistic principles exists for freeliving nematodes (Lorenzen, 1981, 1994). This measure has the distinct advantage of being unbiased by sample size (Clarke & Warwick, 1998). From data consisting only of presence or absence of species (i.e. species lists) it is defined mathematically as:

$$\Delta^+ = [\Sigma\Sigma_{i<j}\omega_{ij}]/[s(s-1)/2],$$

where s is the number of species present, the double summation is over the set $\{i = 1\ s; j=1,\ldots, s$, such that $i<j\}$ and ω_{ij} is the 'distinctness weight' between species i and j. Equal step lengths are normally assumed between each level in the taxonomic hierarchy (species to genus, genus to family, etc), and Clarke & Warwick, (1999) suggest that they be standardized so that the distinctness of two species connected at the highest level (the taxonomically most distant pairing used in a batch of analyses) is set equal to 100. In this case there are six taxonomic levels used: species, genus, family, suborder, order and subclass. Thus the weighting between taxonomic levels for different species in the same genus is 16.667, species in different genera but the same family is 33.33,* etc.

The degree to which certain taxa from the potential species pool are over- or under-represented is another biodiversity attribute of ecological relevance. This is reflected in *variability* of the full set of pairwise distinctness weights making up the average (Clarke & Warwick, 2001). Variation in taxonomic distinctness $\Lambda^+$is defined mathematically as:

$$\Lambda^+ = [\Sigma\Sigma_{i\neq j}(\omega_{ij} - \bar{\omega}^2][s(s-1)].$$

This measure is not exactly unbiased as sample size changes (Clarke & Warwick, in press), but the bias is very small and is manifested by a slight underestimate at very low species numbers.

Determining representativeness

For Δ^+ and Λ^+a simple permutation test of the hypothesis that the assemblage has a taxonomic structure that is representative of the full biodiversity of the regional species pool can be constructed (Clarke & Warwick, 1998, 2001). Say the Salton Sea assemblage comprises m species, then the measured values of Δ^+ and Λ^+can be compared with the range of values from, perhaps, 1000 random selections of m species from the potential source pool of species from marine coastal habitats in North America. If the measured value falls outside the 95% probability limits of this null distribution, then statistically it cannot be considered representative of the full list. If the values fall within these limits, then the assemblage is not significantly different in taxonomic structure than the regional pool, at least in terms of these summary criteria. Results of this type can be visualized as histograms for the simulated null distribution, with an indication of the comparative position of the measured value.

Marine nematodes from the coasts of North America are not well studied, and there is no comprehensive listing of species occurring on the Pacific coast, the most likely source of colonisers of the Salton Sea. However, it is the hierarchical taxonomic structure of coastal marine assemblages that is relevant here, rather than the identities of the actual species involved. The most comprehensive listing (of 118 species) is from the coast of Florida (Wieser & Hopper, 1967), which includes their own inventory from a range of habitat types, plus a number of previous records from other published sources. This listing is regarded as representative of the taxonomic structure of coastal marine nematode assemblages in North America for the purposes of comparison with the Salton Sea.

All the above analyses were undertaken using the software package PRIMER for Windows, developed at the Plymouth Marine Laboratory (Clarke & Warwick, 1994). In each case, the input data consist of an 'aggregation file', indicating the way in which the species present are aggregated up to higher taxonomic levels.

Results and discussion

Altogether, 13 species or putative species of freeliving nematodes belonging to 11 genera were found in the 19 samples (Table 2). The only positively identified species, *Paracyatholaimus pesavis* Wieser & Hopper, 1967 is also found on the coast of Florida. Five species also have close affinities to species found on the Florida coast: *Daptonema erecta* (Wieser & Hopper, 1967), *Ptycholaimellus pandispiculatus* (Wieser & Hopper, 1967), *Terschellingia longicaudata* de Man, 1907, *Terschellingia monohystera* Wieser & Hopper, 1967 and *Thalassomonyhstera parva* (Bastian, 1865). With more detailed taxonomic examination, these identities are likely to be confirmed. In addition, a single juvenile of *Dorylaimopsis* sp. has no characters that unequivocally distinguish it from *D. pellucidum* (Cobb, 1920) from the Florida coast. It is thus reasonable to deduce that the nematode fauna of the Salton

Table 2. Species of nematodes present (x) in each of the samples

Species	Sample no.																		
	1	2	3	4	5	6	7	8	9	10	12	13	14	15	16	17	18	19	20
Daptonema aff. *erecta*	x	x		x					x		x			x		x			
Dorylaimopsis sp.						x													
Leptolaimus sp.	x		x																
Oncholaimus sp.															x		x	x	
Paracyatholaimus pesavis		x	x			x												x	
Ptycholaimellus aff. *pandispiculatus*	x	x	x	x									x	x	x	x		x	x
Sabatieria sp.																x			
Terschellingia aff. *longicaudata*	x	x																	
Terschellingia aff. *monohystera*	x	x					x		x	x	x	x				x		x	
Theristus sp.	x	x		x	x	x	x	x			x	x	x	x	x	x	x	x	x
Thalassomonhystera aff. *parva*		x		x	x													x	
Thalassomonhystera sp.		x		x	x		x	x										x	
?*Trefusia* sp.								x											

Sea derives from the coastal fauna of typical marine habitats.

The head ends of nematodes belonging to the 11 genera are illustrated in Figure 1, to show their buccal structures. Note that these are idealized 'caricatures' of each genus and not exact representations of the actual species present in the Salton Sea. Representatives of each of the feeding groups 1A (4 species), 1B (5 species), 2A (3 species), and 2B (1species) are present, suggesting that they play a full range of ecological roles.

The heterogeneous shoreline substrata (samples 1&2) had a relatively high number of species (6–8), with a preponderance of the (probable) diatom-feeder *Ptycholaimellus* aff. *pandispiculatus*. *Daptonema* aff. *erecta* (a non-selective deposit feeder) was strongly dominant in the mud at Garst Road (sample 17). *Theristus* sp. (another non-selective deposit feeder) was dominant in the algal mats at Bombay Beach (sample 16) and also in the 45 g l^{-1} *Gammarus* culture (sample 4). The predator/omnivore *Oncholaimus* sp. was dominant among attached barnacles in Varner Harbor (sample 15). In other samples, the distribution of species abundances was more even, with no overall dominance by single species. Nematodes were present in reasonable numbers under the most stressful of conditions, the 60 g.l^{-1} *Gammarus* cultures (3 species, sample 7) and at 6 m depth in offshore sediments (2 species, sample 14).

The Salton Sea contains representatives of all the four orders of marine nematodes: Enoplida, Trefusiida, Chromadorida and Monhysterida. The average taxonomic distinctness (Δ^+) of the 13 species is 73.7. This is at the lower end of the range of values derived from 1000 random subsets of 13 species from the 118 in Wieser & Hopper's (1967) marine coastal assemblage (Fig. 2), but falls within the 95% confidence intervals of this distribution (mean Δ^+ 79.3, lower bound 71.2, upper bound 83.3). Thus, the taxonomic spread of species found in the Salton Sea is not significantly different from the null expectation that it is a random selection from the spread of marine coastal taxa.

Similarly, the variation in taxonomic distinctness (Λ^+) is 530.8, rather close to the mean of the simulated random distribution (Fig. 2), and well within its 95% confidence intervals (mean Λ^+ 501.5, lower bound 373.9, upper bound 679.1). Thus, no higher taxa of nematodes from the marine coastal assemblage can be regarded as over- or under-represented in the Salton Sea.

The only previous record of marine nematodes from the Salton Sea is by Linsley & Carpelan (1961) who identified nematodes occuring in algal mats and detritus as belonging the genus *Spilophorella*. No specimens of *Spilophorella* were found in the present samples. However, this genus closely resembles *Ptycholaimellus* (large dorsal tooth in the buccal cavity, double esophageal bulb, punctated cuticle with lateral differentiation). *Ptycholaimellus* aff. *pandispiculatus* was one of the most frequently encountered species in this study. We can not rule out the presence of *Spilo-*

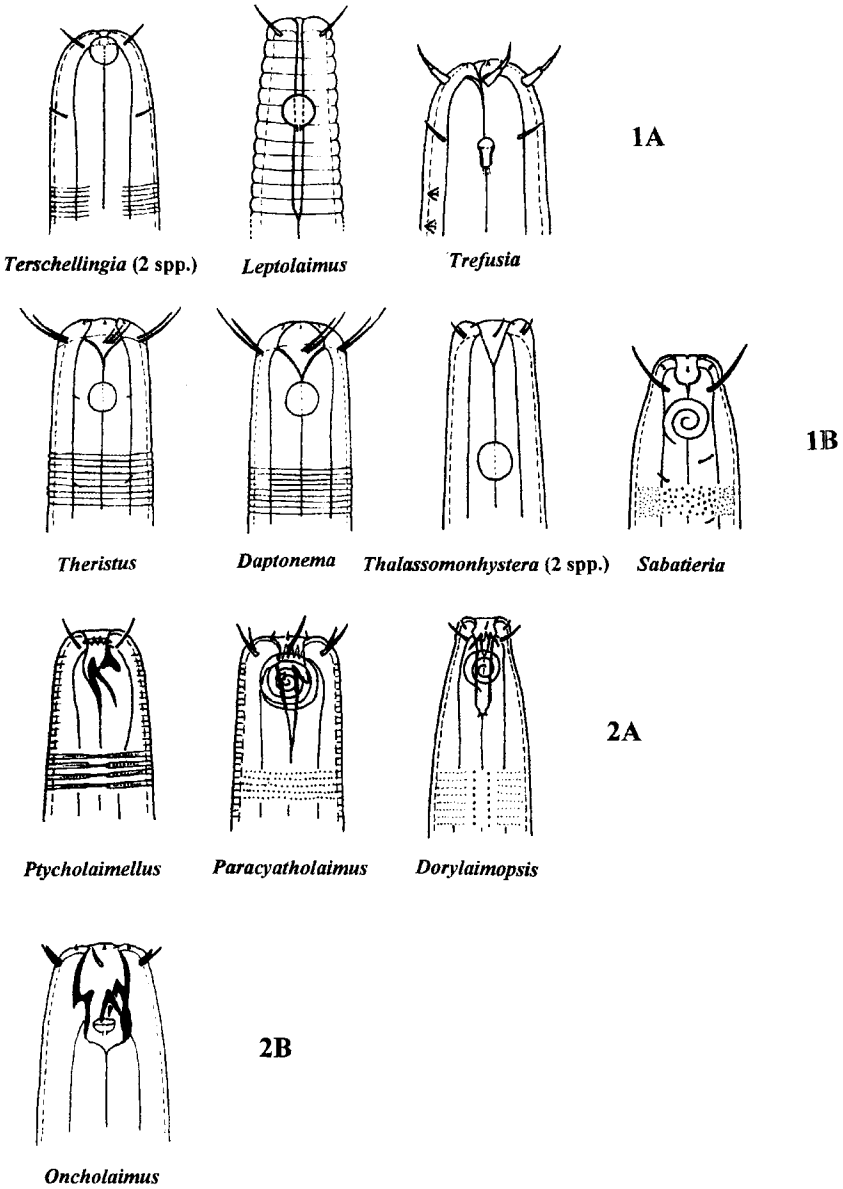


Figure 1. Sketches of the head ends of the 11 genera of freeliving nematodes from the Salton Sea, divided into the four feeding groups 1A, 1B, 2A and 2B.

phorella either now or when salinity was at 35 g l^{-1} in the 1950s, nor can we rule out the possibility of mistaken identity.

Conclusions

The finding of 13 species of freeliving nematodes doubles the number of metazoan invertebrate species so far recorded from the Salton Sea. All the nematode species found are regarded as having a marine coastal origin. This preliminary study suggests that a wide range of marine nematode taxa are capable of adapting to the hypersaline conditions. The broad spectrum of feeding types present suggests that nematodes play a variety of ecological roles within the Sea, which merits further more detailed study. In particular, more quantitative information is required.

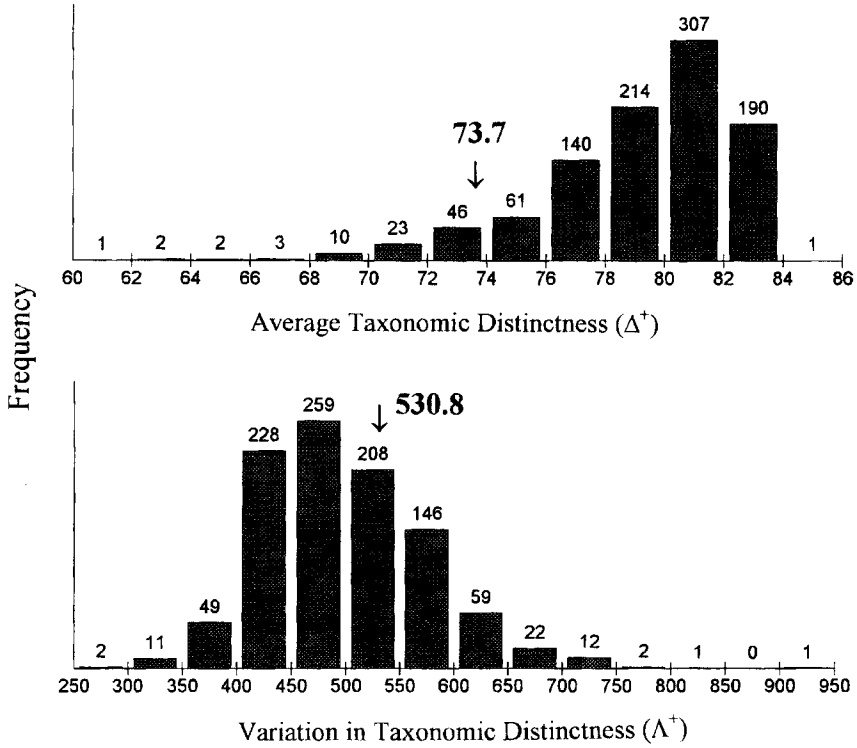


Figure 2. Histograms showing the frequency distribution of Δ^+ and Λ^+values for 1000 random subsets of 13 species drawn from the 118 species recorded from the Florida coast. The measured values for the 13 species in the Salton Sea are indicated by arrows.

Acknowledgements

We thank Sarah Dashfield for preparing the nematode samples for microscopic examination. The research described in this article has been funded in part by the United States Environmental Protection Agency through grant #R826552-01-0 to the Salton Sea Authority. The research results have not been subjected, however, to the Agency's required peer review and therefore do not necessarily reflect the views of the Agency. Therefore, no official endorsement should be inferred. RMW's contribution to the work is part of the Biodiversity core-strategic research project of the Plymouth Marine Laboratory, and was supported in part by the U.K. Department of the Environment, Transport and the Regions under Contract No. CDEP 84/5/295 and the U.K. Ministry of Agriculture, Fisheries and Food under Contract No. AE 1137.

References

Clarke, K. R. & R. M. Warwick, 1994. Change in Marine Communities: An Approach to Statistical Analysis and Interpretation. Plymouth Marine Laboratory, U.K.

Clarke, K. R. & R. M. Warwick, 1998. A taxonomic distinctness index and its statistical properties. J. appl. Ecol. 35: 523–531.

Clarke, K. R. & R. M. Warwick, 1999. The taxonomic distinctness measure of biodiversity: weighting of step lengths between hierarchical levels. Mar. Ecol. Prog. Ser. 184: 21–29.

Clarke, K. R. & R. M. Warwick, 2001. A further biodiversity index applicable to species lists: variation in taxonomic distinctness. Mar. Ecol. Prog. Ser. 216: 265–278.

Detwiler, P. M., M. F. Coe & D. M. Dexter, 2002. The benthic invertebrates of the Salton Sea: distribution and seasonal dynamics. Hydrobiologia 473/Dev. Hydrobiol. 161: 139–160.

Harper, J. L. & D. L. Hawksworth,. 1994. Biodiversity: measurement and estimation. Preface. Phil. Trans. r. Soc. London Ser. B, 345: 5–12.

Kuperman, B., V. E. Matey, D. M. Dexter & M. A. Tiffany, 2001. Invertebrates of the Salton Sea: a scanning electron microscope portfolio. Hydrobiologia (submitted).

Linsley, R. H. & L. N. Carpelan, 1961. Invertebrate Fauna. In Walker, B. W. (ed.), The Ecology of the Salton Sea, California, in Relation to the Sportfishery. Calif. Fish Game Fish Bulletin 113: 43–47.

Lorenzen, S., 1981. Entwurf eines phylogenetischen Systems der freilebenden Nematoden. Verh. int. Meeresforsch. Bremerhaven, Suppl. 7: 1–449.

Lorenzen, S., 1994. The Phylogenetic Systematics of Freeliving Nematodes. Ray Society, London: 755 pp.

Moens, T. & M. Vincx, 1997 Observations on the feeding ecology of estuarine nematodes. J. mar. biol. Ass. U. K. 77: 211–227.

Platt, H. M. & R. M. Warwick, 1980. The significance of free-living nematodes to the littoral ecosystem. In Price, J. H., D. E. G. Irvine & W. F. Farnham (eds), The Shore Environment. Vol. 2. Ecosystems. Academic Press, Cambridge: 729–759.

Somerfield, P. J. & R. M. Warwick, 1996. Meiofauna in marine pollution monitoring programmes: a laboratory manual. MAFF Directorate of Fisheries Research, Lowestoft: 71 pp.

Walker, B. W., 1961. The ecology of the Salton Sea, California in relation to the sportfishery. Calif. Fish. Game Fish. Bull. 113: 1–204.

Watts, J. M., B. K. Swan, M. A. Tiffany & S. H. Hurlbert, 2001. Thermal, mixing, and oyxgen regimes of the Salton Sea, California, 1997–1999. Hydrobiologia 466/Dev. Hydrobiol. 162: 159–176.

Warwick, R. M. & K. R. Clarke, 1995. New 'biodiversity' measures reveal a decrease in taxonomic distinctness with increasing stress. Mar. Ecol. Prog. Ser. 129: 301–305.

Wieser, W., 1953. Die Beziehung Mundhöhlengestalt, Ernärungsweise und Vorkommen bei freilebenden marinen Nematoden. Arkiv Zool. 4: 439–484.

Wieser, W. & B. E. Hopper, 1967. Marine nematodes of the East coast of North America. 1. Florida. Bull. Mus. Comp. Zool. 135: 239–344.

Hydrobiologia **473:** 129–137, 2002.
D.A. Barnum, J.F. Elder, D. Stephens & M. Friend (eds), The Salton Sea.
© 2002 *Kluwer Academic Publishers. Printed in the Netherlands.*

Cryptomonads from the Salton Sea, California

S. B. Barlow[1] & P. Kugrens[2]
[1]*EM Facility/Biology Department, San Diego State University, 5500 Campanile Drive, San Diego, CA 92182-4614, U.S.A.*
[2]*Department of Biology, Colorado State University, Fort Collins, CO 80523, U.S.A.*

Key words: cryptomonads, Salton Sea, phytoplankton kathablepharid

Abstract

Using freshly collected field samples and enrichment cultures, eight genera of cryptomonads from the Salton Sea are recorded for the first time. Comparative data from light and scanning electron microscopy were utilized to identify these genera and species. The genera included *Chroomonas*, *Falcomonas*, *Hemiselmis*, *Plagioselmis*, *Pyrenomonas/Rhodomonas*, *Storeatula*, *Teleaulax*, and the kathablepharid *Leucocryptos*. One putative genus remains unidentified and may represent a new taxon. SEM has not been conducted on this cryptomonad, but it has been isolated and is being maintained in culture. The genera and species identified from the Salton Sea are typical of marine rather then freshwater environments and may play an important role in primary productivity and as preferred food organisms for zooplankton.

Introduction

Cryptomonads, cryptoprotists, or cryptophytes, are unicellular, biflagellate protists. They belong to the Phylum Cryptophyta, Class Cryptophyceae, Order Cryptomonadales (Clay et al., 1999). Cryptomonads are important primary producers in freshwater and marine habitats (Klaveness, 1988; Gillott, 1990), and many are cosmopolitan in their distribution, although they appear to be more common in cooler water. Many are collected in phytoplankton samples but their cells are extremely delicate and rupture when fixatives are added or when temperatures are elevated. As a consequence, their numbers generally are low in preserved samples, and therefore are assumed to be a small and obscure taxonomic group. However, a three year long survey of the mid-lake phytoplankton of the Salton Sea in 1997–1999 revealed that cryptomonads, despite their relatively small size, often represented 10–20% of the total biovolume of the eukaryotic phytoplankton (M. Tiffany, pers. com.). Their small size and delicate construction require electron microscopy for proper identification and specialized electron microscopic techniques to preserve their cell structure (Hill & Wetherbee, 1986, 1988, 1989; Kugrens & Lee, 1986, 1991; Kugrens et al., 1986, 1987; Lee & Kugrens, 1986; Hill, 1991a, b; Clay & Kugrens, 1999b; Clay et al., 1999).

The primary objectives of this report are to provide an inventory of cryptomonad species in the phytoplankton population of Salton Sea and to provide details of some features that can used in identifying cryptomonads. To accomplish these objectives, SEM and light microscopy had to be utilized to determine genera and species since pigmentation is one of the major characteristics used in distinguishing among some genera.

Materials and methods

Water samples from October, 1999 from Garst Road and the State Park Headquarters sites at the Salton Sea were examined using scanning electron microscopy. Fresh samples were fixed by addition of 1 volume of 0.2 M cacodylate buffer, pH 7.2 containing 4% glutaraldehyde to an equal volume of Salton Sea sample. The sample was briefly mixed, and a half volume of aqueous 4% osmium tetroxide immediately added. After 20 min fixation at room temperature in the dark, samples were collected on 1μm-pore size nucleopore filters, dehydrated in an alcohol series,

and critical point dried in a Samdri-790 critical point drier. Dried filters were mounted on stubs, coated with gold/palladium in an Anatech Hummer VI coater and viewed with a Hitachi S-2700 SEM. Digital images were recorded using a Princeton-Gamma-Tech IMIX image collection system. A second set of water samples, collected in February 2000 from Red Hill Marina, was examined by SEM, as well as subcultured in an attempt to produce clonal isolates. Subcultures of Salton Sea water were either diluted into fresh ES-enriched seawater (Provasoli, 1963), or ES-enrichment solution was added to Salton Sea water and subcultured at 18 °C on a 16:8 light cycle.

Observations and discussion

Taxonomic considerations

The structures used as primary characters for identifying cryptomonad genera are the furrow/gullet complex and the cell covering called a periplast. Variations in either of these are used to delineate genera. Cryptomonad cells are asymmetrical with two unequal flagella subapically inserted on the right side of the vestibulum, which is a shallow anterior depression. There may be one or two chloroplats per cell, often with prominent pyrenoids. Pigments in cryptomonads include chlorophylls *a* and *c*, but their differences in coloration are due to the various types of phycobiliproteins in the chloroplasts. Specific phycobiliproteins impart a brown, red or blue-green color to the various genera and species. Furthermore, pigmentation appears to be a major characteristic in delineating some genera whose cell structure otherwise is similar when viewed with the SEM.

A furrow is a ventral groove, of variable length, that begins in the vestibular region of the cell and extends posteriorly (Munawar & Bistricki, 1979; Hill & Wetherbee, 1986, 1989; Kugrens et al., 1986). A tubular invagination called the gullet may extend posteriorly from the vestibulum or the end of the furrow (Hill & Wetherbee, 1986, 1989). Ejectisomes flank the furrow and/or gullet. Several types of furrows have been described in cryptomonads (Kugrens et al., 1986) and these variations have become, and should remain, major features in cryptomonad systematics (Hill & Wetherbee, 1986, 1988, 1989; Hill, 1991a, b, c). There may be only a gullet, only a furrow, or a combination of a furrow-gullet present in cells. Nevertheless, the furrow gullet/complex imparts an asymmetrical shape to the cells, which may be oval, compressed, lunulate, caudate, acute, elongate, sigmoid, reniform or contorted. In addition, all cells possess a vestibulum, which is a shallow anterior depression, where the flagella are inserted on the right side.

Periplasts are unique cell coverings found only in cryptomonads and consist of inner and surface components (Hill & Wetherbee, 1986, 1988, 1989; Kugrens & Lee, 1986, 1991; Brett & Wetherbee, 1986; Wetherbee et al., 1986; Hill, 1991a, b, c). The inner periplast component (IPC) consists either of multiple plates having various shapes (Kugrens & Lee, 1986; Hill & Wetherbee, 1986, 1988, 1989; Hill, 1991a, b, c) or it may consist of a single sheet. The surface periplast component (SPC) is more variable and may consist of plates, heptagonal scales, mucilage or a combination of any of the preceding. Generally, plates cannot be resolved with SEM, but occasionally their shapes can be inferred when some cell shrinkage occurs.

Ejectisomes are a characteristic feature of all cryptomonad cells (Kugrens et al., 1994). They are coiled extrusive organelles, and they appear to be identical in all genera that have been investigated. Large ejectisomes are associated with the furrow/gullet and small ejectisomes are found in other regions of the cell. Large ejectisomes are easily seen with light microscopy, but the small ejectisomes cannot be resolved. However, the presence of small ejectisomes can be detected with SEM and can be used to infer a periplast sheet. Whenever the small ejectisomes appear in close association as slight elevations they provide indirect evidence of a periplast sheet.

Cryptomonads are preferred food organisms for zooplankton (Guillard, 1975; Klaveness, 1984; Stemberger & Gilbert, 1985; Sarnelle, 1993; Li et al., 1996). Additionally, they are routinely ingested by various colorless dinoflagellates, ciliates, and by *Kathablepharis* sp. (Stemberger & Gilbert, 1985; Clay & Kugrens, 1999a, c; Lewitus et al., 1999). Various studies suggest that rotifers appear to select cryptomonads preferentially (Stemberger & Gilbert, 1985), and the presence of cryptomonads enhances the reproduction of planktonic rotifers (Edmondson, 1965). Pejler (1977) observed that various rotifers prefer *Rhodomonas* to the prymnesiophyte *Chrysochromulina*. Since many zooplankton selectively choose cryptomonads as prey, grazing probably plays a significant role in regulating planktonic cryptomonad population dynamics (Sarnelle, 1993). Cryptomonad populations generally reach a maximum following periods of mod-

erate turbulence, when they are disseminated throughout the water column and mixed with higher nutrient waters (Reynolds, 1984), and when grazing is reduced.

Perhaps one of the most interesting aspects involving cryptomonads is the phenomenon known as kleptoplastidy, when the chloroplast of an ingested photoautotroph is retained and remains functional for a period of time (Schnepf et al., 1989; Lewitus et al., 1999). Kleptoplastidy of cryptomonad chloroplasts occurs in ciliates (Stoecker & Silver, 1990) and dinoflagellates (Skovgaard, 1988; Schnepf et al., 1989; Putt, 1990), and these chloroplasts photosynthesize and produce starch, which may be an available carbon source for the host (Larsen, 1988; Putt, 1990; Schnepf & Elbrächter, 1992), or it may fulfill metabolic requirements under limited food availability (Lewitus et al., 1999). Whether this occurs in the Salton Sea could be determined in future studies on ciliates and dinoflagellates.

While cryptomonads represent a well circumscribed group of algae, there is another group of colorless flagellates that historically has been included in the Cryptophyta, known as the kathablepharids, and include the genera *Leucocryptos* and *Kahtablepharis*. These genera are common in both freshwater and marine habitats, although *Leucocryptos* is reported only from marine habitats. Except for the presence of ejectisomes and placement of flagella, their other cellular features do not support the placement of this group within the cryptomonads (Lee & Kugrens, 1991; Lee et al., 1991; Vørs, 1992a, b; Clay & Kugrens, 1999a, c). Currently their systematic and phylogenetic positions remain undetermined, but for the purposes of this study, the kathablepharids are considered as part of the Cryptophyta.

Salton Sea cryptomonads

Enumerations were not conducted; however, cryptomonads were most dominant in the February 2000 samples, with *Teleaulax* and *Plagioselmis* being dominant in the phytoplankton samples. Relative abundances are provided, and a description of the species identified follows. Table 1 provides characteristics for each genus identified in this report.

Blue-green cryptomonads

These genera contain either Cr-phycocyanin 645 (sometimes 615) or 569 and have a blue-green chloroplast. Periplast plates are either rectangular or hexagonal and are present in both the IPC and SPC. A furrow occurs only in *Falcomonas*, whereas only a gullet is present in *Chroomonas* and *Hemiselmis*.

a. *Hemiselmis simplex* **Butcher.** Cells are 5–6 long, × 3–3.5 deep and 2.5–3 μm wide. Cells are laterally compressed and appear bean-shaped or reniform in lateral view. Cells lack a furrow; however, a short gullet originates near the middle of the cell and extends posteriorly and obliquely from the vestibulum (Figs 1 and 2). The superficial periplast component consists of large elongate hexagonal plates, and the IPC is a sheet (Clay & Kugrens, 1999b). A single parietal chloroplast contains the accessory pigment Cr-phycocyanin 615. An eyespot is lacking, but a round, orange refractive body is located in the posterior half of the cell. SEM of a ventral view of the cell (Fig. 2) shows two subequal flagella arising from a slight depression or vestibulum that is located approximately one-third the distance from the cell anterior.

b. *Chroomonas* **sp. Hansgirg** (Fig. 3). Cells measure approximately 8–12 μm in length and 4–7 μm in width. Cells are blue-green in color, due to the presence of Cr-phycocyanin 645. Cells are slightly oval with a slight indentation on the ventral side. Periplast plates of the IPC and SPC are rectangular and are the major diagnostic feature of *Chroomonas*. In Figure 3, the plates are slightly curved and conform to the cell shape. A furrow is absent. Since this cryptomonad was not observed with light microscopy, a species designation was not possible.

c. *Falcomonas daucoides* **(Conrad et Kufferath) Hill** (Figs 4 and 5). Cells are 7–12 μm long and 3–5 μm wide, circular in cross section, and their color is deep blue-green due to the presence of Cr-phycocyanin 569 (Hill & Rowan, 1989; Clay & Kugrens, 1999b). Cells are falcate, ranging to comma or tear-drop shapes, with the anterior end rounded, and the cell tapering to an acute, pointed and slightly ventrally curved posterior end. The posterior end varies from being short and acute to being long, pointed and tail-like. Sometimes the posterior end may be acutely to bluntly rounded. Figures 4 and 5 probably are *F. daucoides* since it has a surface component of hexagonal plates (Hill, 1991a; Clay & Kugrens, 1999b) that would be visible with the SEM. If it had only hexagonal plates in the IPC, then these would not be as distinct as shown in Figures 4 and 5. Furthermore, Figure 5 clearly indicates a falcate shape, and the pointed tail.

A few blue-green falcate cells were observed in the crude sample. Enrichment did not promote growth of this species. When viewed with the SEM, *F. daucoides*

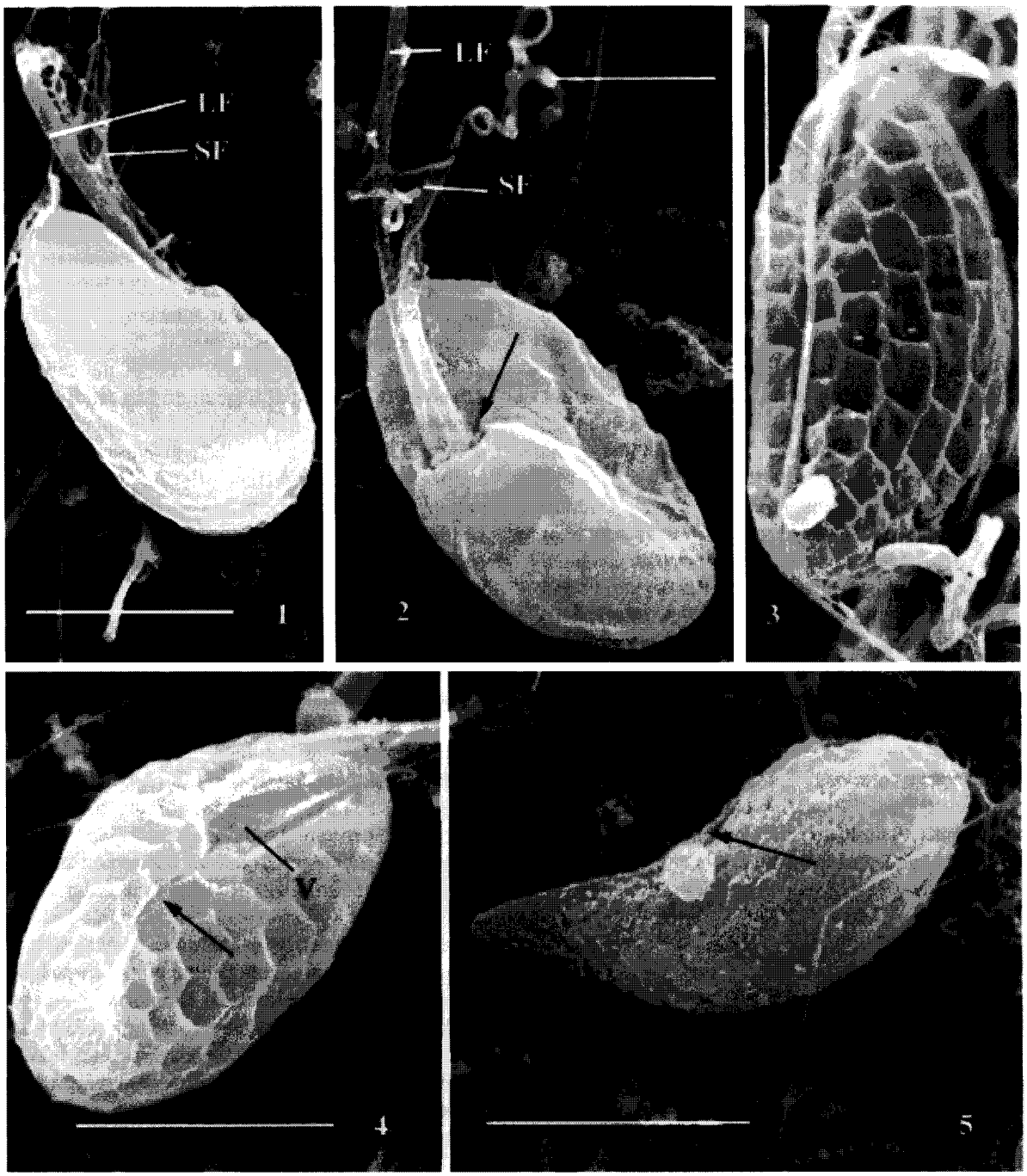


Figure 1. SEM of *Hemiselmis simplex*. Note the insertion of the long (LF) and short (SF) flagellum and the reniform cell shape. Scale bar = 5 μm. *Figure 2.* SEM from the ventral side of *Hemiselmis simplex*. Note the location of the vestibulum (arrow). The cell is slightly flattened from the left side. Scale bar = 5 μm. *Figure 3.* SEM of *Chroomonas* sp. showing the rectangular periplast plates of the surface periplast component. Scale bar = 10 μm. *Figure 4.* Ventral view of *Falcomonas daucoides* cell showing the vestibulum (V) and furrow (arrow). The furrow is barely visible due to cell shrinkage during fixation. Note the hexagonal periplast plates of the surface periplast component. Scale bar = 10 μm. *Figure 5.* Lateral view of *Falcomonas daucoides* showing the falcate cell shape and the pointed posterior of the cell. Surface hexagonal plates also are evident. Scale bar = 10 μm.

Table 1. Cryptomonad genera and the most significant cellular characteristics used in identification

Genus	Furrow/Gullet	Inner Periplast	Outer Periplast	Chloroplast Color
Hemiselmis	Gullet only	Sheet (?)	Elongate Hexagonal Plates	Blue-green
Chroomonas	Gullet only	Rectangular Plates	Rectangular Plates	Blue-green
Falcomonas	Furrow only	Hexagonal Plates	Hexagonal Plates	Blue-green
Storeatula	Gullet only	Sheet	Coarse Fibrils	Red
Rhodomonas	Short Furrow	Square/Rectangular	Coarse Fibrils	Red
Teleaulax	Long Furrow only	Sheet	Heptagonal Scales	Red/Brown
Plagioselmis	3/4 Furrow	Hexagonal Plates	????????	Red/Brown
Leucocryptos	No Gullet/Furrow	Absent	Striated Material	No Chloroplast

is similar in morphology to *Plagioselmis prolonga*, and must be separated by the difference in the phycocyanins. *P. Prolonga* contains phycoerythrin and is red colored.

Red cryptomonads

Red cryptomonads have Cr-phycocyanin 545 as their major accessory (Hill & Rowan, 1989). Four red colored species were found in the samples, with the highest numbers in February 2000.

a. *Storeatula major* **Hill** (Figs 6–8). Cells are 14–18 μm long and 6–8 μm in diameter. Cells lack a furrow, and the tubular gullet opening is ventral to the vestibulum. The figures clearly show that a furrow is absent. The periplast has an IPC consisting of a sheet and an SPC consisting of a thick mat of coarse fibrils that is clearly identifiable in Figures 6–8. The SEMs from this study resemble Figures 35 and 36 by Hill (1991c), confirming that it is the species in this sample.

b. *Pyrenomonas salina* **(Wislousch) Santore** (Fig. 9). This genus and species still are placed in *Rhodomonas* by some authors. For a rationale refer to Kugrens et al. (1999). It is a widely distributed species in the marine environment and perhaps is the most common cosmopolitan species. Cells are 10–14 μm long and 5–7 μm wide, and slightly ellipsoid. The major accessory pigment is Cr-phycoerythrin 545. Cells have a short furrow and deep gullet. The periplast appears serrated in surface view due to a slight anterior elevation of the plates. The IPC consists of small rectangular plates with beveled corners, and the SPC consists of a mat of coarse fibrils (Hill & Wetherbee, 1989; Kugrens et al., 1999).

c. *Teleaulax acuta* **(Butcher) Hill** (Figs 10–12). Cells are falcate, measuring 15–25 μm in length, 10–15 μm in width. The cells may be somewhat flattened. The posterior end is narrower and is slightly recurved with a blunt end. The main accessory pigment is Cr-phycoerythrin 545, imparting a reddish coloration to cells. The cells have a long furrow that extends longitudinally to form the vestibulum, which is located approximately one fourth the cell length from the anterior. The furrow extends almost to the posterior end. Hill (1991c) noted that this exaggerated feature may be responsible for the delicate nature of the cells and renders preservation difficult, especially for SEM. The shape of the cells from light micrographs by Hill (1991c) provides the basis for the current identification.

The periplast consists of an inner sheet that is interrupted by numerous small ejectisome vesicles, seen as slight elevations on the surface in Figures 10–12. The SPC should consist of an imbricate layer of heptagonal scales that cannot be resolved with the SEM. This species was the dominant cryptomonad, if not the dominant phytoplankton species in the February 2000 samples. However, culturing of this cryptomonad was unsuccessful. Counts were not conducted since the primary objective was identification.

d. *Plagioselmis prolonga* **Butcher**. This also was a dominant in the February 2000 samples but not as numerous as *T. acuta*. Unfortunately, SEMs of this species were not obtained and its identification is based strictly on light microscopic observations and the diagrams by Butcher (1967), the publication by Novarino et al. (1994) and unpublished data from Clay & Kugrens. Cells are 9–12 μm long, 5–7 μm wide and 4–7 μm deep, convex, and slightly compressed in lateral view. The cell anterior is rounded, and the posterior end is acute. The vestibulum is subapical. The furrow extends posteriorly from the vestibulum and a short gullet may be present posterior to the furrow. The periplast has an IPC of hexagonal plates that

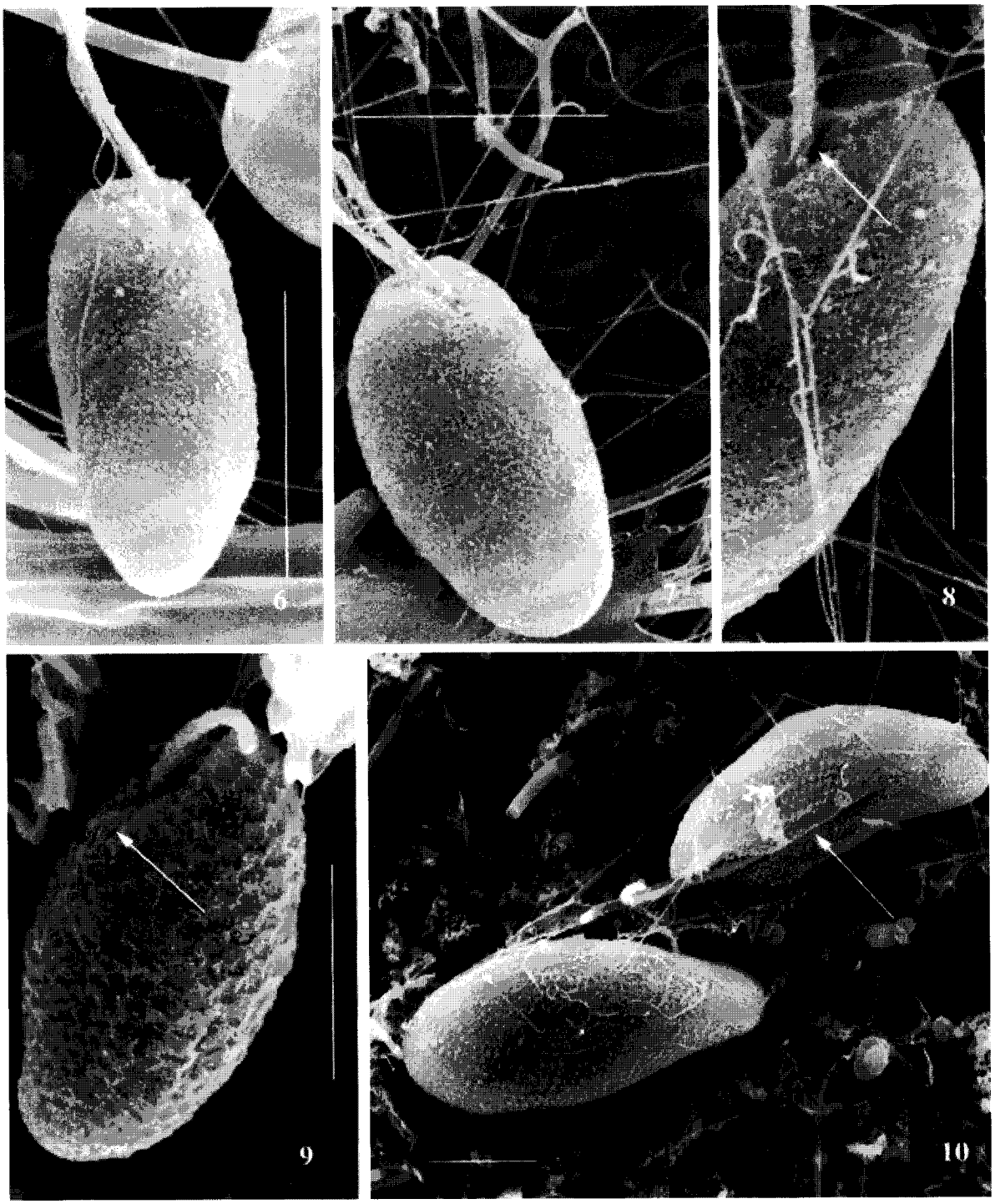


Figure 6. SEM of *Storeatula major*. Note the absence of a furrow and the coarse fibrils on the cell surface. Scale bar = 10 μm. *Figure 7.* SEM of *Storeatula major*. Scale bar = 10 μm. *Figure 8.* Higher magnification of a *Storeatula major* cell showing the presence of a vestibulum (arrow) but an absence of a furrow. Scale bar = 10 μm. *Figure 9.* SEM of a *Pyrenomonas salina* cell showing the periplast plates and short furrow (arrow). Scale bar = 10 μm. *Figure 10. Teleaulax acuta* cells in dorsal and oblique views. The dotted surface represents elevated small ejectisome vesicles. A long furrow is evident in one of the cells (arrow). Scale bar = 10 μm.

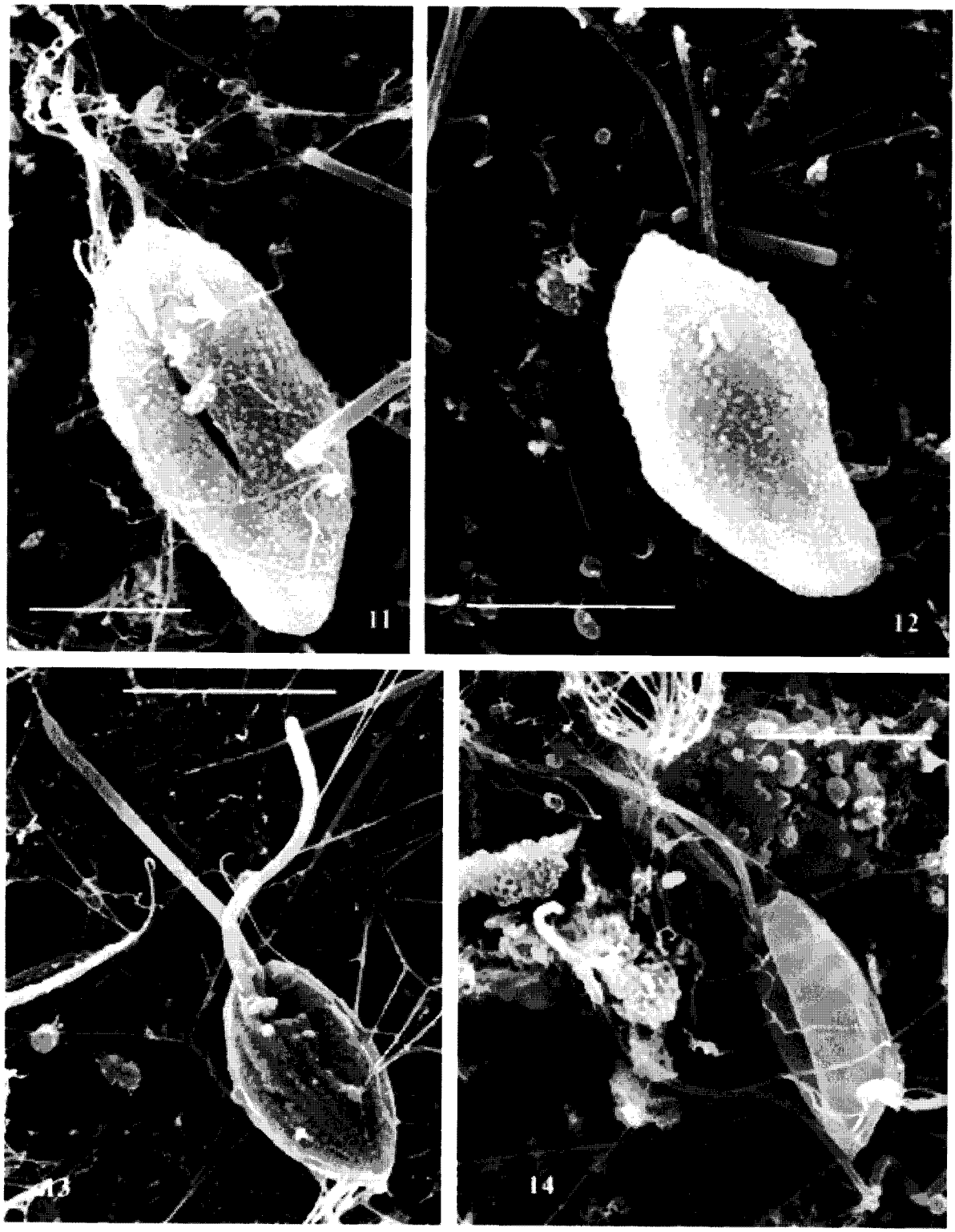


Figure 11. Ventral view of a *Teleaulax acuta* cell showing the furrow and elevated ejectisomes over the cell surface. Scale bar = 10 μm. *Figure 12.* Lateral view of a *Teleaulax* cell showing the curved shape of the cell. Scale bar = 10 μm. *Figure 13. Leucocryptos* sp. cell with two unequal flagella and longitudinal strips on the cell surface. Scale bar = 10 μm. *Figure 14.* Lateral view of a putative *Leucocryptos* with unequal flagella. The ventral portion of the cell indicates some cellular collapse probably resulting from fixation. Scale bar = 10 μm.

are slightly protracted anteriorly. There is a chloroplast with Cr-phycoerythrin 545 accessory pigment. The SPC consists of heptagonal scales and/or fibrils that are not resolved with electron microscopy.

Kathablepharids

Kathablepharids are characterized by being colorless and phagocytic. Cells may be falcate, ovoid, flattened, or ellipsoid. The cell covering consists of imbricate scales or overlapping strips of material that appear striated in cross section (Lee & Kugrens, 1991; Vørs, 1992a, b; Clay & Kugrens, 1999a, c). *Leucocryptos marina* (Braarud) Butcher displays large longitudinal ridges (Vørs, 1992a) similar to those displayed in Figure 13. They are allied with cryptomonads primarily due to the presence of ejectisomes (Lee & Kugrens, 1991; Vørs, 1992a, b; Clay & Kugrens, 1999a, c). Their classification at this time is unknown.

a. *Leucocryptos* **sp. Butcher (Figs 13 and 14).** Small cells of an asymmetric droplet shaped cell with a posterior end were found with the light and scanning electron microscopes. The flagella appear thicker than normal, perhaps due to the thick cell covering over the flagella. A few of these cells were observed in enriched samples but they did not proliferate in culture. These cells were considerably smaller than the only marine species described, which is *L. marina* (Braarud) Butcher and measures approximately 25–30 μm in length. Cells of *Leucocryptos* from the Salton Sea measured 7–12 μm in length and approximately 5 μm in diameter. Cells had ejectisomes, but further details could not be observed due to their rapid movement under the microscope. Whether this represents a small representative of *L. marina* or is a new species remains to be determined.

Conclusions

The cryptomonads identified during this study are typical for marine samples. While some genera are also found in freshwater habitats, the species are strictly marine. A previous report of *Cryptomonas* from the Salton Sea (Carpelan, 1961) is probably incorrect since this genus is found only in freshwater. If *Cryptomonas* indeed is confirmed from the Salton Sea, then it would represent the first confirmed *Cryptomonas* from a saline habitat. An eighth cryptomonad species was isolated from enrichment cultures and is currently being maintained at Colorado State University for future study. It was not observed in crude samples and SEMs were not obtained. It has red pigmentation, and superficially appears to represent a new genus. The cryptomonads may play an important role in primary productivity in the Salton Sea, despite their small size. A survey of the Salton Sea mid-lake phytoplankton from 1997–1999 revealed that cryptomonads often represented 10–20% of the total biovolume of the eukaryotic phytoplankton. Although their population density was greatly diminished during and after the fall turnover, at other times, densities were in the 2000–10 000 cells ml^{-1} range and occasionally even higher (M. Tiffany, pers. com.). Continued analyses of water samples from the Salton Sea is expected to provide additional genera and species of these small flagellates.

References

Brett, S. J. & R. Wetherbee, 1986. A comparative study of periplast structure in *Cryptomonas cryophila* and *C. ovata* (Cryptophyceae). Protoplasma 131: 23–31.

Butcher, R. W., 1967. An Introductory Account of the Smaller Algae of British Coastal Waters IV. Cryptophyceae. Fishery Invest., Ser. 4, London: 1–54.

Carpelan, L. H., 1961. Phytoplankton and plant productivity. In Walker, B. W. (ed.), The Ecology of the Salton Sea, California in Relation to the Sportfishery. Calif. Fish and Game, Fish Bull. 113: 33–43.

Clay, B. L. & P. Kugrens, 1999a. Systematics of the enigmatic kathablepharids, including EM characterization of the type species, *Kathablepharis phoenikoston*, and new observations on *K. remigera* comb. nov. Protist. 150: 43–59.

Clay, B. L. & P. Kugrens, 1999b. Characterization of *Hemiselmis amylosa* sp. nov. and phylogenetic placement of the blue-green cryptomonads *H. amylosa* and *Falcomonas daucoides*. Protist. 150: 297–310.

Clay, B. L. & P. Kugrens, 1999c. Description and ultrastructure of *Kathablepharis tenuis* sp. nov. and *K. obesa* sp. nov. – two new freshwater kathablepharids (Kathablepharididae) from Colorado and Wyoming. Europ. J. Protist. 35: 435–447.

Clay, B. L., P. Kugrens & R. E. Lee, 1999. A revised classification of Cryptophyta. J. linn. Soc. Bot. 131: 131–151.

Edmondson, W. T., 1965. Reproductive rate of planktonic rotifers as related to food and temperature in nature. Ecol. Monogr. 35: 61–111.

Gillot, M., 1990. Phylum Cryptophyta (Cryptomonads). In Margulis, L., J. O. Corliss, M. Melkonian & D. J. Chapman (eds), Handbook of Protoctista. Jones & Bartlett Publishers, Boston: 139–151.

Guillard, R. R. L., 1975. Culture of phytoplankton for feeding marine invertebrates. In Smith, W. L. & M. H. Chanley (eds), Culture of Marine Invertebrate Animals. Plenum Press, New York: 29–60.

Hill, D. R. A., 1991a. *Chroomonas* and other blue-green cryptomonads. J. Phycol. 27: 133–145.

Hill, D. R. A., 1991b. Diversity of heterotrophic cryptomonads. In Patterson, D. J. & J. Larsen (eds), The Biology of Free-Living Heterotrophic Flagellates. Systematics Association Special Volume 45: 235–240.

Hill, D. R. A., 1991c. A revised circumscription of *Cryptomonas* (Cryptophyceae) based on examination of Australian strains. Phycologia 30: 170–188.

Hill, D. R. A. & K. S. Rowan, 1989. Biliproteins of the Cryptophyceae. Phycologia 28: 455–463.

Hill, D. R. A. & R. Wetherbee, 1986. *Proteomonas sulcata* gen. et sp. nov. (Cryptophyceae) a cryptomonad with two morphologically distinct and alternating forms. Phycologia 27: 521–543.

Hill, D. R. A. & R. Wetherbee, 1988. The structure and taxonomy of *Rhinomonas pauca* gen. et sp. nov. (Cryptophyceae). Phycologia 27: 355–365.

Hill, D. R. A. & R. Wetherbee, 1989. A reappraisal of the genus *Rhodomonas* (Cryptophyceae). Phycologia 28: 143–158.

Klaveness, D., 1984. Studies on the morphology, food selection and growth of two planktonic freshwater strains of *Coleps* sp. *Protistologica* 20: 335–349.

Klaveness, D., 1988. Ecology of the Cryptomonadida: a first review. In Sandgren, C. D. (ed.), Growth and Reproductive Strategies of Freshwater Phytoplankton. Cambridge Univ. Press, New York: 105–133.

Kugrens P. & R. E. Lee, 1986. An ultrastructural survey of cryptomonad periplasts using quick-freezing freeze-fracture techniques. J. Phycol. 23: 365–376.

Kugrens, P. & R. E. Lee, 1991. Organization of cryptomonads. In Patterson, D. J. & J. Larsen (eds), The Biology of Free-Living Heterotrophic Flagellates. The Systematics Association Special Volume 45: 219–233.

Kugrens, P., B. L. Clay & R. E. Lee, 1999. Ultrastructure and systematics of two new freshwater cryptomonads, *Pyrenomonas ovalis* and *Storeatula rhinosa* sp. nov. J. Phycol. 35: 1079–1089.

Kugrens, P., R. E. Lee & R. E. Andersen, 1986. Cell form and surface patterns in *Chroomonas* and *Cryptomonas* cells (Cryptophyta) as revealed by scanning electron microscopy. J. Phycol. 22: 512–522.

Kugrens, P., R. E. Lee & R. E. Andersen, 1987. Ultrastructural variations in cryptomonad flagella. J. Phycol. 23: 511–518.

Kugrens, P., R. E. Lee & J. O. Corliss, 1994. Ultrastructure, function and biogenesis of extrusive organelles in selected non-ciliate protists. Protoplasma 181: 164–190.

Larsen, J., 1988. An ultrastructural study of *Amphidinium poecilochroum* (Dinophyceae), a phagotrophic dinoflagellate feeding on small species of cryptophytes. Phycologia 27: 366–377.

Lee, R. E. & P. Kugrens, 1986. The occurrence and structure of flagellar scales in some freshwater cryptophytes. J. Phycol. 22: 549–552.

Lee, R. E. & P. Kugrens, 1991. *Katablepharis ovalis*, a colorless flagellate with interesting cytological characteristics. J. Phycol. 27: 505–513.

Lee, R. E., P. Kugrens & A. P. Mylnikov, 1991. Feeding apparatus of the colorless flagellate *Katablepharis* (Cryptophyceae). J. Phycol. 27: 725–733.

Lewitus, A. J., H. B. Glasgow & J. M. Burkholder, 1999. Kleptoplastidy in the toxic dinoflagellate *Pfiesteria piscicida* (Dinophyceae). J. Phycol. 35: 303–312.

Li, A., D. K. Soecker, D. W. Coats & E. J. Ada, 1996. Ingestion of fluorescently labeled and phycoerythrin containing prey by mixotrophic dinoflagellates. Aquat. Microbiol. Res. 10: 139–147.

Munawar, M. & T. Bistricki, 1979. Scanning electron microscopy of some nanoplankton cryptomonads. Scanning Electr. Micros. 3: 247–252.

Novarino, G., I. A. N. Lucas & S. Morrall, 1994. Observations on the genus *Plagioselmis* (Cryptophyceae). Cryptogamie, Algologie 15: 87–96.

Pejler, B., 1977. Experience with rotifer cultures based on *Rhodomonas*. Arch. Hydrobiol. Beih. Ergebn. Limnol. 8: 264–266.

Provasoli, L., 1963. Growing marine seaweeds Proc. Int. Seaweed Symp. Pergamon Press, New York: 9–17.

Putt, M., 1990. Metabolism of photosynthate in the chloroplast-retaining ciliate *Loboea strobila*. Mar. Ecol. Prog. Ser. 60: 271–282.

Reynolds, C. S., 1984. Phytoplankton periodicity: the interactions of form, function and environmental variability. Freshwat. Biol. 14: 111–142.

Sarnelle, O., 1993. Herbivore effects on phytoplankton succession in a eutrophic lake. Ecol. Monogr. 63: 129–149.

Schnepf, E. & M. Elbrächter, 1992. Nutritional strategies in dinoflagellates: a review with emphasis on cell biological aspects. Eur. J. Protist. 28: 3–24.

Schnepf, E., S. Winter & D. Mollenhauer, 1989. *Gymnodinium aeruginosum* (Dinophyta): a blue-green dinoflagellate with a vestigial, anucleate, cryptophycean endosymbiont. Plant Syst. Evol. 164: 75–91.

Skovgaard, A., 1998. Role of chloroplast retention in a marine dinoflagellate. Aquat. Microbiol. Ecol. 15: 293–301.

Stemberger, R. S. & J. J. Gilbert, 1985. Body size, food concentration, and population growth in planktonic rotifers. Ecology 66: 1151–1159.

Stoecker, D. K. & M. W. Silver, 1990. Replacement and aging of chloroplasts in *Strombidium capitatum* (Ciliophora: Oligotrichida). Mar. Biol. 107: 491–502.

Vørs, N., 1992a. Heterotrophic amoebae, flagellates and Heliozoa from the Tvarminne area, Gulf Of Finland, in 1988–1990. Ophelia 36: 1–109.

Vørs, N., 1992b. Ultrastructure and autecology of the marine, heterotrophic flagellate *Leucocryptos marina* (Braarud) Butcher 1967 (Katablepharidaceae/Kathablepharidae), with a discussion of the genera *Leucocryptos* and *Katablepharis/Kathablepharis*. Eur. J. Protist. 28: 369–389.

Wetherbee, R., D. R. A. Hill & G. I. McFadden, 1986. Periplast structure of the cryptomonad flagellate *Hemiselmis brunnescens*. Protoplasma 131: 11–22.

Hydrobiologia **473:** 139–160, 2002.
D.A. Barnum, J.F. Elder, D. Stephens & M. Friend (eds), The Salton Sea.
© 2002 *Kluwer Academic Publishers. Printed in the Netherlands.*

The benthic invertebrates of the Salton Sea: distribution and seasonal dynamics

P. M. Detwiler, Marie F. Coe & Deborah M. Dexter
Department of Biology, San Diego State University, San Diego, CA 92182, U.S.A.

Key words: saline lakes, *Neanthes succinea*, *Balanus amphitrite*, *Gammarus mucronatus*, *Corophium louisianum*, *Streblospio benedicti*, *Thalassodrilides*

Abstract

The Salton Sea, California's largest inland water body, is an athalassic saline lake with an invertebrate fauna dominated by marine species. The distribution and seasonal dynamics of the benthic macroinvertebrate populations of the Salton Sea were investigated during 1999 in the first survey of the benthos since 1956. Invertebrates were sampled from sediments at depths of 2–12 m, shallow water rocky substrates, and littoral barnacle shell substrates. The macroinvertebrates of the Salton Sea consist of a few invasive, euryhaline species, several of which thrive on different substrates. The principal infaunal organisms are the polychaetes *Neanthes succinea* Frey & Leuckart and *Streblospio benedicti* Webster, and the oligochaetes *Thalassodrilides gurwitschi* Cook, *T. belli* Hrabe, and an enchytraeid. All but *Neanthes* are new records for the Sea. Benthic crustacean species are the amphipods *Gammarus mucronatus* Say, *Corophium louisianum* Shoemaker, and the barnacle *Balanus amphitrite* Darwin. *Neanthes succinea* is the dominant infaunal species on the Sea bottom at depths of 2–12 m. Area-weighted estimates of *N. succinea* standing stock in September and November 1999 were two orders of magnitude lower than biomass estimated in the same months in 1956. During 1999, population density varied spatially and temporally. Abundance declined greatly in offshore sediments at depths >2 m during spring and summer due to decreasing oxygen levels at the sediment surface, eventually resulting in the absence of *Neanthes* from all offshore sites >2 m between July and November. In contrast, on shoreline rocky substrate, *Neanthes* persisted year round, and biomass density increased nearly one order of magnitude between January and November. The rocky shoreline had the highest numbers of invertebrates per unit area, exceeding those reported by other published sources for *Neanthes*, *Gammarus mucronatus*, *Corophium louisianum*, and *Balanus amphitrite* in marine coastal habitats. The rocky shoreline habitat is highly productive, and is an important refuge during periods of seasonal anoxia for *Neanthes* and for the other invertebrates that also serve as prey for fish and birds.

Introduction

The Salton Sea has great ecological importance within the Pacific Flyway due in part to the abundant invertebrate populations that serve as a food base for migratory and resident bird species. Restoration objectives of the Salton Sea Reclamation Act of 1998 recognize this importance, and mandate the maintenance of habitat components for waterfowl as well as the present fishery. The infaunal polychaete *Neanthes succinea* is the key benthic link between detritus accumulating on the sediments and higher trophic level organisms, including predaceous birds and fish. *Neanthes* constitutes a major portion of the diet of adult bairdiella (*Bairdiella icistia* Jordan & Gilbert) and juvenile corvina *Cynoscion xanthulus* Jordan & Gilbert (Quast, 1961; Whitney, 1961) and is heavily preyed upon by eared grebes (*Podiceps nigricollis* Brehm) staging at the Sea (J. Jehl, pers.com.). Despite the importance of *Neanthes* within the Sea, few *in situ* studies on the species have been attempted. The abundance of *Neanthes* in offshore sediments was last estimated in 1956 by Carpelan & Linsley (1961a), and monthly abundance of *Neanthes* at one shoreline location was recorded throughout 1972 when salinity was 38 g l^{-1} (Reilly, 1974). More recent surveys of the Salton Sea biota examined contaminants and potential toxins associated with invertebrate fauna, but did

not include quantitative information on distribution, abundance, or seasonal trends (Setmire et al., 1990, 1993; Schroeder et al., 1993). Furthermore, there is no information on the seasonality of the invertebrate communities associated with the rocky substrates and barnacle shell substrates found along the perimeter of the Sea.

From the 1930s to 1961, California Department of Fish and Game introduced at least 29 species of marine invertebrates into the Sea to develop potential commercial fisheries and to create a food base for emerging sportfisheries (Carpelan & Linsley, 1961a). Of those species, only *Neanthes succinea* remains, persisting under highly eutrophic conditions, a 19–21 °C range in seasonal mean water temperature, and sulfate concentration nearly 3 times greater than in seawater (S. Hurlbert, unpubl. data; Watts et al., 2001). The present species composition of benthic macroinvertebrates represents inocula from the Gulf of California, Pacific Ocean, and the Gulf of Mexico.

As adults, *Neanthes* and the other invertebrate species provide food for fish and birds that forage on the bottom; their juveniles and reproductive stages provide food for fish feeding in the water column and at the water surface. Because there are so few species in the food chain, changes in the physical and chemical environment in the Salton Sea have the potential for destabilizing the food base, adversely affecting fish and birds. The purpose of this study is to document the species composition, abundance, and seasonality of macroinvertebrates associated with specific benthic habitats. We sampled the sublittoral sediments of the Sea at depths of 2–12 m, and the shoreline habitats comprising barnacle shell substrates, barnacle-covered rocks, and algae-covered rocks. Also, we determined the seasonal abundance of swarming heteronereids of *Neanthes succinea* to quantify their availability to fish and birds foraging at night.

Description of major species

Neanthes succinea is a euryhaline nereid polychaete first reported in the Sea by Hartman (1936) and was probably introduced in 1930 from Mission Bay, San Diego (Carpelan & Linsley, 1961a). At sexual maturity, benthic adults metamorphose into nektonic heteronereids, which are distinguished from nonreproductive adults by the presence of natatory setae and an enlarged medial region for gamete storage. Reproduction occurs when heteronereids swim to the surface and release gametes through ruptures in the body wall. After spawning, individuals die. Fertilized eggs develop within 24 h into pelagic trochophore larvae which settle on the bottom after approximately 2 weeks (Carpelan & Linsley, 1961b).

Balanus amphitrite Darwin is a common midlittoral barnacle found throughout temperate and tropical waters, and tolerates eutrophic and polluted marine environments and salinity levels of up to 78 g l^{-1} (Simmons, 1957; Calcagno et al., 1998). Introduction of this species into the Salton Sea probably occurred in 1944 via military seaplanes or buoys brought in from the Pacific coast (Cockerell, 1945; Rogers, 1949).

The amphipod *Gammarus mucronatus* Say is found throughout the Atlantic Seaboard (Quebec to the Gulf of Mexico) inhabiting estuaries, other brackish intertidal zones, and hypersaline lagoons. This crustacean is often associated with seagrasses and/or chlorophytes (Barnard & Gray, 1968; Bousfield, 1973). In the Salton Sea it is epibenthic in the littoral zone, and also neritic. It most likely became established in the Salton Sea after 1956, as no amphipod was recorded by Carpelan & Linsley (1961a) during their study. In the laboratory, *Gammarus* reproduces over increasing salinities of Salton Sea water up to 65 g l^{-1} (D. Dexter & P. McNair, unpubl. data).

This study confirms the tentative identification by Barnard & Gray (1968) of *Corophium louisianum* Shoemaker in the Salton Sea. *Corophium* is a euryhaline amphipod distributed along the entire Gulf coast, and is found in brackish and marine waters up to 75 g l^{-1} (Hedgpeth, 1959). In those locations, *C. louisianum* lives in self-constructed tubes attached to roots of marsh grass or other firm substrates, and forms an important component in the diet of estuarine fish (Thomas, 1976; Heard, 1982; Rozas & LaSalle, 1990). Both *C. louisianum* and *G. mucronatus* may have been introduced into the Salton Sea in 1957 when California Dept. Fish and Game planted stands of shoal grass (*Diplantha wighti*) from Texas for wildfowl food (Barnard & Gray, 1968).

The spionid polychaete *Streblospio benedicti* Webster inhabits the upper 2–3 cm of muddy to slightly sandy sediments in marine environments throughout the world and can recruit to disturbed and polluted environments (McCall, 1977; Pearson & Rosenberg, 1978; Levin, 1986; Chandler et al., 1997). This species can exploit both suspension and surface-deposit feeding (Levin, 1986). The presence of *Streblospio* represents a new report for the Salton Sea, and pos-

sibly a new salinity record for this species. Based on its lecithotrophic mode of development (L. Levin, pers. com.), the origin of the Salton Sea population appears to be the Pacific Coast of North America.

The tubificid oligochaetes *Thalassodrilides belli* Cook and *T. gurwitschi* Hrabe are commonly found in marine and brackish sediments both intertidally and subtidally throughout the Caribbean and the Gulf of Mexico, while *T. gurwitschi* also has a circumtropical distribution (Milligan, 1986; Erséus, 1990). The enchytraeid could not be identified from preserved specimens, but is most likely a species of *Marionina*, a genus with a cosmopolitan distribution commonly found in intertidal and supralittoral habitats (Giere & Pfannkuche, 1982).

We did not quantitatively sample for other marine taxa present in the Sea (the turbellarian *Macrostomum pusillum* Ax, the ostracod *Cyprideis beaconensis* LeRoy, and the harpacticoid copepod *Cletocamptus deitersi* Richard). Thirteen putative species of nematodes were distinguished in benthic samples collected from a variety of habitats, and are discussed in Warwick et al. (2002). Two non-marine insects, the corixid *Trichocorixa reticulata* Guérin–Menéville and larvae of the brine fly *Ephydra cinerea* Jones, can be abundant within hypersaline pools in shoreline regions around the Sea, but are rarely found in the Sea proper, and thus were not included in our study. Scanning electron micrographs of all these species are presented in Kuperman et al. (2002).

Methods

Benthic fauna of the soft offshore sediments

Benthic grab samples were taken at stations along 3 transects extending out from shore. These transects were selected in relation to the three stations (S1, S2, S3) used for plankton sampling and water quality monitoring during 1997–1999 (Fig. 1). Transect 1 began at the State Recreation Area and extended along a course of 165° toward S1. Transect 2 began offshore of Bombay Beach and extended on a course of 261° toward S2. Transect 3 began off of the shoreline approximately 8 km south of Bombay Beach, and extended on a course of 244° toward S3. Stations S1, S2 and S3 are located at 115° 55′ W, 33° 25′ N (9.6 km south of State Recreation Area); 115° 51′ W, 33° 21′ N (8.0 km northeast of Salton City); and 115° 48′ W, 33° 18′ N (9.0 km east of Salton City), respectively. The angle of Transect 3, the southernmost transect, was selected with the expectation that laminated sediments reported by Walker (1996) would be encountered along that trajectory.

The infaunal benthos was sampled on January 18–19, March 27, April 16–17, May 19, July 13, September 27–28, and November 20, 1999. Triplicate grab samples were taken along each transect at each of 6 stations corresponding to depths of 2, 4, 6, 8, 10, and 12 m. We used a petite Ponar grab, which samples an area of 15 × 15 cm to a depth of 15 cm. The grab always filled during our sampling. GPS coordinates for each station were recorded on each sampling date. Because the sediment was impenetrable at Station 2 on Transect 3 in January, the replicates for that station were obtained at a slightly deeper (2.3 m) location nearby. The contents of each grab were rinsed on a 1000 μ sieve and material remaining on the screen was preserved in a solution of buffered 3.4% formaldehyde with rose bengal added.

On March 27, stations 4 to 12 m on Transect 3 were sampled but the Ponar grab was lost at station 2 m as a result of a cable break. Thus, T3-2 m and Transects 1 and 2 were sampled on April 16–17. The counts of benthic invertebrates for the March and April sampling dates were not treated separately during data analysis.

Sediment analysis

Sediment characteristics can be important factors affecting the distribution of infaunal invertebrates. Replicate samples of the top 15 cm of sediment were collected at each station in March and September. Total carbon, total nitrogen, and organic carbon content were determined using a CE Instruments NCS 2500 elemental analyzer calibrated against Montana Pine standard. Particle size analysis was performed on sediments collected in March utilizing a combination of wet sieving through a US standard sieve series and the hydrometer technique (Cox, 1996). A Mettler electronic balance was used to weigh dried sediment fractions to the nearest mg to determine size distributions.

Macrozooplankton tows

On each sample date beginning at sunset, we conducted 3 replicate tows for macrozooplankton to determine the abundance and biomass of nektonic heteronereids of *Neanthes succinea*. A 1000 μ mesh net (0.8 m in diameter, 2.5 m long) was towed along a course of 280° from the mouth of Varner Harbor at

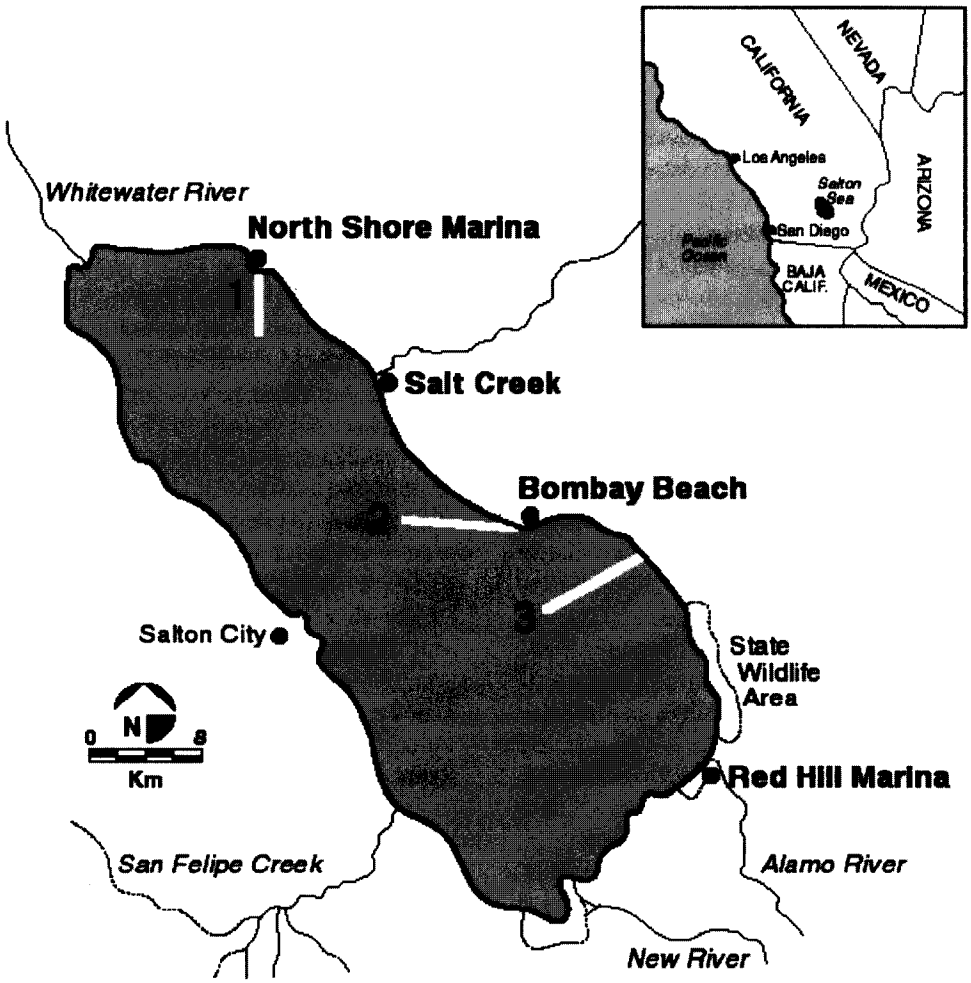


Figure 1. Location of sites sampled bimonthly throughout 1999. Benthic transects are numbered 1–3. Barnacle sand sampling occurred at North Shore, Salt Creek, and Bombay Beach. Rocky substrata were sampled at Red Hill Marina

0.8 km/h for 10 min, sampling ~67 m^3 if we assume 100% filtration efficiency. Water depth along this trajectory ranged from 2.7 m to 6.2 m. Organisms were preserved on site in a solution of buffered 3.4% formaldehyde with rose bengal added. The lengths of heteronereids from each collection were measured to the nearest mm. In collections where there were >50 heteronereids, 50 individuals were randomly selected for measurement using a plankton splitter.

Benthic flora and fauna associated with shoreline littoral substrates

Rocky substrates

Hard substrates available in the Salton Sea for epifaunal colonization consist of rocks, submerged structures, construction materials, imported fill (e.g. concrete riprap) and precipitated calcium carbonate deposits. Quadrat sampling of invertebrates on hard substrates was carried out on the southern jetty at Red Hill Marina on two substrate types: rocky substrate lacking macroscopic algae (and dominated by *Balanus amphitrite*) and rocky substrate dominated by the chlorophytes *Chaetomorpha linum* Müller and *Enteromorpha intestinalis* (L.) Link. The locations of five quadrats on barnacle-covered rock were haphazardly selected along the exposed side of the jetty, while five quadrats on algae-covered rock were selected along both the exposed and protected sides of the jetty. Quadrat sites were restricted to smooth surfaces between 0 and 90° slope. All samples were collected within 15 cm of the water surface, and sites were selected at least 3 m apart from each other.

Each quadrat was sampled using a scraping device constructed specifically for this purpose. The device is a stainless steel box measuring 15 × 15 × 5 cm. The bottom surface of the box has a sharpened flange directed 45° downward, creating a 10 × 1.5 cm opening into which the sample is scraped. The top face of the box is screened with 1000 μ mesh to prevent loss of organisms, and is hinged to allow removal of collected material. On both sides of the box are handles 10 cm long, which were used to delimit a 10 × 10 cm area for scraping. Samples were preserved in a solution of buffered 3.4% formaldehyde with rose bengal added.

Barnacle shell substrates

A major shoreline habitat all around the Salton Sea, especially at very shallow depths (less than 0.3 m), consists of intact and broken barnacle shells and associated unconsolidated sediments, ranging in particle size from coarse sand to gravel. Invertebrates present in barnacle shell substrates were sampled on open shoreline sites at Bombay Beach, Salt Creek, and State Recreation Area Headquarters (Fig. 1).

Three replicate samples at each site were collected using a stainless steel corer (area 0.01 m^2) which penetrated the sediment 10 cm. Samples were collected at 0.3 m depth, within 0.5 m of the shoreline. Each sample was rinsed on a 1000 μ sieve, and all of the remaining material on the sieve was preserved in the field with a solution of buffered 3.4% formaldehyde with rose bengal added. In the laboratory, each sample was divided using a Folsom plankton splitter to obtain a subsample with 1/8th the original volume of the field-collected sample. This sample was transferred into 70% ethyl alcohol for later enumeration of organisms.

Sample processing

In the laboratory, organisms were separated from the associated debris, identified under a dissecting microscope, and transferred to 70% ethyl alcohol. Count data of polychaetes and amphipods represented intact individuals and head segments. Specimens were identified to the lowest taxonomic level possible. In the case of unknown species, representative specimens were sent to taxonomic specialists for further identification.

Complete collections of preserved *Neanthes* from grabs and from all quadrats collected on algae-covered rocks were blotted on filter paper and weighed on an analytical balance to determine weight per individual and biomass per m^2. Individual *Neanthes* were weighed live and after preservation to determine a factor to convert alcohol wet weight biomass to wet weight:

$$\text{Wet weight} = \text{alcohol wet wt.} \times 1.0649.$$

Wet weights were averaged over transects, and the overall mean was multiplied by geometric mean density of *Neanthes* along each transect per date, then those numbers were averaged into the means plotted in Figure 3B.

The proportion of gravid amphipods collected from algae covered rock quadrats was determined on each sampling date by examining individuals under the dissecting microscope for the presence of eggs or young in the brood pouch.

Data analysis

For the various sorts of abundance data, geometric means were calculated. The first step was to add a constant (c) to each raw datum, corresponding to the smallest non-zero value possible based upon the sampling and counting methods used. When the entirety of each sample is examined and results are reported as number per sample, the constant is 1, as in the case of grab and quadrat sampling. For macrozooplankton tows, the constant is 0.015 and for sand cores, the constant is 8. For weight data, the constant corresponds to the weight of the smallest individual encountered (0.0015 g). Standard errors were determined from log transformed data. Backtransformation of the standard error (SE) from log units yields the standard error factor (SEF). The value of SEF includes the constant. Thus for geometric means, the upper and lower boundaries (B) of the 'mean ± standard error' are obtained as follows:

$$B_{\text{upper}} = [(\text{Geom. Mean}) \times \text{SEF}] - c$$

$$B_{\text{lower}} = [(\text{Geom. Mean}) \div \text{SEF}] - c$$

Values for *Neanthes* density in offshore sediments represent the mean of 9 replicates taken on each sampling date at each depth. Standard errors are based on 3 means, one from each transect.

To estimate the area-weighted standing stock of *Neanthes* on each sample date, we used lake surface area as a proxy for bottom area. First, we computed the area of lake surface that would be exposed if the lake elevation dropped 2, 4, 6, 8, 10 and 12 m in depth, using recent bathymetric data (Ferrari & Weghorst,

1997). We assumed an initial lake elevation of −69 m sea level. Next, we subtracted those areas from the present lake area to obtain areas of lake bottom lying at 0–2, 2–4, 4–6, 6–8, 8–10,10–12, and 12– 14 m depth. Each final area was multiplied by the mean density of *Neanthes* at each depth, and this product was then multiplied by the average mass per individual at each station. We assumed that numerical and biomass density of *Neanthes* at ≥12 m were equivalent to values at 12 m, and that 14 m represented the bottom of the Sea. Estimated standing stock of *Neanthes* in 1956 was recomputed using more accurate measurements of area as described above. September and November 1956 biomass density data were separately analyzed. Data from 2 m depth intervals were converted to geometric means for comparison to 1999 data. When there was no data for a given depth, biomass density at the next lower depth was used. Mean values at a given depth were multiplied by the area of lake bottom at that depth, and all depth values summed to determine standing stock.

Water column and sediment properties

Oxygen concentration and temperature values reported in Figure 3 represent the means of all temperature and oxygen measurements recorded from the mid-lake vertical profiles along S1, S2, and S3 for each month when benthic sampling occurred (Watts et al., 2001, see their 'Methods'). We assumed that the oxygen concentration at the mid lake stations at a particular depth represents the mean oxygen concentration on the sediment surface at the depth we sampled.

We compared differences in carbon, nitrogen, and C:N ratios of sediments collected in March and September by multiple *t* tests on means of log-transformed data, and compared the relationship between sediment elemental content and depth using Spearmann rank correlation analysis.

Results

Sediment characteristics

The sediment characteristics of all stations sampled by grab are shown in Figure 2. Most of the sediments at depths below 2 m consist of coarse silt (mean particle size 59 μ). While there was little evidence of difference in mean silt content of sediments at T2 and T3 stations between 4 and 12 m ($P = 0.11$, paired *t* test), mean silt content of 4–12 m sediments along T1 was

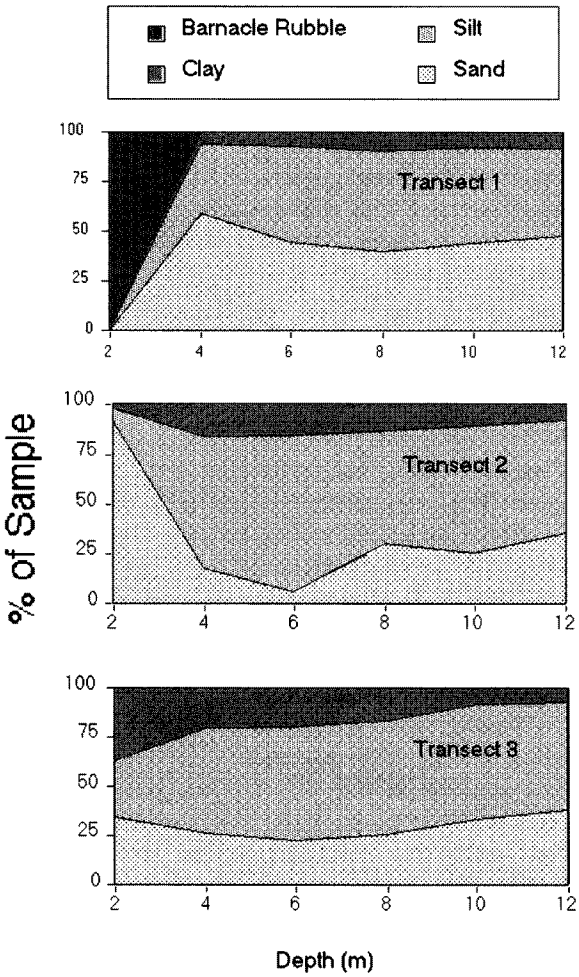


Figure 2. Sediment composition of samples from six stations along three transects in the Salton Sea, California in March 1999.

lower than along T2 and T3. Sediment characteristics at 2 m differed markedly among transects. At T1-2 m, a surprising finding was that much of the substrate was composed of loose clusters of live barnacles at high densities (up to 18 026 m^{-2}), and this precluded the determination of C and N content of those sediments. At T2-2 m, the bottom was sandy with moderately-sorted sediments, while the sediments at T3-2m consisted of moderately-sorted clay.

Mean total carbon content, organic carbon content, nitrogen content, and C:N ratio all varied between locations and sampling dates (Table 1). Along T3, both mean total carbon and nitrogen content were higher in March than in September, but distinctive seasonal differences were not apparent along the other two

Table 1. Seasonal changes in carbon and nitrogen content of sediments sampled along three transects in the Salton Sea, California. Nitrogen and carbon content was not determined for T1–2 sediments. Values presented are means of 4 replicates. Correlation coefficients relating elemental content to depth are compared below. 2 m stations were not included in the calculation of mean values

Station		Total Carbon Content (mg C g dry wt^{-12} ± SD)			Organic Carbon Content (mg C g dry wt^{-12} ± SD)			Nitrogen Content (mg C g dry wt^{-12} ± SD)			C:N molar ratio ± SD		
		March	Sept.	*P*	March	Sept.	*P*	March	Sept.	*P*	March	Sept.	*P*
1-4		5.98±0.13	7.22±0.15		2.82±0.51	5.97±0.14		0.46±0.04	0.41±0.08		15.2 ± 1.32	21.22± 4.07	
1-6		6.36±0.41	7.11±0.12		5.43±0.69	5.48±0.19		0.50±0.06	0.35±0.04		14.9 ± 2.16	23.83± 2.41	
1-8		6.78±0.11	7.09±0.47		5.42±0.85	5.26±0.41		0.45±0.01	0.25±0.06		17.4 ± 0.70	34.16± 6.03	
1-10		7.46±0.29	8.87±0.34		6.37±0.19	7.58±0.26		0.56±0.10	0.52±0.07		15.9 ± 3.53	20.15± 1.79	
1-12		7.21±0.60	8.41±0.86		6.66±0.28	7.02±0.34		0.52±0.02	0.48±0.06		16.1 ± 0.72	20.60± 0.76	
	Mean	6.76±0.60	7.74±0.84	0.06	5.34±1.51	6.26±1.00	0.29	0.50±0.05	0.40±0.11	0.12	15.9 ± 0.98	23.99± 5.86	0.01
	r	0.80	0.70		0.73	0.55		0.39	0.43		0.18	−0.23	
	P	0.000	0.001		0.000	0.013		0.088	0.057		0.45	0.32	
2-2		0.60±0.07	1.13±0.03		0.24±0.04	0.57±0.05		no data	0±0[A]		-	-	
2-4		3.21±0.20	4.17±0.24		1.78±0.14	2.10±0.22		0.29±0.06	0.08±0.03		13.5 ± 2.97	69.3 ± 28.06	
2-6		4.13±0.06	5.16±0.56		2.35±0.05	2.53±0.73		0.32±0.02	0.11±0.03		14.9 ± 1.12	55.15± 11.73	
2-8		5.69±0.16	4.15±0.28		3.17±0.27	2.93±1.04		0.26±0.02	0.10±0.03		26.0 ± 1.16	51.83± 14.77	
2-10		5.51±0.22	4.16±0.13		3.37±0.14	3.58±0.53		0.29±0.01	0.15±0.02		22.1 ± 1.33	31.98± 3.76	
2-12		6.04±0.36	7.81±0.66		4.44±0.77	7.64±0.33		0.36±0.01	0.51±0.07		19.5 ± 0.84	18.12± 1.50	
	Mean	4.92±1.19	5.09±1.58	0.29	3.02±1.02	3.76±2.24	0.18	0.30±0.04	0.19±0.18	0.21	19.2 ± 5.12	45.3 ± 20.2	0.02
	r	0.91	0.63		0.97	0.90		0.39	0.62		0.56	−0.75	
	P	0.000	0.001		0.000	0.000		0.09	0.003		0.01	0.000	
3-2		3.32±0.31	2.78±0.08		0.69±0.17	1.14±0.10		0.10±0.01	0.01±0.01		40.4 ± 0.82	141.8 ±195.7	
3-4		5.40±0.21	4.54±0.33		2.03±0.25	2.05±0.08		0.18±0.01	0.05±0.04		34.8 ± 1.33	64.43± 46.92	
3-6		5.62±0.40	4.52±0.06		2.95±0.44	2.20±0.06		0.20±0.01	0.09±0.02		32.6 ± 1.38	58.35± 11.75	
3-8		5.53±0.46	3.77±0.10		2.98±0.62	2.15±0.14		0.23±0.01	0.10±0.04		28.6 ± 0.68	47.49± 17.05	
3-10		5.81±0.73	3.84±0.26		3.23±0.23	2.52±0.14		0.27±0.02	0.15±0.03		24.7 ± 1.73	30.58± 3.83	
3-12		6.31±0.54	4.40±0.61		5.17±0.26	3.97±0.69		0.38±0.02	0.26±0.07		19.1 ± 0.77	20.69± 2.75	
	Mean	5.73±0.35	4.21±0.38	0.00	3.27±1.15	2.58±0.08	0.48	0.25±0.08	0.13±0.08	0.04	27.96± 6.2	44.3 ± 18.4	0.16
	r	0.72	0.21		0.91	0.92		0.98	0.93		−0.97	−0.95	
	P	0.000	0.32		0.000	0.000		0.000	0.000		0.000	0.000	

[a]Below detection limits.

transects. Sediment organic carbon content remained similar between seasons along all transects. Mean nitrogen and total carbon content at T1 at any given depth on both dates ($n = 10$) was up to 2.5 times higher than at the same depth along T2 and T3. Total carbon and organic carbon content were lowest in the sandy sediments at T2-2 m.

Total carbon increased with depth along all 3 transects in March, but this relationship decoupled along T3 in September. Organic carbon increased with depth along all transects in both March and September, while nitrogen content increased with depth at each transect in September. C:N ratios were consistently greater in September than in March, and showed clear decreases with depth along T3 on both dates, but less obvious patterns at the other transects.

Benthos of soft sediments

Neanthes succinea was the dominant benthic species, present at all depths along the three transects during late winter and early spring (Fig. 3). Density of *Neanthes* was consistently highest at the 2 m stations, particularly in July at 2 m (8325 ind m^{-2}), and biomass density at that depth was also greatest (32.19 g m^{-2}). However, density declined over the summer throughout the lake, as oxygen content decreased and mean water temperature remained elevated. In July, worms were present only at 2 and 4 m stations. By September, pileworm density was reduced 95% relative to July, and worms were present only at the 2 m stations. By November, *Neanthes* had begun to recolonize sediments at 12 m.

During January and March, mean biomass of individual *Neanthes* from 4 to 12 m stations was 3 times greater than for specimens collected at 2 m

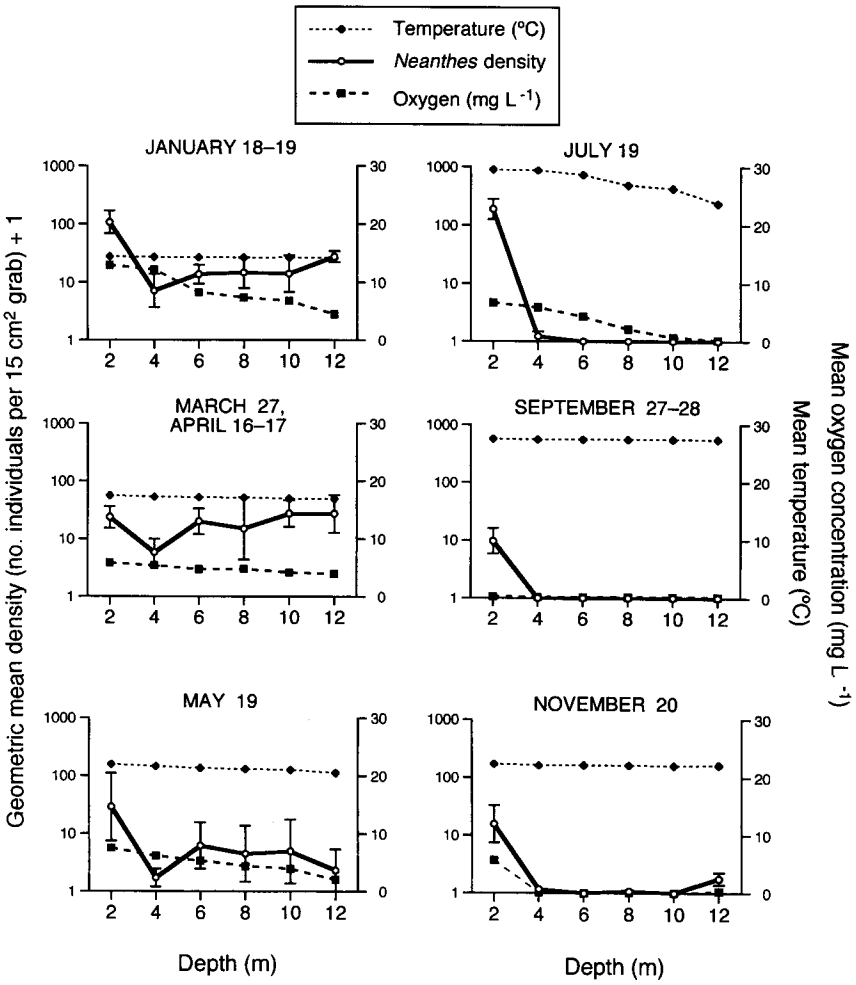


Figure 3. Variation of *Neanthes* density, oxygen concentration, and temperature with depth on six sampling dates, 1999. Each density value at each depth represents the geometric mean ± SE of 3 transects, and includes the constant (c=1). Oxygen concentrations and temperature at sediment surface are estimated from the mid-lake vertical profiles of Watts et al. (2001) (see 'Methods').

depth (Table 2). Mean size and mean biomass per m^2 were greatest in March, and lowest in September (Fig. 4A,B). The standing stock of *Neanthes* was highest in March, and about 6.5% of the total standing stock was found between 0 and 4 m depth, increasing to 41% in May. From July to November, 99% of the standing stock was restricted to sediments 0–4 m depth (Table 2). During September, there was little correlation between density of *Neanthes* and sediment organic content (Spearmann $r = -0.40$, $P = 0.12$).

The other infaunal macroinvertebrates present in offshore sediments were the oligochaete *Thalassodrilides belli* and the spionid *Streblospio benedicti*. *Thalassodrilides belli* was observed only once during 1999 (within barnacle clusters at T1–2 m in July) at high density (13 542 m^{-2}). *Streblospio* was found in sporadically and in low numbers at shallow (2 & 4 m) stations along T1 and T2, but was always present at station T3-2 m, where clays composed nearly 40% of the sediments. Maximum density of *Streblospio* reached 2797 m^{-2} in January 1999. On rare occasions, *Gammarus* was present at 2 m stations but at low density (<0.01 m^{-2}).

Macrozooplankton

Nektonic macroinvertebrates were present in the water column on each sampling date, although abundance varied greatly between dates (Table 3). The main period of *Neanthes* spawning occurred during March, and heteronereid length ranged from 15 to 35 mm

Table 2. Biomass of *N. succinea* in the Salton Sea during 1999. Area estimates used in computation of standing stock were based on recent bathymetric date (Ferrari & Weghorst, 1977)

Date	Depth stratum (m)	Weight per worm mg (SEF)	Biomass Density g wet wt m^{-2} (SEF)	Standing stock for specified depth (metric tons)
January	0–4	4.58 (1.40)	23.15 (1.15)	3510
	4–14	13.62 (1.17)	9.08 (1.23)	7223
	Whole lake	–	–	10 733
March	0–4	7.06 (1.25)	7.88 (1.86)	1195
	4–14	22.27 (1.24)	17.50 (1.49)	13 930
	Whole lake	–	–	15 125
May	0–4	1.51 (2.72)	1.48 (8.07)	224
	4–14	1.46 (4.61)	0.25 (10.21)	199
	Whole lake	–	–	423
July	0–4	3.63 (1.31)	32.19 (1.55)	4881
	4–14	0.003 (1.03)	0.005 (1.07)	4
	Whole lake	–	–	4885
September	0–4	0.97 (1.29)	0.44 (1.79)	67
	4–14	[a]	–	0
	Whole lake	–	–	67
November	0–4	3.52 (1.64)	2.61 (3.10)	396
	4–14	0.13 (1.26)	0.007 (1.36)	6
	Whole lake	–	–	402

[a] In September there were no individuals present from 4 to 12 m depth.

Table 3. Abundance of swarming *N. succinea* heteronereids and nektonic organisms collected per 67 m^3 tow conducted within 2 h after sunset. $n = 3$ tows on each date

Date	Heteronereid length (mm) mean ± SE	Density no. per 67 m^3 (SEF)			
		Neanthes Heteronereids	*Neanthes* Nectochaetes	*Gammarus mucronatus*	Fish juveniles
January 18	0	0	0	1.0 (1.00)	0
March	23.5 ± 0.70[A]	7.3 (22.50)	0	34.4 (1.69)	0
May 16	0	0	4.5 (1.55)	0.3 (4.63)	0
July 19	14.1 ± 1.36	0.1 (7.37)	55.9 (1.31)	0.1 (9.54)	6.2 (1.30)
September 27	14.4 ± 0.89	2.0 (1.99)	0	0	7.9 (1.63)
November 20	14.5 ± 2.83[A]	35.7 (1.85)	0	0	11.0 (1.09)

[A] $n = 50$.

(mean 23.5 mm). A second peak of reproductive activity occurred in November, and those heteronereids were smaller (10.9–20.1 mm, mean 14.5 mm). Juvenile fish appeared in the plankton in July, and became more abundant in following months.

Benthos of shoreline substrates

Rocky substrates

This survey revealed that rocky shoreline habitats serve as important refuges for invertebrates during

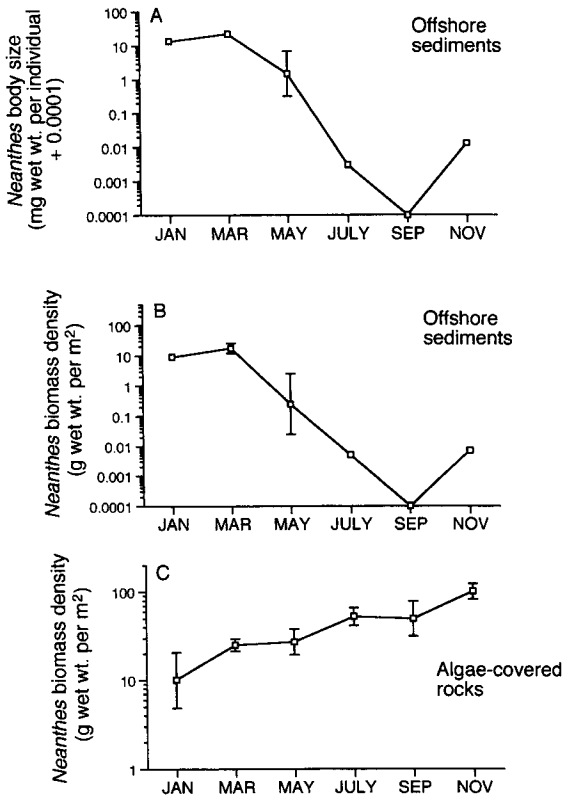


Figure 4. (A) Body weight of *Neanthes* in offshore sediments (depths≥ m); n=3 transects. (B) Biomass density of *Neanthes* in offshore sediments. (C) Biomass density of *Neanthes* on algae-covered rocks at Red Hill Marina, n=5 quadrats for each date. All values represent mean ± SE.

periods when the lake is stratified and hypoxic conditions prevail (e.g. much of summer and fall). Invertebrates were abundant on rocky substrates even when they were scarce or absent from other shoreline habitats, and in September 1999, biomass density of *Neanthes* on algae-covered rocks was nearly two orders of magnitude greater than in offshore sediments (Table 2, Fig. 4C). Biomass density on algae-covered rocks nearly doubled to 101 g.m^{-2} between July and November.

In January, there were clear differences in abundance of species on algae-covered rocks, and on rocks lacking algae (and dominated by barnacles). Organisms were consistently more numerous on the former (Fig. 5). Abundance of each species tended to increase in spring and summer on both substrates, though *Balanus* density dropped nearly tenfold on algae-covered rocks in September. Between January and July, mean alcohol wet weight biomass of algae increased 370%, from 0.30 kg per m^{-2} to 1.42 kg m^{-2}. Mean density of

Table 4. Percentage of total number of amphipods which were gravid on each collecting date in 1999

Date	*C. louisianum* total no. examined	*C. louisianum* % gravid	*G. mucronatus* total no. examined	*G. mucronatus* % gravid
January 19	323	15.2	167	10.2
March 28	31	9.6	3909	5.7
May 20	68	16.2	6122	5.5
July 13	300	15.3	3035	0.6
September 28	1064	21.1	583	15.8
November 21	580	14.1	1231	10.1

Gammarus on algae-covered rocks followed a similar pattern, increasing an order of magnitude from 2050 m^{-2} in January to 84 300 m^{-2} in May. In July, *Gammarus* density on algae-covered rocks was 50 times greater than on barnacle-covered rocks.

Seasonal recruitment of *Balanus* and *Neanthes* occurred in late winter. On barnacle-covered rocks, density of those species increased by nearly two orders of magnitude between January and May; in contrast, densities of *Balanus* and of *Neanthes* on algae-covered rocks did not change appreciably during the same period. *Neanthes* showed alternating bimonthly patterns of abundance between the two microhabitats from May through September, and highest mean density occurred in July on algae-covered rocks (81 100 m^{-2}). Mean density of *Corophium* increased throughout the year in both habitats, to a high of 18 160 m^{-2} in September.

Timing of amphipod reproduction

Gravid amphipods were recorded on each sample date but the greatest proportions were present in September, when 15.8% of all *Gammarus* and 21.1% of all *Corophium* examined contained either eggs or juveniles in their brood pouches (Table 4). The percentage of gravid *Corophium* was always greater than for *Gammarus*. At all times, the population of *Gammarus* was dominated by juveniles.

Shoreline barnacle shell substrates

While the shoreline barnacle shell substrate appears depauperate to the observer in the field, it is an important habitat for juvenile *Neanthes* and for oligochaetes. *Neanthes* was the most abundant species, found at all three sites and on all dates except September (Fig. 6). Most *Neanthes* collected were small recruits (<3 mm)

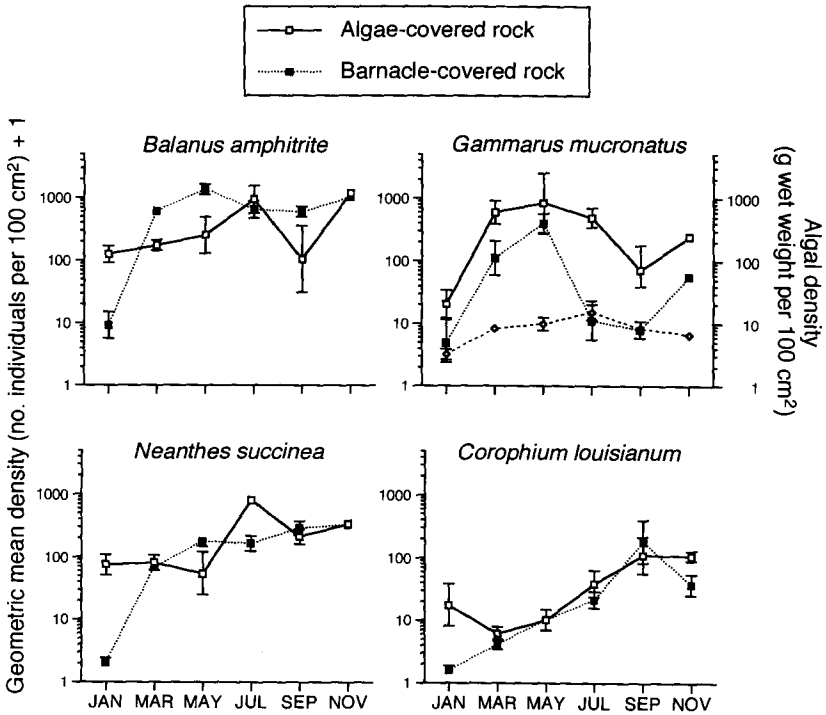


Figure 5. Densities of macroinvertebrates and macroalgae collected on rocky substrata at Red Hill, Marina, 1999. n=5 quadrats for each date. Mean values included the constant (c=1). Error bars represent ± 1 SE.

and density was highest in May at the State Recreation Area site (45 856 per m^{-2}). *Gammarus* and *Balanus* were also present, but in low density.

The tubificid *Thalassodrilides gurwitschi* and the enchytraeid were most abundant at the shoreline site near the terminus of Salt Creek. Mean oligochaete density was greatest in January 2000, at 13 808 m^{-2}. Immature tubificids were present throughout the year.

Various small taxa (nematodes, the copepods *Apocyclops dengizicus* (Lepeschkin) and *Cletocamptus dietersi* Richard, the ostracod *Cyprideis beaconensis* LeRoy, and *B. amphitrite* cyprids) were present in our core samples but could not be quantitatively sampled, so those species were excluded from data analysis. Additionally, we never encountered the corixid *Trichocorixa reticulata* or larvae of the brine fly *Ephydra cinerea* while sampling the barnacle shell substrate.

Comparison of densities across substrate types

Abundances of the five macroinvertebrate taxa are compared among 6 substrate types in Table 5, where we have converted annual mean densities to a standard area (1 m^2). *Neanthes* density showed nearly a four-fold difference among the three 2 m offshore substrates, with the barnacle rubble substrate at Station T1 2 m supporting the highest density of this organism. The highest numbers of *Neanthes* and crustaceans are found on both algae-covered and barnacle-covered rocks along the shoreline.

Discussion

Dynamics of Neanthes *in offshore sediments*

It is clear that seasonal hypoxia is the major factor influencing the distribution and abundance of *N. succinea* in the Salton Sea. Although *Neanthes* can tolerate complete anoxia for up to 27 h and survive for at least a month at 1.8 mg O_2/l in the laboratory (Carpelan & Linsley, 1961a; Martin, 1974; Kristensen, 1983), widespread hypoxic conditions in the Sea typically persist much longer. Nearly 60% of the Sea bottom was anoxic for up to five months during 1999, and the entire lake was anoxic from surface to bottom for several days in September (Watts et al., 2001: Fig. 3B, C). The abundance of *Neanthes* varied spatially and temporally between the northern and southern basins, reflecting decreases in oxygen

Table 5. Geometric mean density per m^2 of 6 dominant macroinvertebrate taxa collected from 6 substrata types at the Salton Sea on 6 sample dates in 1999. Organisms never found in a particular substratum are indicated by (Ø)

Substrate[d]	Taxon and Density [no. m^{-2} (SEF)]					
	N. succinea	*G. mucronatus*	*C. louisianum*	*B. amphitrite*	Oligochaeta	*S. benedicti*
Sand $n = 18$	830 (1.454)	11.65 (1.183)	Ø	Ø	Ø	Ø
Clay $n = 18$	1512 (1.347)	3.50 (1.054)	2.79 (1.063)	Ø	Ø	3.90 (1.472)
Barnacle rubble $n = 18$	3171 (1.538)	6.58 (1.080)	15.80 (3.017)	1946 (1.989)	18.29[a] (6.639)	Ø
Shoreline barnacle sand $n = 3$ sites, 56 reps	4043 (1.074)	118 (1.005)	Ø	526 (1.019)	1342[b] (1.048)	Ø
Barnacle-covered rocks $n = 30$	8593 (1.398)	3200 (1.449)	1218 (1.392)	37 956 (1.470)	[c]	Ø
Algae-covered rocks $n = 30$	16 367 (1.262)	21 338 (1.337)	2159 (1.334)	29 387 (1.264)	Ø	Ø

[a]Geometric mean of *T. belli* in 3 grabs at T1-2 m in July. At all other times, this species was absent from this habitat.
[b]Oligochaetes consisted of *T. gurwitschi* and *Marionina* sp.
[c]Two unidentified individuals present in 5 quadrats in July, 31 in 5 quadrats in September.
[d]Each of the substrate types except shoreline barnacle sand was sampled at one location.

concentrations throughout the water column. For example, during January and March, *Neanthes* density below 6 m depth along T1 was 2–6 times lower than along T3 and T2, respectively. In May, pileworms were absent below 6 m along T1, but were present below 10 m along T2 and T3 located within the southern basin, which is shallower and thus is more readily oxygenated through wind mixing than the northern basin (Watts et al., 2001: Figs 4 and 5).

For sediments collected in both March and September, the trend is for organic carbon to be lower where *Neanthes* density is higher, i.e. the 2 m stations. At those stations, *Neanthes* can reduce organic carbon abundance by utilizing it as a food source (Cammen, 1980). Also, it is possible that greater turbulence at 2 m results in lower net deposition rates of fine particulate organic matter. In early summer, the deeper stations become devoid of fauna and this condition can last for several months, allowing organic carbon to accumulate from input of dead organisms sinking from planktonic and nektonic communities.

To our knowledge, the Salton Sea harbors the highest densities reported for *N. succinea*, exceeding values observed in brackish and marine habitats on Atlantic and Gulf coasts (Table 6). The highest density of *Neanthes* in offshore sediments (21 267 m^{-2}) was seen within barnacle clusters and rubble at T1 2 m in May and July. Pileworms were frequently found inside empty barnacle shells. The structural heterogeneity and vertical relief of the barnacle substrate may provide refugia from fish predation, as well as reduce the frequency of intraspecific aggressive encounters (Reish & Alosi, 1968), allowing more polychaetes to coexist per unit area. Also, the loose rubble samples were usually oxygenated to 15 cm, with the reducing layer existing further below the sediment surface. Though we did not determine organic content at station T1-2 m, it is likely to be high due to

Table 6. Maximum abundance of dominant benthic macrofaunal species at Salton Sea compared to marine and estuarine environments. Values reported from this study except for *S. benedicti* are geometric means of replicated samples for a given site or station. Values reported from other studies are maximum values of individual samples, except the following studies which reported means: Shalla et al., 1995 (n = 4), Shkedy et al., 1995 (n = 4); Calcagno et al., 1998 (n = 17); LaSalle & Rozas, 1991 (n = 11); Tudorancea & Harrison, 1988 (n = 2); Galat et al., 1981 (n = 13)

Species	Habitat	Maximum density (no. per m^2)	Reference
Balamus amphitrite	Salton Sea	136 506[a]	This study
	Salton Sea	326 000	Vittor, 1968
	Lake Timsah, Egypt	99 900	Shalla et al., 1995
	Mikhmoret, Israel	4079	Shkedy et al., 1995
	Quequén, Argentina	320	Calcagno et al., 1998
Neanthes succinea	Salton Sea (algae-covered rocks)	81 153[b]	This study
	Salton Sea (mud < 1 m depth)	24 600	Reilly, 1974
	Salton Sea (mud 4 m depth)	18 781	Carpelan & Linsley, 1961a
	Salton Sea (mud 4 m depth)	1150[c]	This study
	Cape Cod, Massachusetts	3165	Sardá et al., 1995
	Newport River, North Carolina	1370	Cammen, 1979
	Black Sea	936	Murina & Mikhailova, 1994
	St. Louis Bay, Mississippi	92	LaSalle & Rozas, 1991
Streblospio benedicti	Salton Sea	632[d]	This study
	St. Louis Bay, Mississippi	1842	LaSalle & Rozas, 1991
	Newport River North CArolina	5430	Cammen, 1979
	Mission Bay, Diego	16 000	Levin, 1981
	Cape Cod, Massachusetts	42 206	Sardá et al., 1995
	San Francisco Bay mudflat	60 000	Nichols & Thompson, 1985
	Rehoboth Bay, Delaware	103 500	Watling, 1975
	Virginia estuary	140 000	Virnstein, 1979
Gammarus mucronatus	Salton Sea	84 300[e]	This study
	Parker River, Massachusetts	16 000	LaFrance & Ruber, 1985
	Chesapeake Bay	6800	Fredette & Diaz, 1986
Corophium louisianum	Salton Sea	18 157[f]	This study
	St. Louis Bay, Mississippi		LaSalle & Rozas, 1991
	in *Eleocharis* roots	7919	
	on bare mud	5525	
	San Jose Island, Texas[i]	409	Whorff et al., 1995
Oligochaeta	Cape Cod, Massachusetts	19 439[g]	Sardá et al., 1995
	Salton Sea	13 808[h]	This study
	Lake Shala, Ethiopia	8485	Turorancea & Harrison, 1988
	Newport River, North Carolina	7980	Cammen, 1979
	St. Louis Bay, Mississippi	1049	LaSalle & Rozas, 1991
	Pyramid Lake, Nevada	480	Galat et al., 1981

[a] n = 5 quadrats, barnacle-covered rocks, May 1999.
[b] n = 5 quadrats, July 1999.
[c] n = 3 grabs (T2, 4 m in January 1999). Maximum sample at 4 m: 1466 m^{-2} at T2 in January.
[d] value of individual sample T3 2 m in January 1999.
[e] n = 5 quadrats, algae-covered rocks, May 1999.
[f] n = 5 quadrrats, barnacle-covered rocks, September 1999.
[g] sum of means of *Monopylephorus evertus*, *M.* sp.2, and *Paranais litoralis* in fertilized muddy sites.
[h] n = 3 cores, Salt Creek in January 2000.
[i] *Corophium* was not identified to species.

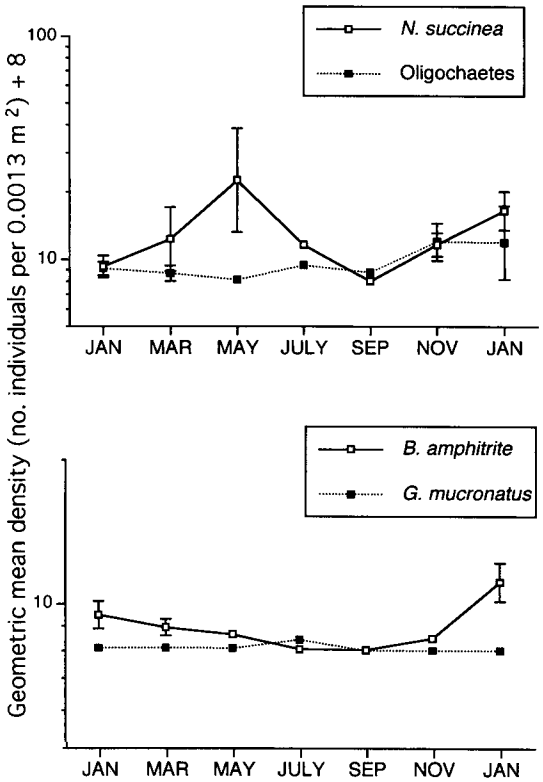


Figure 6. Densities of four invertebrates in shoreline barnacle shell substrata, n=3 shoreline sites. Mean values include the constant (c=8). Error bars represent ± 1 SE.

inputs of waste and exuviae from the living barnacle aggregations which constituted much of the substrate.

Neanthes was 2–3 times more abundant in the barnacle rubble substrate at T1-2 m than in the clay and sand substrates at T3-2 m and T2-2 m, respectively (Table 5). However, we cannot generalize these results to the rest of the Sea because we did not replicate our 2 m sites, and furthermore, the extent of Sea bottom covered by each sediment type was not determined.

We did not sample for *N. succinea* in the southernmost region of the Sea, where inflows from the Alamo and New rivers produce salinity gradients (Watts et al., 2001: Fig. 6). *Neanthes* may also be abundant 1–5 km from the mouths of the rivers, because *N. succinea* shows considerable local adaptation to lowered salinity and survives well to 29 g l^{-1} (Oglesby, 1965; Martin, 1974).

Change since 1950s

Of the 32 stations sampled for *Neanthes succinea* in 1956 (Carpelan & Linsley, 1961a: Tables 23 and 24), 17 were located on the eastern side of the Sea and within 8 km of our transects. Also, sampling was not replicated spatially or temporally in 1956, nor was the mesh size used in screening sediments reported. Despite these differences and unknowns in sampling effort, a comparison of *Neanthes* abundance across decades is worth attempting.

We compared numerical and biomass densities of *Neanthes* in 1956 and 1999 from 2 to 3 m and 4 to 12 m stations located in the northern end of the Sea. In September 1956, 5 of 17 stations sampled were between 2 and 3 m, and the remaining 12 stations were at depths ≥4 m. On November 29, 1956, 4 of 9 stations were ≤3 m. Data from 6 similar stations sampled on December 3 1956 were also included in the analysis.

There is a clear difference in *Neanthes* biomass between 1956 and 1999 (Table 7). At shallow (2–3 m) stations, geometric mean abundance of *Neanthes* in September and November 1956 was 8–10 times greater than that seen during the same months in 1999; additionally, mean biomass per m^2 at this depth was up to 50 times greater in 1956 than in 1999. This trend continued at deeper stations. Carpelan & Linsley (1961a) recorded biomass up to 75.9 g m^{-2} at 6 m in November 1956, and in the same month, mean biomass of *Neanthes* at their 11m station was 4.5 g m^{-2}. However, in November 1999 *Neanthes* was absent from our 6 m stations, and biomass at our 12 m stations averaged only 0.017 g m^{-2}.

The area-weighted estimated standing stock of *Neanthes* throughout the Salton Sea was highest in March and lowest in September (Table 2). The biomass we calculated for November 1999 (0.39×10^6 kg) was two orders of magnitude lower than Carpelan & Linsley's original estimate for the entire Sea in November 1956 (13.2×10^6 kg). Using Carpelan & Linsley's data and recent bathymetric information (Ferrari & Weghorst, 1997), we calculated standing stock as 4.9 $\times 10^6$ kg in September 1956; our data give an estimated standing stock of 0.067×10^6 kg in September 1999.

The extent and duration of anoxia during 1999 may help explain the differences in *Neanthes* abundance observed between historic periods. Interannual variation in hypoxic conditions was marked between 1997 and 1999. Anoxia did not occur above 6 m in 1997, but prior to our sampling in September 1999, the en-

Table 7. Comparison of geometric mean density and biomass of *Neanthes succinea* collected in 1956 and 1999 from offshore sediments during September and November at 2–3 m stations and 4–12 m stations

Month and depth		Numerical density no. m^{-2} (SEF)			Biomass density g m^{-2} (SEF)		
		1956	1999	*P*	1956	1999	*P*
September							
1-3 m	$\bar{x}$ (SEF)	3256 (1.17)	377.3 (1.76)	0.003	18.6 (1.32)	0.37[a] (1.76)	<0.001
	95% C.I.	1004–10 554	922–2858		5.1–68.2	0.1–4.3	
	n	5	3		5	3	
4–12 m							
	$\bar{x}$ (SEF)	282.5 (1.97)	0		0.05 (6.97)	0	
	95% C.I.	65–1222	-		0.004–0.84	-	
	n	12	3		8	3	
November							
2–3 m	$\bar{x}$ (SEF)	7402 (1.14)	596.4 (2.24)	0.08	17.3 (1.11)	2.10[b] (2.24)	0.12
	95% C.I.	2709–20 224	1146–5743		6.4–47	0.2–20.2	
	n	7	3		7	3	
4–12 m							
	$\bar{x}$ (SEF)	5395 (1.28)	6.23 (1.45)	<0.001	23.15 (1.42)	0.02 (1.45)	<0.001
	95% C.I.	1723–16 885	0.9–38.9		13.5–80.6	0.003–0.13	
	n	7	3		7	3	

[a]Mean density per m^2 of each transect was multipled by 0.97 mg (Table 2).
[b]Mean density per m^2 of each transect was multipled by 3.25 mg (Table 2).

tire surface of the Sea was almost completely anoxic for several days (Watts et al., 2001: Fig. 3B). In contrast, the Sea was oxygenated to 8 m during July and September 1956 (Carpelan & Linsley, 1961a).

Several decades of nutrient enrichment from inflow sources are likely to have increased production relative to 1956, as well as increasing the area and extent of the consequent hypoxic field when planktonic producers die, sink, and decompose on benthic sediments. Between 1907 and 1957 in the central (8–12 m) region of the Sea, approximately 22.5 mm of sediment accumulated on the bottom, composed of fine particles with mean silt content of 24% (Arnal, 1961). We noted a greater abundance of fine particles (mean silt content 51%, $n = 17$ stations), reflecting 42 additional years of sedimentation, but an increase in sediment organic carbon content relative to 1956 cannot be demonstrated from our data. Similarly, the amounts of total C and N determined in sediments in 1999 (n=128 for each) are similar to levels reported in October and November 1968 by Bain et al. (1970) (grand mean N content March, September 1999: 0.28% vs. 0.3% [n=7]; mean total C content: 5.4% vs. 4.0% [n=7]).

Predation by tilapia (*Oreochromis mossambicus* Peters), a cichlid fish not present in the Sea before the 1960s (Riedel et al., 2001), seems a likely factor contributing to the reduced abundance of *Neanthes* in nearshore (2–3 m) sediments relative to 1956. Predation by tilapia and other fish species is likely to intensify during summer months when the majority of fish are distributed close to shore due to hypoxic conditions in the main body of the Sea.

Seasonality of spawning by N. succinea

Temperature affects the seasonal reproductive cycle in *Neanthes*. Maximum frequency of heteronereid metamorphosis and spawning occurs between 15 and 20° C (Hardege et al., 1990), corresponding to mean water temperatures in the Salton Sea during spring and fall. *Neanthes* reproduces throughout the year, indicated by the presence of pelagic larvae each month with a maximum peak during spring and a secondary peak in fall (Tiffany et al., 2002). This trend was also observed by Carpelan & Linsley (1961a, b), when 65% of total settlement occurred between March and June and 27% during November and February 1956. Heteronereid lengths (Table 3) reflect pre-spawning seasonal growth and the loss of larger infaunal individuals as nektonic heteronereids. In September 1999, heteronereids were 60% shorter than in spring, and

this may be partially due to growth limitation by low nitrogen content in 2 m sediments (Table 1) as well as physiological stress from hypoxic summer conditions. The larger size of the spring heteronereid cohort reflects a longer development time experienced by the population overwintering under more favorable conditions.

Streblospio benedicti

Streblospio was found in greatest abundance at T3 2 m in sediments consisting of red and gray clay. These sediments were not easily washed through the sieve, and thus retained many *S. benedicti*, which are approximately 2–4 mm long and less than 0.5 mm wide.

Streblospio tolerates low oxygen (Ritter & Montagna, 1999) and displays opportunistic life history traits contributing to its dominance in organically enriched environments (Levin, 1986; Ibarzabal, 1997; Mendez-Ubach, 1997). Nevertheless, its density at the Salton Sea is lower than at other locations (Table 6). The low density of *Neanthes* at T3-2 m rules out competition with *Streblospio* as a controlling factor, so it is more likely that abiotic stress depresses abundance of *Streblospio* in the Salton Sea. Sardá and Martin (1993: Fig. 7a, b) examined 8 populations of *S. benedicti* in North America and Europe, and determined a positive relationship between numerical density and mean annual water temperature. Given that the mean annual water temperature at the Salton Sea is 22 °C (Watts et al., 2001), the regression equation of Sardá & Martin (1993) would predict a density 80 times higher than what we observed. They also found a negative relationship between the annual range of water temperature and mean abundance, and this would predict a density about 2.6 times greater than what we observed. Other factors, such as the high concentration of sulfate and possibly high levels of parasitization (Kuperman et al., 2002), may operate in conjunction with temperature to adversely affect physiological processes and fecundity. Experimental tests of these hypotheses would provide insight. Additionally, predation by fish and *Gammarus* may be an important factor, as *Gammarus* can capture and consume motile organisms similar in size to *Streblospio* (Hart et al., 1998).

Seasonal patterns of Gammarus mucronatus *abundance*

The seasonal increase in *G. mucronatus* paralleled the increase in macroalgal biomass. Large scale variations in the abundance of gammarids can be related to the availability of ephemeral chlorophytes (LaFrance & Ruber, 1985; Fredette & Diaz , 1986), and amphipods often comprise the numerically dominant invertebrates associated with shallow water macroalgal mats (Shannon et al., 1994). Algae can serve as a food source for *G. mucronatus* directly, and as a substrate colonized by epiphytic microflora which are also fed upon by the amphipods (Sanders et al., 1962; Zimmerman et al., 1979; Simpson et al., 1998). Algae can alter local hydrodynamic flow by dissipating wave energy, decreasing water velocity and increasing deposition of sediments onto the algal substrate. *Enteromorpha* thalli are tubular, smooth, and may be branched or unbranched. This architecture appears to trap less debris and harbors fewer epiphytes than the long, entangled filaments of *Chaetomorpha*. *C. linum* may enhance abundance of *Gammarus* by entraining more detritus, favoring the development of microflora. Additionally, algal thalli provide additional attachment surfaces which help *Gammarus* resist dislodgment by wave action (Whorff et al., 1995).

Predation by tilapia and other fish species on *Gammarus* is likely to be significant, since tilapia reduced the abundance of *G. mucronatus* in experimental microcosms (Hart et al., 1998; Simpson et al., 1998), and during the summer, fish juveniles and larvae were common in our plankton tows and numerous inside the jetty (Table 4). The high density of *Gammarus* on algae-covered rocks at the Salton Sea during summer 1999 may be due in part to a reduction in predator capture efficiency (Drake et al., 1995).

Because we did not sample *Gammarus* frequently enough to track cohort growth through size distributions (Wetzel & Likens, 1991), we could not estimate secondary production, which can reach 10 g dry wt m^{-2} yr^{-2} in temperate coastal regions (LaFrance & Ruber, 1985). Nevertheless, production by *Gammarus* is likely to be higher in the Salton Sea, due to the hypereutrophic conditions and warm water temperatures occurring throughout the year.

Information on the ecology of *C. louisianum* is scant, but it appears that its abundance at the Salton Sea is relatively high on rocky substrata (Table 7). One quadrat sampled in September yielded 109 000 ind m^{-2}, which is comparable to the density recor-

ded for *Corophium volutator* on mudflats in southern England (Gerdol & Hughes, 1994). The structural complexity of the empty barnacle shell microhabitat on rocky shorelines in the Sea increases the availability of sites for tube construction, and may provide protection from fish predation.

Seasonality of Balanus amphitrite *abundance*

Ecological theories seeking to explain patterns in spatial and temporal abundance of barnacles have traditionally invoked hypotheses examining the relative importance of postsettlement processes versus planktonic larval supply dynamics. Gaines & Roughgarden (1985) suggest that postsettlement processes determine barnacle distribution and abundance when settlement is high.

The increase in barnacle density from January forwards (Fig. 5) is in accord with heavy spring recruitment. Vittor (1968) also noted recruitment in late winter at the Salton Sea, and a general increase in density of adults from December to July. These trends reflect the seasonality of nauplii and cyprid abundance (Tiffany et al., 2002). In the Salton Sea, settlement can reach 30 ind. cm^{-2} d^{-1}, and up to 307 700 m^{-2} (Carpelan & Linsley, 1961a). Shalla et al. (1995) estimated even greater settlement (1 500 000 m^{-2}) in the Suez Canal at Lake Timsah, a saline lake ranging from 20 to 44 g l^{-1}. However, their studies did not quantify seasonal abundance of adults.

It is clear that the lack of available hard substrates in the Salton Sea is a major limiting factor for *Balanus*. Because reproductive output is high and larvae are abundant in the water column, intraspecific competition for space is high. This is readily observed at T1-2 m, where barnacles overgrew each other, forming large clusters unattached to any solid substrate.

The life history characteristics of *B. amphitrite* in the Salton Sea feature increased reproductive output and growth under elevated temperature and salinity. During most of the year, water temperatures at the Salton Sea are within the range reported by Patel & Crisp (1960) as optimal for fertilization and brood formation (22–32 °C). Hart et al. (1998) determined that nauplii production is highest at 48 g l^{-1}, near the present salinity of the Sea. Additionally, Simpson & Hurlbert (1998) found that individual basal diameter growth (mm d^{-1}) of *B. amphitrite* was 50% more rapid at 48 g l^{-1} compared to the summer growth rate (0.3 mm d^{-1}) reported by Carpelan & Linsley (1961a). Although the survival rate of adult *Balanus* in the present Salton Sea environment are not known, prior estimates of mean lifespan (4 weeks, max. 20 weeks) were made when salinity was 37 g l^{-1} (Vittor, 1968). This is less than half the lifespan of *B. amphitrite* in a fouling community on the Mediterranean shore of Israel (Shkedy et al., 1995). It is likely that the favorable breeding conditions in the Salton Sea result in several short-lived generations each year, maintaining population stability despite seasonal mortality.

Several biotic factors usually cited to explain the distribution patterns of barnacles are not operant in the Salton Sea ecosystem. For instance, there are no invertebrate predators on settled barnacles in the Salton Sea, nor are there interspecific invertebrate competitors for space. While Shkedy et al. (1995) suspected that dense cover of the algae *Spyridia filamentosa* contributed to mortality of *B. amphitrite* in the lower intertidal in Israel, it does not appear that *Enteromorpha intestinalis* or *Chaetomorpha linum* adversely affects the survival of adult *Balanus* in the Salton Sea. However, those algae may co-opt space available for settlement by cyprids, which may explain the 75-fold increase in density of *Balanus* between January and March on rocks devoid of algae (Fig. 5).

Physical disturbance may be an important postsettlement process affecting *Balanus* survival. Intraspecific crowding and heavy juvenile settlement contribute to the formation of dense clumps of elongated barnacles, and the unusual ion composition of Salton Sea water together with the lower availability of Ca^{2+} relative to seawater results in decreased shell strength (Simpson & Hurlbert, 1998). As a result, barnacle clumps can be easily detached from the substrate, and it is likely that seasonal storms cause significant barnacle mortality.

The Salton Sea lacks tidal fluctuations to structure the vertical distribution of *Balanus*, but the lake elevation varies annually due to the seasonal inflows of agricultural runoff. During 1999, lake elevation fluctuated 2 dm, and was highest during March through July (Fig. 2D, Watts et al., 2001). Barnacles settling at the waterline during that interval would eventually perish from exposure.

Seasonality of amphipod reproduction

On all sample dates in 1999, the Salton Sea population of *G. mucronatus* was dominated by juveniles, indicating year-round recruitment. In contrast, *Gammarus* recruits from spring through fall on the east coast of North America and produces 6–9 cohorts yr^{-1}

(LaFrance & Ruber, 1985; Fredette & Diaz, 1986). We observed the highest percentage of gravid *Gammarus* in September, when water temperatures were highest. The elevated water temperatures at the Salton Sea during summer would certainly affect growth and maturity rate and contribute to short generation times. Total development time in *G. mucronatus* (from ovulation to emergence of young from the brood pouch) may be as short as 4.5–6.5 d when water temperature reaches 22 °C (Borowsky, 1980), and maturation may occur sooner than the 3–5 week period reported for *G. mucronatus* in temperate regions (Fredette & Diaz, 1986).

Our sampling methods certainly did not collect all the juvenile *Corophium*, so their abundance is underestimated, but juveniles of *Gammarus* are better represented in our samples. Although there is little information on the life history characteristics of *C. louisianum*, other corophiids are known to produce 4 or more generations per year with generation times of 4–5 weeks (Birklund, 1977; Nair & Anger, 1979; Omori et al., 1982).

Seasonal abundance of species found in shoreline barnacle shell substrates

Several factors may work in concert to drive the seasonal dynamics of *Neanthes* in littoral sediments. During summer months, water temperature in the shallow littoral zone occasionally exceeds 36 °C, the 96 h LT_{100} reported for a Salton Sea population of *Neanthes* (Martin, 1974). Additionally, in summer larval supply is low (Tiffany et al., 2002), and predation intensity on adults and larvae is likely to be high in nearshore regions, because juvenile and adult fish are concentrated there by the hypoxic conditions in the main body of the Sea (Riedel et al., 2002, Watts et al., 2001). Moreover, localized die-offs of *Neanthes* may result from onshore movement of sulfide-laden 'green water' after certain wind and current conditions in spring and summer (Watts et al., 2001). Any of these factors may have occurred singly or in concert during September 1999, resulting in the extirpation of *Neanthes* from all the littoral stations we sampled.

Immature tubificids and adult *Thalassodrilides gurwitschi* and the enchytraeid were present in barnacle shell substrates throughout the year, including September. Oligochaetes are tolerant of low oxygen conditions and this allows them to exploit deeper horizons below the sediment surface (Giere & Pfannkuche, 1982). This may reduce their susceptibility to elevated temperatures and sulfide concentrations. Abundance of *T. gurwitschi* was always higher at Salt Creek than at Bombay Beach and State Recreation Area. This might possibly be due to reduced salinity conditions via freshwater seepage from Salt Creek, although we did not measure salinity while sampling.

While sediment characteristics can mediate distribution and abundance for many species of marine tubificids (reviewed in Cook, 1971), tubificids were collected from a variety of sediment types in the Salton Sea. We collected *T. gurwitschi* from much coarser sediments (mean particle size range 1.1–3.8 mm) than have been reported for this species (Diaz & Erséus, 1994). Furthermore, while *T. belli* was found only to inhabit fine silts and silty clays in a Baja California bight (Cook, 1974), we found it exclusively in barnacle rubble. The patchy distribution of these species in the Salton Sea may reflect a heterogeneous distribution of preferred prey microorganisms (Giere, 1975), though little is known of the feeding ecology of these oligochaetes in the Sea.

Oligochaetes reached a maximum density of 13 808 m^{-2} in January 2000 at Salt Creek, representing 51% of the invertebrates collected. This is similar to the combined abundance of *Monopylephorus evertus* and *Paranais litoralis* at muddy sites in a Cape Cod marsh (Table 6). However, we sampled oligochaetes with a 1000 μ mesh, a size which failed to retain up to 74% of a mixed collection of preserved tubificids (Giere & Pfannkuche, 1982) so our data are undoubtedly underestimated. Nevertheless, oligochaete density at the Salton Sea is high relative to several other habitats, since all investigators listed in Table 6 sieved sediments through screens with mesh sizes $\leq 800\ \mu$.

Oligochaetes can be abundant over a range of depths in other saline lakes (Galat et al., 1981; Tudorancea & Harrison, 1988), but oligochaetes at the Sea were only present at stations ≤ 2 m. Oligochaetes may be restricted to the littoral zone because they lack a planktonic larval phase necessary to colonize areas farther offshore after seasonal anoxia. Additionally, predation by *Neanthes* may reduce or eliminate oligochaetes from shallow (2–4 m) depths.

While there is little information on the upper salinity tolerances of the individual oligochaete species in the Salton Sea, some or all may be able to survive at greater salinity. At the conclusion of a 15-month long study, Simpson et al. (1998) found an uniden-

tified oligochaete within an experimental Salton Sea microcosm maintained at 65 g l^{-1} salinity.

Comparison with other saline lakes

The macrobenthic invertebrate community differs in several ways from benthic communities in other North American saline lakes. First, North American saline lakes are dominated mainly by crustaceans, chironomids and other diptera (Hammer, 1986; Hammer et al., 1990). Marine species are rarely present, and other than the Laguna Salada in Baja California, no other inland saline lake in North America supports a barnacle population (S. Hurlbert, pers. com.). Also, invertebrate community structure in the Salton Sea does not vary seasonally, in contrast to North American saline lakes which have characteristic spring and summer faunas corresponding to the emergence times of different insect groups (Timms et al., 1986; Hammer et al., 1990).

Because the Salton Sea receives continuous freshwater inflows from agricultural runoff, salinity varies <10% in the main body of the lake throughout the year (presently 41.0–44.7 g l^{-1}, Watts et al., 2001). In contrast, shallow saline lakes fed by precipitation can show greater fluctuations in salinity, which influence the seasonal composition of invertebrate species (Wollhem & Lovvorn, 1995).

The Salton Sea macroinvertebrate fauna presently consists of 14 species (excluding nematodes), 8 of which were sampled in our study. This taxonomic diversity is greater than at three mesosaline lakes in central Canada with salinities of 33, 42.5, and 54 g l^{-1}, respectively. Benthic macroinvertebrates were limited to Chironomidae in each of the first 2, and other dipteran insects dominated the latter (Timms et al., 1986). Macroinvertebrate species richness in the Salton Sea is also 1.4–2.8 times higher than Australian lakes within a comparable salinity range (Timms, 1981, 1998). Because benthic species richness declines with increasing salinity, comparisons have to be made between lakes of comparable salinity, and few North American lakes studied are similar in salinity to the Salton Sea (Timms et al., 1986), or are as eutrophic.

In addition to species richness, invertebrate biomass in salt lakes tends to decrease with increasing salinity (Timms et al., 1986, Hammer et al., 1990), yet biomass per m^2 of *Neanthes* in offshore sediments at the Salton Sea in July was greater than the total spring benthic biomass per m^2 in 18 of 20 less saline lakes (range 0.9–42.5 g l^{-1}) in Canada (Timms et al., 1986: Table 4). However, these comparisons do not take into account production and turnover rates, presently unknown in the Salton Sea.

Potential implications of management actions on the invertebrate community

Although the resident population of *N. succinea* has acclimated over several decades to increasing salinity, its future may be tenuous. *Neanthes* will ultimately become extinct from the Sea when the salinity level eventually exceeds the physiological limits of the species to osmoregulate. Experimental studies show that fertilization success and early cleavage of *Neanthes* zygotes raised at 45 g l^{-1} are reduced 50% compared to that seen at 36 g l^{-1}; moreover, larval development does not proceed above 50 g l^{-1} (Kuhl & Oglesby, 1979). Presently, there are no data to assess whether reproduction in the Salton Sea population is depressed relative to coastal populations of *Neanthes* due to elevated salinity. Although Tiffany et al. (2001) found similar abundance of planktonic nectochaetes as Carpelan & Linsley (1961a), differences in sampling methodologies do not permit direct comparisons. Following the loss of *Neanthes* from the ecosystem, fish would suffer from the loss of a major food source, impacting fish-eating birds. With the absence of *Neanthes*, *Gammarus* would assume increased prominence in nearshore habitats (Simpson et al., 1998).

The preferred engineering projects proposed for reversing the rising salinity at the Salton Sea involve minor reductions in lake volume. However, if continued supplies of fresh water into the Salton Sea cannot be ensured, then government-mandated water conservation measures and future water transfers to coastal municipalities will foster major decreases in lake elevation. These events would theoretically result in more frequent mixing of the water mass by decreasing the amount of wind energy necessary to turnover the lake (Watts et al., 2001), which could conceivably expose benthic invertebrates to shorter, less frequent periods of anoxia. Additionally, the bottom topography of the Sea is such that decreases in lake elevation would slightly increase the area of shallow water habitat that is currently available for *Neanthes*, mainly in the southern end of the Sea. If we assume that *Neanthes* can only utilize sediments between 0–4 m depth during the warm season, then 16 083 ha (16%) of lake bottom lie within that range at the present lake elevation of −69 m. Decreasing the lake elevation to −70 m, −71 m, or −72 m would result in 17, 19, and

21% of total lake bottom between the 0 and 4 m range. Using our data from Table 2 and assuming all else being equal, total standing stock of *Neanthes* at a lake elevation of −70 and −71 m would be slightly greater than the total standing stock at −69 m in winter and spring months, but up to 11 and 17% greater, respectively, than the total standing stock at −69 m during summer and fall.

In contrast, a 1 m drop in water level would contribute to either a complete loss of or a major reduction in the present hard substrate habitats. The construction of impoundment structures made of rip rap or similar material would ameliorate the loss but may or may not offset it. Should the latter case be true, then a net reduction in habitat available for barnacle and algal attachment may translate into a decrease in the availability of food for fish and birds feeding on the associated organisms. The influence of such a decrease would be especially magnified during summer months, when *Neanthes* is absent or is found in low densities in the other habitats.

Acknowledgements

We thank the Salton Sea Research Management Committee and the Salton Sea Science Subcommittee for funding support, our project officer D. Stephens for his enthusiasm and guidance, and S. Horowitz for facilitating our research in the State Recreation Area. The following taxonomists aided with identifications: L. Lovell (Polychaeta), M. Milligan (Oligochaeta), S. Murray and P. Fong (Chlorophyta), J. Thomas (Amphipoda), and R. Warwick (Nematoda). Field and laboratory assistance was provided by L. Harrington, B. Harper, G. Morris, S. Phelps, L. Thurn, and J. Zimmer. This manuscript was improved by comments from S. Hurlbert, D. Herbst, and an anonymous reviewer. This research has been funded in part by the United States Environmental Protection Agency through grant #R826552-01-0 to the Salton Sea Authority. The research results have not been subjected to the Agency's required peer review and therefore do not necessarily reflect the views of the Agency. Therefore, no official endorsement should be inferred.

References

Arnal, R. E., 1961. Limnology, sedimentation, and microorganisms of the Salton Sea, California. Bull. geol. Soc. am. 72: 427–478.

Bain, R. C., A. M. Caldwell, R. H. Clawson, H. L. Scotten & R. G. Wills, 1970. Salton Sea, California: water quality and ecological management considerations. U.S. Dept. Interior, Fed. Wat. Qual. Administration, Pacific Southwest Region: 54 pp.

Barnard, J. L. & W. S. Gray, 1968. Introduction of an amphipod crustacean in the Salton Sea, California. Bull. S. Calif. Acad. Sci. 67: 219–232.

Birklund, J., 1977. Biomass, growth, and production of the amphipod *Corophium insidiosum* Crawford, and preliminary notes on *Corophium volutator* (Pallas). Ophelia 16: 187–203.

Borowsky, B., 1980. Reproductive patterns of three intertidal salt marsh Gammaridean amphipods. Mar. Biol. 55: 327–334.

Bousfield, E. L., 1973. Shallow Water Gammaridean Amphipoda of New England. Cornell University Press, Ithaca, New York, U.S.A.: 312 pp.

Brinkhurst, R. O., 1982. British and Other Marine and Estuarine Oligochaetes: Keys and Notes for the Identification of the Species. Cambridge University Press, Cambridge: 127 pp.

Calcagno, J. A., J. López Gappa & A. Tablado, 1998. Population dynamics of the barnacle *Balanus amphitrite* in an intertidal area affected by sewage pollution. J. crust. Biol. 18(10): 128–137.

Cammen, L. M., 1979. The macro-infauna of a North Carolina salt marsh. Am. midl. Nat. 102(2): 244–253.

Cammen, L. M., 1980. The significance of microbial carbon in the nutrition of the deposit feeding polychaete *Nereis succinea*. Mar. Biol. 61: 9–20.

Carpelan, L. H., 1961. Zooplankton. In Walker, B. W. (ed.), The Ecology of the Salton Sea, California, in Relation to the Sportfishery. Calif. Fish Game Fish Bull. 113: 49–62.

Carpelan, L. H. & R. H. Linsley, 1961a. The pile worm, *Neanthes succinea* (Frey and Leuckart). In Walker, B. W. (ed.), The Ecology of the Salton Sea, California, in Relation to the Sportfishery. Calif. Fish Game Fish Bull. 113: 63–76.

Carpelan, L. H. & R. H. Linsley, 1961b. The spawning of *Neanthes succinea* in the Salton Sea. Ecology 42: 189–190.

Chandler, G. T., M. R. Shipp & T. L. Donelan, 1997. Bioaccumulation, growth and larval settlement effects of sediment-associated polynuclear aromatic hydrocarbons on the estuarine polychaete, *Streblospio benedicti* (Webster). J. exp. mar. Biol. Ecol. 213: 95–110.

Cockerell, T. D. A., 1945. The Colorado desert of California: its origin and biota. Trans. Kansas Acad. Sci. 48: 1–39.

Cook, D. G., 1971. The Tubificidae (Annelida, Oligochaeta) of Cape Cod Bay. II. Ecology and systematics with the description of *Phallodrilus parviatriatus* nov. sp. Biol. Bull. 141: 203–221.

Cook, D. G., 1974. The systematics and distribution of marine Tubificidae (Annelida: Oligochaeta) in the Bahia de San Quintin, Baja California, with description of five new species. Bull. S. Calif. Acad. Sci. 73: 126–140.

Cox, G., 1996. Laboratory Manual of General Ecology. 7th edn. Wm. C. Brown Publishers, Dubuque: 278 pp.

Diaz, R. J. & C. Erséus, 1994. Habitat preferences and species associations of shallow-water marine Tubificidae (Oligochaeta) from the barrier reef ecosystems off Belize, Central America. Hydrobiologia 278: 93–105.

Drake, C., P. J. Behr & I. Valiela, 1995. Effect of algal cover on size-selective predation of *Gammarus mucronatus* by the striped killifish *Fundulus majalis*. Biol. Bull. 189: 243–244.

Erséus, C., 1990. The marine Tubificidae (Oligochaeta) of the barrier reef ecosystems at Carrie Bow Cay, Belize, and other parts of the Caribbean Sea, with descriptions of twenty-seven new species and revision of *Heterodrilus, Thalassodrilides* and *Smithsonidrilus*. Zool. Scr. 19: 243–303.

Ferrari, R. L. & P. Weghorst, 1997. Salton Sea 1995 hydrographic GPS survey. Water Resources Services, Technical Service Center. Denver, Colorado.

Fredette, T. J. & R. J. Diaz, 1986. Life history of *Gammarus mucronatus* Say (Amphipoda: Gammaridae) in warm temperate estuarine habitats, York River, Virginia. J. crust. Biol. 6: 57–78.

Gaines, S. & J. Roughgarden, 1985. Larval settlement rate: a leading determinant of structure in an ecological community of the marine intertidal zone. Proc. natn. Acad. Sci. U.S.A. 82: 3707–3711.

Galat, D. L., E. L. Lider, S. Vigg & S. R. Robertson, 1981. Limnology of a large, deep, North American terminal lake, Pyramid Lake, Nevada, U.S.A. Hydrobiologia 82: 281–317.

Gerdol, V. & R. G. Hughes, 1994. Effect of *Corophium volutator* on the abundance of benthic diatoms, bacteria and sediment stability in two estuaries in southeastern England. Mar. Ecol. Prog. Ser. 114: 109–115.

Giere, O., 1975. Population structure, food relations, and ecological role of marine oligochaetes, with special reference to meiobenthic species. Mar. Biol. 31: 139–156.

Giere, O. & O. Pfannkuche, 1982. Biology and ecology of marine oligochaeta, a review. Oceanogr. Mar. biol. ann. Rev. 20: 173–308.

Hammer, U. T., 1986. Saline Lake Ecosystems of the World. Dr W. Junk Publishers, Dordrecht: 613 pp.

Hammer, U. T., J. S. Sheard & J. K. Kranabetter. 1990. Distribution and abundance of littoral benthic fauna in Canadian prairie saline lakes. Hydrobiologia 197: 173–192.

Hardege, J. D., H. D. Bartels-Hardege, E. Zeeck & F. T. Grimm, 1990. Induction of swarming of *Neanthes succinea*. Mar. Biol. 104: 291–295.

Hart, C. M., M. R. González, E. P. Simpson & S. H. Hurlbert, 1998. Salinity and fish effects on Salton Sea microecosystems: zooplankton and nekton. Hydrobiologia 381: 129–152.

Hartman, O., 1936. New species of polychaetous annelids of the family Nereidae from California. Proc. U.S. Nat. Mus. 83: 467–480.

Heard, R. W., 1982. A guide to common tidal marsh invertebrates of the northeast Gulf of Mexico. Mississippi Alabama Sea Grant Consortium, MASGP publication 79-004: 82 pp.

Hedgpeth, J. W., 1959. Some preliminary considerations of the biology of inland mineral waters. Archivio di Oceanografiae Limnologia Suppl. 11: 111–141.

Ibarzabal, D. R., 1997. Benthonic polychaetes of Havana Bay, Cuba. Revista de Biologia Tropical. 44–45: 341–359.

Kristensen, E., 1983. Ventilation and oxygen uptake by three species of *Nereis* (Annelida: Polychaeta) I. Effects of hypoxia. Mar. Ecol. Prog. Ser. 12: 289–297.

Kuhl, D. I. & L. C. Oglesby, 1979. Reproduction and survival of the pileworm *Nereis succinea* in higher Salton Sea salinities. Biol. Bull. 157: 153–165.

Kuperman, B.I., V.E. Matey, D. M. Dexter & M. A. Tiffany, 2002. Invertebrates of the Salton Sea: a scanning electron microscopy portfolio. Hydrobiologia 473/Dev. Hydrobiol. 161: 203–216.

LaFrance, K. & E. Ruber, 1985. The life cycle and productivity of the amphipod *Gammarus mucronatus* on a northern Massachusetts salt marsh. Limnol. Oceanogr. 30(5): 1067–1077.

LaSalle, M. W. & L. P. Rozas, 1991. Comparing benthic macrofaunal assemblages of creekbank beds of the spikerush *Eleocharis parvula* (R&S) Link and adjacent unvegetated areas in a Mississippi brackish marsh. Wetlands 11: 229–224.

Levin, L. A., 1981. Dispersion, feeding behavior, and competition in 2 spionid polychaetes. J. mar. Res. 39: 99–117.

Levin, L. A., 1984. Multiple patterns of development in *Streblospio benedicti* Webster (Spionidae) from three coasts of North America. Biol. Bull. 166: 494–508.

Levin, L. A., 1986. Effects of enrichment on reproduction in the opportunistic polychaete *Streblospio benedicti* (Webster): a mesocosm study. Biol. Bull. 171: 143–160.

Martin, J. M., 1974. The effects of dissolved oxygen, salinity, and temperature on two populations of the polychaetous annelid *Neanthes succinea*. M.S. Thesis, California State University, Long Beach. Long Beach, California: 89 pp.

McCall, P. L., 1977. Community patterns and adaptive strategies of the infaunal benthos of Long Island Sound. J. mar. Res. 35: 221–265.

Mendez-Ubach, N., 1997. Polychaetes inhabiting soft bottoms subjected to organic enrichment in the Topolobampo lagoon complex, Sinaloa, Mexico. Oceanides 12: 79–88.

Milligan, M. R., 1996. Identification Manual for the Oligochaetes of Florida – Volume II: Estuarine and Nearshore Marine Oligochaetes. FL. Dept. Environ. Protect. Contract Number WM550: 239 pp.

Murina, V. V. & T. V. Mikhailova, 1994. The spread of the polychaete *Neanthes succinea* in the benthic and pelagic zones of Zerov's phylophora field in the northwest part of the Black Sea. Gidrobiologicheskiai zhurnal 30(1): 19–27. [Russian]

Nair, K. K. C. & K. Anger, 1979. Life cycle of *Corophium insidiosum* (Crustacea: Amphipoda) in laboratory culture. Helgoländer wiss. Meerresunter. 32: 279–294.

Oglesby, L. C., 1965. Steady state parameters of water and chloride regulation in estuarine nereid polychaetes. Comp. Biochem. Physiol. 14: 621–640.

Omori, K., M. Tanaka & T. Kikuchi, 1982. Seasonal changes of short-term reproductive cycle in *Corophium volutator* (Crustacea: Amphipoda) – semi-lunar or lunar cycle? Publications of the Amakusa Marine Biological Laboratory, Kyushu University 6: 105–117.

Patel, B. & D. J. Crisp, 1960. The influence of temperature on the breeding and moulting of some warm water species of operculate barnacles. J. mar. biol. Ass. U.K. 39: 667–680.

Pearson, T. H. & R. Rosenberg, 1978. Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. Oceanogr. mar. biol. Ann. Rev. 16: 229-311.

Quast, J. C., 1961. The food of the Bairdiella. In Walker, B. W. (ed.), The Ecology of the Salton Sea, California, in Relation to the Sportfishery. Calif. Fish Game Fish Bull. 113: 153–164.

Reilly, G. B., 1974. A comparison of two geographically isolated populations of *Neanthes succinea* (polychaetous annelid) with special reference to physical and chemical parameters. M.S. Thesis, California State University Long Beach, Long Beach, California: 62 pp.

Reish, D. J. & M. C. Alosi, 1968. Aggressive behavior in the polychaetous annelid family Nereidae. Bull. S. Calif. Acad. Sci. 67: 21–28.

Riedel, R., L. Caskey & B.A. Costa-Pierce, 2002. Fish biology and fisheries ecology of the Salton Sea, California. Hydrobiologia 473/Dev. Hydrobiol. 161: 229–244.

Ritter, M. & P. A. Montagna, 1999. Seasonal hypoxia and models of benthic response in a Texas Bay. Estuaries 22: 7–20.

Rogers, F. L., 1949. Three new subspecies of *Balanus amphitrite* from California. J. Ent. Zool. 41: 23–32.

Rozas, L. P. & M. W. LaSalle, 1990. A comparison of the diets of Gulf killifish, *Fundulus grandis* Baird and Girard, entering and leaving a Mississippi brackish marsh. Estuaries 13(3): 332–336.

Sanders, H. L., E. M. Goodsmith, E. L. Mills & G. E. Hampson, 1962. A study of the intertidal fauna of Barnstable Harbor, Massachusetts. Limnol. Oceanogr. 7: 63–79.

Sardá, R. & D. Martin, 1993. Populations of *Streblospio* (Polychaeta: Spionidae) in temperate zones: demography and production. J. mar. biol. Ass. U.K. 73: 769–784.

Sardá, R., K. Foreman & I. Valiela, 1995. Macroinfauna of a southern New England salt marsh: seasonal dynamics and production. Mar. Biol. 121: 431–445.

Schroeder, R. A., M. Rivera, B. J. Redfield, J. N. Densmore, R. L. Michel, D. R. Norton, D. J. Audet, J. G. Audet & S. L. Goodbred, 1993. Physical, chemical, and biological data for detailed study of irrigation drainage in the Salton Sea Area, California, 1988–1990. U.S. Geol. Surv. OFR 93-83: 179 pp.

Setmire, J. G., J. C. Wolfe & A. K. Stroud, 1990. Reconnaissance investigation of water quality, bottom sediment, and biota associated with irrigation drainage in the Salton Sea area, California, 1986–1987. U.S. Geol. Surv. Water-Resources Investigations Report 89–4102: 68 pp.

Setmire, J. G., R. A. Schroeder, J. H. Densmore, S. L. Goodbred, D. J. Audet & W. R. Radke, 1993. Detailed study of water quality, bottom sediment, and biota associated with irrigation drainage in the Salton Sea area, California, 1988–1990. U. S. Geol. Surv. WRIR 93-4014: 102 pp.

Shalla, S. H. A., A. F. A. Ghobashy & R. G. Hartnoll, 1995. Studies on the barnacle *Balanus amphitrite* Darwin 1854 (Cirripedia) from Lake Timsah in the Suez Canal. Crustaceana 68(4): 503–517.

Shannon, J. P., D. W. Blinn & L. E. Stevens, 1994. Trophic interactions and benthic animal community structure in the Colorado River, Arizona, U.S.A. Freshwat. Biol. 31: 213–220.

Shkedy, Y., U. N. Safriel & T. Keasar, 1995. Life-history of *Balanus amphitrite* and *Chthamalus stellatus* recruited to settlement panels in the Mediterranean coast of Israel. Israel J. Zool. 41: 147–161.

Simmons, E. G., 1957. An ecological survey of the Upper Laguna Madre. Pub. Inst. mar. Sci., Port Aransas, Texas 4: 156–200.

Simpson, E. P. & S. H. Hurlbert, 1998. Salinity effects on the growth, mortality and shell strength of *Balanus amphitrite* from the Salton Sea, California. Hydrobiologia 381: 179–190.

Simpson, E. P., M. Gonzales, C. Hart & S. H. Hurlbert, 1998. Salinity and fish effects on Salton Sea microecosystems: benthos. Hydrobiologia 381: 153–177.

Thomas, J. D., 1976. A survey of gammarid amphipods of the Barataria Bay, Louisiana Region. Contrib. mar. Sci. 20: 87–111.

Tiffany, M. A., B. K. Swan, J. M. Watts & S. H. Hurlbert, 2001. Metazooplankton dynamics in the Salton Sea, California. 1997–1999. Hydrobiologia 473/Dev. Hydrobiol. 161: 103–120.

Timms, B. V., 1981. Animal communities in 3 Victorian lakes of differing salinities. Hydrobiologia 81: 181–193.

Timms, B. V., U. T. Hammer & J. W. Sheard, 1986. A study of benthic communities in some saline lakes in Saskatchewan and Alberta, Canada. Int. Rev. ges. Hydrobiol. 71: 759–777.

Timms, B. V., 1998. Further studies on the saline lakes of the eastern Paroo, inland New South Wales, Australia. Hydrobiologia 381: 31–42.

Tudorancea, C. & A. D. Harrison, 1988. The benthic communities of the saline lakes Abijata and Shala (Ethiopia). Hydrobiologia 158: 117–123.

Virstein, R. W., 1979. Predation on estuarine infauna: response patterns of component species. Estuaries 2: 69–86.

Vittor, B. A., 1968. The effects of oxygen tension, salinity, temperature, and crowding on the distribution, growth, and survival of *Balanus amphitrite* Darwin in the Salton Sea, California. M. A. Thesis, San Diego State University, San Diego, California. 151 pp.

Walker, J. J., 1996. Fresh-water inflow and distribution of laminated sediments in the Salton Sea, California: M.S. Thesis. Loma Linda University, Loma Linda, California: 31 pp.

Warwick, R., D. M. Dexter & B. Kupermann, 2002. Freeliving nematodes from the Salton Sea. Hydrobiologia 473/Dev. Hydrobiol. 161: 121–128.

Watts, J., B. K. Swan, M. A. Tiffany & S. H. Hurlbert, 2001. Thermal, mixing, and oxygen regimes of the Salton Sea, California, 1997–1999. Hydrobiologia 466/Dev. Hydrobiol. 162: 159–176.

Wetzel, R. G. & G. E. Likens, 1991. Limnological Analysis. 2nd edn. Springer-Verlag New York, Inc., New York: 391 pp.

Whitney, R. R., 1961. The orangemouth corvina, *Cynoscion xanthulus* Jordan and Gilbert. In Walker, B. W. (ed.), The Ecology of the Salton Sea, California, in Relation to the Sportfishery. Calif. Fish Game Fish Bull. 113: 165–184.

Whorff, J. S., L. L. Whorff & M. H. Sweet III, 1995. Spatial variation in an algal turf community with respect to substrate slope and wave height. J. exp. biol. Ass. U.K. 75: 429–444.

Wollheim, M. W. & J. R. Lovvorn. 1995. Salinity effects on macroinvertebrate assemblages and waterbird food webs in shallow lakes of the Wyoming high plains. Hydrobiologia 310: 207–223.

Zimmerman, R., R. Gibson & J. Harrington, 1979. Herbivory and detritivory among gammaridean amphipods in a Florida Seagrass community. Mar. Biol. 54: 41–47.

Hydrobiologia **473:** 161–177, 2002.
D.A. Barnum, J.F. Elder, D. Stephens & M. Friend (eds), The Salton Sea.
© 2002 *Kluwer Academic Publishers. Printed in the Netherlands.*

Naked amoebae (Protozoa) of the Salton Sea, California

Andrew Rogerson & Gwen Hauer
Oceanographic Center, Nova Southeastern University, 8000 N Ocean Drive, Dania Beach, FL 33004, U.S.A.
E-mail: arogerso@nova.edu

Key words: abundance, gymnamoebae, hypersaline, identification, salinity tolerance

Abstract

The Salton Sea is an inland lake in California with an average salinity of ca. 44 g l^{-1}. This productive water body, which supports substantial fish and migratory bird populations, is under threat because of increasing salinity levels. The present study was the first to examine the naked amoeboid protozoa of the Salton Sea and provide a first estimate of their numerical importance. Over a six-month sampling period (June–December, 1999), 45 different morphospecies (considered to be species) of amoebae were isolated. Wherever possible, isolates were identified to species or genus using diagnostic features recognizable by light microscopy. For each isolate, illustrations and brief notes on the diagnostic characters used in the identifications are given. These will allow this paper to be used as an identification guide to amoebae of the Salton Sea in future studies. Of the 45 taxa, around 18 of the isolates (i.e. 40%) are probably new to Science. Preliminary counts, based on enrichment cultivation methods, showed that amoebae in shoreline waters ranged from 14 560 to 237 120 cells l^{-1} (mean 117 312 ± 86 075 S.D.). The ecological importance of high numbers and high diversity of amoebae is unknown. But it should be noted that several of the amoebae were actively grazing cyanobacterial and algal filaments and filaments of the bacterium *Beggiatoa*. Others were predominately associated with suspended particulates. As such, amoebae may be important in the cycling of carbon and nutrients in the Salton Sea.

Introduction

A recent series of studies has shown that naked amoebae can be numerically important in the plankton of a wide range of water bodies (see references in Table 3). Despite this attention, naked amoebae remain an understudied group of protozoa relative to the more conspicuous heterotrophic flagellates and ciliates. This is because amoebae are slow-moving and often small, transparent and frequently attached to surfaces. Moreover, naked amoebae have few rigid morphological features on which identifications can be based so microbial ecologists tend to shy away from these protozoa.

In view of the paucity of information on amoebae in general, it is not surprising that virtually nothing is known about amoebae inhabiting very saline environments. The Great Salt Lake, with an average salinity of 122 g l^{-1}, was found to support 77 different species (reviewed by Javor, 1989). Of these, only 3 species were naked amoebae. Vorhies (1917) reported 2 species of limax (elongate) amoebae and Jones (1944) named a new species, *Amoeba flowersi*, although his illustrations do not show an amoeba of the genus *Amoeba*. The Dead Sea is also a well-studied hypersaline water body, but so far only one unidentified species of amoeba (probably a Heterolobosean) has been found. This was isolated from benthic mud and grew in the laboratory at ca. 150–180 g l^{-1} salinity (Elazari-Volcani, 1943). Others have reported protozoa (without details) from a variety of hypersaline sites worldwide (Melack, 1983; Purser, 1985; Javor, 1989; Oren, 1999).

The Salton Sea is the largest inland lake in California with a salinity of ca. 44 g l^{-1}. Specific details about the water chemistry and formation of this unique water body can be found elsewhere (González et al., 1998; Hart et al., 1998). Today, the Sea is important to numerous migrating, wintering and breeding bird species that are supported by its varied biota, especially its impressive fish stocks. But there is concern about salinity levels which are increasing at a rate of about

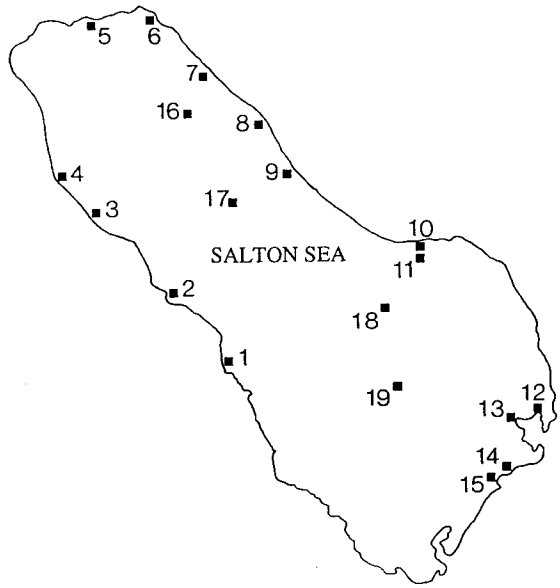


Figure 1. Map of Salton Sea showing sampling sites (1–19). The Salton Sea is the largest inland body of water in the state of California located 35 miles north of the US–Mexico border. It is about 53 km long, 13–22 km wide, has about 180 km of shoreline and averages 8 m in depth. The Sea's elevation is ca. 69 m below sea level.

0.2–0.3 g l^{-1} yr^{-1} (S. Hurlbert, pers.com). Moreover, this rate will increase if lake levels decline. Such salinity increases will undoubtedly have a dramatic effect on the biota of the Sea in the years ahead.

The present study is the first to catalogue the morphospecies of naked amoebae present in the Salton Sea. The term naked amoebae is used to include all amoebae without an obvious wall or test with a defined aperture through which pseudopodia emerge for feeding and locomotion. The majority of naked amoebae have broad, lobose pseudopodia (gymnamoebae, sensu Page, 1987) but a few have fine filose pseudopodia either with or without granules (extrusomes). Amoebae constitute a heterogeneous group of protists and some have temporary flagellate stages in their life cycle. These amoeboid protozoa, considered to be flagellates by some (D.J. Patterson, pers. comm.), are also included in this survey. The present study also gives first indications of the numbers of amoebae in the plankton of the Salton Sea and compares these levels to available published data for other marine water bodies.

Materials and methods

Study sites

Samples were collected between June and December 1999 from 19 sites in the Salton Sea (15 shore samples, and 4 open water samples; Fig. 1). Shore samples were collected in sterile collecting bottles taking care to include floating debris or algal mats that are often rich in amoebae. Some surface sediment was also included in these combined samples. Sites were sampled at least twice over the 6-month sampling period. Sample 15 at Obsidian Butte was a hypersaline pond (ca. 160 g l^{-1} salt) in close proximity to the Sea. The open water sites 16, 17 and 18 were tow samples taken with a plankton net pulled through the entire water column (2–12 m depth). Sample 19 was collected from mid-lake surface water as a tow sample through floating algal detritus. Apart from the hypersaline pond sample, salinities at the sites ranged between 37 and 52 g l^{-1} over the sampling period. Salinities were measured using a refractometer (Atago, Japan).

Identifications

In all cases, identifications were based on diagnostic features discernable at the light microscope level using a phase contrast inverted microscope (Olympus IX70). These included the general morphology of an 'average' locomotive cell, its floating form, size, type of locomotion (steady or eruptive), presence of distinctive cytoplasmic inclusions such as crystals or vacuoles, and appearance of the posterior uroid (if present). The main identification keys used were by Page (1983, 1988), Page & Seimensma (1991), Lee et al. (1985) and Bovee & Sawyer (1979) in addition to the treatise by Schaeffer (1926). To facilitate identification, amoebae were first enriched in the laboratory to obtain large numbers of each strain; it is imperative to observe several cells when identifying amoebae to obtain an impression of an 'average' locomotive cell. Amoebae that are inactive or changing direction are rarely true to the description. In all cases, samples were inoculated into seawater adjusted to either ca. 46 or 160 g^{-1}depending on where the sample was collected. All seawater was adjusted by the addition of sea salts (Sigma Chemical Co., St. Louis, MO, U.S.A.). One sterile rice grain was added to each culture to stimulate the growth of indigenous prey bacteria. Cultures were incubated in the dark at 20 °C and examined every week for the presence of different species. Ob-

servations were carried out over several months since different species of amoebae appeared over time.

Enumeration of amoebae

The number of amoebae in the water column was estimated for a series of samples collected in November 1999. Ten sites were sampled by collecting 10 ml of water in sterile, capped, centrifuge tubes. All samples were from the water column (i.e. plankton) in shallow water (ca. 1 m deep) along the shoreline. Because amoebae are small, transparent and frequently attached to surfaces, they are difficult to observe in fresh samples. Consequently, most workers rely on counting amoebae indirectly after growing them in the laboratory. The aliquot counting method was used in the present study (full details in Rogerson & Gwaltney, 2000). In brief, water was vortexed on high for 1 min to disperse amoebae evenly in the sample. Aliquots (10 μl) were pipetted into the 48 wells of tissue culture plates containing seawater (adjusted to 46 g l^{-1}salt) and a small fragment of rice grain to stimulate the growth of indigenous bacterial prey. All samples were processed within 2 h of collection. After incubation at 20 °C in the dark (to favor the growth of heterotrophic protists), the number of wells with amoebae was scored; it was assumed that the presence of a population of amoebae in a culture well indicated that at least one individual of that species was present in the original inoculum. The number of amoebae ml^{-1} (N) in the original sample was computed as:

$$N = (n \times 10^3)/V,$$

where n is the number of positive scores of amoebae in the 48 wells and V is the total volume (μl) deposited into the wells (in this case 480 μl). By assuming that the initial distribution of cells in the wells is Poisson-based and counting the wells with no amoebae, one can obtain a slightly higher maximum likelihood estimate (MLE) for the counts (Halvorson & Ziegler, 1933). However, this conversion factor does not greatly affect the numbers, particularly when growth only occurs in a few wells (O.R. Anderson, pers. comm.), thus it was not applied to the current data.

For each of the 10 samples, the dry weight of particulate material in the water column (mg ml^{-1}) was recorded.

Salinity tolerance

Preliminary experiments on the tolerance of amoebae to rapid salinity changes were carried out. Eleven strains of amoebae were isolated from the hypersaline pond (site 15) at a salinity of ca. 160 g l^{-1} (strains 5, 15,17, 20, 21, 22, 24,25,26, 27, 28). After establishing cultures in the laboratory at this high salinity, amoebae were inoculated directly, without any preconditioning, into dishes containing water at 60, 46, 40 and 32 g l^{-1}. In all cases, natural seawater was adjusted with the addition of the appropriate weight of sea salts (Sigma Chemical Co., St. Louis, U.S.A.). A further 4 strains of amoebae from cultures at ca. 48 g l^{-1} were transferred directly into water adjusted to the salinities 32, 40, and 60 g l^{-1}. Cultures were incubated and observed regularly for evidence of amoebae growth.

Results

For convenience, the morphospecies (presumed species) of amoebae found in this study are grouped into 6 categories based on morphological features easily recognized using light microscopy. Category 1 amoebae have subpseudopodia extending usually from the anterior hyaline zone. Category 2 amoebae are thecates with a thickened covering, or theca. When viewed by the light microscope, these amoebae appear to have a thickened skin often with wrinkles or folds. Category 3 amoebae are limax, having an elongate and cylindrical form. Movement of limax amoebae can be steady or eruptive. Category 4 amoebae have a raised, domed cytoplasmic mass with a surrounding hyaline zone. The dome can be central or posterior. Category 5 amoebae are more or less flattened amoebae with an extensive anterior hyaline zone. Cells are fan-shaped (flabellate) or tongue-shaped (linguiform) or ovoid. Category 6 amoebae include those with fine or filose pseudopodia and those unusual amoebae of uncertain taxonomic affinity.

Below are brief descriptions of the 45 morphospecies of amoebae encountered in this study. The isolate numbers are consistent with the line-drawings given in Figure 2 and with the numbers in Table 1. The information given builds upon and extends existing knowledge about named species and provides first information on the unidentified isolates. The notes given, in combination with the line drawings and light micrographs, will allow future researchers to identify

Table 1. List of naked amoebae from the Salton Sea with site location at which they were found. Note that the numbers 1–45 correspond to the isolate numbers in Figure 2

No.	Identity	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
1	*Hartmannella* sp.				O	O	O	O				O							O	
2	*H. abertawensis*						O								O		O			O
3	*H. vacuolata*						O	O												
4	*Vahlkampfia dumnonica*	O			O			O			O		O	O				O	O	
5	Unidentified (*Pernina*-like)		O				O	O			O		O		O	O			O	O
6	*V. salina*			O	O			O			O		O		O					
7	*Stygamoeba polymorpha*	O		O	O			O	O		O				O			O		
8	*Mayorella gemmifera*						O	O			O									
9	*M. corlissi*		O		O			O												
10	*Mayorella/Dactylamoeba*			O			O	O			O		O	O						
11	*Mayorella/Dactylamoeba*							O						O						
12	*Mayorella* sp.						O	O					O	O	O					
13	*Vexillifera telmathalassa*				O		O	O			O				O				O	
14	*Vexillifera* sp.	O		O							O		O		O			O		
15	*V. aurea*										O					O				
16	*Thecamoeba hilla*					O														
17	*Parvamoeba rugata*			O				O					O		O	O				
18	Unidentified genus	O		O	O			O	O					O				O		
19	Unidentified genus							O												
20	Unidentified genus	O			O		O	O								O		O		
21	Unidentified genus	O	O	O				O							O	O				
22	Unidentified genus	O		O	O			O	O		O	O	O			O			O	
23	*Cochliopodium*-like	O						O										O		
24	*Cochliopodium* sp.							O								O	O	O		
25	Unidentified genus			O				O	O				O		O	O	O	O	O	O
26	*Vannella mira*	O						O	O							O	O	O	O	O
27	*Vannella/Platyamoeba*			O					O				O		O	O		O		O
28	*V. septentrionalis*						O									O		O		O
29	*V. aberdonica*				O		O	O										O		O
30	*V. sensilis*			O					O		O									
31	*Vannella* sp.	O	O		O				O				O		O		O	O	O	O
32	*Vannella* sp.												O					O		
33	*Vannella/Platyamoeba*							O										O		
34	*P. langae*		O							O		O				O				
35	*Platyamoeba* sp.	O		O				O			O				O		O	O		O
36	*Platyamoeba* sp.							O			O									
37	*Unda schaefferi*			O				O	O									O		
38	Unidentified genus							O	O		O			O			O	O		O
39	Unidentified genus							O												
40	Unidentified genus								O		O	O								
41	*Vampyrellidium*-like										O						O	O	O	
42	Unidentified vampyrellid										O		O						O	
43	Unidentified genus							O					O				O	O	O	
44	*Nuclearia*-like							O					O						O	
45	Unidentified genus				O			O	O					O						

Figure 2
given in

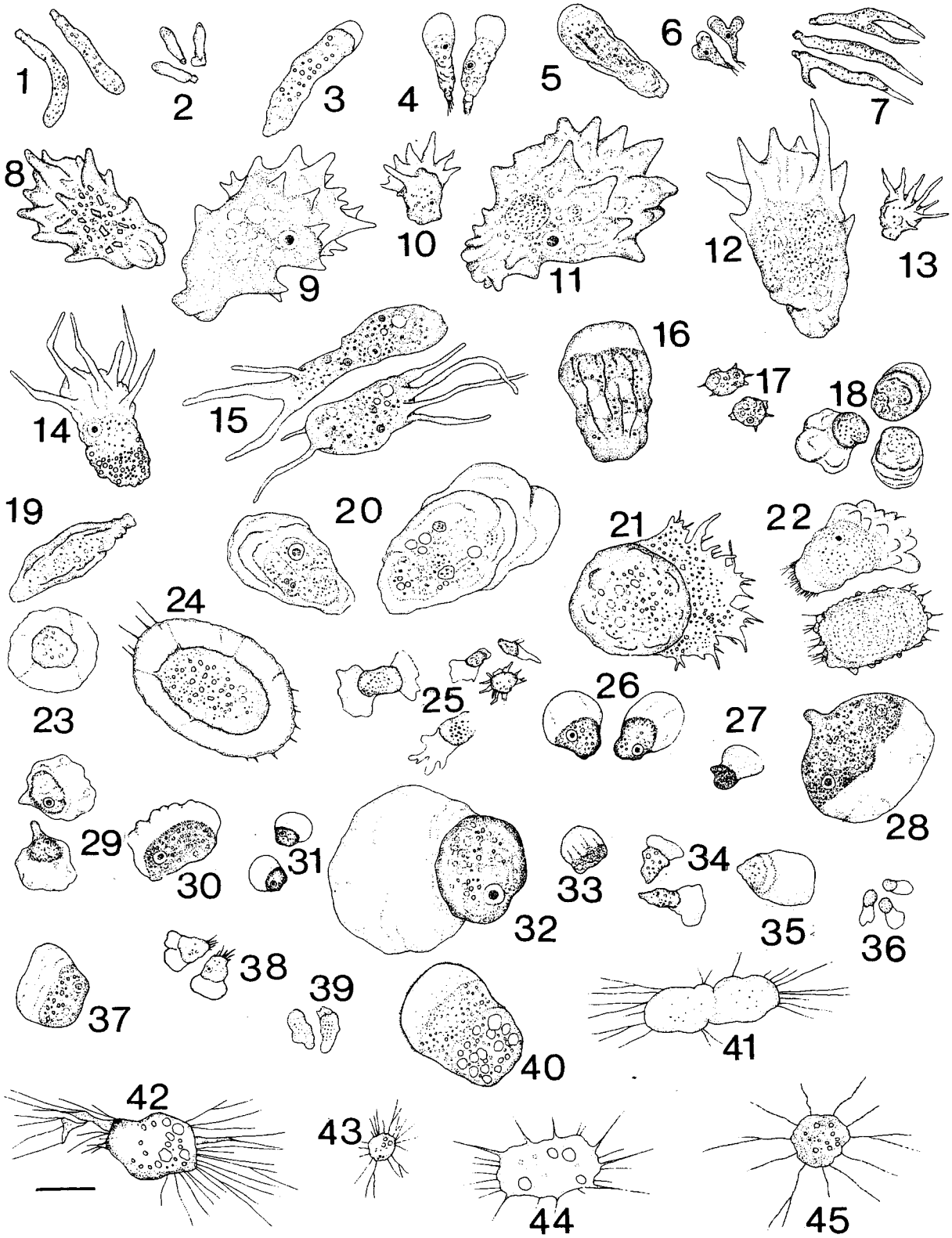


Figure 2. Line drawings of the morphotypes of naked amoebae isolated from the Salton Sea. Numbers 1–45 correspond to the identifications given in Table 1. Scale bar (bottom left) = 10 μm throughout except for the large isolates 9, 15, and 16 (scale bar = 30 μm).

naked amoebae in the Salton Sea. The complete list of naked amoebae isolated from 19 sites is given in Table 1. It is clear that some amoebae were rare, only present at one or two sites (e.g. *H. vacuolata, T. hilla, V. aurea*) while other amoebae were common, such as the *Perninia*-like amoeba (isolate 5) which occurred in 42% of the samples. The Table also shows that some sites had greater diversities of amoebae than at other locations. Site 7 at Varner Harbor, for example, contained 73% of all the amoebae species found in the Sea. On the other hand, site 9 yielded no amoebae, although this might be misleading and due to heavy bacterial contamination that developed in laboratory cultures.

Category 1 amoebae

1. *Hartmannella* sp. (Alexieff, 1912) (Figs 2.1 and 3a). Limax amoeba with steady, non-eruptive motion. Cell length between 20 and 32 μm (mean 25 μm), with a thin anterior hyaline zone, a granular cytoplasm with inclusions and a spherical nucleus. Posterior uroid bulbous without trailing filaments. Relatively common in the Salton Sea occurring at 5 sites. A similar isolate was found by Butler & Rogerson (2000) from the Clyde estuary, Scotland. This isolate is probably a new species since it does not match the three named species. It is smaller than *H. lobifera*, larger than *H. abertawensis*, and lacks the conspicuous vacuolar inclusions of *H. vacuolata* (Page, 1983; Smirnov, 1997; Anderson et al., 1997a).

2. *Hartmannella abertawensis* Page, 1980 (Fig. 2.2). Limax amoeba (7–12 μm) with steady locomotion. Reduced hyaline zone but distinct, nonetheless, as a shallow anterior crescent cap. Uroidal knob present, but not as a villous bulb uroid. These features are consistent with the description of *H. abertawensis* given by Page (1983). It should be noted, however, that the anterior hyaline cap of the Salton Sea isolate is less pronounced than in most *Hartmannella*. The genus description (Page, 1974) points out that the hyaline cap is nearly always present during locomotion and is usually as deep antero-posteriorly as broad.

3. *Hartmannella vacuolata* Anderson, Rogerson & Hannnah, 1997 (Figs 2.3 and 3b). Limax amoeba with steady, non-eruptive locomotion. Cytoplasm with numerous vacuoles. Prominent anterior hyaline zone and posterior without a uroid. Mean length of 23 μm (range 20–26 μm). Previously reported from the Clyde estuary (salinity ca. 32 g l^{-1}) by Anderson et al. (1997a). The Salton Sea isolate is slightly smaller than the Clyde isolate which ranged from 23 to 45 μm. A smaller, vacuolated, *Hartmannella* (up to 20 μm) was found in mangrove waters by Rogerson & Gwaltney (2000).

4. *Vahlkampfia dumnonica* Page, 1983 (Figs 2.4 and 3c). Limax, eruptive amoeba (14–37 μm; mean 20 μm) often with pronounced hyaline margin and trailing uroidal filaments. This heterolobosean amoeba (sensu Page, 1983) produces neither flagellates nor cysts (the Heterolobosea typically exhibit eruptive motion and/or flagellated and/or encysted forms). Previously reported from European waters. Similar to *V. longicauda* and *V. baltica* (Bovee & Sawyer, 1979).

5. Unidentified amoeba (*Pernina*-like). (Fig 2.5 and 3d,e,f). Common, limax amoeba from 10 sites in the Salton Sea, and from the hypersaline pond (ca. 160 g l^{-1}). Movement slowly eruptive and cysts were common suggesting the class Heterolobosea (Page, 1973). The cell had a narrow anterior hyaline zone and a blunt posterior without trailing uroidal filaments. In some features, this amoeba resembled the marine species *Pernina chaumonti*, with regard to size, locomotion, and the formation of cysts with pores and plugs (Fig. 5e). However, *Pernina* reportedly has common uroidal filaments (Kadiri et al., 1992) which were never observed. The Salton Sea isolate voraciously consumed algal/cyanobacterial or bacterial filaments (Fig. 5f) and large food vacuoles containing ingesta were common in the cytoplasm.

6. *Vahlkampfia salina* (Hamburger, 1905) (Figs 2.6 and 3g). A small, eruptive, limax amoeba (8–17 μm; mean 11 μm). Moving cells have a shallow hyaline anterior margin and long, trailing posterior filaments. Cytoplasm finely granular with a prominent nucleus with a central nucleolus. No cysts observed. The existence of cysts in this species is in doubt since Page (1983) believed that Hamburger (1905) mistook fungal spores for cysts. Bovee & Sawyer (1979) commented that this species has a worldwide distribution.

7. *Stygamoeba polymorpha* Sawyer, 1975 (Figs 2.7 and 3h). Thin, elongate amoebae, sometimes branching and often with lateral hyaline extensions (mean length 18 μm). Locomotion steady although frequently changes direction and shape; stationary forms often leaf-like. This amoeba was common in the Salton Sea. It has been reported from the Atlantic Ocean, Gulf of Mexico, Georgia coastal waters and southeastern Florida, and the west coast of Scotland (Sawyer, 1980; Munson, 1992; Butler & Rogerson, 2000; Rogerson & Gwaltney, 2000). Only other described marine species is *S. regulata* (Smirnov, 1996).

Figure
vacuol
(f). (g)
Vexillif
genus (

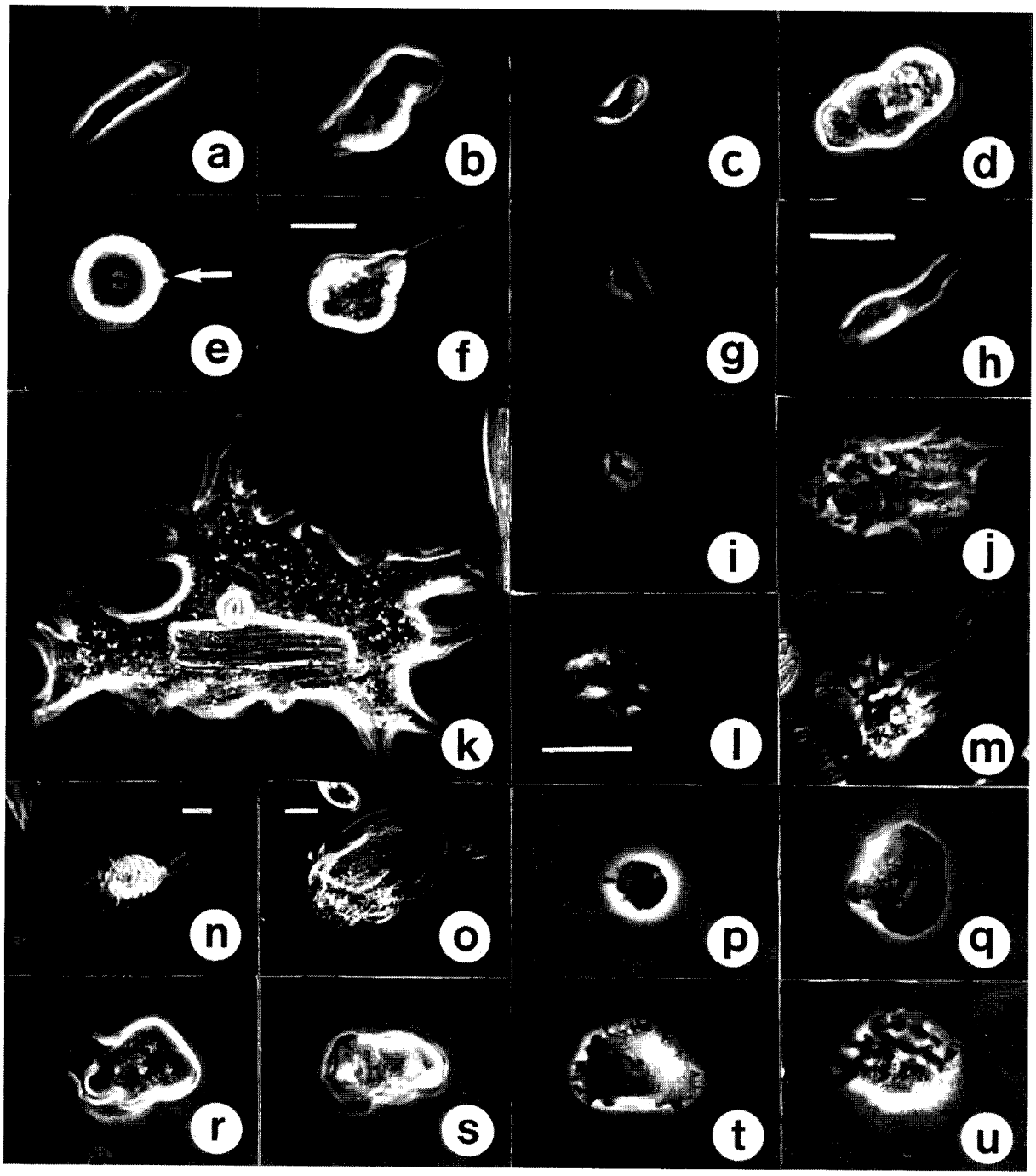


Figure 3. (a–u) Light micrographs of Salton Sea amoebae with isolate identification numbers in parentheses. (a) *Hartmannella* (1). (b) *H. vacuolata*. (2). (c) *Vahlkampfia dumnonica* (4). (d–f) *Pernina*-like amoeba (5). Note the cyst in e with pores (arrow) and ingestion of *Beggiatoa* (f). (g) *V. salina* (6). (h) *Stygamoeba polymorpha* (7). (i) *Mayorella/Dactylamoeba* (10). (j) *Mayorella* (12). (k) *Mayorella corlissi* (9). (l) *Vexillifera telmathalassa* (13). (m) *Vexillifera* (14). (n) *V. aurea* (15). (o) *Thecamoeba hilla* (16). (p) *Parvamoeba rugata* (17). (q) Unidentified genus (18). (r–s) Unidentified genus (20). (t–u) Unidentified genus (22). Scale bars = 10 μm throughout.

Category 2 amoebae

8. *Mayorella gemmifera* Schaeffer, 1926 (Fig. 2.8). Large mayorellid amoeba (34–54 μm; mean 42 μm) with blunt mamilliform subpseudopodia extending from anterior hyaloplasm. Movement rapid, but steady, with obvious streaming of a cytoplasm rich in distinct crystals. *Mayorella* is a widely distributed genus (Page, 1983) and this species has previously been reported from along the west coast of the US and from waters off southern England.

It should be noted that the genus *Dactylamoeba* resembles *Mayorella* under the light microscope. The two genera can only be distinguished by transmission electron microscopy; the cell surface of *Dactylamoeba* has micro-scales while the surface of *Mayorella* has a cuticle (Page, 1988). It should also be noted that Goodkov (1988) maintains that the application of the generic name *Dactylamoeba* is taxonomically incorrect and offers the alternative *Korotnevella*. However, *Dactylamoeba* has been retained throughout the present paper.

9. *Mayorella corlissi* Sawyer (Figs 2.9 and 3k). Similar morphology to *M. gemmifera* but larger (50–100 μm; mean 60 μm). Cytoplasm without crystals but with many vacuoles. This species has previously been isolated from a salt pond at Woods Hole and from Virginia to Massachusetts (Bovee & Sawyer, 1979).

10. *Mayorella* Schaeffer, 1926/ *Dactylamoeba* Korotneff, 1880 (Figs 2.10 and 3i). See comments on distinguishing between these two genera under *M. gemmifera*. Small mayorellid only 12 μm in length (range 10–13 μm). This isolate is smaller than any previously named mayorellid amoeba.

11. *Mayorella* Schaeffer, 1926/*Dactylamoeba* Korotneff, 1880 (Fig. 2.11). Mayorellid with a mean locomotive length of 17 μm (range 15–20 μm). Typically with several blunt subpseudopodia originating from the anterior edge. Cytoplasm without crystals although often with a few large food vacuoles packed with ingested bacteria.

12. *Mayorella* Schaeffer, 1926. (Figs 2.12 and 3j). Mayorellid similar to *M. gemmifera* but lacking the conspicuous cytoplasmic crystals. Generally within the size range 25–40 μm (mean 32 μm). Changes shape rapidly and with larger subpseudopodia that occasionally extend with a sweeping motion. Relatively common at 5 sites in the Salton Sea.

13. *Vexillifera telmathalassa* Bovee, 1956 (Figs 2.13 and 3l). Amoeba with long, slender, subpseudopodia. The spiny appearance is typical of the genus. Size range (8–17 μm) and appearance consistent with features of *V. telmathalassa* (7–17 μm) (Page, 1983). Widely distributed in Atlantic, North Sea, Gulf of Mexico and west coast of Scotland (Butler & Rogerson, 2000) and at 6 sites in the Salton Sea.

Note that *Vexillifera* has similar characters to *Mayorella* except that the subpseudopodia are as long, or longer, than the body mass.

14. *Vexillifera* Schaeffer, 1926 (Figs 2.14 and 3m). Amoeba with classical long 'vexilliferan' pseudopodia. Generally 40 μm in length although variable (34–61 μm). Morphologically similar to *V. browni* (14–23 μm) and *V. ottoi* (18–27 μm) but larger than either of these species (Bovee & Sawyer, 1979).

15. *Vexillifera aurea* Schaeffer (Figs 2.15 and 3n). According to Bovee & Sawyer (1979) this is the largest named *Vexillifera* (60–80 μm). The Salton Sea isolate is larger (75–110 μm) but is nevertheless tentatively identified as *V. aurea*. Butler & Rogerson (2000) described a similar isolate (ca. 90 μm) as *V. aurea* from the west coast of Scotland. It was found at two sites in the Salton Sea; within an algal mat, which is consistant with the herbivorous designation given by Bovee & Sawyer (1979) and in the hypersaline pond at 160 g l^{-1}.

Category 3 amoebae

16. *Thecamoeba hilla* Schaeffer, 1926 (Figs 2.16 and 3o). Flattened amoeba, up to 75 μm in length, oval in outline without subpseudopodia or uroidal filaments. Distinct anterior hyaloplasm as a lateral crescent. Pellicle-like surface with several parallel dorsal folds or wrinkles running longitudinally. Cytoplasm granular with large food vacuoles containing algal remnants (e.g. diatoms). Rare, only at one site in the Salton Sea.

17. *Parvamoeba rugata* Rogerson, 1993 (Figs 2.17 and 3p). Small, inconspicuous amoeba (mean length 5 μm; range 3–8 μm) with a central raised mass with random wrinkles of folds. Locomotion by extension of lobed hyaline lobopodia which occasionally taper to fine points. Salton Sea isolate commonly with a few distinct cytoplasmic granules. This isolate slightly larger than previously reported for *P. rugata* (Rogerson, 1993). Probably a common species but easily overlooked because of its small size. Also reported from west coast of Scotland and Florida (Rogerson, 1993; Rogerson & Gwaltney, 2000). Present in the hypersaline pond (160 g l^{-1}).

18. Unidentified genus (Figs 2.18 and 3q). Unusual thecate amoeba with irregular surface folds. Usually oval (10–30 μm; mean 13 μm). Hyaline zone reduced in most cells except in the occasional fan-shaped

morphologies (Fig. 18q). Markedly raised posterior cytoplasmic mass with obvious granules and vesicles. Very slow moving.

19. Unidentified genus (Figure 2.19). Thecate amoeba with no hyaline zone. Cells elongate with distinct lateral folds running longitudinally and a posterior uroidal knob. Locomotion is steady. Rare in the Salton Sea, observed in only one sample.

20. Unidentified genus (Figs 2.20 and 3r,s) . Thecate amoeba ranging in length from 17 to 47 μm (mean 31 μm). Oval or oblong when moving and rounded when stationary. Surface with obvious irregular folds or wrinkles. Cytoplasm rich in vacuoles and cellular inclusions. Prominent nucleus (5–7 μm diameter) with a central nucleolus. This amoeba was found amongst algal mats at 4 sites and also from the hypersaline pond (site 15 ca.160 g l^{-1}) although at high salinity its morphology was different.

Category 4 amoebae

21. Unidentified genus (Fig. 2.21). Around 30 μm in length (range 17–42 μm) and distinctive because of the numerous granules or crystals throughout the cell, including the hyaline zone. Reflection from these bodies gave the amoeba a bright appearance under the light microscope. Anterior edge with numerous short subpseudopodia up to 8 μm in length which were actively extending and retracting. Posterior cell body was markedly raised and brownish in color under phase contrast microscopy. Despite the movement of the anterior pseudopodia, locomotion of the entire cell was slow. Also present at 160 g l^{-1}in the hypersaline pond.

22. Unidentified genus (Figs 2.22, 3 t,u and 4a). Polymorphic amoeba that adopted several shapes between 14 and 60 μm in length (mean 22 μm). When stationary, cell oval with numerous short subpseudopodial extensions that may or may not taper to fine tips. At other times, periphery of cell with either numerous tooth-like processes or irregular blunt projections. Cell raised into a dome. Surface with distinctive pattern either due to fine granules or possibly a covering of short pseudopodial bosses. Locomotion generally slow, often moving with blunt pseudopodia advancing from the anterior edge. Posterior trailing filaments common. On rare occasions, cell forms eruptive bulges. This, together with the collopodial holdfasts around the periphery are reminiscent of *Rhizamoeba* (Page, 1983), however, none of the named species resemble this isolate. The amoeba was common in the Salton Sea occurring at 9 sites including the hypersaline pond (160 g l^{-1}).

23. *Cochliopodium*-like amoeba (Figs 2.23 and 4b). Body discoid to broadly ovoid with an extensive peripheral hyaline zone (length ca. 15 μm). No surface scales (a diagnostic feature of *Cochliopodium*) were detected by light microscopy. Smaller than the two named marine cochliopodia; *C. clarum* (40 μm) and *C. gulosum* (80 μm).

24. *Cochliopodium* Hertwig & Lesser, 1874 (Figs 2.24 and 4c) . Cell rounded or oval (ca. 35 μm in length) with a prominent hyaline border completely surrounding a raised central hump rich in granules/crystals. Occasional fine, short pseudopodia extending from anterior edge and trailing filaments at the posterior. *Cochliopodium* is enclosed by a tectum of microscales (which were not observed by light microscopy in this isolate). Because of this covering, some classify *Cochliopodium* as a testate amoeba rather than a naked amoeba (see Page, 1987). Two marine species have previously been described; *C. clarum* and *C. gulosum*. A freshwater species, *C. bilimbosum*, has been reported from the low salinity waters of the Baltic Sea (Vørs, 1992). This isolate also found in the hypersaline pond (160 g l^{-1}).

25. Unidentified genus (Figs 2.25 and 4d). Amoebae with distinct raised granular hump. Range of cell sizes (6–16 μm) and morphologies. When moving, cells have emerging hyaline zone that can extend into finger–like pseudopodia. Stationary cells have finger-like lobopodia emerging from around periphery. Cell changes shape frequently and peripheral pseudopodia are rapidly extended and retracted. This unusual amoeba is unlike any previously described. It bears a superficial resemblance to *Parvamoeba rugata* (Rogerson, 1993), but is larger and without surface wrinkles. This isolate also found in the hypersaline pond (160 g l^{-1}).

Category 5 amoebae

26. *Vannella mira* (Schaeffer, 1926) (Figs 2.26 and 4e,f). Fan-shaped amoeba (9–17 μm in length) with a floating form with radiating pseudopodia (Fig. 4f) that taper to points (overall width 24–34 μm). Found at 8 sites in the Sea including the hypersaline pond (160 g l^{-1}).

27. *Vannella* Bovee, 1965/*Platyamoeba* Page, 1969 (Figs 2.27 and 4g). Small, fan-shaped to oval amoeba ca. 7 μm in length. Hyaline zone and granular posterior cytoplasm both markedly flattened giving the entire cell a dark appearance under phase contrast microscopy. Unlike other small vannellids and platyamoebae which include *P. langae* and *V. aberdon-*

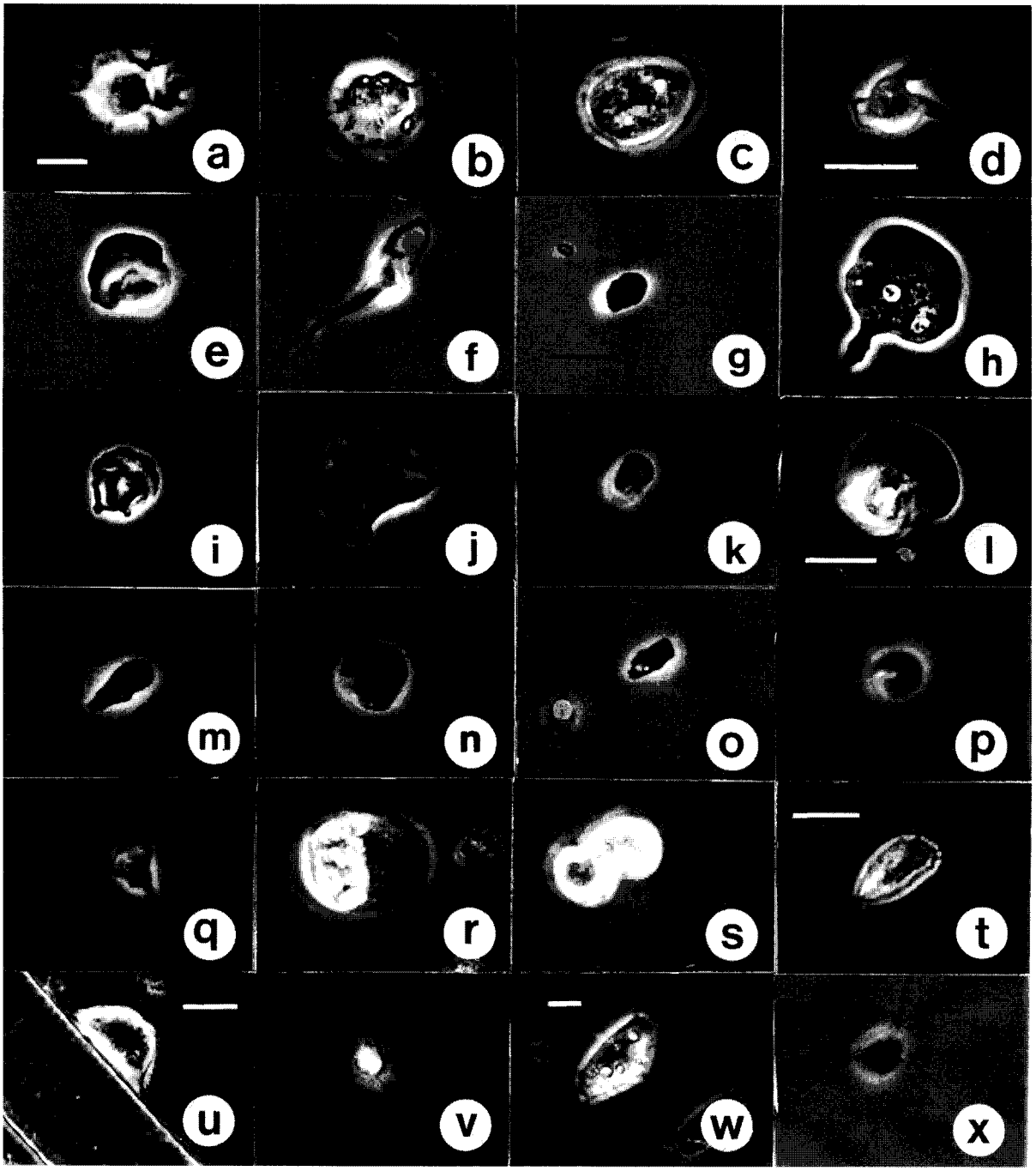


Figure 4. (a–x) Light micrographs Micrographs of Salton Sea amoebae with isolate identification numbers in parentheses. (a) Unidentified genus (22). (b) *Cochliopodium*-like (23). (c) *Cochliopodium* (24). (d) Unidentified genus (25). (e–f) *Vannella mira* (26). Note floating form in (f). (g) *Vannella/Platyamoeba* (27). (h) *V. septentrionalis* (28). (i) *V. aberdonica* (29). (j) *V. sensilis* (30). (k) *Vannella* (31). (l) *Vannella* (32). (m) *Platyamoeba langae* (34). (n) *Platyamoeba* (35). (o) *Platyamoeba* (36). (p) *Unda schaefferi* (37). (q) Unidentified genus (38). (r) Unidentified genus (40). (s) *Vampyrellidium*-like (41). (t–u) Unidentified vampyrellid (42). Note feeding amoeba on surface of algal filament (u). (v) Unidentified genus (43). (w) *Nuclearia*-like (44). (x) Unidentified genus (45). Scale bars = 10 μm throughout.

ica (Page, 1983). Common in the Sea and also found in the hypersaline pond (160 g l^{-1}).

Note, it is often difficult to distinguish these genera by light microscopy. *Vannella* tends to be more fan-shaped while *Platyamoeba* is often tongue-shaped. Moreover, the floating form of *Vannella* often has pointed radiating pseudopodia while *Platyamoeba* has blunt pseudopodia. But neither of these features are without exceptions. Both genera are very common in marine habitats (Page, 1983, 1988).

28. *Vannella septentrionalis*. Page, 1980 (Figs 2.28 and 4h). Fan-shaped amoeba ca. 25 μm in length frequently with a spatulate posterior. Also found in the hypersaline pond (160 g l^{-1}).

29. *Vannella aberdonica* Page, 1980 (Figs 2.29 and 4i). Fan-shaped amoeba often with a spatulate posterior (overall length 7–13 μm). Floating form without pointed radiate pseudopodia. Instead, when floating, the cell appears thickly flattened or twisted. These features are consistent with the species description.

30. *Vannella sensilis* Bovee & Sawyer, 1979 (Figs 2.30 and 4j) . Flattened, fan-shaped amoeba with distinctive wavy anterior hyaline edge. Advancing clear margin often finely dentate. Breadth generally wider (ca. 17 μm) than the length (ca. 11 μm).

31. *Vannella* Bovee, 1965 (Figs 2.31 and 4k). Very common small, unidentified vannellid (ca. 6 μm). Small fan-shaped amoebae (4–8 μm) were commonly found in the Clyde estuary, Scotland by Butler & Rogerson (2000). Small representatives of the genera *Vannella* and *Platyamoeba* are probably very common in all waters yet overlooked in most studies due to their size.

32. *Vannella* Bovee, 1965 (Figs 2.32 and 4l). Fan-shaped amoeba with extensive flattened hyaline occupying at least half the length of the cell. Locomotive cell between 20 and 38 μm in length. Shape generally oval with a thick, posterior granular mass. During locomotion, hyaline often extends around the sides of the cytoplasmic mass and occasional wrinkles move over the hyaline. Posterior never observed to be spatulate. Shares features with *V. anglica*.

33. *Vannella* Bovee, 1965/*Platyamoeba* Page 1969 (Fig. 2.33). Small (ca. 7 μm) unidentified vannellid with cytoplasmic extensions extending into the hyaline zone. Amoeba very slow moving. Rare, found in only one sample.

34. *Platyamoeba langae* Sawyer, 1975 (Figs 2.34 and 4m). Small, linguiform (tongue-shaped) amoeba with hyaline zone occupying one third to one half cell length. Some cells take on fan-shaped appearance. Amoebae small, usually less than 10 μm in length (5–14 μm). Cytoplasm with granular appearance and pale yellow color under phase contrast microscopy. Hyaloplasm clear with occasional transient lateral folds. Widespread distribution around the U.S.A. (Bovee & Sawyer, 1979) and off the west coast of Scotland (Butler & Rogerson, 2000).

35. *Platyamoeba* Page 1969 (Figs 2.35 and 4n). A small platyamoeba (8–17 μm; mean 11 μm) with distinctive row of cytoplasmic granules which may be diagnostically important. This isolate could also adopt a spatulate shape reminiscent of the genus *Vannella*. However, electron microscopical examination of the cell surface confirmed that it is a species of *Platyamoeba* and a new species has been proposed, *P. pseudovannellida* (Hauer, Rogerson & Anderson, in press).

36. *Platyamoeba* Page, 1969 (Figs 2.36 and 4o). Locomotive form commonly oblong with an extensive anterior hyaline zone. Cell length always less than 10 μm. Similar to *P. langae*. Small platyamoebae (e.g. isolates 35 and 36) are common when care is taken to search for small amoebae in water samples.

37. *Unda schaefferi* Sawyer, 1975 (Figs 2.37 and 4p). Flattened ovoid cell advancing along a broad hyaline edge. When moving, cell ca. 14 μm wide and 10 μm long. Anterior hyaloplasm moves forward in waves giving the cell a characteristic steady rolling motion (rate 1 μm s^{-1}). Cytoplasm with many small granules. This species was common amongst algal material at 4 sites in the Sea. Described from Atlantic coastal waters of the U.S. (Sawyer, 1975).

Category 6 amoebae

38. Unidentified genus (Figs 2.38 and 4q). This small amoebae (6–10 μm in length) had a distinctive, rapid, rolling motion with a very prominent hyaline edge evident in moving cells. Cells frequently with trailing, posterior filaments. The hyaline zone was markedly transparent; the posterior cytoplasm was granular. This amoeba has been found in mangrove waters of southern Florida (Rogerson & Gwaltney, 2000).

39. Unidentified genus (Fig. 2.39). Small, flattened amoeba that frequently changes shape. Cytoplasm with granules. Only found on one occasion in one sample.

40. Unidentified genus; *Hyalodiscus*-like (Figs 2.40 and 4 r). Oval amoeba (14–28 μm in length) with hyaloplasm occupying half the length of the cell. The hyaline region is in two zones; an anterior clear zone and a finely granular zone leading into the raised

posterior hump. Cell cytoplasm with large, conspicuous granules/inclusions. The most distinctive feature of this isolate is the fine pseudopodial fringe around the periphery of the cell. When moving, cell has a rolling motion often with parallel ridges that 'roll' over the hyaloplasm. This isolate was recently found on the surface of sea grass in southern Florida (unpublished observation, the authors).

41. *Vampyrellidium*-like amoeba (Figs 2.41 and 4s). Body finely granular between 20 and 26 μm in length. Pseudopodia filose, occasionally branched. Cells commonly show bipolarity with pseudopodia emerging from both ends of the cell.

According to Cann & Page (1979), the naked filose amoebae comprise two families. The Nucleariidae with the genus *Nuclearia* and the Vampyrellidae with the genus *Vampyrella*. A third genus, *Vampyrellidium* was shown by Patterson et al. (1987) to have affinities with the nucleariid amoebae. The three genera are distinguished by life cycle, pseudopodia and feeding behavior. Not enough information was gained in this study to identify the filose amoebae (strains 41–44). Moreover, most isolates of the above genera are freshwater.

42. Unidentified vampyrellid amoeba (Figs 2.42 and 4t). Filose amoeba with numerous active pseudopodia extending from both poles of the cell, although one pole predominates. Body oval, ca. 16 μm in length, with pseudopodia extending up to 20 μm. Posterior pseudopodia often trailing and merged into a cytoplasmic sheet. Consistent with members of the Vampyrellidae, this amoeba consumed green algal filaments by penetrating the cells (Fig. 4u).

43. Unidentified filose amoeba (Figs 2.43 and 4v). Small filose amoeba with a body between 3 μm and 8 μm in length. Very fine pseudopodia extend from periphery reaching up to 8 μm in length. Pseudopodia often branched but never anastomizing. Cell slow moving and body with several obvious inclusions. Observed to attach, and possibly penetrate and prey on cyanobacterial filaments. Some resemblance to *Diplophrys* (see Patterson, 1989). *Diplophrys* is a saprotroph associatied with aquatic vegetation (Dykstra & Porter, 1984) that has been reported from the Baltic Sea (Vørs, 1992). This protist has microscopic, organic plate-scales which can only be observed by electron microscopy.

44. *Nuclearia*-like amoeba (Figs 2.44 and 4w). Filose amoeba conforming to the description of *Nuclearia* although usually a freshwater genus. Body ca. 35 μm in length. Cytoplasm with a prominent nucleus, vacuoles and fine granular inclusions. Cells commonly with green vacuoles containing algal/cyanobacterial ingesta. Nucleariid amoebae engulf, rather than penetrate, algal prey.

45. Unidentified filose amoeba (Figs 2.45 and 4x). Body length 8–18 μm with fine pseudopodia extending from periphery of flattened cell. Pseudopodia often branched with granules (extrusomes). Cytoplasm granular with occasional larger inclusions. Cell yellowish in color under phase contrast microscopy. Relatively common at 4 sites in salinities ranging from 41 to 50 g l^{-1}. Larger, but similar to the flagellate *Massisteria marina* which has similar pseudopodia and a flagella which is hard to see in living cells (Patterson & Fenchel, 1990).

Although only 29 out of the 45 isolates could be identified to species or genus, all named amoebae were of marine origin. Given the short history of the Salton Sea endemic species were not expected. Moreover, the preliminary salinity experiments showed that amoebae are remarkably salt tolerant. Of the 14 strains of amoebae tested, 10 of the amoebae grew at 3 out of the 4 test salinities (32, 40, 46 and 60 g l^{-1}) without any prior acclimatization to culture conditions. Ten of the amoebae were isolated from the hypersaline pond (salinity ca. 160 g l-1) and all of these could be grown down to 40 g l^{-1}. Three isolates were particularly salt tolerant; isolate 5 (*Perninia*-like amoeba) and *V. septentrionalis* (isolate 28) grew at all salinities between 32 and 160 g l^{-1} and *V. mira* grew at all salinities apart from 32 g l^{-1}. Clearly, none of the amoebae from the hypersaline pond are obligate halophiles. Instead, they should be described as halotolerant (Javor, 1989), at this time.

The number of amoebae in the water column, estimated by the aliquot enrichment method, showed that amoebae are abundant in the water column (Table 2). Numbers ranged from 14 560 to 237 120 amoebae l^{-1} with an overall mean of 117 312 cells l^{-1} ($\pm$ 86 075 S.D.). There was considerable variation in the numbers of amoebae at the different sites, however, it is believed that this was related to the amount of suspended material in the water column. Since amoebae are frequently surface-associated protists, it follows that greater surface areas will result in higher abundances. This is indicated in Figure 5 which shows that as the weight of particulates in the water column increases, so does the number of amoebae. No distinction was made between living and dead particulates, however, it is worth pointing out that several amoebae were observed to be consuming algal and cyanobac-

Table 2. Numbers (l^{-1}) of naked amoebae (am), ciliates (cil), heterotrophic dinoflagellates (dino), heliozoans (hel) and *Labyrinthula* (lab) in the water column of the Salton Sea. Ten sites were sampled (see Fig. 1) and all counts by the enrichment cultivation method. Samples were collected November 1999

Site	Biotic group				
no.	am	cil	dino	hel	lab
5	212 160	8320	b.d.[a]	2080	b.d
6	39 520	4160	2080	4160	4160
7	237 120	68 640	12 480	b.d.	b.d.
8	128 960	b.d.	b.d.	12 480	b.d.
9	14 560	8320	4160	b.d.	4160
10	180 960	8320	4160	b.d.	b.d
11	193 440	4160	b.d.	16 640	2080
12	114 400	8320	2080	2080	b.d.
13	20 800	24 960	b.d.	b.d.	2080
14	31 200	6240	4160	b.d.	b.d.

[a]b.d. = below detection.

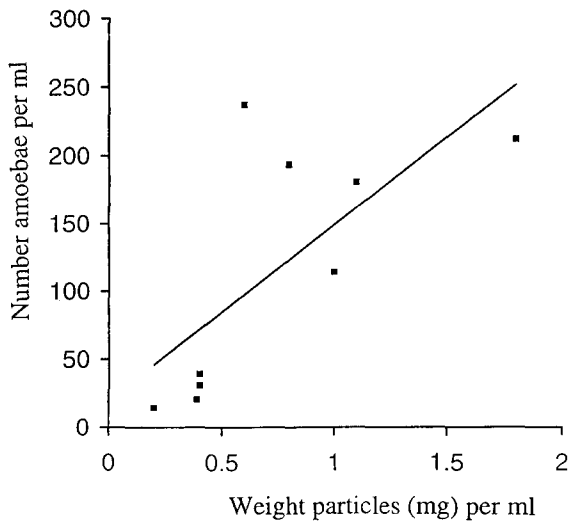


Figure 5. Relationship between the weight of suspended particles (mg ml^{-1}) in the water column and the numbers of naked amoebae (ml^{-1}); $y = 98.77x + 33.88$ ($r = 0.7271$).

terial filaments and the suspended mats of *Beggiatoa* (Fig. 3f).

The enrichment cultivation method used for amoebae also estimated the numbers of ciliates, heterotrophic dinoflagellates and heliozoans in the water. These averaged 14 144 l^{-1} (S.D. 20 233), 2912 l^{-1} (S.D. 3823), and 3744 l^{-1} (S.D. 5948), respectively. The method also estimated the abundance of the unusual heterokont aquatic fungi, *Labyrinthula* spp. (Beakes, 1998), which are saprophytes of marine plants. The enrichment cultivation method is inappropriate for heterotrophic flagellates since the method is thought to underestimate this group about 10-fold (Rogerson & Gwaltney, 2000). In this study, the count was 105 248 flagellates l^{-1} (S.D. 34,863) suggesting that the true heterotrophic flagellate count may be around 1 052 480 l^{-1}.

Discussion

The 45 taxa of amoebae isolated from the Salton Sea is undoubtedly an underestimate of the true diversity present in this water body. Because amoebae are difficult to observe in freshly collected samples, all observations were made on enriched cultures after days or weeks in the laboratory. It is unrealistic to expect all amoebae to be amenable to laboratory cultivation methods especially since only one culture method was used (i.e. seawater with rice grains). Moreover, although samples were collected as frequently as possible, only a few liters of water were processed over the six-month sampling period. Many sites within the Sea, possibly harboring additional species, were inevitably overlooked. Finally, only samples from aerobic and microaerophilic sites were collected and processed. This means that any anaerobic species of amoebae were overlooked. A recent examination of anaerobic sediments from Varner Harbor revealed two eruptive limax amoebae that did not survive in the presence of oxygen. One of these was the eruptive limax, *Vahlkampfia anaerobica* (Smirnov & Fenchel, 1996), while the other was a larger, unidentified, eruptive limax amoeba. Smirnov (1999) recently reported isolating twelve species of amoebae from anaerobic sediments, although only one was an anaerobic species.

Although 45 species is an underestimate, for the aforementioned reasons, it is an impressive diversity for a single water body. Butler & Rogerson (2000) found approximately 70 taxa of naked amoebae in a comprehensive year-long study of various benthic sediments from the Clyde estuary, Scotland. Other biodiversity investigations have tended to show fewer numbers of species. A total of 37 different naked amoebae were reported from mangrove waters in Southern Florida (Rogerson & Gwaltney, 2000). Sawyer (1980) found 35 species in sediments in the Atlantic Ocean and Gulf of Mexico and Sawyer & Bodammer (1983) recorded 20 species in the New York Bight. Studies on sublittoral beach sands yielded 18 species (Fernandez-

Leborans & Novillo, 1993) while beach sands in Japan contained 15 species (Sudzuki, 1979). Perhaps the best comparative data comes from a review of the literature by Rogerson & Goodkov (1999, unpublished) who concluded that there are 74 valid species of amoebae inhabiting European marine waters.

The Salton Sea survey has shown that as many as 18 (i.e. 40%) of the amoebae isolated in this study are new species. A recent study of mangrove waters also concluded that about 43% of the amoebae isolated were new to Science (Rogerson & Gwaltney, 2000). This clearly shows that amoebae are an overlooked group of protozoa in previous taxonomic studies and dramatically support Vørs' (1992) view that many of the protists encountered in nature are as yet undescribed. At this time we are unsure about the total numbers of species of marine amoebae globally (including undescribed species), but the final total is likely to be in the hundreds rather than the thousands. This is based on an estimate of the global diversity of freshwater and soil amoebae. Finlay & Esteban (1998) reviewed the literature on these naked amoebae and concluded that there are about 211 species globally.

The Salton Sea is a recent water body, hence the amoebae are all introduced marine forms rather than endemic species. Because of efficient dispersal means (Rogerson & Detwiler, 1999), protozoa tend to occupy similar habitats in geographically isolated locations (Finlay, 1998). In other words, most protozoa are cosmopolitan and endemics are rare (Esteban et al., 2000). The preliminary salinity tolerance experiments conducted on Salton Sea amoebae support this view since most 'hypersaline' amoebae readily adapted to being grown in normal seawater. Even amoebae from the hypersaline pond, at 5 times the salinity of natural seawater, could be grown without acclimatization at lower salinities, often down to 32 g l^{-1}. In fact, a review of the limited published information on the salt tolerance of amoebae suggests that they are highly tolerant of salinity changes and that the strict categorization into 'marine' or 'freshwater' forms is a poor diagnostic feature.

The marine testate amoeba, *Ovulinata parva* (Anderson et al., 1996, 1997b) showed remarkable salinty tolerance growing in media ranging from 0 to 35 g l^{-1}. Similarly, Vørs (1992) found the 'marine' amoebae *Flabellula demetica* and *Vannella aberdonica* to survive down to a salinity of 5 g l^{-1} and the 'freshwater' amoebae *V. platypodia* and *V. simplex* to tolerate up to 29 and 28 g l^{-1} salt, respectively. The marine amoeba, *Vexillifera telmathalassa,* was able to adjust to a gradual decline in salinity from 36 to 16 g l^{-1} (Anderson, 1994). Finally, Mast & Hopkins grew *Amoeba mira* (= *Vannella mira*) in water ranging from 3.2 to 320 g l^{-1}.

Knowledge about the diversity of amoebae is essential to understanding the ecological role of these organisms. Likewise, knowledge about the numbers of amoebae is a vital ecological parameter. This study gives the first information about abundances of naked amoebae in the shoreline waters of the Salton Sea, where they averaged 117 312 cells l^{-1}. There was considerable variation in the data but most of this could be attributed to variations in the quantity of suspended material (living and dead) in the water column. This is not surprising since amoebae are usually surface associated and consume attached bacteria. Others were associated with the luxuriant algal mats that periodically formed in the Sea. Here, some amoebae were observed to be consuming algae or bacterial filaments. Eight species of amoebae were found to consume cyanobacterial filaments, 1 species voraciously consumed diatoms and a further 3 species had unidentified 'algal' ingesta. The highest density of amoebae recorded in the Salton Sea (237 120 amoebae l^{-1}) is among the highest ever reported for marine waters worldwide (see Table 3).

Protozoa are common in hypersaline lakes and solar ponds although this list is heavily biased towards ciliates (Javor, 1989). Nevertheless, it attests to the relative success of protozoans in these habitats. Very little is known about naked amoebae despite the results of the present study that have shown them to be diverse and abundant in the hypersaline waters of the Salton Sea. Much remains to be investigated about the physiology of these protozoa and about their ecological role in the Sea, where their sheer abundance suggests that they may play an important role in the cycling of carbon and nutrients.

Acknowledgements

The research described in this article has been funded in part by the United States Environmental Protection Agency through grant #R826552-01-0 to the Salton Sea Authority. The research results have not been subjected, however, to the Agency's required peer review and therefore do not necessarily reflect the views of the Agency. No official endorsement should be inferred. We thank Christina Gwaltney for editorial comments.

Table 3. Comparison of numbers of naked amoebae (l^{-1}) from different marine or brackish planktonic sites

Location	Numbers l^{-1}		Reference
	Mean	Range	
Open ocean	n.d.[a]	1–10	Davis et al. (1978)
Open ocean	n.d.	4–37	Caron et al. (1986)
Open ocean (aggregates)	n.d.	1900–53 ,200	Caron et al. (1986)
Hudson estuary	2869	up to 8000	Anderson & Rogerson (1995)
Clyde estuary	n.d.	800–15 600	Anderson & Rogerson (1995)
Clyde estuary	n.d.	0–43 000	Rogerson & Laybourn-Parry (1992)
Clyde estuary	n.d.	up to 19 000	Armstrong et al. (2000)
Black Sea	n.d.	0–380 000	Murzov & Caron (1996)
Bermuda	75 000	n.d.	Anderson (1998)
Pacific, Antarctica (160 m)	n.d.	up to 68 000	Kopylov & Sashin (1988)
Pacific, Antarctica (surface)	n.d.	up to 30 000	Kopylov & Sashin (1988)
Coastal Antarctica	2048	n.d.	Mayes et al. (1998)
Mangroves	19 430	2000–104 000	Rogerson & Gwaltney (2000)

[a]n.d. = no data.

References

Anderson, O. R., 1994. Fine structure of the marine amoeba *Vexillifera telmathalassa* collected from a coastal site near Barbados with a description of salinity tolerance, feeding behavior and prey. J. Eukaryot. Microbiol. 4: 124–128.

Anderson, O. R., 1998. Densities and diversity of gymnamoebae in relation to some inshore aquatic habitats in Bermuda. J. Eukaryot. Microbiol. 45: 151–155.

Anderson, O. R. & A. Rogerson, 1995. Annual abundances and growth potential of gymnamoebae in the Hudson estuary with comparative data from the Firth of Clyde. Eur. J. Protistol. 31: 223–233.

Anderson, O. R., A. Rogerson & F. Hannah, 1996. A description of the testate amoeba *Ovulina parva* gen.nov., sp. nov. from coastal marine sediments. J. mar. biol. Ass. U.K. 76: 851–865.

Anderson, O. R, A. Rogerson & F. Hannah, 1997a. Three new limax amoebae isolated from marine surface sediments: *Vahlkampfia caledonica* n.sp., *Saccamoeba marina* n.sp., and *Hartmannella vacuolata* n.sp. J. Eukaryot. Microbiol. 44: 33–42.

Anderson, O. R., A. Rogerson & F. Hannah, 1997b. *Ovulinata* nom.nov., a replacement name for *Ovulina* Anderson, Rogerson & Hannah, 1996 (Protista:Filosea). J. mar. biol. Ass. U.K. 77: 1259.

Armstrong, E., A. Rogerson & J. W. Leftley, 2000. The abundance of heterotrophic protists associated with intertidal seaweeds. Estuar. coast. shelf Sci. 50: 415–424.

Beakes, G. W., 1998. Relationships between lower fungi and protozoa. In Coombs, G. H., K. Vickerman, M. A. Sleigh & A. Warren (eds), Evolutionary Relationships among Protozoa. Kluwer Academic Publishers, London: 351–373.

Bovee, E. C. & T. K. Sawyer, 1979. Marine flora and fauna of the northeastern United States. Protozoa: Sarcodina: Amoebae. NOAA Technical Report 419, U.S. Department of Commerce: 55 pp.

Butler, H. & A. Rogerson, 1995. Temproal and spatial abundance of naked amoebae (Gymnamoebae) in marine benthic sediments of the Clyde Sea area, Scotland. J. Eukyot. Microbiol. 42: 724–730.

Butler, H. & A. Rogerson, 2000 Naked amoebae from benthic sediments in the Clyde Sea area, Scotland. Ophelia 53: 37–54.

Cann, J. P. & F. C. Page, 1979. *Nucleosphaerium tuckeri* nov. gen., nov. sp. – A new freshwater filose amoeba without motile form in a new family Nucleariidae (Filosea: Aconchulinida) feeding only by ingestion only. Arch. Protistenkd. 122: 226–240.

Caron, D. A., P. G. Davis, L. P. Madin & J. McN. Sieburth, 1986. Enrichment of microbial populations in macroaggregates (marine snow) from surface North Atlantic. J. mar. Res. 44: 543–565.

Davis, P. G., D. A. Caron & J. McN. Sieburth, 1978. Oceanic amoebae from the North Atlantic: culture, distribution and taxonomy. Trans. am. Micros. Soc. 97: 73–86.

Dykstra, M. J. & D. Porter, 1984. *Diplophrys marina*, a new scale-forming protist with labyrinthulid affinities. Mycologia 76: 626–632.

Elazari-Volcani, B., 1943. Bacteria on the bottom of the Dead Sea. Nature 152: 274–275.

Esteban, G. F., B. J. Finlay, J. L. Olmo & P. A. Tyler, 2000. Ciliated protozoa from a volcanic crater-lake in Victoria, Australia. J. Nat. Hist. 34: 159–189.

Fernandez-Leborans, G. & A. Novillo, 1993. Sublittoral protistan communities of the shores of the Sea of Cantabria (Bay of Biscay). Int. Rev. ges. Hydrobiol. 78: 201–218.

Finlay, B. J., 1998. The global diversity of protozoa and other small species. Int. J. Parasitol. 28: 29–48.

Finlay, B. J. & G. F. Esteban, 1998. Freshwater protozoa: biodiversity and ecological function . Biodiversity and Conservation 7: 1163–1186.

Goodkov, A. V., 1988. *Korotnevella* nom, nov. – new generic name for scale-bearing *Mayorella*-like amoebae. Zool. J. 67: 1728–1730 (in Russian).

González, M. R., C. M. Hart, J. Verfaillie & S. H. Hurlbert, 1998. Salinity and fish effects on Salton Sea microecosystems: water chemistry and nutrient cycling. Hydrobiologia 381: 105–128.

Halvorson, H. O. & N. R. Ziegler, 1933. Application of statistics to problems in bacteriology 1. A means of determining bacterial population by the dilution method. J. Bacteriol. 26: 101–121.

Hamburger, C., 1905. Zur Kenntnis der *Dunaliella salina* und einer Amöbe aus Salinenwasser von Cagliari. Arch. Protistenkd. 6: 111–130.

Hart, C. M., M. R. González, E. P. Simpson & S. H. Hurlbert, 1998. Salinity and fish effects on Salton Sea microecosystems: zooplankton and nekton. Hydrobiologia 381: 129–152.

Javor, B. J., 1989. Hypersaline Environments, Microbiology and Biochemistry. Springer-Verlag New York: 328 pp.

Jones, D. T., 1944. Two protozoans from the Great Salt Lake. Bulletin University of Utah 35: 1–11.

Kadiri, G. E., L. Joyon & M. Pussard, 1992. *Pernina chaumonti*, n.g., n.sp., a new marine amoeba (Rhizopoda, Heterolobosea). Eur. J. Protistol. 28: 43–50.

Kopylov, A. I. & A. F. Sashin, 1988. Heterotrophic nanoplankton; its composition, abundance and trophic characteristics. In Vinogradov, M. E. & M. V. Flint (eds), Ekosistemy Subantarktitsheskoi Sony Tichova Okeana (Ecosystems of the Subantarctic Zone of the Pacific). Nauka, Moscow.

Lee, J. J., S. H. Hutner & E. C. Bovee (eds), 1985. An Illustrated Guide to the Protozoa, Society of Protozoologists, Lawrence, Kansas.

Mast, S. O. & D. L. Hopkins, 1941. Regulation of the water content of *Amoeba mira* and adaptation to changes in the osmotic concentrations of the surrounding medium. J. cell. Comp. Physiol. 41: 31–48.

Mayes, D. F., A. Rogerson, H. Marchant & J. Laybourn-Parry, 1998. Temporal abundance of naked bacterivore amoebae in coastal east Antarctica. Estuar. coast. shelf Sci. 46: 565–572.

Melack, J. M., 1983. Large, deep salt lakes: a comparative limnological analysis. Hydrobiologia 105: 223–230.

Munson, D. A., 1992. Marine amoebae from Georgia coastal surface waters. Trans. am. Micros. Soc. 111: 360–364.

Murzov, S. & D. A. Caron, 1996. Sporadic abundances of naked amoebae in Black Sea plankton. Aquat. Microbial. Ecol. 11: 161–169.

Oren, A., 1999. Microbiology and Biogeochemisty of Hypersaline Environments. Division of Microbial and Molecular Ecology, CRC Press, Boca Raton: 359 pp.

Page, F. C., 1974. A further study of taxonomic criteria for limax amoebae, with descriptions of new species and a key to genera. Arch. Protistenkd. 116: 149–184.

Page, F. C., 1983. Marine Gymnamoebae. Cambridge. Institute of Terrestrial Ecology: 54 pp.

Page, F. C., 1987. The classification of 'naked' amoebae (Phylum Rhizopoda). Arch. Protistenkd. 133: 199–217.

Page, F. C., 1988. A New Key to Freshwater and Soil Gymnamoebae. Culture Collection of Algae and Protozoa, Freshwater Biological Association, Ambleside, Cumbria: 122 pp.

Page, F. C. & F. J. Siemensma, 1991. Nackte Rhizopoda und Heliozoea, Gustav Fischer Verlag, Stuttgart: 297 pp.

Patterson, D. J., B. Surek & M. Melkonian, 1987. The ultrastructure of *Vampyrellidium perforans* Surek & Melkonian and its taxonomic position among the naked filose amoebae. J. Protozool. 34: 63–67.

Patterson, D. J, 1989. Stramenopiles: Chromophytes from a protistan perspective. In Green J. C., B. S. C. Leadbeater & W. L. Diver (eds), The Chromophyte Algae: Problems and Perspectives. Clarendon Press, Oxford: 357–379.

Patterson, D. J. & T. Fenchel, 1990. *Massisteria marina* Larsen & Patterson 1990, a widespread and abundant bacterivorous protist associated with marine detritus. Mar. Ecol. Prog. Ser. 62: 11–19.

Purser, B. H., 1985. Coastal evaporitic systems. In Friedman, G. M. & W. E. Krumbein (eds), Hypersaline Ecosystems. The Gavish Sabkha. Ecological Studies 53, Springer-Verlag, New York: 72–102.

Rogerson, A., 1993. *Parvamoeba rugata* n.g., n.sp. (Gymnoamoebia, Thecamoebidae): an exceptionally small marine naked amoeba. Eur. J. Protistol. 29: 446–452.

Rogerson, A. & J. Laybourn–Parry, 1992. The abundance of marine naked amoebae in the water column of the Clyde estuary. Estuar. coast. shelf Sci. 34: 187–196.

Rogerson, A. & A. Detwiler, 1999. Abundance of airborne heterotrophic protists in ground level air of South Dakota. Atmospheric Res. 51: 35–44.

Rogerson, A. & C. Gwaltney, 2000. High numbers of naked amoebae in the planktonic waters of a mangrove stand in Southern Florida, U.S.A. J. Eukaryot. Microbiol. 47: 235–241.

Sawyer, T. K., 1975. Marine amoebae from surface waters of Chincoteague Bay, Virginia: one new genus and eleven new species within the families Thecamoebidae and Hyalodiscidae. Trans. am. Micros. Soc. 94: 305–333.

Sawyer, T. K., 1980. Marine amoebae from clean and stressed bottom sediments of the Atlantic Ocean and Gulf of Mexico. J. Protozool. 27: 13–32.

Sawyer, T. K. & S. M. Bodammer, 1983. Marine amoebae (Protozoa: Sarcodina) as indicators of healthy or impacted sediments in the New York Bight Apex. In Duedall, I. W., B. H. Ketchum, P. K. Park & D. R. Kester (eds), Wastes in the Ocean, Vol 1; Industrial and Sewage Wastes in the Ocean. Wiley-Interscience, New York: 337–352.

Schaeffer, A. A., 1926. Taxonomy of the amebas with descriptions of thirty-nine new marine and freshwater species. Paper Dept Mar Biol Carnegie Institution Washington: 24: 116 pp.

Smirnov, A. V., 1996. *Stygamoeba regulata* n.sp. (Rhizopoda) – A marine amoeba with an unusual combination of light-microscopical and ultrastructural features. Arch. Protistenkd. 146: 299–307.

Smirnov, A. V., 1997. Two new species of marine amoebae: *Hartmanella lobifera* n.sp. and *Korotnevella nivo* n.sp. (Lobosea, Gynamoebida). Arch. Protistenkd. 147: 283–292.

Smirnov, A. V., 1999. An illustrated survey of gymnamoebae isolated from anaerobic sediments of the Nivå Bay (The Sound) (Rhizopoda, Lobosea). Ophelia 50: 113–148.

Smirnov, A. V. & T. Fenchel, 1996. *Vahlkampfia anaerobica* n. sp. and *Vannella peregrinia* n. sp. (Rhizopoda) – from a marine sediment. Arch. Protistenkd. 147: 189–198.

Sudzuki, M., 1979. Psammobiont Rhizopoda and Actinopoda from marine beaches of Japan. Acta Protozool. 18: 293–304.

Vorhies, C. T., 1917. Notes of the fauna of the Great Salt Lakes. Am. Nat. 51: 494–499.

Vørs, N., 1992. Heterotrophic amoebae, flagellates and heliozoa from the Tvärminne area, Gulf of Finland, in 1988–1990. Ophelia 36: 1–109.

Hydrobiologia **473:** 179–201, 2002.
D.A. Barnum, J.F. Elder, D. Stephens & M. Friend (eds), The Salton Sea.
© 2002 *Kluwer Academic Publishers. Printed in the Netherlands.*

The diatom flora of the Salton Sea, California

Carina B. Lange[1] & Mary Ann Tiffany[2,*]
[1]*Departamento de Oceanografia, Universidad de Concepcion, Casilla 160-C, Concepcion, Chile*
[2]*Dept. of Biology and Center for Inland Waters, San Diego State University, San Diego, CA 92182-4614, U.S.A.*
*(*Author for correspondence)*

Key words: diatoms, saline lakes, Salton Sea, California

Abstract

We report on diatom species of the Salton Sea, a highly saline (43 g l^{-1}) inland lake in California. We identified and photographed all diatom taxa encountered in the phytoplankton and benthos of the Salton Sea and its immediate tributaries. Ninety-four taxa were distinguished based on their morphological features using light- and electron microscopy. In the Salton Sea, there are four general categories of diatom assemblages related to their habitats: (1) A planktonic assemblage composed of *Chaetoceros muelleri* var. *subsalsum*, *Cyclotella choctawhatcheeana*, *Cyclotella* sp., *Cylindrotheca closterium*, *Pleurosigma ambrosianum*, *Thalassionema* sp.; (2) a benthic assemblage with diatoms that live on the bottom (e.g. genera *Caloneis*, *Diploneis*, *Entomoneis*, *Gyrosigma*, *Plagiotropis*, *Pleurosigma*, *Surirella* and *Tryblionella*), or in algal mats (*Proschkinia bulnheimii*, several species of *Navicula* and *Seminavis gracilenta*); (3) an epiphytic community attached to the macroscopic green algae which grow on the rocks and other hard surfaces near shore (e.g. *Achnanthes brevipes*, *Licmophora ehrenbergii*, *Tabularia parva*); and (4) a freshwater assemblage composed of species that get washed in by the rivers and other inflows discharging into the Sea (e.g. *Achnanthidium minutissimum*, *Cocconeis pediculus*, *Cyclotella atomus*, *C. scaldensis*, *Nitzschia elegantula*, *T. weissflogii*). The most striking feature of the phytoplankton is the abundance of species formerly known only from marine environments; this is not surprising given the high salinity and the peculiar history of the lake.

Introduction

Salton Sea waters are rich in phytoplankters. Diatom, dinoflagellate and flagellate abundances and species composition vary seasonally; for example, flagellates dominate in summer (Tiffany, 1999) whereas diatoms and dinoflagellates co-dominate the remainder of the year. Phytoplankton in the Sea plays three principal roles: (1) it constitutes the base of the food web supporting a highly productive sport fishery (Riedel et al., 2002); (2) high production rates of phytoplankton combined with high temperatures, low levels of dissolved oxygen and periodic stratification create severe water quality problems (Cohen et al., 1999); and (3) toxin-producing algae cause intoxication of fish and wildlife, and may be involved in massive fish-kills (Reifel et al., 2002; Tiffany et al., 2001).

Although phytoplankton dynamics is a fundamental issue for understanding the biology of the Sea, only two previous reports have provided substantive information on the algae (mainly diatoms and dinoflagellates) that occurred in the Sea in 1954–56 (Carpelan, 1961) and in 1968–69 (Bain et al., 1970). Maximum observed densities for a short list of dominant taxa (5 diatoms and 3 dinoflagellates) were given, but many were not identified to species level. With the objective of documenting the diversity of diatoms in the Salton Sea and thus expanding the limited knowledge of these single-celled algae from this extreme environment, we present here a compilation of all diatom taxa observed in the lake from shore and open water sites. This may serve as a guide to the diatom flora of the Salton Sea for use by students and researchers interested in highly saline inland waters. This study is part of an intensive, multidisciplinary investigation of the key physical, chemical and biological components and processes of the Salton Sea ecosystem.

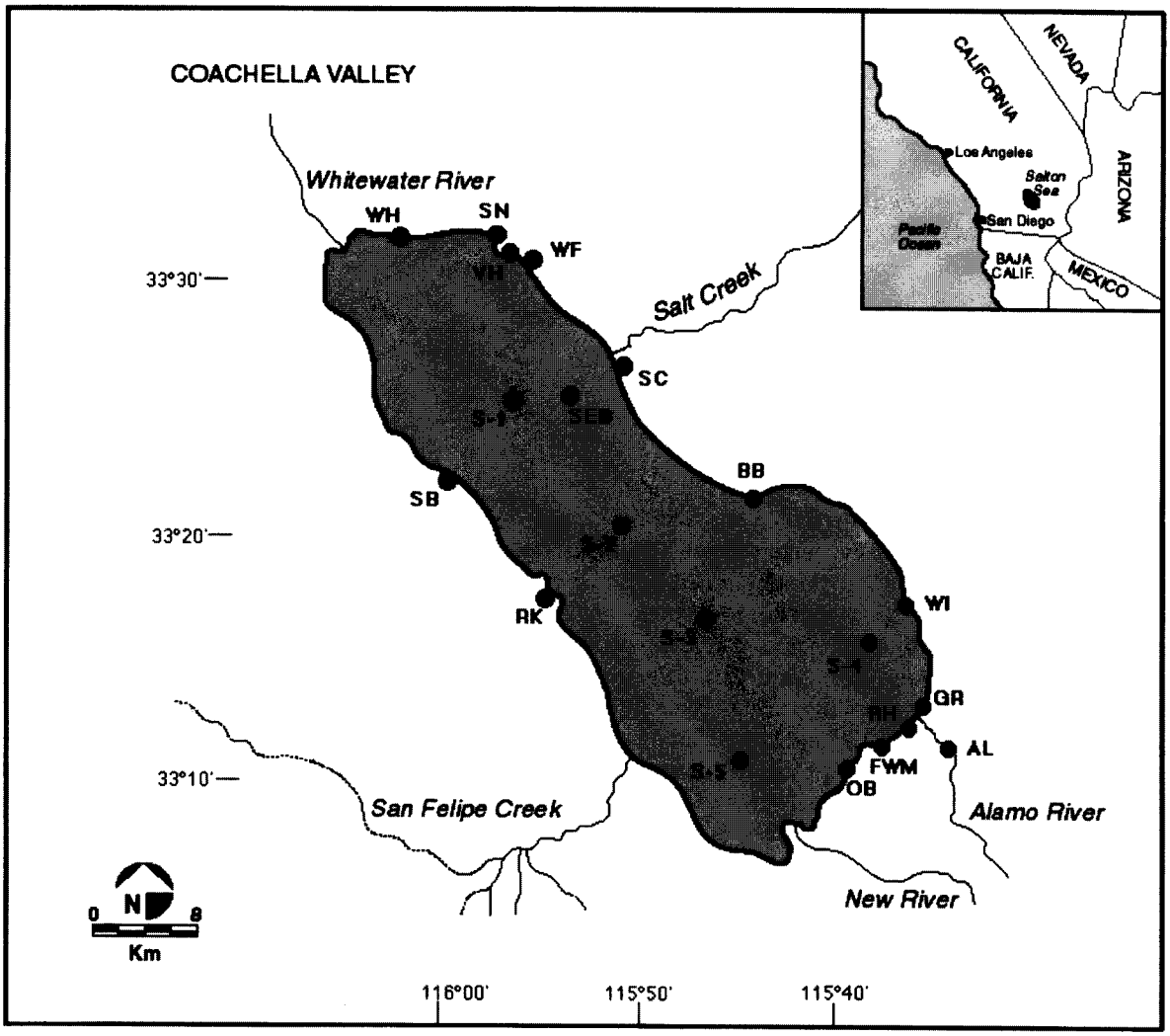


Figure 1. The Salton Sea and its tributaries. Sampling stations S-1 through S-5 = plankton water column; SED = surface sediment; BB = Bombay Beach; RK = Riviera Keys; SB = Salton Sea Beach; SC = Salton Sea at Salt Creek; SN = Sneaker Beach; VH = Varner Harbor; GR = Garst Road; OB = Obsidian Butte; RH = Red Hill (RH); WI = Wister; AL = Alamo River; FMW = freshwater marsh; WH = Wheeler Road; WF = Whitefield Creek. Insert: Location of Salton Sea in California.

Description of study area

The Salton Sea is the largest body of water in California (Fig. 1). It is approximately 53 km long, 13–22 km wide and has about 180 km of shoreline. Its elevation is ca. 69 m below sea level; the average water depth is ca. 8 m (see review in Cohen et al., 1999). The Salton Sea's physical characteristics are a result of a complex interplay of natural and human influences that have taken place in the course of this century (Kaiser, 1999). It is an artificial ecosystem, initially formed in 1905 by flooding of the Colorado River. For a review of the Sea's history, see Cohen et al. (1999).

The present Salton Sea is sustained by agricultural drainage from the Coachella, Imperial and Mexicali Valleys (Whitewater, Alamo and New rivers); smaller volumes of municipal effluent and stormwater runoff also flow to the Sea (Fig. 1). Water entering the Sea is only removed through evaporation (Cohen et al., 1999). The Salton Sea has thus become a highly saline water body. Its current salinity is ca. 43 g l^{-1} for most of the lake, dropping to 3–4 g l^{-1} at the mouths of the Alamo and New rivers. In isolated shore pools, much higher salinities are found (see Cohen et al., 1999, and references therein). Average water temperatures in the Salton Sea vary seasonally from ca. 12

°C in winter to 40 °C in summer (Watts et al., 2001). Dissolved silica values range from 4 to 10 mg l^{-1} (J. Watts, unpublished data). Nutrient-rich conditions in the Sea sustain high biomass production, large numbers of invertebrates and a productive fishery that in turn supports large avian populations of high diversity.

Materials and methods

We examined diatoms from the water column, surface sediment, surfaces of macroalgae and rocks, and floating algal mats (Table 1). Samples for taxonomic purposes were collected at 20 different sites from 1998 through 2000 (Fig. 1; Tables 1 and 2). Some sampling sites were sampled only once, others on multiple occasions. Stations S-1 through S-3 represent the main water mass of the lake, and stations S-4 and S-5 are characteristic of shallower water conditions at the lake's southern end. The five plankton stations and stations Bombay Beach (BB), Riviera Keys (RK), Salton Sea Beach (SB), Salton Sea at Salt Creek (SC), Sneaker Beach (SN) and Varner Harbor (VH), always had high salinities of >40 g l^{-1}. Intermediate salinities of 20–40 g l^{-1} characterized sampling stations Garst Road (GR), Obsidian Butte (OB), Red Hill (RH) and Wister (WI). Sampling stations Alamo River (AL), freshwater marsh (FWM), Wheeler Road (WH) and Whitefield Creek (WF) had the lowest salinities, 3–20 g l^{-1}.

Water samples from the lake were collected with a bottle or bucket and centrifuged to concentrate the planktonic organisms. Surface sediment was sampled with a 50 ml syringe. Epiphytic and epilithic diatoms were gathered by collecting macroalgae and by scraping submerged rocks. Shoreline sand provided epipsammic diatom species.

All samples for diatom analysis were examined in the natural state before acid-treatment, and again after oxidation with HNO_3 and H_2SO_4 and rinsing with distilled water (Von Stosch method in Hasle & Syvertsen, 1997). Naphrax mounts were used for light microscopy (Zeiss Photomicroscope III and Reichert Diastar). For SEM (Hitachi S-5200 at 10 KV accelerating voltage), samples were either rinsed with distilled water or acid-cleaned and then air-dried before mounting on aluminum stubs, and coating with Au/Pd. Critical point drying (Cohen, 1974) was used for examination of intact frustules. Samples, permanent slides and scanning electron microscopy (SEM)

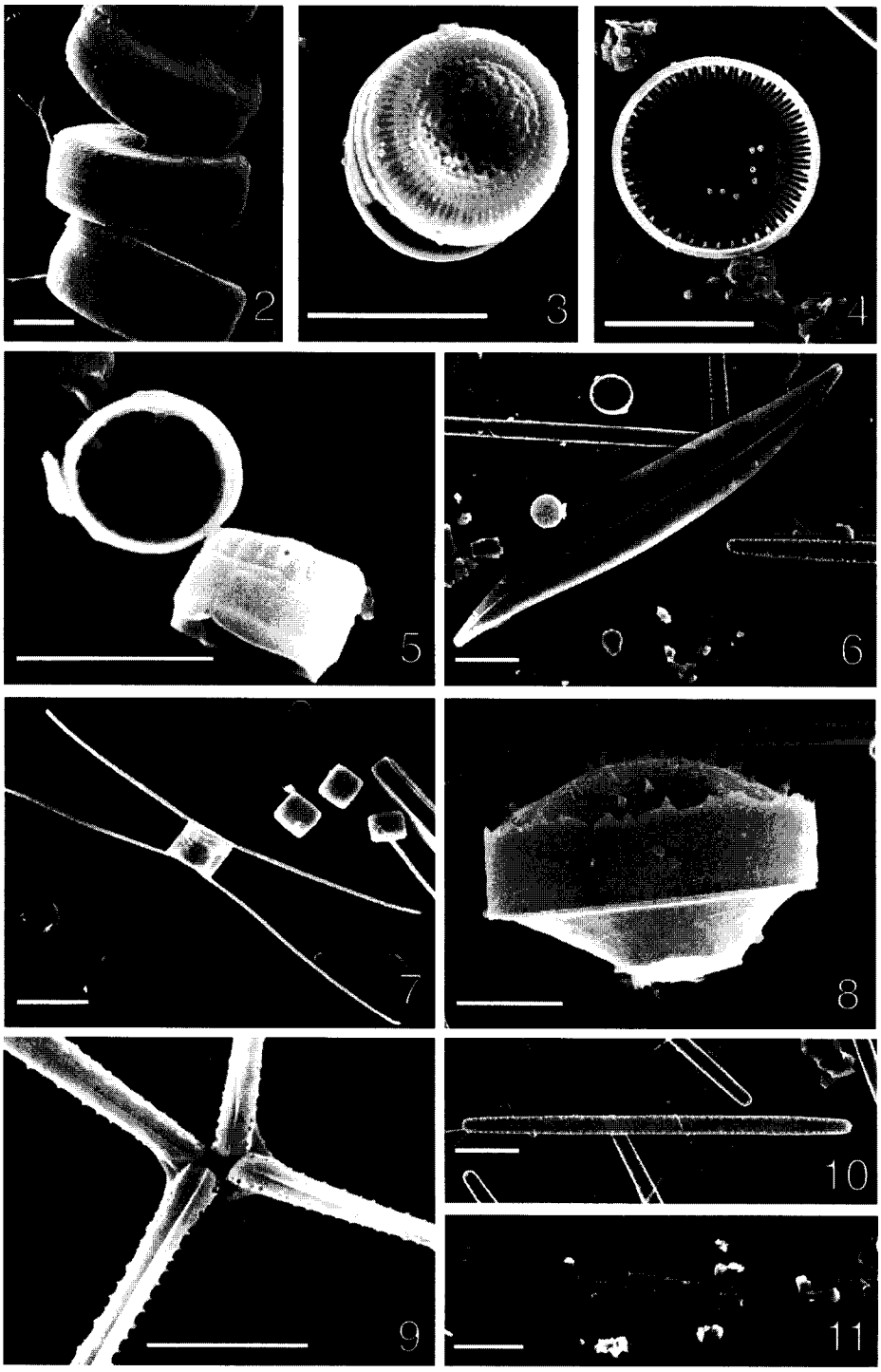
Table 1. Sampling dates and locations

Location	Date	Type of sample
Alamo River	26/04/1999	plankton
Alamo River	03/07/1999	plankton
Alamo River	11/12/1999	plankton
Bombay Beach	12/12/1998	epiphytic-Enteromorpha
Bombay Beach	19/02/1999	surface sediment
Bombay Beach	26/04/1999	surface sediment
Bombay Beach	12/06/1999	epiphytic-Cladophora
Bombay Beach	29/08/1999	surface sediment
Bombay Beach	15/10/1999	foam at shore
Bombay Beach	04/01/2000	surface sediment
Desert Shores	13/01/1999	epiphytic-Chaetomorpha
Freshwater Marsh	27/12/1999	surface sediment
Garst Road	12/06/1999	surface sediment
Garst Road	03/07/1999	surface sediment
Garst Road	15/10/1999	foam
Garst Road	15/10/1999	plankton
Garst Road	27/12/1999	surface sediment
Obsidian Butte	13/01/1999	epiphytic-Chaetomorpha
Obsidian Butte	12/06/1999	surface sediment
Obsidian Butte	12/08/1999	surface sediment
Obsidian Butte	27/12/1999	epiphytic-Chaetomorpha
Red Hill Marina	23/02/1999	surface sediment
Red Hill Marina	16/04/1999	epiphytic-Chaetomorpha
Red Hill Marina	16/04/1999	surface sediment
Red Hill Marina	16/04/1999	plankton
Red Hill Marina	12/06/1999	surface sediment
Red Hill Marina	15/10/1999	epiphytic-Chaetomorpha
Red Hill Marina	15/10/1999	plankton
Riviera Keys	02/10/1998	surface sediment
Riviera Keys	12/12/1998	epiphytic-Chaetomorpha
Riviera Keys	12/01/1999	epiphytic-Chaetomorpha
Riviera Keys	12/06/1999	plankton
Riviera Keys	12/06/1999	surface sediment
Riviera Keys	02/07/1999	algal mat
Riviera Keys	11/08/1999	surface sediment
S-1	24/08/1998	plankton
S-1	01/25 to 05/25/1999	plankton
S-2	04/25 to 05/10/1999	plankton
S-3	03/16 to 05/10/1999	plankton
S-3	04/01/2000	plankton
S-4	28/02/1999	plankton
S-4	28/02/1999	surface scum
S-4	04/07 to 12/07/1999	plankton
S-5	10/05/1999	plankton
Salt Creek	12/06/1999	barnacle sand
Salton Sea Beach	12/01/1999	epiphytic-Chaetomorpha
Salton Sea Beach	12/06/1999	epiphytic-Chaetomorpha
Salton Sea Beach	12/06/1999	plankton
Sneaker Beach	24/01/1999	epiphytic-filamentous cyanobacteria
Sneaker Beach	16/04/1999	surface sediment
Varner Harbor	24/08/1998	plankton
Varner Harbor	07/11/1998	algal mat
Varner Harbor	12/12/1998	algal mat
Varner Harbor	10/01/1999	algal mat
Varner Harbor	25/01/1999	algal mat
Varner Harbor	26/01/1999	plankton
Varner Harbor	16/04/1999	algal mat
Varner Harbor	09/06/1999	algal mat
Varner Harbor	23/06/1999	barnacle sand
Varner Harbor	24/06/1999	algal mat
Varner Harbor	02/07/1999	algal mat
Varner Harbor	15/10/1999	algal mat
Varner Harbor	23/11/1999	plankton
Varner Harbor	01/12/1999	epiphytic-algae on barnacles
Wheeler Road	27/12/1999	surface sediment
Whitefield Creek	12/08/1999	attached epiphytic filaments
Whitefield Creek	15/10/1999	attached epiphytic filaments
Wister	15/10/1999	surface sediment

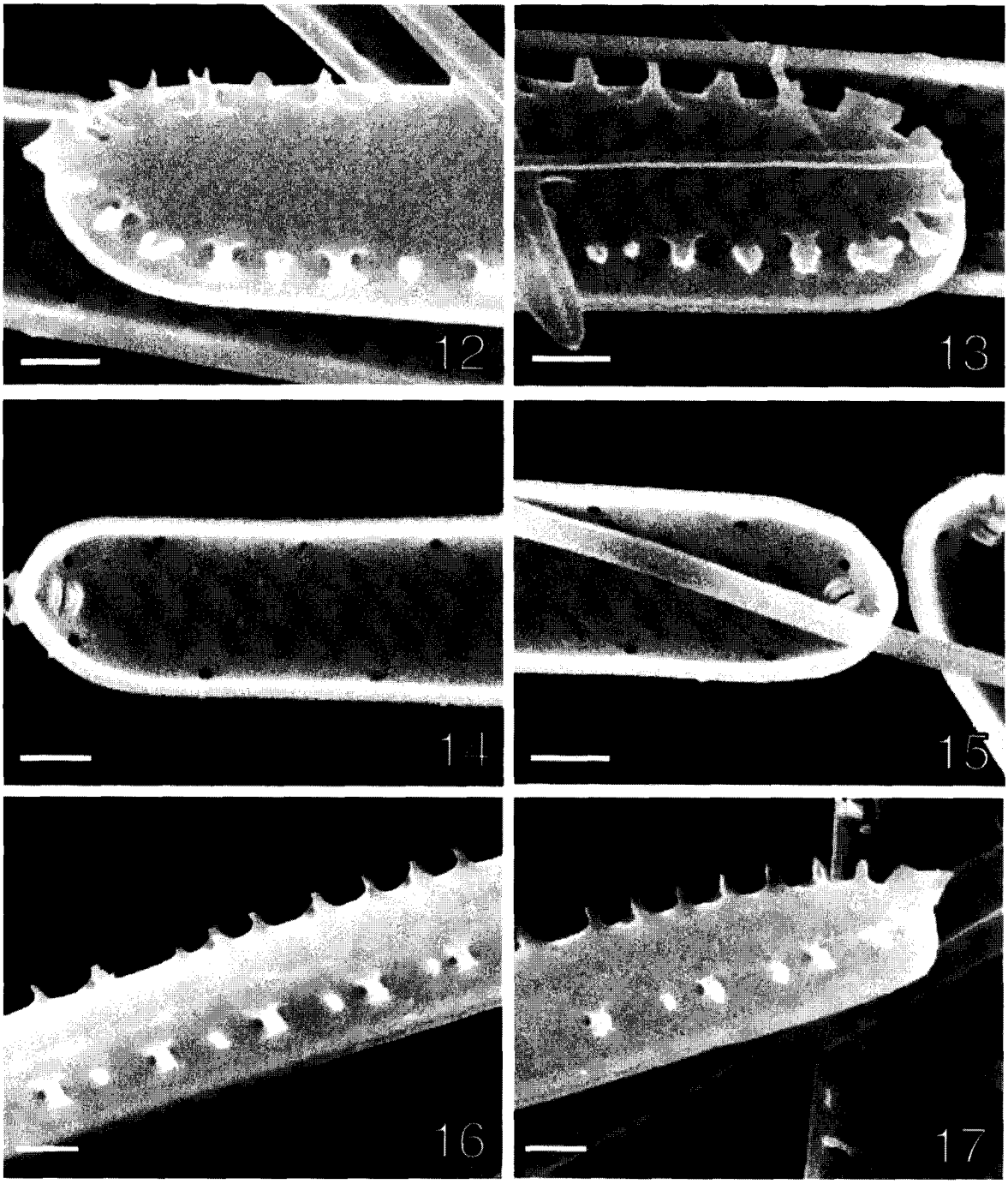
Table 2. Diatom flora of the Salton Sea (list of identified taxa, each taxon's primary habitat, known distribution, and occurrence in the Salton Sea)

Nr. Taxon	Primary habitat	Comments	Occurrence	
1	*Achnanthes amoena* Hustedt	epiphyte	freshwater, on *Terpsinoë musica*	WF
2	*Achnanthes brevipes* C. A. Agardh	epiphyte	marine, on *Chaetomorpha* sp.	OB, RK, SB
3	*Achnanthes submarina* Hustedt	epipsammic	brackish	VH, SB
4	*Achnanthidium minitussimum* (Kütz.) Czarnecki	epiphyte	freshwater	S-4 scum
5	*Amphora beaufortiana* Hustedt	epipelic	predominantly marine	S-4 scum, BB
6	*Amphora coffeaeformis* (C. A. Agardh) Kützing 'complex'	epipelic, epilithic	predominantly marine	SB, GR, VH
7	*Amphora copulata* (Kütz.) Schoeman & Archibald	epipelic, epilithic	freshwater	RK, SB, VH
8	*Amphora ovalis* (Kütz.) Kützing	epipelic, epilithic	freshwater	BB
9	*Amphora pediculus* (Kütz.) Grunow	epipsammic	freshwater	BB, SC
10	*Amphora thermalis* Hustedt	benthic	thermal springs and saline lakes	BB
11	*Anomoeoneis sphaerophora* (Kg.) Pfitzer f.*sphaerophora*	epipelic	brackish	S-4 scum, BB
12	*Auricula holsatica* (Helmcke & Krieger) Paddock & Sims	benthic	occasionally found in the plankton	OB, RK, VH
13	*Bacillaria paxillifer* (O. F. Müller) Hendey	epipelic, epilithic	freshwater, motile colonies	AL
14	*Berkeleya scopulorum* (Brébisson ex Kütz.) E.J. Cox	benthic	marine	BB, RH, S-4 scum
15	*Brachysira aponina* Kützing	epipelic, epilithic	predominantly marine	RK, VH, S-4 scum
16	*Brachysira vitrea* (Grunow) R. Ross	epipelic, epilithic	freshwater	RH
17	*Caloneis africana* (Giffen) Stidolph	epipelic	littoral, sandy beaches	GR, RH, S-4 scum
18	*Caloneis amphisbaena* f. *subsalina* (Donkin) Van der Werff & Huls	epipelic	wash-in	S-1
19	*Caloneis* aff.*C. westii* (Wm. Smith) Hendey	epipelic	brackish/marine	VH, SC, SB, OB, WH
20	*Campylodiscus bicostatus* Wm. Smith	epipelic	freshwater and brackish	WF
21	*Chaetoceros muelleri* var. *subsalsum* Johansen & Rushforth	planktonic	common in summer, forms resting spores	S1-5, SED
22	*Cocconeis pediculus* Ehrenberg	epiphyte	freshwater	S-4 scum
23	*Cocconeis placentula* var*euglypta* (Ehrenberg) Grunow	epiphyte	freshwater	RH, S-4 scum
24	*Craspedostauros britannicus* E.J. Cox	epipelic	marine	BB, S-4 scum
25	*Craticula ambigua* (Ehrenberg) D. G. Mann	epipelic	freshwater	S-4 scum
26	*Ctenophora pulchella* (Ralfs ex Kütz.) Williams & Round	epiphytic	fresh/brackish	SED
27	*Cyclotella atomus* Hustedt	planktonic	freshwater and brackish	AL, S-4
28	*Cyclotella choctawhatcheeana* Prasad	planktonic	brackish, solitary in the Salton Sea	S1-5
29	*Cyclotella meneghiniana* Kützing	planktonic	freshwater and brackish	AL, S2-5
30	*Cyclotella scaldensis* Muylaert & Sabbe	planktonic	freshwater	S-4
31	*Cyclotella wulfiae* Meyer & Håkansson	planktonic	brackish	S-4
32	*Cyclotella* sp.	planktonic	solitary, sometimes in long chains	S1-5
33	*Cylindrotheca closterium* (Ehrenberg) Reimann & Lewin	planktonic, epipelic	marine	S1-5
34	*Cymbella affinis* Kützing	epilithic, epiphytic	freshwater	S-4 scum, AL
35	*Didymosphenia geminata* (Lyngbye) M. Schmidt	epilithic	freshwater	AL
36	*Diploneis boldtiana* Cleve	epipelic	freshwater	VH, RH, SB
37	*Diploneis bombus* Ehrenberg	epipelic	predominantly marine	VH, SED, S-4 scum
38	*Diploneis obliqua* (Brun) Hustedt	epipelic	brackish/marine	SED, BB
39	*Diploneis smithii* var.*dilatata* (M. Peragallo) Boyer	epipelic	fresh and brackish	S-1
40	*Entomoneis paludosa* (W. Smith) Reimer	epipelic	predominantly freshwater	AL, S-4
41	*Entomoneis* aff.*E.pulchra* (J.W. Bail.) Reimer	epipelic	mesohalobe	RH, GR
42	*Fallacia forcipata* (Greville) A. J. Stickle & D. G. Mann	epipelic	predominantly marine	GR, RH, BB, OB
43	*Fallacia pygmea* (Kütz.) A. J. Stickle & D. G. Mann	epipelic	brackish	SED, OB, RH, BB
44	*Gomphonema parvulum* (Kütz.) Kützing	epiphytic, epilithic	freshwater	S-1, S-4 scum, SED
45	*Gomphonemopsis* aff.*G. exigua* (Kütz.) Medlin	epiphytic, epizoic?	on *Chaetomorpha* and *Zoothamium*	RH
46	*Gyrosigma balticum* (Ehrenberg) Rabenhorst	benthic	first report from an inland body of water	BB, RH, RK, GR, VH

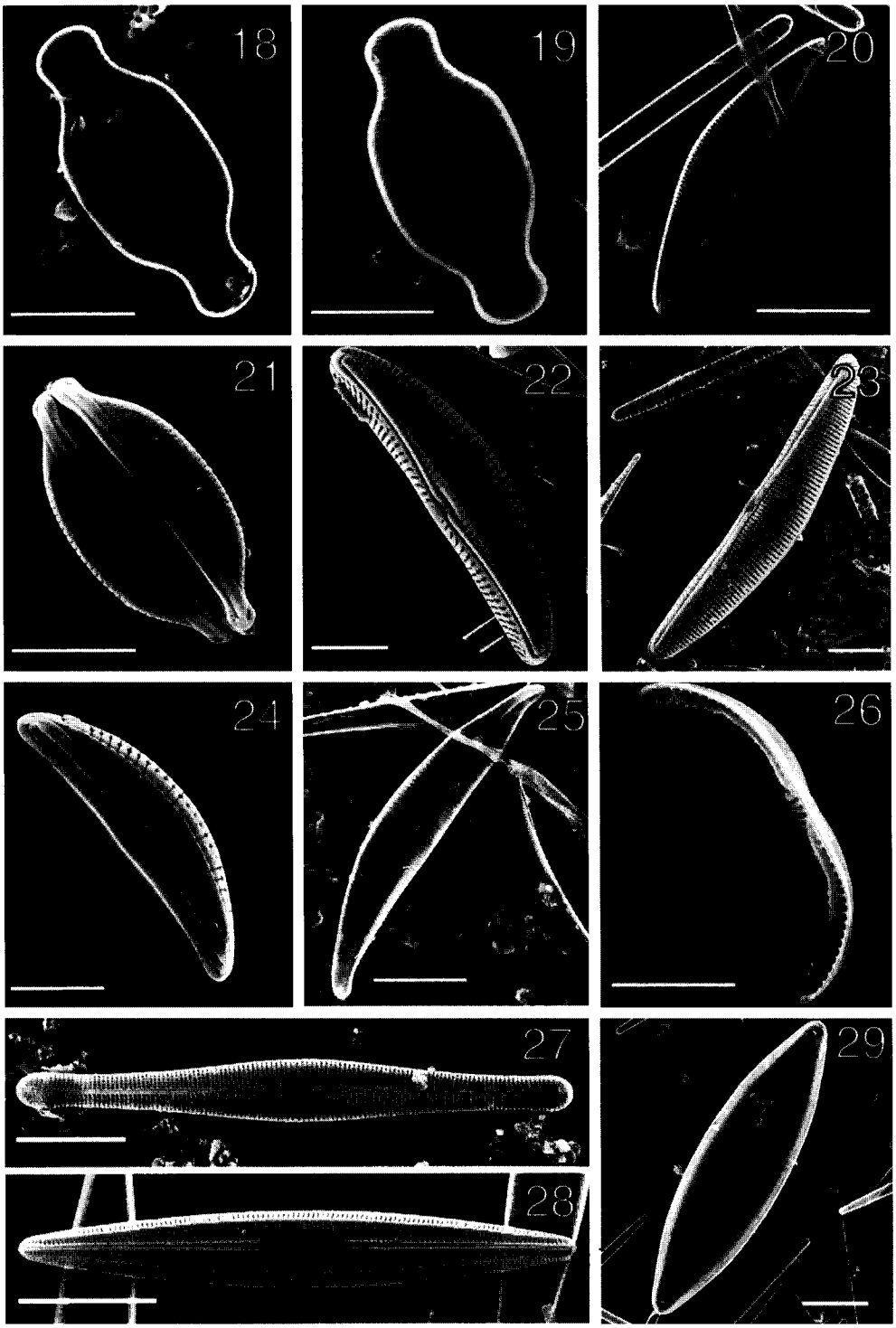
46	*Gyrosigma balticum* (Ehrenberg) Rabenhorst	benthic	first report from an inland body of water	BB, RH, RK, GR, VH
47	*Gyrosigma fasciola* (Ehrenberg) Griffith & Henfry	epipelic, planktonic	brackish/marine	GR
48	*Gyrosigma wormleyi* (Sullivant) Boyer	benthic	known previously from freshwater only	GR, RK
49	*Licmophora ehrenbergii* (Kütz.) Grunow	epiphytic	marine, on*Chaetomorpha* sp., rare	SB, S-4 scum
50	*Nanofrustulum shiloi* (Lee, Reim.& McEmery) Round, Hallsteinsen & Paasche	free or symbiotic	marine	FWM
51	*Navicula capitata* var.*hungarica* (Grunow) R. Ross	epipelic	freshwater	AL
52	*Navicula gregaria* Donkin	epiphytic, epilithic	brackish, eutrophic freshwater	S-4 scum
53	*Navicula menisculus* Schumann	benthic	found abundantly in algal mat	VH, BB
54	*Navicula pavillardii* Hustedt	epipelic	marine	OB
55	*Navicula pseudocrassirostris* Hustedt	epipelic	probably belongs to genus *Sellaphora*	SB, S-1
56	*Navicula veneta* Kützing	epipelic	brackish	S-1, S-4
57	*Nitzschia distans* Gregory	epipelic	brackish	VH, OB
58	*Nitzschia elegantula* Grunow	epiphytic, epilithic	freshwater	AL, GR, S-4 scum
59	*Nitzschia frustulum* (Kützing) Grunow	epilithic	occasionally found in winter plankton	S1-5, VH, BB, GR
60	*Nitzschia obtusa* W. Smith	benthic	brackish	RH, S-4 scum
61	*Nitzschia reversa* W. Smith	planktonic	marine, brackish	S-4 scum, AL
62	*Nitzschia sigma* (Kütz.) W. Smith	epipelic	brackish	VH, RH, BB, S-4 scum
63	*Nitzschia sigmoidea* (Nitzsch) W. Smith	epipelic	fresh/brackish	RH
64	*Nitzschia* (wide) sp.			VH, RH
65	*Opephora naveana* Le Cohu	epipsammic	freshwater to marine	SC, VH, RH, SB
66	*Petroneis marina* (Ralfs in Pritchard) D. G. Mann	epipelic	marine	BB
67	*Placoneis* sp.	epipelic	fresh and brackish	S-4 scum
68	*Plagiotropis* sp. [*P. lepidoptera* (Gregory) Kuntze ?]	epipelic	marine?	GR, VH
69	*Planothidium delicatulum* (Kütz.) Round & Bukhtiyarova	epipsammic, epilithic	freshwater	S-4 scum
70	*Planothidium lanceolatum* (Bréb) Round & Bukhtiyarova	epipsammic, epilithic	freshwater	WF
71	*Pleurosigma ambrosianum* Sterrenburg, Tiffany & Lange	planktonic	common in winter	S1-5
72	*Pleurosigma strigosum* W. Smith	benthic	brackish	RH, S-4 scum
73	*Pleurosira laevis* (Ehr.) Compère	epiphytic	brackish wash-in, zig-zag colonies	WF, RH, GR
74	*Pleurosira* sp.	epiphytic		AL
75	*Proschkinia bulnheimii* (Grunow) Karayeva	benthic	marine, found in Salton Sea algal mat	VH
76	*Rhopalodia* sp.	epipelic		BB
77	*Sellaphora pupula* (Kütz.) Mereschkowsky	epipelic	freshwater	AL
78	*Sellaphora* sp.			S-4
79	*Seminavis gracilenta* (Grunow ex A. Schmidt) Mann	epipelic	marine, large and small populations	VH, BB, GR, RK
80	*Stephanodiscus niagarae* Ehrenberg complex	planktonic	freshwater	S-4 scum
81	*Surirella brebissonii* var.*kuetzingii* Krammer & Lange–Bertalot	epipelic	freshwater to brackish	S-4 scum
82	*Surirella minuta* Brébisson ex Kütz.	epipelic, epilithic	freshwater	BB, VH
83	*Surirella striatula* Turpin	epipelic	brackish	S-4 scum
84	*Tabularia investiens* (W. Smith) Williams & Round	epiphytic	on *Pleurosira laevis* and *Terpsinöe musica*	WF
85	*Tabularia parva* (Kütz.) Williams & Round	epiphytic	*on Chaetomorpha* sp.	SN, OB, RK, VH
86	*Terpsinoë musica* Ehrenberg	epiphytic	fresh to brackish, zig-zag colonies	WF, AL
87	*Thalassionema* sp.	planktonic	summer, solitary or in stellate colonies	S1-5, SED
88	*Thalassiosira pseudonana* Hasle & Heimdal	planktonic	freshwater	AL, S-4 scum
89	*Thalassiosira weissflogii* (Grunow) Fryxell & Hasle	planktonic	fresh/brackish	WI, RH, S-4 scum
90	*Tryblionella apiculata* Gregory	epipelic	brackish	VH, RK, AL
91	*Tryblionella granulata* Grunow	epipelic	brackish and marine	RH, S-4 scum
92	*Tryblionella hungarica* (Grunow) D. G. Mann	epipelic	brackish	RH, BB, AL
93	*Tryblionella littoralis* (Grunow in Cleve & Grunow) D. G. Mann	epipelic	marine	WI, S-1, S-4 scum
94	*Tryblionella punctata* W. Smith	epipelic	marine, occasionally in winter plankton	S1-5, BB, VH, SED



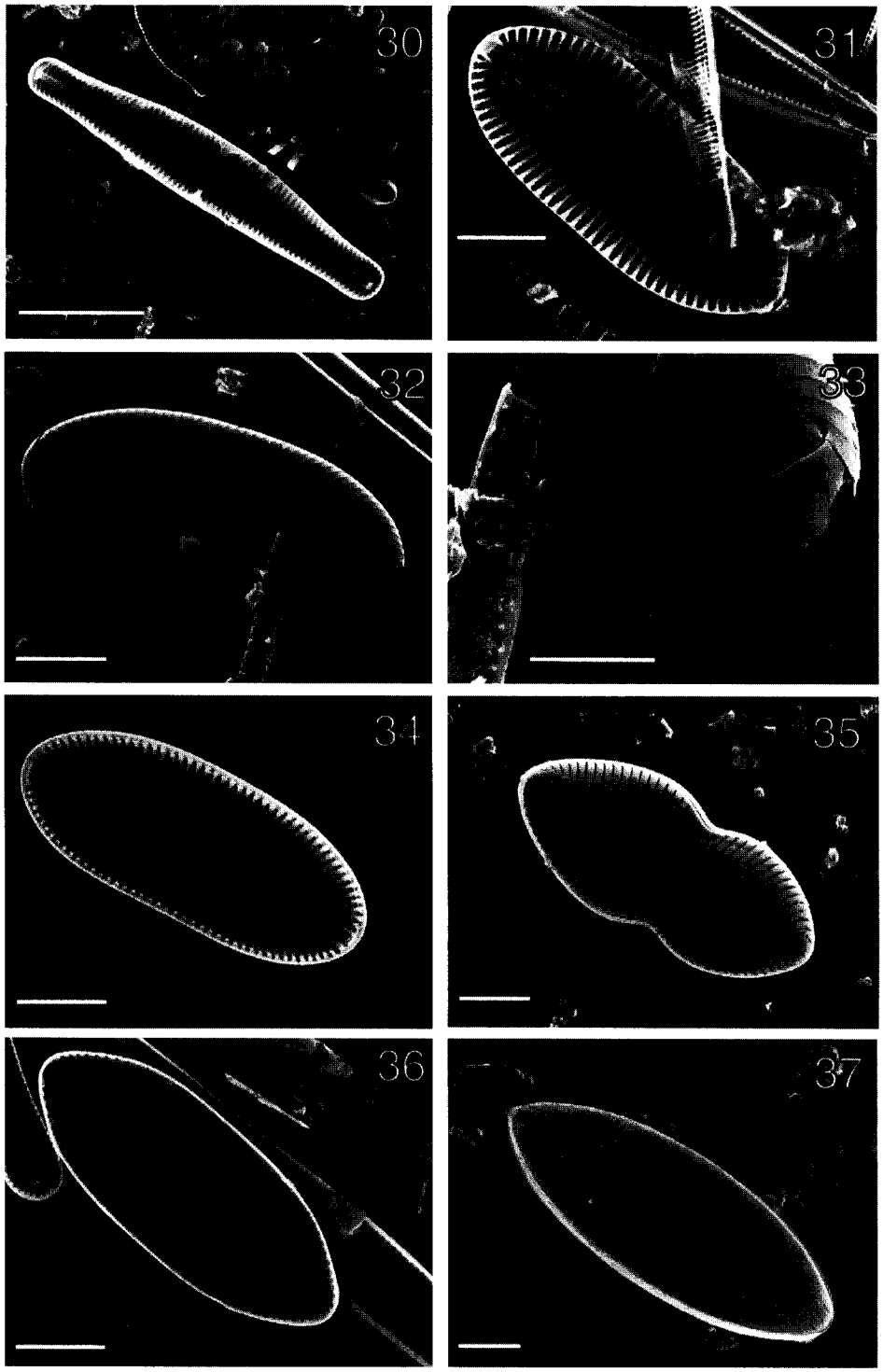
Figures 2–11 **Planktonic assemblage**, SEM. *Figures 2–4. Cyclotella* sp. Chain (2), and external view of frustule (3); note undulation of valve face. *Figure 4.* Internal view, note central fultoportulae and ring of marginal fultoportulae; rimoportula at 11 o'clock. *Figures 5. Cyclotella choctawhatcheeana*, girdle view of valve with bands attached, and internal view of another valve. *Figure 6. Pleurosigma ambrosianum* general view, valve interior. *Figures 7 & 8. Chaetoceros muelleri* var. *subsalsum*, vegetative cell (7) and resting spore (8). *Figures 9 & 10. Thalassionema* sp. *Figure 9.* Detail of stellate colony, note mucous pads at foot-poles. *Figure 10.* Valve view (external), both poles are smoothly rounded. *Figure 11. Cylindrotheca closterium*, general view. Scale bars = 5 μm in Figures 2, 5, 8; bars = 10 μm in Figures 3–4, 6–7, 9–11.



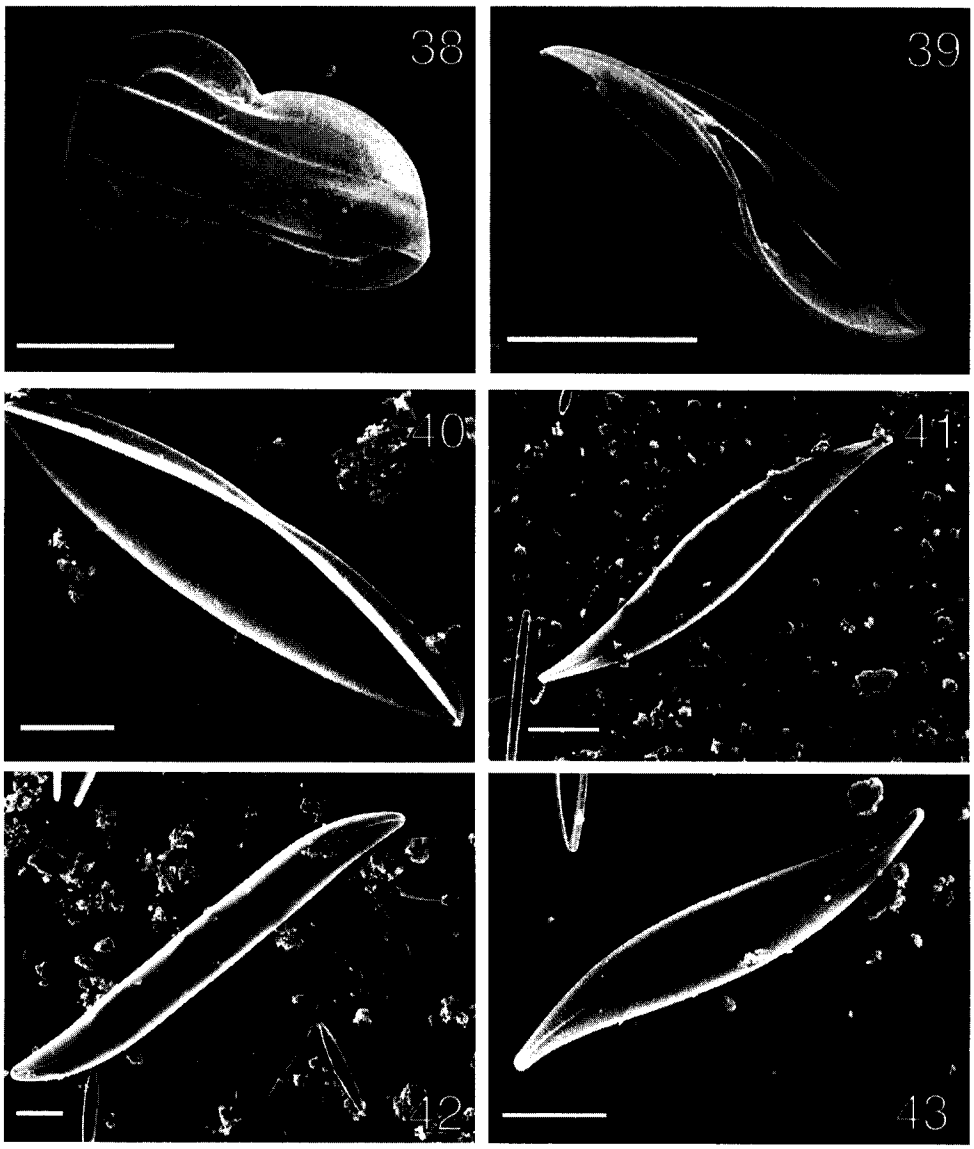
Figures 12–17 Thalassionema **sp.**, SEM. *Figures 12, 13, 16, 17.* External views; tilt is 45 ° in Figures 16 & 17. Sternum wide; areolae located at the border between valve face and mantle; external openings of areolae are large grooves crossed by simple silicified arches (12, 16). Spines are present externally between areolae (16, 17). Each valve end bears an apical protrusion, one which is arrow-shaped, much more prominent than the other (12, 17). *Figures 14 & 15.* Internal views. Internal openings of areolae small (14,15); one rimoportula at each pole, located obliquely (15) or almost perpendicular to the apical axis (14). All scale bars = 1 μm.



Figures 18–29 **Benthic assemblage**, SEM. *Figures 18 & 19. Achnanthes submarina*; raphid valve, internal view (18); araphid valve, external view (19). *Figure 20. Amphora beaufortiana*, internal view of valve. *Figure 21. Amphora coffeaeformis*, external view of frustule. *Figure 22. Amphora copulata*, external view of valve. *Figure 23. Amphora ovalis*, valve exterior. *Figure 24. Amphora pediculus*, valve exterior. *Figure 25. Amphora thermalis*, valve interior. *Figure 26. Auricula holsatica*; crescent-shaped valve, internal view. *Figure 27. Berkeleya scopulorum*, valve exterior. *Figure 28. Brachysira aponina*, internal view of valve. *Figure 29. Caloneis africana*, internal view. Scale bars = 20 μm in Figure 29; 5 μm in Figures 18, 19, 24, 26; all others = 10 μm.



Figures 30–37 **Benthic assemblage** (cont.), SEM. *Figure 30. Craspedostaurus britannicus*, internal view. *Figure 31. Diploneis boldtiana*, internal view. *Figures 32–34. Diploneis obliqua. Figure 32.* Asymmetric valve, external view. *Figure 33.* External view, detail of marginal area showing narrow slits running the whole length of the stria, and 'grappling hooks' at the external marginal end of each elongated slit. *Figure 34.* Asymmetric valve, internal view. *Figure 35. Diploneis bombus*, external view. *Figure 36. Fallacia forcipata*, valve interior. *Figure 37. Fallacia pygmea*, valve exterior. Scale bars = 5 μm in Figures 31, 33, 36, 37; bars = 10 μm in Figures 30, 32, 34, 35.

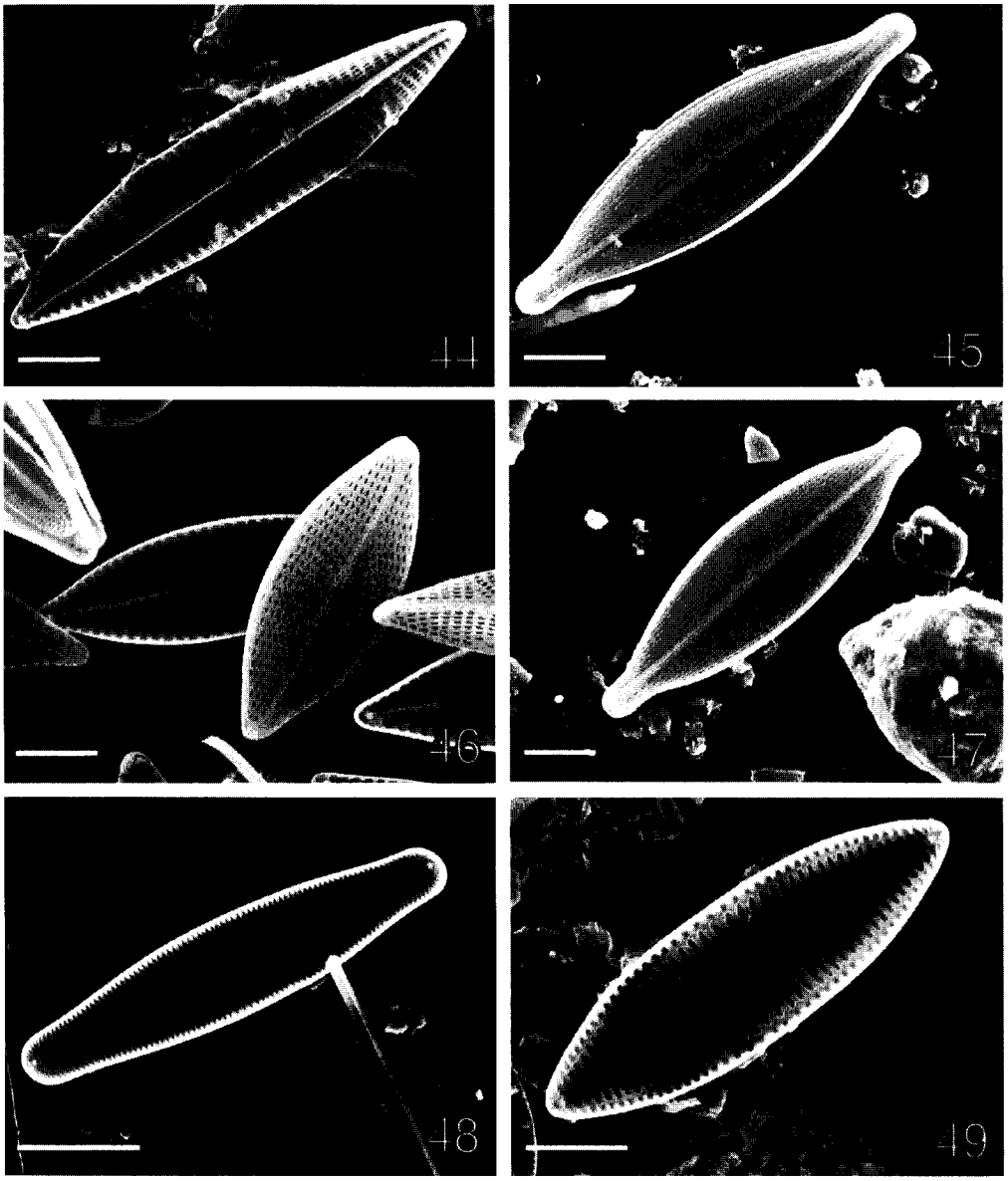


Figures 38–43 **Benthic assemblage** (cont.), SEM. *Figures 38, 39. Entomoneis* aff. *E. pulchra*, girdle view (38) and general view showing torsion of cell (39). *Figure 40. Plagiotropis lepidoptera*?, general aspect of valve. *Figure 41. Pleurosigma strigosum*, general aspect, valve interior. *Figure 42. Gyrosigma balticum*, general aspect, valve interior. *Figure 43. Gyrosigma wormleyi*, general aspect, valve interior. All scale bars = 20 μm.

stubs are kept in the collections of SDSU and Scripps Institution of Oceanography.

Diatom taxa were identified to the lowest taxonomic level possible (Table 2; Figs 2–105). A few taxa showed peculiar morphological features, probably as a response to adaptation to the extreme salinity environment of the Salton Sea. Although these organisms are in need of further taxonomic work, they are documented here and listed in Table 2 as 'sp.' (e.g. *Cyclotella* sp., *Pleurosira* sp., *Sellaphora* sp.) or 'aff.' (e.g. *Entomoneis* aff. *E. pulchra*).

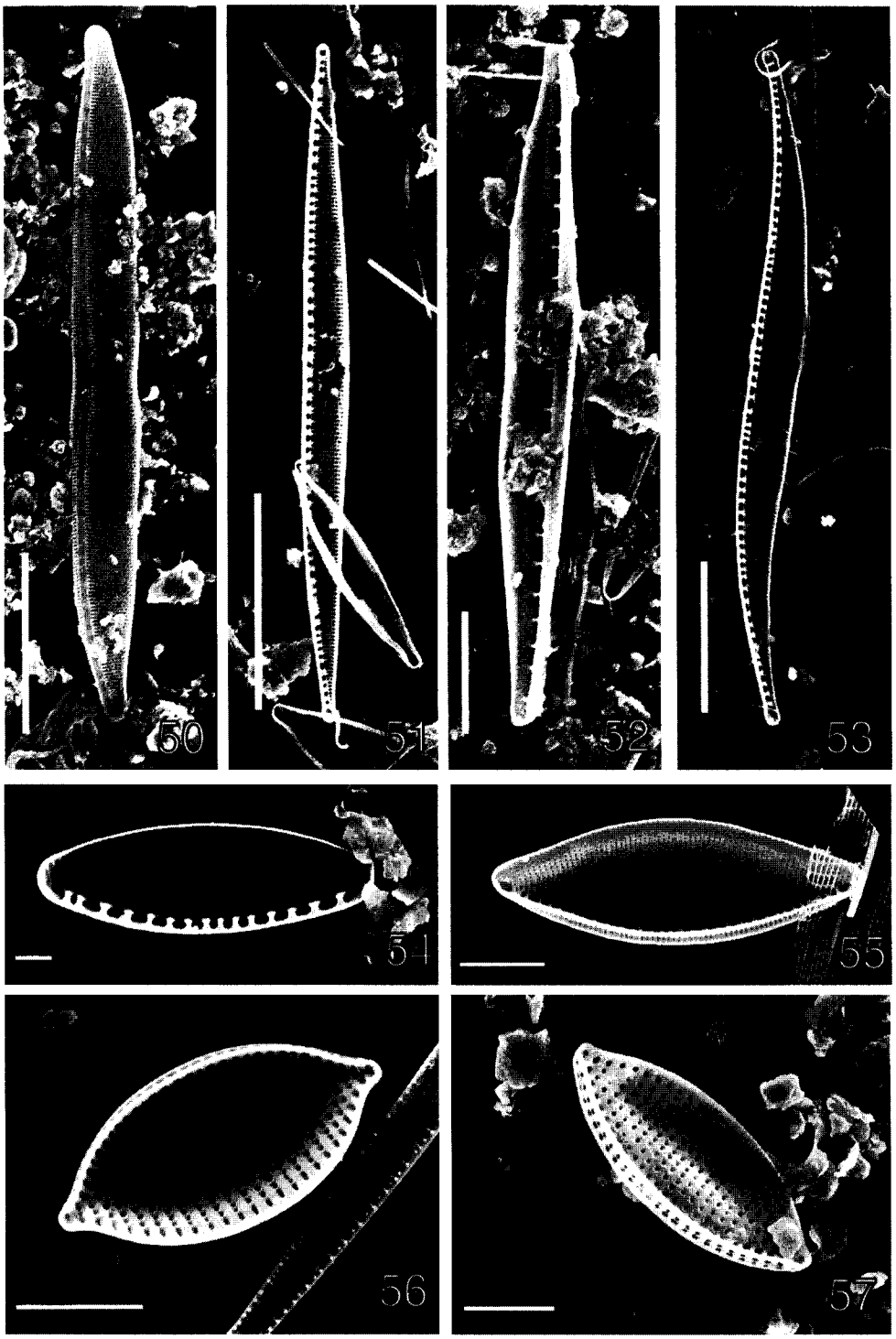
For each taxon, we include its original distribution known from the literature (e.g. Round et al., 1990; Snoeijs, 1993; Snoeijs & Vilbaste, 1994; Ehrlich, 1995; Snoeijs & Potapova, 1995; Snoeijs & Kasperovičiene, 1996; Sims, 1996; Snoeijs & Balashova, 1998), and its occurrence in the Salton Sea (Table 2). Although any taxon living in the Salton Sea may



Figures 44-49 **Benthic assemblage** (cont.), SEM. *Navicula pavillardii*, internal view. *Figure 45. Navicula veneta*, external view. *Figure 46. Navicula menisculus*, external and internal views. *Figure 47. Navicula gregaria*, external view. *Figure 48. Navicula pseudocrassirostris*, internal view. *Figure 49. Oestrupia* sp., internal view. Scale bars = 5 μm in Figures 44–47; bars = 10 μm in Figures 48, 49.

be considered as a 'saline lake' species that is adapted to high salinity and eutrophic conditions, the terminology we use here refers to its environmental distribution hitherto known. Thus, we use 'marine' to characterize species which heretofore are known only from marine environments; 'brackish' for species with known distribution only in mesosaline waters of estuarine and marine littoral areas; and 'freshwater' for those known only from rivers and lakes with salinities <3 g l^{-1}.

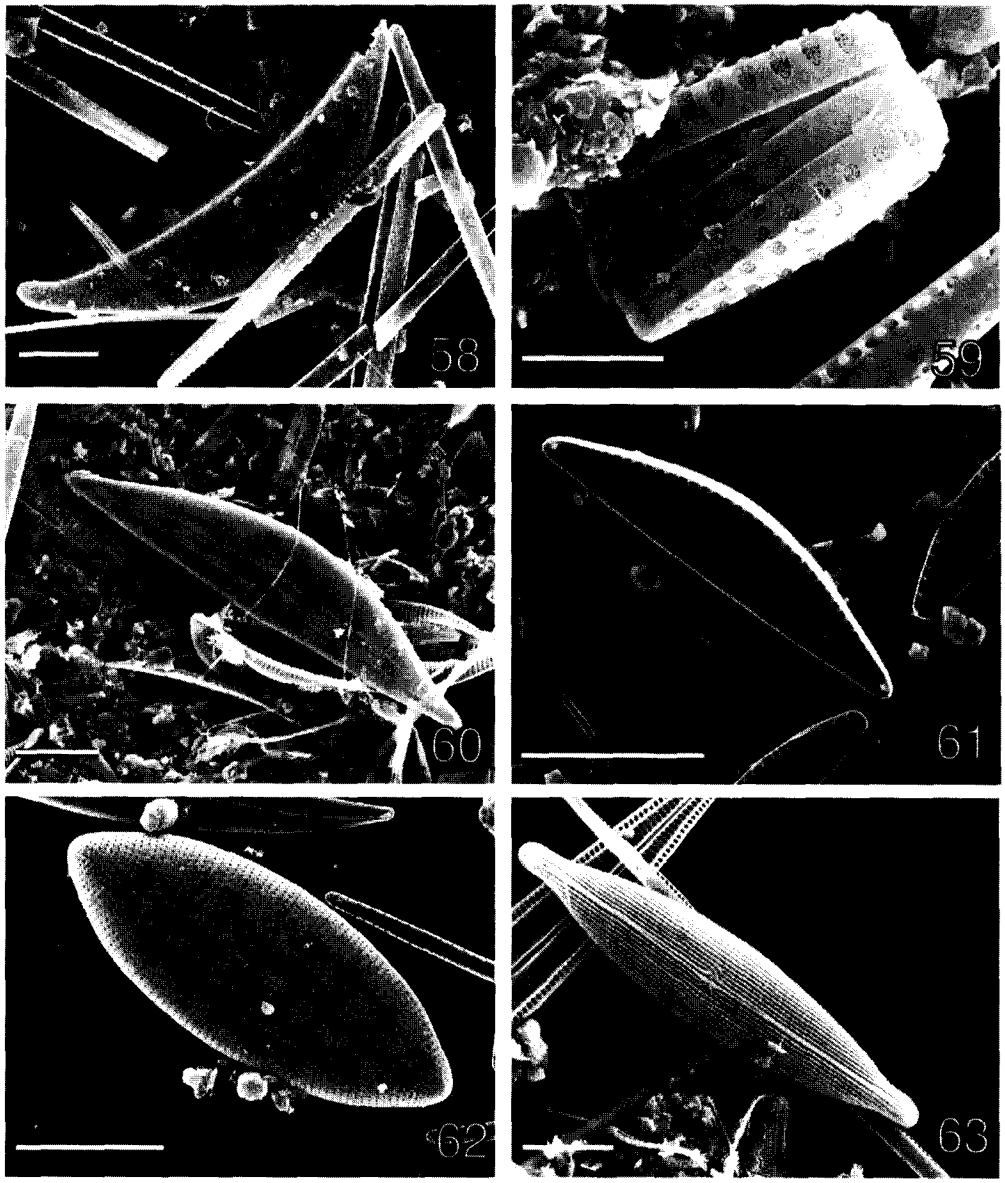
Water samples for phytoplankton enumeration were collected with a 3 m long $\times$ 4 cm diameter PVC tube sampler at depth intervals 0–3 m, 3–6 m and 6–9 m, starting in January 1997. Water from these three depths was pooled, and samples were placed in vials and preserved with 1% Lugol solution. They were kept in darkness until enumerated. Sixteen ml



Figures 50–57 **Benthic assemblage** (cont.), SEM. *Figure 50. Nitzschia obtusa*, valve exterior. *Figures 51–57.* internal views. *Figure 51. Nitzschia sigma. Figure 52. Nitzschia distans. Figure 53. Nitzschia sigmoides. Figure 54. Nitzschia frustulum. Figure 55. Nitzschia ovalis. Figure 56. Trybionella granulata. Figure 57. Trybionella punctata.* Scale bars = 20 μm in Figures 50, 51; 10 μm in Figures 52, 53, 56; 5 μm in Figures 55, 57; 1 μm in Figure 54.

Figure
view. *I*
Petron
61; 5 μ

of sa
invert
identi
across
1997



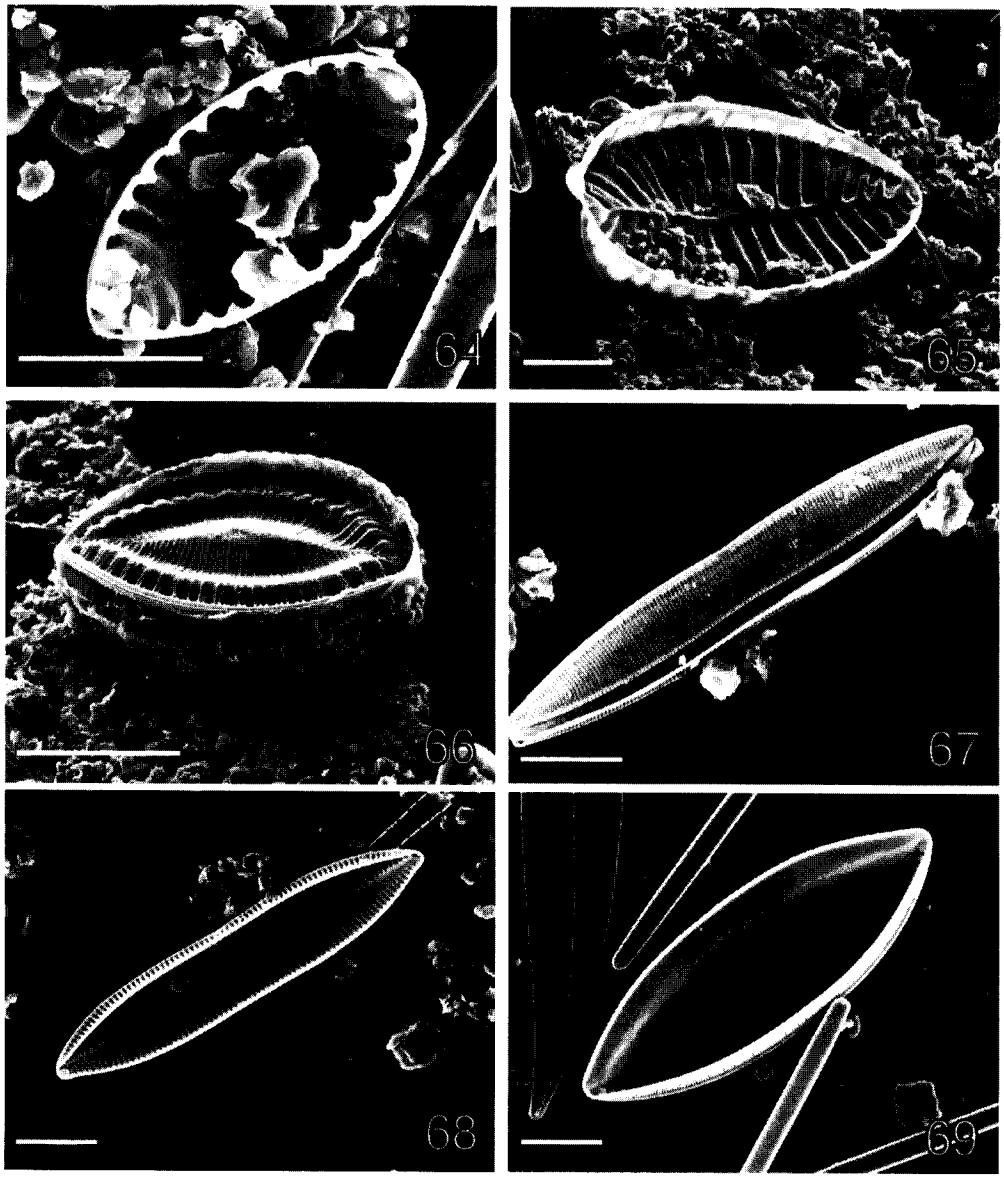
Figures 58–63 **Benthic assemblage** (cont.), SEM. *Figure 58. Rhopalodia* sp., external view. *Figure 59. Opephora naveana*, frustule in girdle view. *Figures 60, 61. Seminavis gracilenta. Figure 60.* Large specimen, external view; *Figure 61.* Small specimen, internal view. *Figure 62. Petroneis marina*, external view. *Figure 63. Proshkinia bulnhemii*, external view. Scale bars = 20 μm in Figure 62; 10 μm in Figures 58, 60, 61; 5 μm in Figures 59, 63.

of sample were settled; counting of diatom cells by inverted microscope technique (Utermöhl, 1958) and identification of taxa was done at 400× magnification across two diameters of the settling chamber. Data for 1997 at station S-1 are represented in Figure 106.

Results and discussion

Composition of the Diatom Flora

We have found 94 taxa in the Salton Sea, its inflows and shoreline pools (Table 2). SEM photographs of almost all diatom taxa encountered in the phytoplankton and benthos are presented in Figures 2–105. We have attempted to divide the diatom flora of the Salton

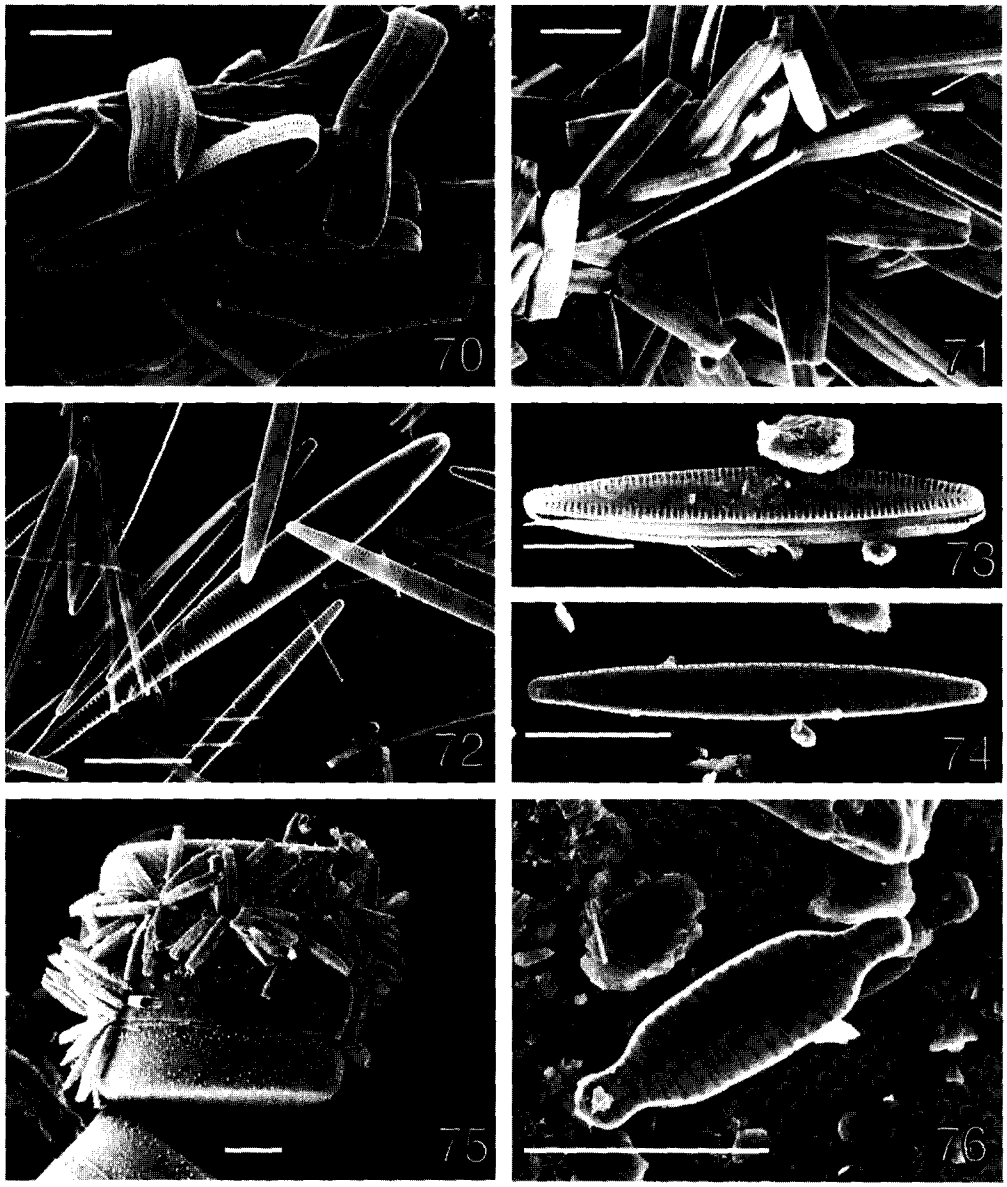


Figures 64–69 **Benthic assemblage** (cont.), SEM. *Figure 64. Surirella minuta*, valve interior. *Figure 65. Surirella striatula*, valve interior, tilt 45 °. *Figure 66. Surirella brébissonii* var. *kuetzingii*, frustule, tilt 45 °. *Figure 67. Tryblionella apiculata*, valve exterior. *Figure 68. Tryblionella hungarica*, valve interior. *Figure 69. Tryblionella littoralis*, valve interior. Scale bars = 20 μm in Figures 65, 66; 10 μm in Figures 64, 67–69.

Sea into four general categories, according to primary habitats: planktonic, benthic, epiphytic and freshwater assemblages. With the exception of the freshwater community, all other diatoms can be considered resident species of the Salton Sea.

The **planktonic assemblage** (Figs 2–17) includes species that live in the plankton and float freely with the water currents. They provide food for zooplankters and fish. It is a mixed assemblage, dominated by marine forms and accompanied by brackish species, and organisms that are regularly found in other saline lakes worldwide. *Chaetoceros muelleri* var. *subsalsum*, *Cyclotella choctawhatcheeana*, *Cyclotella* sp., *Cylindrotheca closterium, Pleurosigma ambrosianum* and *Thalassionema* sp. characterize the planktonic assemblage.

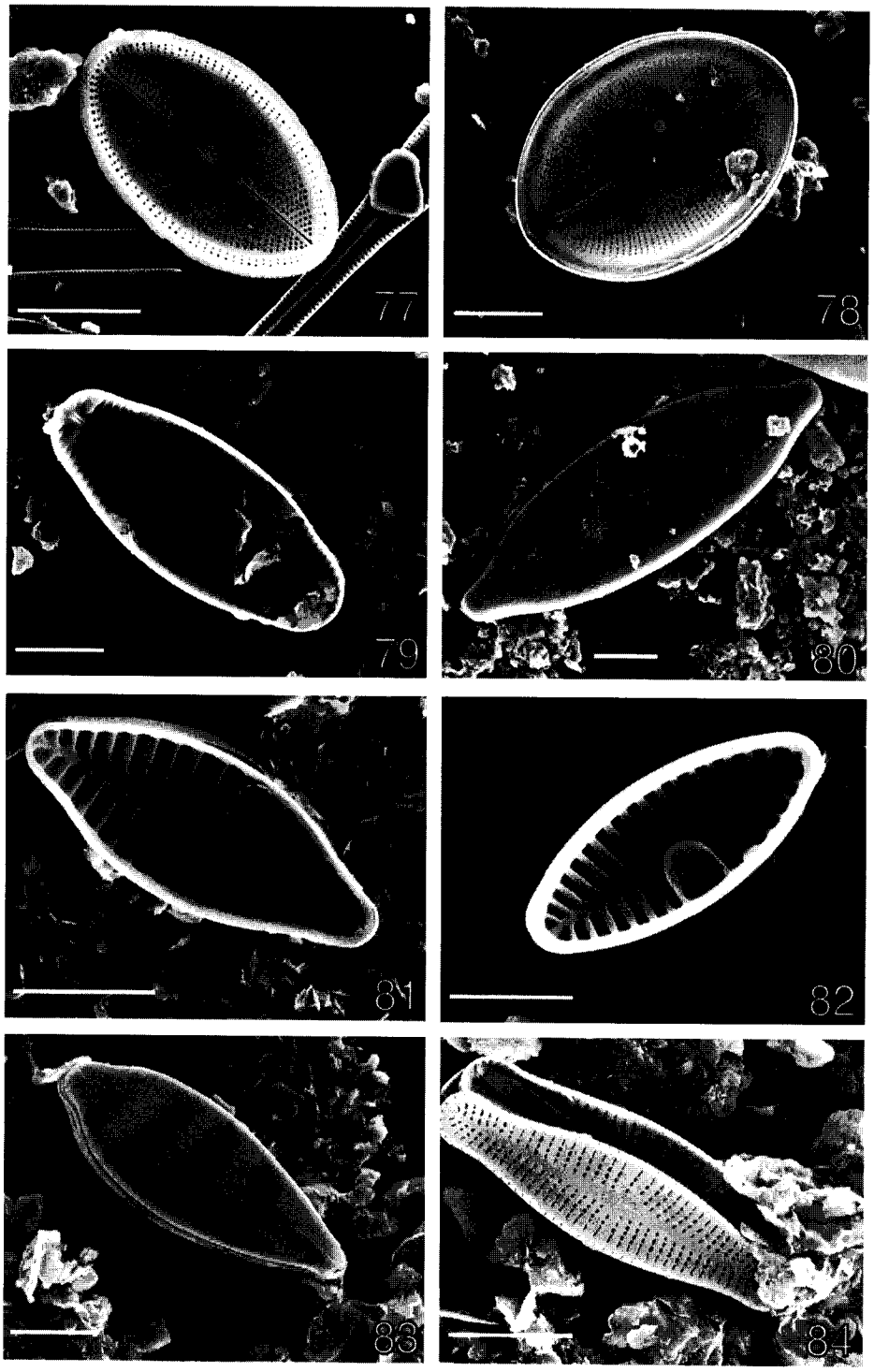
P. ambrosianum (Fig. 6) is a new species characterized by its extremely fine structure, recently described from the Salton Sea by Sterrenburg et al. (2000). *Cylindrotheca closterium* (Fig. 11) is a common diatom in



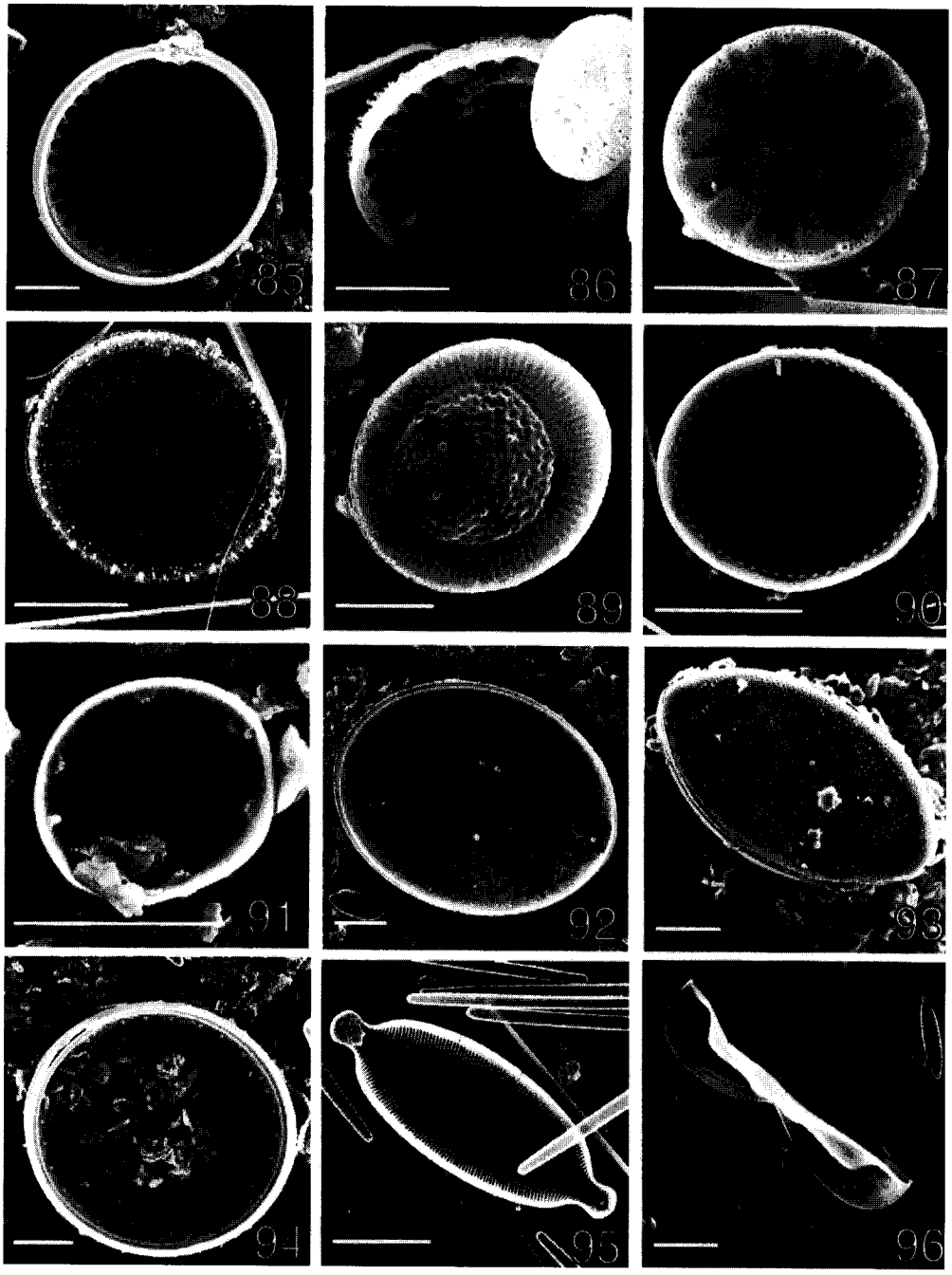
Figures 70–76 **Epiphytic assemblage**, SEM. Cells of *Achnanthes brevipes* (70) and *Tabularia parva* (71) attached on *Chaetomorpha*. *Figure 72. Licmophora ehrenbergii*, internal view. *Figure 73. Tabularia parva*, external view. *Figure 74. Gomphonemopsis* aff. *G. exigua*, internal view, note isopolarity. *Figure 75.* Cells of *Tabularia investiens* attached to girdle of *Pleurosira laevis*. *Figure 76. Achnanthes amoena* (external view) on *Terpsinoë musica*. Scale bars = 20 μm in Figures 70–72, 75; 10 μm in Figures 73, 74, 76.

marine coastal ecosystems (Hasle & Syvertsen, 1997). *C. muelleri* var. *subsalsum* (Fig. 7) is a small species generally reported as developing in brackish waters (mesohalobe), found in various arid saline systems (Johansen & Rushforth, 1985). Its spores are commonly observed in surface sediments of the lake (Fig. 8). The variability of resting spores in terms of shape and ornamentation was great: primary valves usually convex, spinose or smooth; secondary valve surface smooth with one or two spines often visible; secondary valve shaped as chimney-like protrusion though sometimes much reduced. Little variability was evident among vegetative cells.

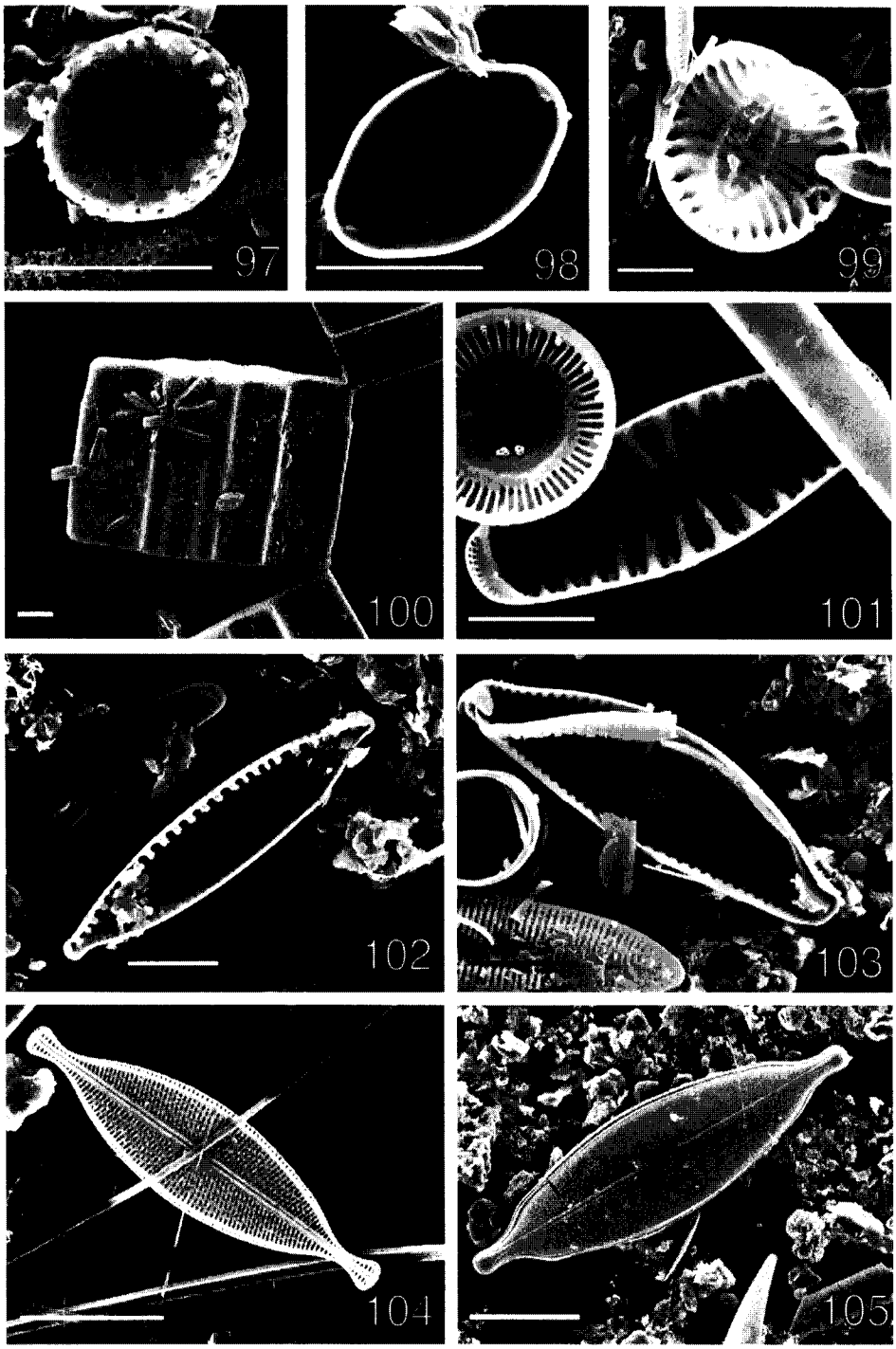
Two euryhaline, planktonic *Cyclotella* species were present year-round in fairly high numbers. The individual cells of *C. choctawhatcheeana* (Fig. 5) are small (<10 μm in diameter) and somewhat resemble those of *C. caspia* Grunow (Prasad et al., 1990). *Cyc-*



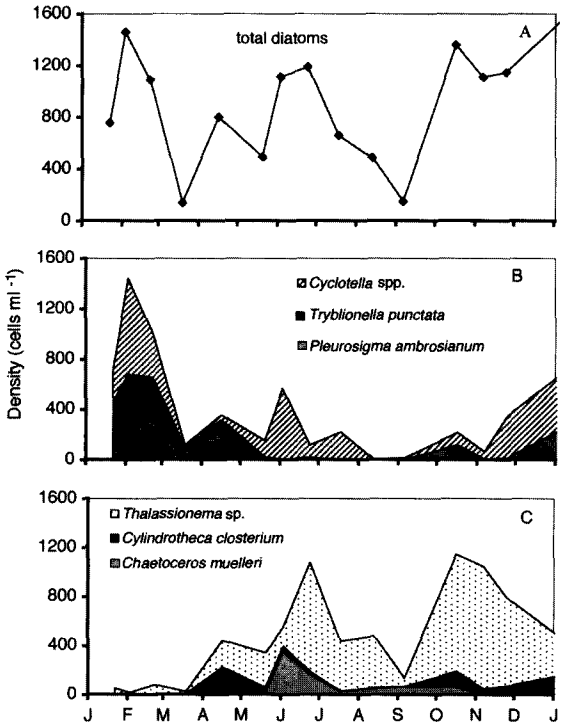
Figures 77–84 **Freshwater assemblage**, SEM. *Figure 77. Cocconeis placentula* var. *euglypta*; raphid valve, external view. *Figure 78. Cocconeis pediculus*; raphid valve, external view. *Figure 79. Sellaphora pupula*, internal view. *Figure 80. Anomoeoneis sphaerophora*, external view. *Figure 81. Planothidium delicatulum*, araphid valve, internal view. *Figure 82. Planothidium lanceolatum*, internal view of araphid valve; note 'hoof-mark' capped structure (see Round & Bukhtiyarova, 1996). Figure 83. *Gomphonema parvulum*, external view of frustule. *Figure 84. Achnanthidium minutissimum*, araphid valve, external view; underneath is raphid valve in internal view. Scale bars = 10 μm in Figures 77, 78, 80; bars = 5 μm in Figures 79, 81–84.



Figures 85–96 **Freshwater assemblage** (cont.), SEM. *Figures 85, 86. Cyclotella scaldensis*, internal views; tilt is 45 ° in Figure 86. *Figure 87. Cyclotella atomus*, external view. *Figure 88. Cyclotella meneghiniana*, external view. *Figure 89. Cyclotella wulfiae*, external view. *Figure 90. Thalassiosira weissflogii*, internal view. *Figure 91. Thalassiosira pseudonana*, internal view. *Figure 92. Pleurosira laevis*, internal view. *Figure 93. Pleurosira* sp., external view. *Figure 94. Stephanodiscus* sp. (*S. niagarae* complex), internal view. *Figure 95. Caloneis amphisbaena*, valve interior. *Figure 96. Entomoneis paludosa*, valve strongly compressed laterally. Scale bars = 20 μm in Figures 92, 95; 10 μm in Figures 90, 93, 94, 96; 5 μm in all other figures.



Figures 97–105 **Freshwater assemblage** (cont.), SEM. *Figure 97. Nanofrustulum shiloi*, external view. *Figure 98. Placoneis* sp., internal view. *Figure 99. Campylodiscus bicostatus*, internal view. *Figure 100. Terpsinoë musica*, frustule in a chain with *Tabularia investiens* attached to girdle bands. *Figure 101. Navicula capitata* var. *hungarica*, internal view. *Figure 102. Nitzschia elegantula*, internal view. *Figure 103. Cymbella affinis*, internal view. *Figure 104. Brachysira vitrea*, valve interior. *Figure 105. Craticula ambigua*, external view. Scale bars = 20 μm in Figures 100, 105; 10 μm in Figures 99, 103, 104; 5 μm in Figures 97, 98, 101, 102.



Figures 106 The annual cycle of diatom abundance in the plankton of the Salton Sea during 1997, station S-1. A. Total diatom cells ml^{-1}. B and C. Cell abundances for the dominant diatom species in the plankton.

lotella sp. (Figs 2–4), on the other hand, is somewhat larger (10–20 μm in diameter) and has a tendency to form long chains (Fig. 2). *C. choctawhatcheeana* has been described as being associated with anthropogenic eutrophication of Chesapeake Bay, U.S.A., and may be an indicator species of such changes in coastal waters (Cooper, 1995). It has also been characterized as a cosmopolitan species in saline closed-basin lakes (Carvalho et al., 1995). In the summer and fall, the most common diatom by far was *Thalassionema* sp.

Taxonomic notes

Cyclotella sp.: The general aspect of *Cyclotella* sp. (Figs 2–4) resembles *C. litoralis* Lange & Syvertsen (Lange & Syvertsen, 1989). However, morphological differences regarding number of striae in 10 μm (20–22 for *C.* sp vs. 9–14 in *C. litoralis*), external opening of marginal rimoportula (placed above the marginal ring of fultoportulae vs. below it in *C. litoralis*), and the undulation of the valve face being restricted to the central field (Fig. 3) lead us to believe that this is a new species. A manuscript is in preparation.

Thalassionema sp.: Morphological features of this species are commonly found in *T. nitzschioides* (Grunow) Mereschkowsky, *T. pseudonitzschioides* (Schuette & Schrader) Hasle and *T. frauenfeldii* (Grunow) Hallegraeff. Cells usually solitary (Fig. 10), or, more seldom, in stellate colonies (as in *T. nitzschioides* and *T. pseudonitzschioides*) formed by mucous pads at the foot-poles (Fig. 9). Valves linear; valve ends similar in width and outline, both poles are smoothly rounded (Figs 10, 14, 15), as in *T. nitzschioides* (Hasle & Syvertsen, 1997). Sternum wide (Figs 10 and 16); areolae are on the border between valve face and mantle; 5–7 in 10 μm, as is the case for *T. frauenfeldii* (Hasle & Syvertsen, 1997). Internal openings of areolae small (Figs 14,15); externally they are manifest as larger grooves crossed by simple silicified arches, as in *T. frauenfeldii* (Figs 12, 16, 17). Spines are present externally between areolae (Figs 12, 13, 16, 17) (see figure f, p. 425 in Round et al., 1990). Each valve end bears an apical protrusion, one which is arrow-shaped, much more prominent than the other (Figs 12, 17). One rimoportula at each pole, located obliquely or almost perpendicular to the apical axis (Figs 14, 15), as in *T. pseudonitzschioides*. A small pore is present between the process and the valve margin. Further investigations, including observations of type material, are certainly required in order to establish the correct identity of this taxon. The three closely related *Thalassionema* species are marine planktonic diatoms. *T. nitzschioides* has an ample distribution worldwide (Hasle & Syvertsen, 1997); *T. pseudonitzschioides* was originally described from the Gulf of California (Schuette & Schrader, 1982) and may be regarded as a subtropical to temperate species; *T. frauenfeldii* has been observed from warm and temperate localities (Hasle & Syvertsen, 1997), including the Gulf of California.

The **benthic assemblage** is highly diverse (>50 species), and includes marine, estuarine and freshwater diatoms (Figs 18–69). Many diatoms can be found in or on nearshore substrates, either attached to sand grains (epipsammic), rocks (epilithic), or plants (epiphytic, see below), or living freely on the surface sediments (epipelic). The epipelic community is composed of motile species (Round et al., 1990) and can form dense patches of brownish color on the substrate. Typical genera of the Salton Sea epipelon include *Caloneis, Diploneis, Entomoneis, Gyrosigma, Plagiotropis, Pleurosigma, Surirella* and *Tryblionella*. The attached communities include adnate forms (Round et al., 1990) with cells closely appressed to the sub-

stratum (e.g. *Amphora pediculus*, *A. ovalis*; Figs 23, 24).

When turbulence is high in the lake, as during strong windstorms, diatoms that are usually associated with benthic and epiphytic habitats get mixed into the plankton (Tiffany, 1999). In the summer, mats of cyanobacteria with benthic diatoms enmeshed in them break free from the bottom to float on the surface. *Pleurosigma* sp. and *Nitzschia sigmoidea* were mentioned by Carpelan (1961) as associated with these mats. We recorded *Proschkinia bulnheimii* (Fig. 63), several species of *Navicula* (Figs 44–47), and *Seminavis gracilenta* (Figs 60, 61) in our mat samples.

Taxonomic notes

Diploneis obliqua (Brun) Hustedt is a brackish water form (Hustedt, 1933) which possesses asymmetric valves (Figs 32–34). Our specimens fit the description given by Hustedt (1933, pp. 686–687, Fig. 1075c). We could not locate electron microscope images of this species in the literature. We illustrate it here with special reference to (a) the chambers that open to the exterior of the valve by a long narrow slit running the whole length of the stria (Figs 32, 33), and (b) the 'grappling hooks' at the external marginal end of each elongated slit (Fig. 33). Slit-like external openings have been described in *D. splendida* (Gregory) Cleve by Droop (1996), and a crescent-shaped opening at the margin of each stria was first discovered by Idei & Kobayashi (1989) in *Diploneis finnica* (Ehrenberg) Cleve.

The lanceolate valves of *Navicula pseudocrassirostris* Hustedt (Fig. 48) have broadly rounded poles, and when seen under SEM, they reveal several morphological features that are characteristic of the genus *Sellaphora* Mereschkowsky (i.e. striae uniseriate; areolae small; internally, the raphe ends in a narrow helictoglossa at the poles; Mann, 1989). Thus, our SEM observations as well as others from the Dead Sea and 'Arava Springs (Ehrlich, 1995) and salt marsh sediments (M. Sullivan, pers. comm.) indicate that this '*Navicula*' species most probably belongs to *Sellaphora*. We have been unable to find a formal transfer of this species in the literature. Mann's (1989) list of new combinations is incomplete, but it is beyond the scope of this paper to deal with nomenclatural changes.

An **epiphytic community** grows attached to the macroscopic green algae (*Chaetomorpha linum* Müller and*Enteromorpha intestinalis* (L.) Link) and filamentous cyanobacteria that grow on the rocks and other hard surfaces near the shore (Figs 70–76). *Tabularia parva* (Figs 71, 73) was the most common epiphyte, often densely covering the host and giving it a deep brownish color. *Achnanthes brevipes* (Fig. 70) and *Licmophora ehrenbergii* (Fig. 72) were also seen growing on *Chaetomorpha*. From our limited sampling, it appears that *A. brevipes* may be primarily restricted to the colder months; *L. ehrenbergii* was rare. A *Chaetomorpha* sample from Red Hill (15 Oct 99, temp 30 °C, sal. 34 g l^{-1}) was covered with the colonial ciliate *Zoothamnium* sp. and with the diatom *Gomphonemopsis* aff. *G. exigua* (Fig. 74). The diatom cells seem to be growing on both the stalk of the ciliate and on *Chaetomorpha*. Taxonomically, *G. exigua* is of interest due to the lack of heteropolarity in our specimens, a condition that is very unusual in this genus (F. Round, pers. comm.) defined as heteropolar (Medlin & Round, 1986).

In addition, large epiphytic and epilithic diatom species hosting other diatoms were also observed in the Salton Sea area at Whitefield Creek. The most commonly encountered hosts were species forming long filaments attached to rocks or macroalgae, *Pleurosira laevis* and *Terpsinoë musica*. These large diatoms often had smaller diatoms attached, usually to the girdle bands. Such was the case for *Tabularia investiens* growing on *P. laevis* (Fig. 75), and of *Achnanthes amoena* on *T. musica* (Fig. 76).

The **freshwater assemblage** is diverse and composed of 30 species (Figs 77–105). Three main tributaries, the Alamo, New and Whitewater rivers flow into the Salton Sea. In addition, there are agricultural drains and some small creeks. These are fresh to slightly saline (1–5 g l^{-1}) environments with their own particular diatom flora. These diatoms get flushed into the Sea and their valves are found in the water column and in the surface sediments. Once in the Sea, many of the species probably do not live long in the high salinity waters. Planktonic (e.g. *Cyclotella atomus*, Fig. 87; *C. scaldensis*, Figs 85, 86; *T. weissflogii*, Fig. 90), benthic (e.g. *Achnanthidium minutissimum*, Fig. 84; *Cocconeis pediculus*, Fig. 78; *Nitzschia elegantula*, Fig. 102) and epiphytic forms (e.g. *Pleurosira laevis*, Figure 92) are included in this assemblage.

The annual cycle in the plankton

The general pattern of seasonal variation of planktonic diatoms in 1997 is shown in Figure 106A. Concentrations of diatoms in the water column were highest (>1000 cells ml^{-1}) in February–March, June–July

and October 1997–January 1998. Minimum values were measured in mid-March and September. This general pattern is similar to the one observed by Carpelan (1961) and Bain et al. (1970). Highest absolute values for 1997 were lower than those reported previously (~1500 cells ml^{-1} in 1997 vs. ~50 000 cells ml^{-1} in 1955 and 1956 (Carpelan, op. cit.), and ~14 000 cells ml^{-1} in 1968 (Bain et al., op. cit.)). Differences in sampling methods and locations, counting procedures, and/or climatic factors may explain this discrepancy.

The diatom species composition varied with the seasons (Fig. 106B, C). In the winter, three planktonic diatoms (*P. ambrosianum, C. choctawhatcheeana* and *Cyclotella* sp.) and one benthic species (*T. punctata*) dominated the plankton assemblage in 1997 (Fig. 106B). As mentioned above, when turbulence is high in the lake benthic and epiphytic diatoms get mixed into the plankton (Tiffany, 1999). This was the case for *T. punctata* which reached densities of 700 cells ml^{-1} in February 1997. In spring–early summer and fall, the most common diatom by far was *Thalassionema* sp. with densities of >1000 cells ml^{-1} (Fig. 106C). It was accompanied by high abundances of *C. closterium*, *Cyclotella* spp. and *C. muelleri* var. *subsalsum* (mainly in early summer).

Earlier studies of Carpelan (1961) and Bain et al. (1970) do not mention the occurrence of *C. muelleri* var. *subsalsum* at all. During our study period, this species reached concentrations of ca. 400 cells ml^{-1} in June 1997, and preliminary downcore studies reveal the presence of *Chaetoceros* spores in older sediments as well (Tiffany, unpubl. data). Although it is small in size, the shape of cells is so characteristic (Fig. 7) that we do not believe this species could have been overlooked in the past. Whether it may be considered a 'newcomer' to the lake will remain unknown until high-resolution downcore studies can be undertaken.

The other planktonic diatom taxa were reported in the earlier studies (though in some cases under a different name), and seasonal population peaks seem to correspond with our observations. For example, *Cyclotella* (identified as "close to *C. caspia*"; Carpelan, 1961, p. 38) and a short *Nitzschia longissima* (suggested to be a variety of *C. closterium*) were considered the two most prevalent diatoms of the Sea (Carpelan, op. cit.), present year-round except in the summer. We suggest these records to coincide with our records of *C. closterium*, and probably also of *Cyclotella* sp. Also, Carpelan's record of *Thalassionema nitzschioides* in July–September 1955 should correspond with our observations of *Thalassionema* sp, and the *Pleurosigma* species reported as dominating the winter plankton may correspond *to P. ambrosianum*.

Outlook: Uniqueness of the Salton Sea diatom flora

Many of the diatoms recorded in the Salton Sea area are typical of saline aquatic habitats in western North America (see summary in Blinn, 1993). Some have been observed worldwide in highly saline waters of, for example, northern Egypt (Compère, 1990), Israel (Ehrlich, 1978, 1995), and Australian saline lakes (Gell & Gasse, 1990), and have been used as indicators of Quaternary climate and hydrology (see summary in Fritz et al., 1999). Others are freshwater representatives linked to the Colorado River ecosystem (Czarnecki & Blinn, 1978). The uniqueness of the Salton Sea phytoplankton, however, lies in the predominantly marine nature of its composition. Marine diatoms (e.g. *C. closterium* (Ehr.) Reimann & Lewin, *Thalassionema* sp.), dinoflagellates (e.g. *Gonyaulax grindleyi* Reinecke, *Gyrodinium uncatenum* Hulburt), and flagellates (e.g. *Chattonella marina* (Subrahmanyan) Hara & Chihara and the cryptomonad *Plagioselmis* sp.) live and grow in the Salton Sea. This is probably the result of intentional and unintentional introductions of marine fauna and flora. In less than 100 years the Salton Sea has changed from a freshwater lake to a highly saline ecosystem dominated by non-native species (Cohen et al., 1999). Most of the marine fish species were introduced from the Gulf of California in the 1940s and 1950s to create a sport fishery (Walker et al., 1961; Setmire et al., 1993). Various invertebrate animals were introduced from the coasts of California or the Gulf of California in the 1950s to provide food for fish populations, or unintentionally during fish transplants (Linsley & Carpelan, 1961). These introductions, as well as the current importance of the Salton Sea to migratory waterbirds have provided a direct route for marine organisms to invade the Sea. We do not know how many marine diatoms were accidentally brought into the Sea and how many of them actually became established. We speculate that accidental introduction may have been the case for the marine genus *Thalassionema*, for example, that is present year-round and dominates the phytoplankton assemblage in early summer and fall. *Thalassionema* sp. valves are well preserved in the surface sediments of the Salton Sea. Densely packed

layers of this species resembling diatom mats can be distinguished downcore (Tiffany, pers. obs.); they may hold clues to the marine evolution of the Salton Sea.

Acknowledgements

We wish to express our gratitude to the many colleagues who have assisted us with the identification of diatoms of the Salton Sea, including H. Håkansson, G. R. Hasle, Y. Likhoshway, N. Navarro, M. Poulin, A.-M. Schmidt, F. A. S. Sterrenburg. Especially, we thank E. Cox, D. Czarnecki, F. Round and M. Sullivan, for their help and unconditional interest in the study of the diatoms of this unusual location. We thank S. Barlow and the SEM Facility at SDSU for unlimited help during endless hours at the microscope; J. Watts, B. Kuperman and V. Matey for all those sampling hours at the lake, and J. Dainer for technical assistance. R. Vogl, R. Henry and D. Dexter kindly supplied sediment samples. S. Hurlbert provided continuous support and encouragement. This study developed from work toward a master degree of M. A. Tiffany under the direction of S. Hurlbert at SDSU. This final version benefited from comments of F. Reid, S. Hurlbert, and an anonymous reviewer. Financial support was provided in part by the United States Environmental Protection Agency through grant #R826552-01-0 to the Salton Sea Authority, and by the Marine Life Research Group of the Scripps Institution of Oceanography (to CBL). The research results have not been subjected, however, to the Agency's required peer review and, therefore, do not necessarily reflect the views of the Agency. Therefore no official endorsement should be inferred.

References

Bain, R. C., A. M. Coldwell, R. H. Clawson, H. L. Scotten & R. G. Wills, 1970. Salton Sea California: water quality and ecological management considerations. U.S. Dept. Interior, Federal Water Quality Administration, Pacific Southwest Region: 53 pp.

Blinn, D. W., 1993. Diatom community structure along physicochemical gradients in saline lakes. Ecology 74: 1246–1263.

Carpelan, L. H., 1961. Phytoplankton and plant productivity. In Walker, B. W. (ed.), The Ecology of the Salton Sea, California, in Relation to the Sportfishery. California Dept. Fish and Game, Fish Bull. 113: 33–42.

Carvalho, L. R., E. J. Cox, S. C. Fritz, S. Juggins, P. A. Sims, F. Gasse & R. W. Batterbee, 1995. Standardizing the taxonomy of saline lake *Cyclotella* spp. Diatom Res. 10: 229–240.

Cohen, A. L., 1974. Critical point drying. In Hyat, A. M. (ed.), Principles and Techniques of Scanning Electron Microscopy 1". Van-Nostrand-Reinhold, New York: 44–112.

Cohen, M. J., J. I. Morrison & E. P. Glenn, 1999. Haven or hazard: The ecology and future of the Salton Sea. Pacific Institute for Studies in Development, Environment, and Security Report, February 1999: 64 pp.

Compère, P., 1990. Diatoms from hypersaline inland waters of Egypt. In Kociolek, J. P. (ed.), Proc. 11th Int. Diatom Symp., 12–17 August 1990, San Francisco. Calif. Acad. Sciences, San Francisco, California: 175–188.

Cooper, S. R., 1995. An abundant small brackish water *Cyclotella* species in Chesapeake Bay, U.S.A. In Kociolek, J. P. & M. J. Sullivan (eds), A Century of Diatom Research in North America: A Tribute to the Distinguished Careers of Charles W. Reimer and Ruth Patrick Koeltz, Champaign: 127–134.

Czarnecki, D. B. & D. W. Blinn, 1978. Diatoms of the Colorado River in Grand Canyon National Park and vicinity. Bibl. Phycologica 38: 181 pp.

Droop, S. J. M., 1996. The identity of *Diploneis splendida* (Bacillariophyta) and some related species. Phycologia 35: 404–420.

Ehrlich, A., 1978. The diatoms of the hyperhaline Solar Lake (NE Sinai). Israel J. Bot. 27: 1–13.

Ehrlich, A., 1995. Flora Palaestina. Atlas of the inland-water diatom flora of Israel. Geol. Surv. Israel, Israel Acad. Sci. Humanities: 166 pp. + 60 plates.

Fritz, S. C., B. F. Cumming, F. Gasse & K. R. Laird, 1999. Diatoms as indicators of hydrologic and climatic change in saline lakes. In Stroemer, E. F. & J. P. Smol (eds), The Diatoms. Applications for Environmental and Earth Sciences. Cambridge University Press, U.K.: 41–72.

Gell, P. A. & F. Gasse, 1990. Relationships between salinity and diatom flora from some Australian saline lakes. In Kociolek, J. P. (ed.), Proc. 11th Int. Diatom Symp., 12–17 August 1990, San Francisco. Calif. Acad. Sciences, San Francisco, California: 631–647.

Hasle, G. R. & E. E. Syvertsen, 1997. Chapter 2. Marine Diatoms. In Tomas, C. R. (ed.), Identifying Marine Phytoplankton. Academic Press, San Diego, California: 5–385.

Hustedt, F., 1933. Die Kieselalgen Deutschlands, Österreichs und der Schweiz mit Berücksichtigung der übrigen Länder Europas sowie der angrenzenden Meeresgebiete, 2. Teil, Lief. 3. In Rabenhort, L. (ed.), Kryptogamen-Flora, Leipzig: 321–432.

Idei, M. & H. Kobayasi, 1989. The fine structure of *Diploneis finnica* with special reference to the marginal openings. Diatom Res. 4: 25–37.

Johansen, J. R. & S. R. Rushforth, 1985. A contribution to the taxonomy of *Chaetoceros muelleri* Lemmermann (Bacillariophyceae) and related taxa. Phycologia 24: 437–447.

Kaiser, J., 1999. Battle over a dying sea. Science, News Focus 284: 28–30.

Lange, C. B. & E. E. Syvertsen, 1989. *Cyclotella litoralis* sp. nov. (Bacillariophyceae), and its relationships to *C. striata* and *C. stylorum*. Nova Hedw. 48: 341–356.

Linsley, R. H. & L. H. Carpelan, 1961. Invertebrate fauna. In Walker, B. W. (ed.), The Ecology of the Salton Sea, California, in Relation to the Sportfishery. California Dept. Fish and Game, Fish Bull. 113: 43–47.

Mann, D. G., 1989. The diatom genus *Sellaphora*: separation from *Navicula*. British Phycol. J. 24: 1–20.

Medlin, L. K. & F. E. Round, 1986. Taxonomic studies of marine Gomphonemoid diatoms. Diatom Res. 1: 205–225.

Prasad, A. K. S. K., J. A. Nienow & R. J. Livingston, 1990. The genus *Cyclotella* (Bacillariophyta) in Choctawhatchee Bay, Florida, with special reference to *C. striata* and *C. choctawhatcheeana* sp. nov. Phycologia 29: 418–436.

Reifel, K. M., M. P. McCoy, T. E. Rocke, M. A. Tiffany, S. H. Hurlbert & D. J. Faulkner, 2002. The possible importance of algal toxins in the Salton Sea, California. Hydrobiologia 473/Dev. Hydrobiol. 161: 275–293.

Riedel, R., L. Caskey & B. A. Costa-Pierce, 2002. Fish biology and fisheries ecology of the Salton Sea. Hydrobiologia 473/Dev. Hydrobiol. 161: 231–246.

Round, F. E. & L. Bukhtiyarova, 1996. Four new genera based on *Achnanthes* (*Achnanthidium*) together with a re-definition of *Achnanthidium*. Diatom Res. 11: 345–361.

Round, F. E., R. M. Crawford & D. G. Mann, 1990. The Diatoms. Biology & Morphology of the genera. Cambridge University Press: 747 pp.

Schuette, G. & H. Schrader, 1982. *Thalassiothrix pseudonitzschioides* sp. nov.: a common pennate diatom from the Gulf of California. Bacillaria 5: 213–223.

Setmire, J. G., R. A. Schroeder, J. N. Densmore, S. L. Goodbred, D. J. Audet & W. R. Radke, 1993. Detailed study of water quality, bottom sediment, and biota associated with irrigation drainage in the Salton Sea area, California, 1988–90. U.S. Geol. Survey Water Res. Invest. Report 93–4014: 102 pp.

Sims, P. A. (ed.), 1996. An Atlas of British Diatoms. Biopress Ltd., Bristol, U.K.: 601 pp.

Snoeijs, P. (ed.), 1993. Intercalibration and Distribution of Diatom Species in the Baltic Sea. Vol 1. Opulus Press, Länna, Sweden: 130 pp.

Snoeijs, P. & S. Vilbaste (eds), 1994. Intercalibration and Distribution of Diatom Species in the Baltic Sea. Vol 2. Opulus Press, Länna, Sweden: 125 pp.

Snoeijs, P. & M. Potapova (eds), 1995. Intercalibration and Distribution of Diatom Species in the Baltic Sea. Vol 3. Opulus Press, Länna, Sweden: 125 pp.

Snoeijs, P. & J. Kasperoviciene (eds), 1996. Intercalibration and Distribution of Diatom Species in the Baltic Sea. Vol 4. Opulus Press, Länna, Sweden, 125 pp.

Snoeijs, P. & N. Balashova (eds), 1998. Intercalibration and Distribution of Diatom Species in the Baltic Sea. Vol 5. Opulus Press, Länna, Sweden: 144 pp.

Sterrenburg, F. A. S., M. A. Tiffany & C. B. Lange, 2000. Studies on the genera *Gyrosigma* and *Pleurosigma* species from the Salton Sea California (U.S.A.). Proc. Acad. Nat. Sciences Philadelphia 105: 305–313.

Tiffany, M. A., 1999. Composition and dynamics of Salton Sea plankton. Abstract in: Science for the Salton Sea Ecosystem Management, University of California, Riverside, 5 January 1999, Riverside: 14–15.

Tiffany, M. A, S. B. Barlow, V. E. Matey & S. H. Hurlbert, 2001. *Chattonella marina* (Raphidophyceae), a potentially toxic alga in the Salton Sea, California. Hydrobiologia, 466/Dev. Hydrobiol. 162: 187–194.

Utermöhl, H., 1958. Zur Vervollkommung der quantitativen Phytoplankton-Methodik. Mitt int. Verein theor. Angew. Limnol. 9: 1–38.

Walker, B. W., 1961. The ecology of the Salton Sea, California, in relation to the sportfishery. California Dept. Fish and Game, Fish Bull. 113: 204 pp.

Watts, J M., B. K. Swan, M. A. Tiffany & S. H. Hurlbert, 2001. Thermal, mixing, and oxygen regimes of the Salton Sea, California, 1997–1999. Hydrobiologia, 466/Dev. Hydrobiol. 162: 159–176.

Hydrobiologia **473:** 203–216, 2002.
D.A. Barnum, J.F. Elder, D. Stephens & M. Friend (eds), The Salton Sea.
© 2002 *Kluwer Academic Publishers. Printed in the Netherlands.*

Invertebrates of the Salton Sea: a scanning electron microscopy portfolio

Boris I. Kuperman, Victoria E. Matey, Deborah M. Dexter & Mary Ann Tiffany
Department of Biology, San Diego State University, San Diego, CA 92182, U.S.A.

Key words: Salton Sea, invertebrates, SEM, Foraminifera, Turbellaria, Rotifera, Polychaeta, Oligochaeta, Cirripedia, Ostracoda, Copepoda, Amphipoda, Insecta

Abstract

Scanning electron microphotographs of 16 Salton Sea invertebrate species are presented within this portfolio. A wide spectrum of invertebrates was investigated including foraminiferans, a flatworm, a rotifer, annelids, crustaceans and insects. Additional information is provided on the morphology and function of structures visible in the images.

Introduction

Invertebrates (>150 μm) inhabiting the Salton Sea are important in both the planktonic and benthic food chains. The Salton Sea was accidentally formed in 1905–06 as a result of an engineering error, and is the largest inland body of water in California (Walker, 1961). It is located in one of the most arid regions of North America and has a high evaporation rate and low water inflow. The present salinity is approximately 44 g l^{-1}, and the water temperature varies seasonally from 13° C in winter to 40° C in late summer while oxygen concentration varies spatially and temporally from 0 to >20 mg l^{-1} (Watts et al., 2001).

The last detailed examination of the invertebrates of the Salton Sea was conducted in the mid 1950s by Carpelan & Linsley (1961). At that time, they identified invertebrates belonging to six phyla: Protozoa (considered as a phylum up to the 1980s), Rotifera, Bryozoa (currently consisting of two phyla, the Ectoprocta and Entoprocta), Nematoda, Annelida, and Arthropoda.

Our goal was to produce a current inventory of invertebrate fauna of the Salton Sea in conjunction with researchers at other universities. The morphology of 16 species belonging to nine taxonomic invertebrate groups is presented in this portfolio of images.

Material and methods

Specimens were collected at the Salton Sea in 1998–2000 at various shoreline and offshore locations and prepared for scanning electron microscopy (SEM). In preparation for SEM, specimens were fixed in cold Karnovsky fixative for 1–2 h, postfixed in 1% osmium tetraoxide for 1 h and dehydrated in a graded ethanol series with a final change in absolute ethanol. Before the drying procedure, small specimens such as foraminiferans, turbellarians, polychaete larvae, barnacle nauplii and cyprids, copepods, ostracods, and rotifers were collected on a millipore filter paper using a syringe equipped with a filter paper holder. Both large and small samples were critical-point-dried with liquid CO_2. Specimens were mounted on the stubs, sputter-coated with gold–palladium and examined in a Hitachi S 2700 scanning microscope at an accelerating voltage of 10 kV.

Results and discussion

In 1998–2000, the invertebrate fauna of the Salton Sea was represented by Protozoa (Ciliophora, Sarcodina, particularly the Foraminifera), Platyhelminthes (Turbellaria), Rotifera, Nematoda, Annelida (Polychaeta and Oligochaeta), and Arthropoda (Crustacea: Ostracoda, Copepoda, Amphipoda, Cirripedia, and Insecta). The nematodes have not yet been identified. Species lists of ciliates and naked amoebae are in-

cluded in separate papers by Small et al. (2002) and Rogerson & Hauer (2002), respectively. The species illustrated in this portfolio include the foraminiferans *Ammonium beccarri* Linneus, *Quinqueloculina bellatula* Bandy and *Q. rhodiensis* Parker, the turbellarian *Macrostomum pusillum* Ax, the rotifer *Brachionus rotundiformis* Tschugunoff, the oligochaetes *Thalassodrilides gurwitschi* Cook, *T. belli* Hrabe, and an unidentified enchytraeid, the polychaetes *Neanthes succinea* Frey and Leuckart and *Streblospio benedicti* Webster, the copepods *Apocyclops dengizicus* Lepeschkin and *Cletocampus deitersi* Richard, the barnacle *Balanus amphitrite* Darwin, an ostracod *Cyprideis beaconensis* Le Roy, the amphipods *Gammarus mucronatus* Say and *Corophium louisianum* Shoemaker, and the insects *Trichocorixa reticulata* Guérin-Menéville and *Ephydra cinerea* Jones.

Foraminifera

The foraminiferans were identified by Anthony Rathburn (Scripps Institute of Oceanography) and Susan Burke (Scripps Institute of Oceanography) from small sediment samples removed from the top 3 cm of the sediment surface in grabs taken at 2, 4, 8, and 12 m along the eastern side of the lake in March 1999 (Detwiler et al., 2002). The sediment was preserved with buffered formalin; samples were stained with Rose Bengal, and allowed to sit for one week. The sediment fraction >150 μm that remained after wet sieving was examined for foraminiferans. There were very low numbers of living specimens, and recently dead foraminiferans were included in the species list. Diversity was very low, and abnormally formed specimens were common, probably as a by-product of the stressful nature of the environment (Rathburn pers. comm.).

Ammonium beccarrii (Fig. 1A) belongs to the Family Rotaliidae which consists of exceptionally small forams having a trochospiral test with calcareous walls. The genus *Ammonium* is characteristic of marginal marine environments, lagoons, estuaries and the inner continental shelf, and *A. beccarrii* is reported from Britain, the Adriatic Sea, the Red Sea (Hedley & Adams, 1978), and Australia (Yassini & Jones, 1995). Arnal (1958) reported that this species was very abundant in the Salton Sea at most of the stations. The species has been cultured using a variety of pennate diatoms and cyanobacteria for food (Hedley & Adams, 1978).

Quinqueloculina bellatula (Fig. 1B) and *Q. rhodiensis* (Fig. 1C) belong to the Family Miliolidae which is characterized by a test of calcite crystals. The genus *Quinqueloculina* is often common in shallow waters. Its five chambers are tubular and are arranged about a longitudinal axis. The aperture is located terminally and is the major opening to the exterior through which pseudopodia extend. In the 1950s *Q. bellatula* was abundant and *Q. belli* was uncommon, but both were widespread and living in the shallow waters of the Salton Sea (Arnal, 1958).

Platyhelminthes

The turbellarian flatworm *Macrostomum pusillum*, (Fig. 1D) was identified by Yuri Mamkaev (Zoological Institute of Russian Academy of Sciences, St. Petersburg, Russia). It is a small free living flatworm belonging to the Family Macrostomidae, has no tentacles or projections and reproduces only sexually.

M. pusillum is present in muddy to sandy substrates in brackish and coastal salinities in Europe, Atlantic coasts of United States and Canada, and Alaska (Faubel, 1974; Rieser & Morse, 1974; Ax & Armonies,1990). At the Salton Sea, specimens were associated with algal mats and muddy substrates in shallow embayments within Varner Harbor and near Red Hill Marina (Garst Road and the shallow bay between Red Hill Marina and Garst Road).

The body is completely ciliated with ventral cilia more numerous and longer than dorsal cilia, with rosettes of long cilia interspersed among the shorter cilia. Ventral ciliation, in conjunction with mucus produced by epithelial cells, provides for locomotion across the substrate. The spatulate posterior end is adhesive for attachment to the substrate, and some spines are present at the posterior end.

Rotifera

Brachionus rotundiformis (Order Monogononta), identified by Russ Shiel (Murray-Darling Freshwater Research Centre, N.S.W., Australia) is a planktonic loricate rotifer in the *Brachionus plicatilis* complex (Fig. 2). It is extremely abundant in the summer (Tiffany et al., 2002). The body can be divided into the head, trunk and foot (with toes). In swimming rotifers, such as this one, the foot may act as a rudder (Donner, 1966). The outer covering, the lorica, is a firm structure into which the head and foot can be retracted. The anterior spines of the lorica are dorsally acute and ventrally cuspate (Fig. 2A,B). The corona

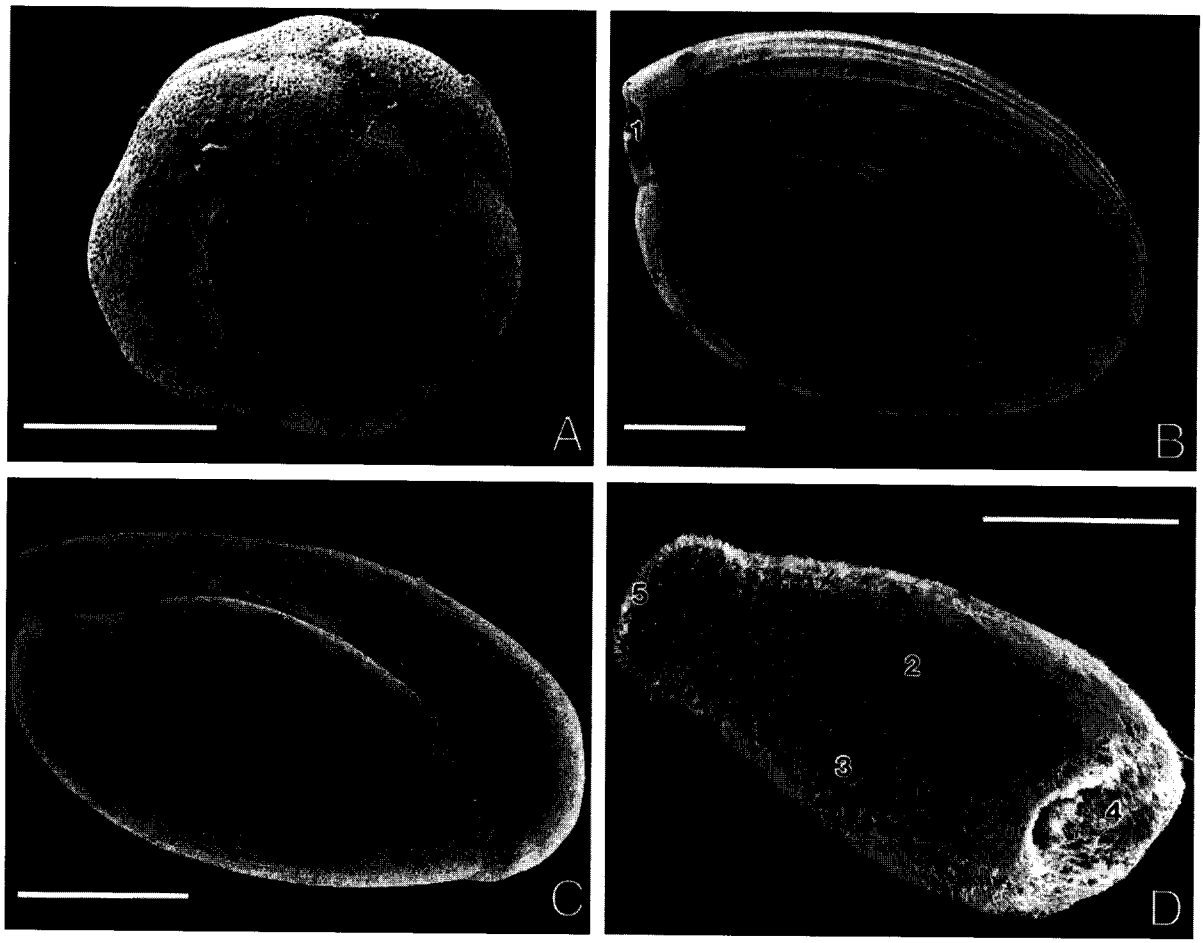


Figure 1. Salton Sea Foraminifera and Platyhelminthes. (A) Foraminifera *Ammonium beccarri*, spiral view. (B) Foraminifera, *Quinqueloculina bellatula*, chambered side. (C) Foraminifera *Quinqueloculina rhodiensis*, chambered side. (D) Turbellaria *Macrostomum pussilum*. (1) Apperture; (2) dorsal ciliation; (3) ventral ciliation; (4) anterior part; (5) posterior part. All scale bars = 100 μm.

is the ciliated portion of the head and consists of the trochus and cingulum (Fig. 2B,C). The beating of the cilia on the corona is used for locomotion and to propel food such as small algal cells toward the mouth which is located between the trochus and the cingulum.

Annelida, Polychaeta

The polychaete *Neanthes succinea* (Family Nereidae) (Fig. 3A), is the dominant benthic organism of the offshore sediments (Detwiler et al., 2002) and its larvae (Fig. 3B,C) are seasonally abundant in the plankton (Tiffany et al., 2002). This cosmopolitan species occurs along the coasts off the Gulf of Mexico, North, Central and South America, Europe, Africa, and the Black Sea (Pettibone, 1963)

The prostomium, the pre-oral segment, has two pairs of eyes which function as photoreceptors, a pair of tentacles, and a pair of large palps, both of which contain tactile and chemical sensory receptors (Fig. 4A,B). The first complete segment, the peristomium, has four pairs of tentacles (or cirri). Two pairs are located dorsally and are longer than the two pairs located on the ventral surface of the peristomium.

The proboscis is everted for feeding and is divided into two rings, the anterior maxillary ring, and the oral ring, both of which have denticles (conical paragnaths) which are used to help macerate food (Fig. 4A). Prey is seized with paired dark jaws located at the tip of the maxillary ring.

The biramous parapodia with associated setae are used for locomotion; the setae grip the substrate and provide traction. Since this species does not possess any branchiae, the parapodia also function in respiration. The parapodia of *N. succinea* change along the

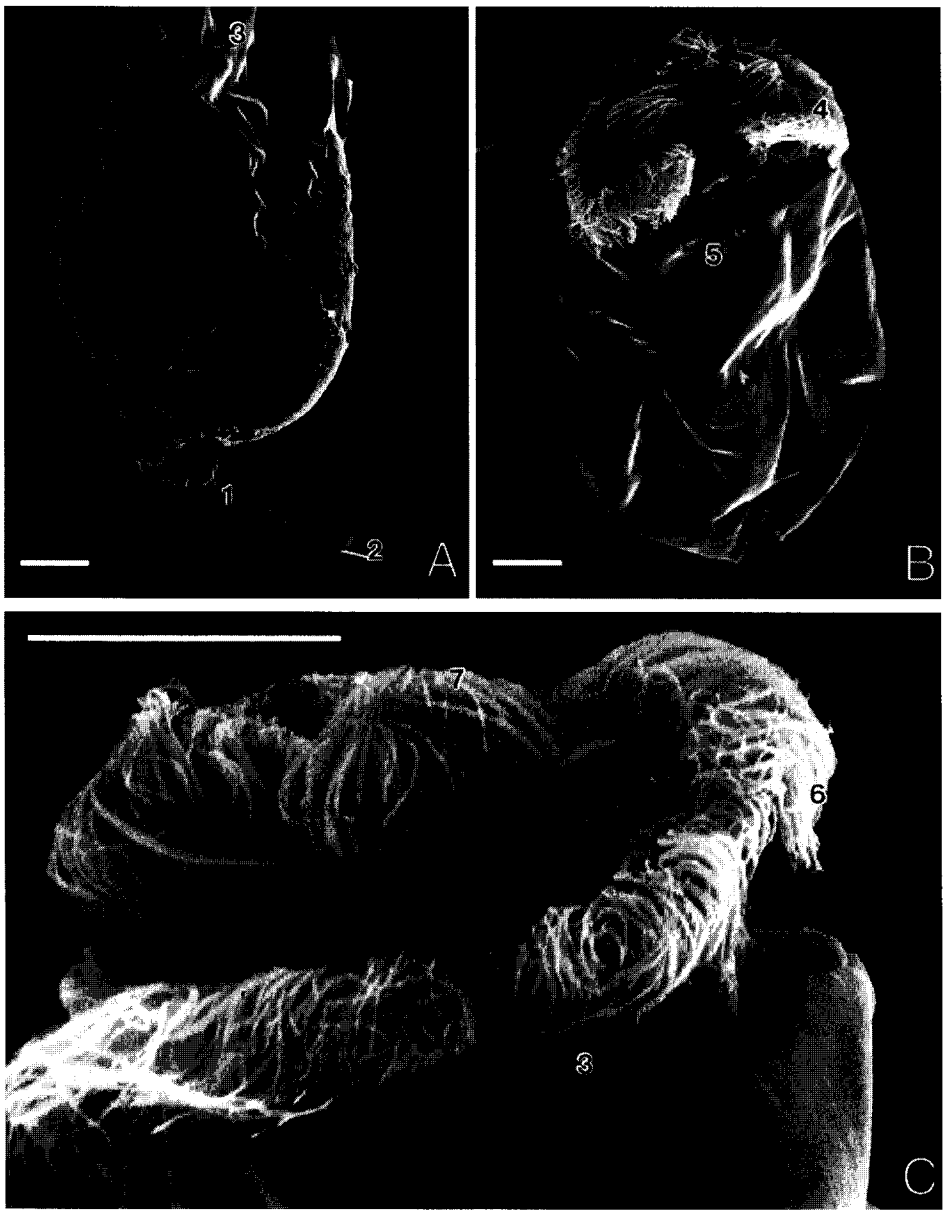


Figure 2. Salton Sea rotifer *Brachionus rotundiformis*. (A) Dorsal view. (B) Ventral view of *B. rotundiformis* with foot retracted. (C) Lateral view of corona. (1) Foot; (2) toes; (3) acute anterior spine of lorica; (4) corona; (5) cuspate anterior spine; (6) cingulum; (7) trochus. All scale bars = 20 μm.

length of the organism, particularly in the sexually mature heteronereids, where the parapodia of the middle region of the body are enlarged and flattened (Fig. 4C,D). Specialized swimming setae with paddle-like surfaces are present and help this benthic organism to reach the water surface for spawning. The dorsal cirrus is extremely large and broad in the posterior segments of all individuals, and the size difference between the smaller ventral neuropodium and associated cirri and the much larger dorsal notopodium and dorsal cirri is clearly shown in Figure 4D.

Sexually mature individuals die after releasing their gametes into the surface water layers (Carpelan & Linsley, 1961). The larvae depicted (Fig. 3B,C) have prostomial tentacles and one pair of peristomial tentacles and are approximately 1–2 weeks old.

Streblospio benedicti (Family Spionidae) (Fig. 5A) was identified by Lawrence Lovell, (Scripps Institute

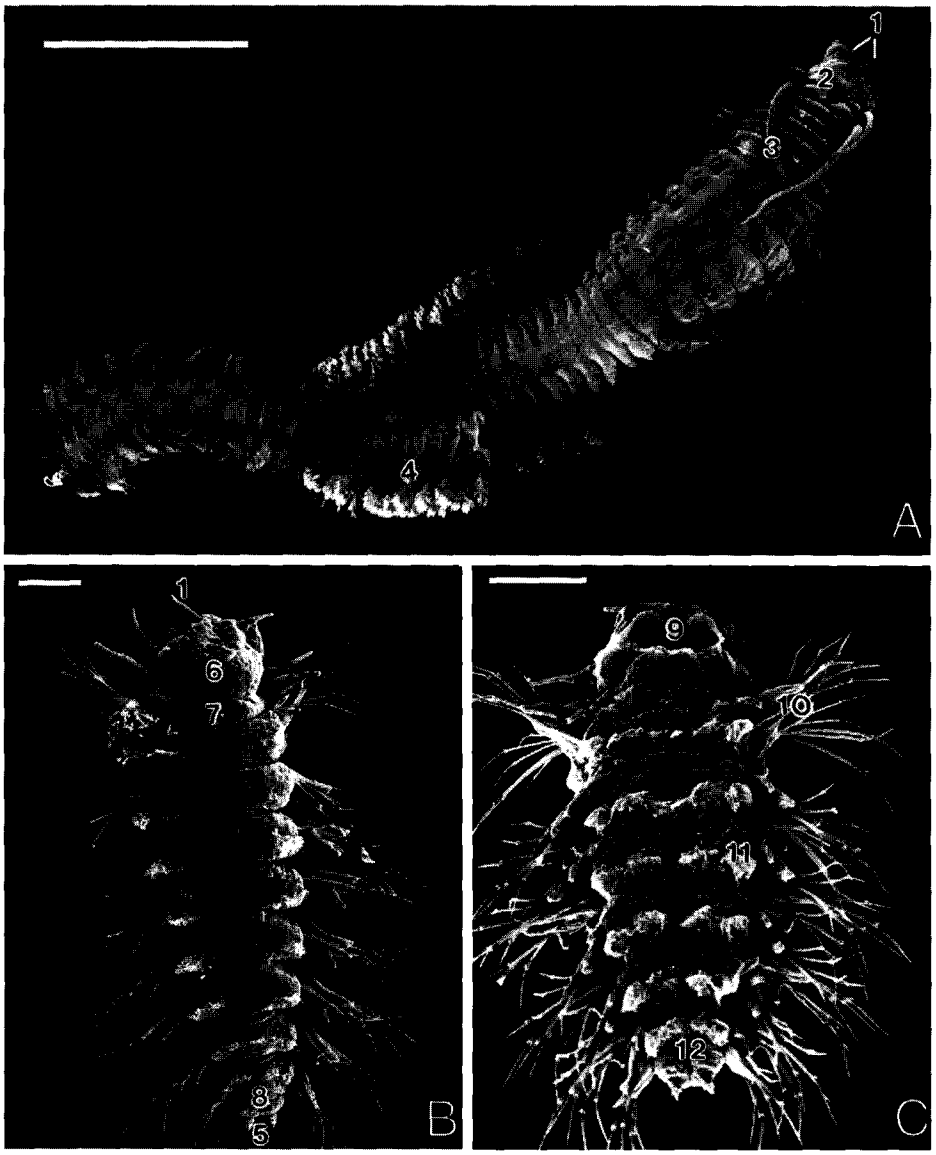


Figure 3. Salton Sea polychaete *Neanthes succinea.* (A) Dorsal view of entire heteronereid of *N. succinea.* (B) Dorsal view of *N. succinea* larva. (C) Ventral view of *N. succinea* larva. (1) Prostomial tentacle; (2) eye; (3) peristomial tentacle; (4) natatory parapodia; (5) anal cirrus; (6) prostomium; (7) peristomium; (8) pygidium; (9) mouth; (10) parapodium; (11) cilia; (12) anus. Scale bars: A =500 μm; B & C = 50 μm.

of Oceanography). This species has a wide geographic distribution occurring along the Atlantic coasts of Europe, North and South America, and the Gulf and Pacific coasts of North America (Levin, 1984). In 1999 it was present at the Salton Sea in greatest abundance in the clay sediments located at 2 m depth (Detwiler et al., 2002). Spionids are easily recognized by the presence of a pair of feeding palps on the prostomium which are used to collect detritus from the sediment surface (Fig. 5B). A pair of branchiae, located on the first segment, function as the main respiratory structure. The dorsal collar or hood is found on the dorsal surface of second the segment between the right and left notopodia.

Annelida, Oligochaeta

Three oligochaetes are abundant within the littoral barnacle shell and sandy substrates (0–0.3 m depth) along the eastern shoreline of the Salton Sea (Detwiler et al., 2002). One of these was abundant in barnacle

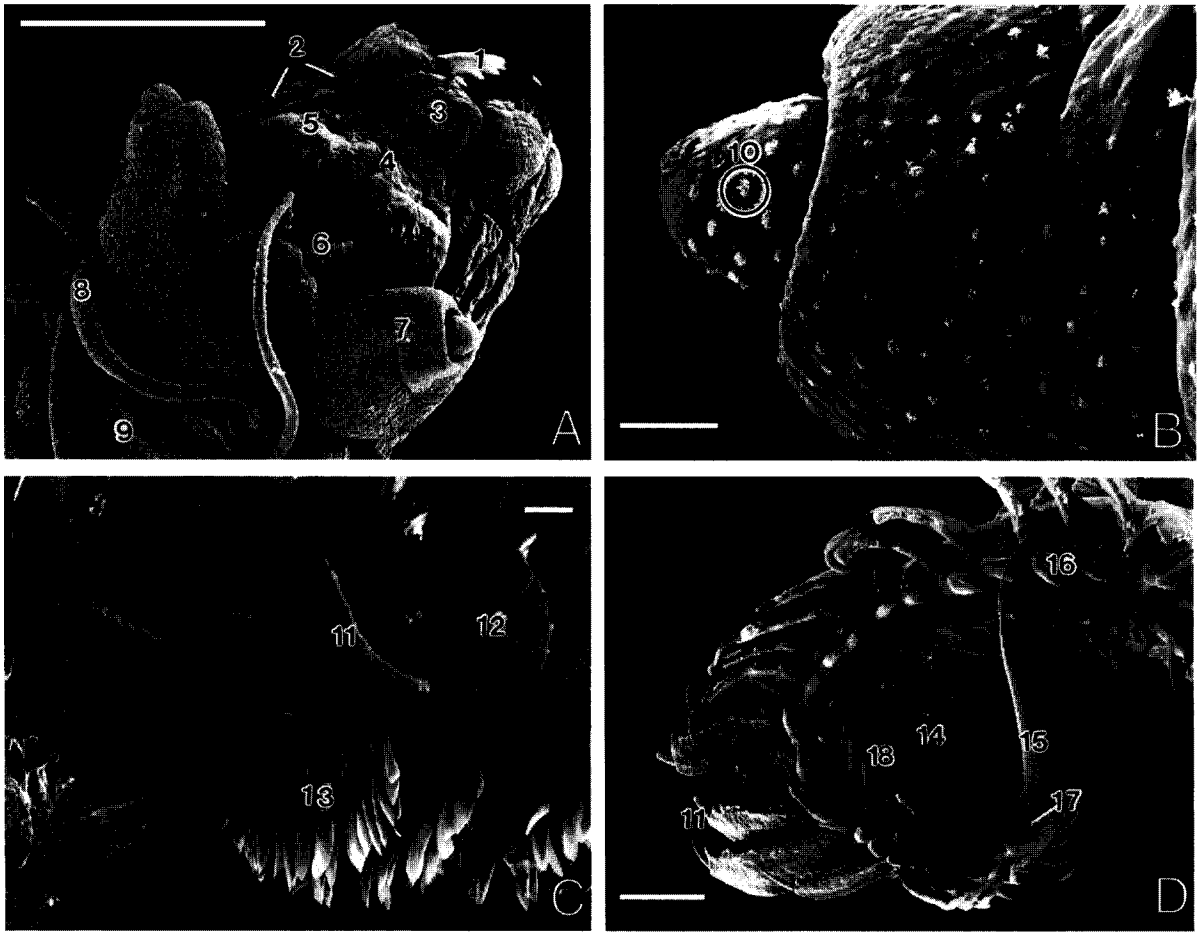


Figure 4. Salton Sea polychaete *Neanthes succinea.* (A) Anterior end, dorsal view. (B) Anterior end of prostomial biarticulated palp. (C) Parapodia in the middle region of a heteronereid, dorsal view. (D) Posterior end. (1)= Jaws; (2) extended proboscis; (3) maxillary ring; (4) oral ring; (5) paragnath; (6) prostomial tentacle; (7) prostomial palp; (8) peristomial tentacle; (9) peristomium; (10) sensory receptor; (11) dorsal cirrus; (12) notopodial lobe; (13) natatory setae; (14) ventral surface; (15) anal cirrus; (16) post-setal lobe; (17) pygidium; (18) neuropodium. Scale bars: A&D =500 μm, B & C= 50 μm.

rubble at 2 m depth. All species were identified by Michael Milligan (Center for Systematics and Taxonomy, Sarasota, Florida).

One oligochaete as yet unidentified (Fig. 5C,D) belongs to the Family Enchytraeidae, diagnosed by the location of the spermathecal pores (segment 5) and the male pores (segment 12). This small oligochaete lacks eyes, possesses paired simple setae in 4 bundles per segment (Fig. 5C), and exhibits only sexual reproduction. The sense organs are evenly distributed on the prostomium (Fig. 5D).

Two members of the Family Tubificidae were present. This family contains some species known for their ability to thrive in polluted waters. This family is identified by the spermathecae being located in segment 10 and the male pores on segment 11. Both species are bright red in color when alive. *Thalassodrilides gurwitschi* (Fig. 5E), is found in the Caribbean and Mediterranean seas, the Persian Gulf, and along the coasts of southern China and western Australia, living mainly in muddy sediments of both intertidal and subtidal marine and brackish waters (Erséus, 1990). The mouth is located on the ventral surface between the prostomium and peristomium. Sense organs are scattered unevenly on the prostomium. Spermathecae are absent on segment 10 which distinguishes this species from *T. belli* (Milligan, pers. comm.). This species exhibits at least three setal types: straight hair setae and bifid hair setae at the anterior end, and bifid sigmoid setae near the posterior end.

Thalassodrilides belli (Fig. 5F) occurs in the Caribbean and Gulf of Mexico (Erséus, 1990), and

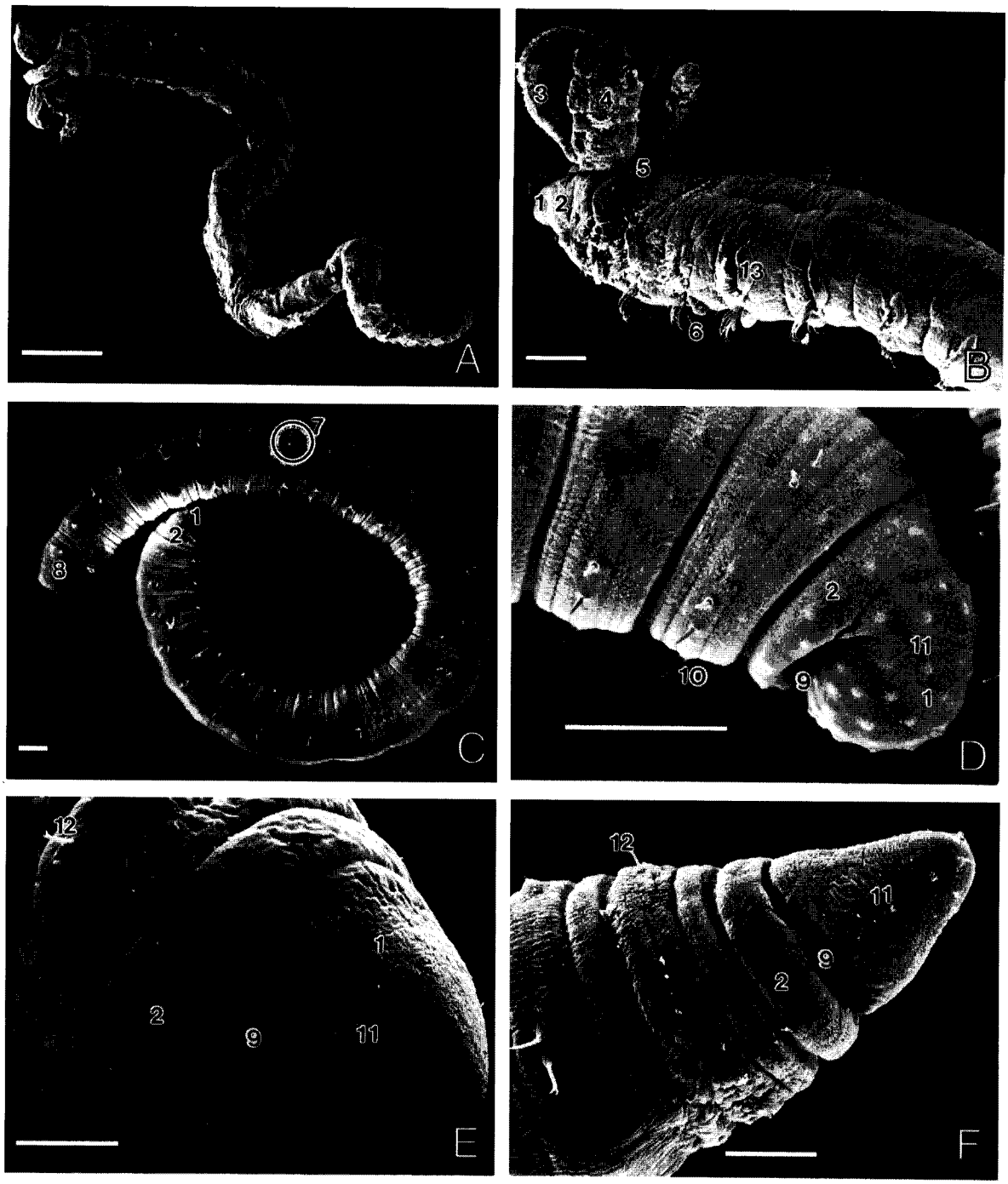


Figure 5. Salton Sea polychaete *Streblospio benedicti* and oligochaetes. (A) *S. benedicti*, general view. (B) Anterior end of *S. benedicti*. (C) Oligochaete, Family Enchytraeidae, general view. (D) Head end of Enchytraeidae. (E) Head end of oligochaete *Thalassodrilides gurwitschi*. (F) Head end of oligochaete *T. belli*. (1) Prostomium; (2) peristomium; (3) prostomial palps; (4) branchiae; (5) dorsal collar; (6) capillary setae; (7) setal bundles; (8) pygidium; (9) mouth; (10) pointed setae; (11) sensory organ; (12) bifid hair setae; (13) parapodium. Scale bars: A= 500 μm, B-F= 50 μm.

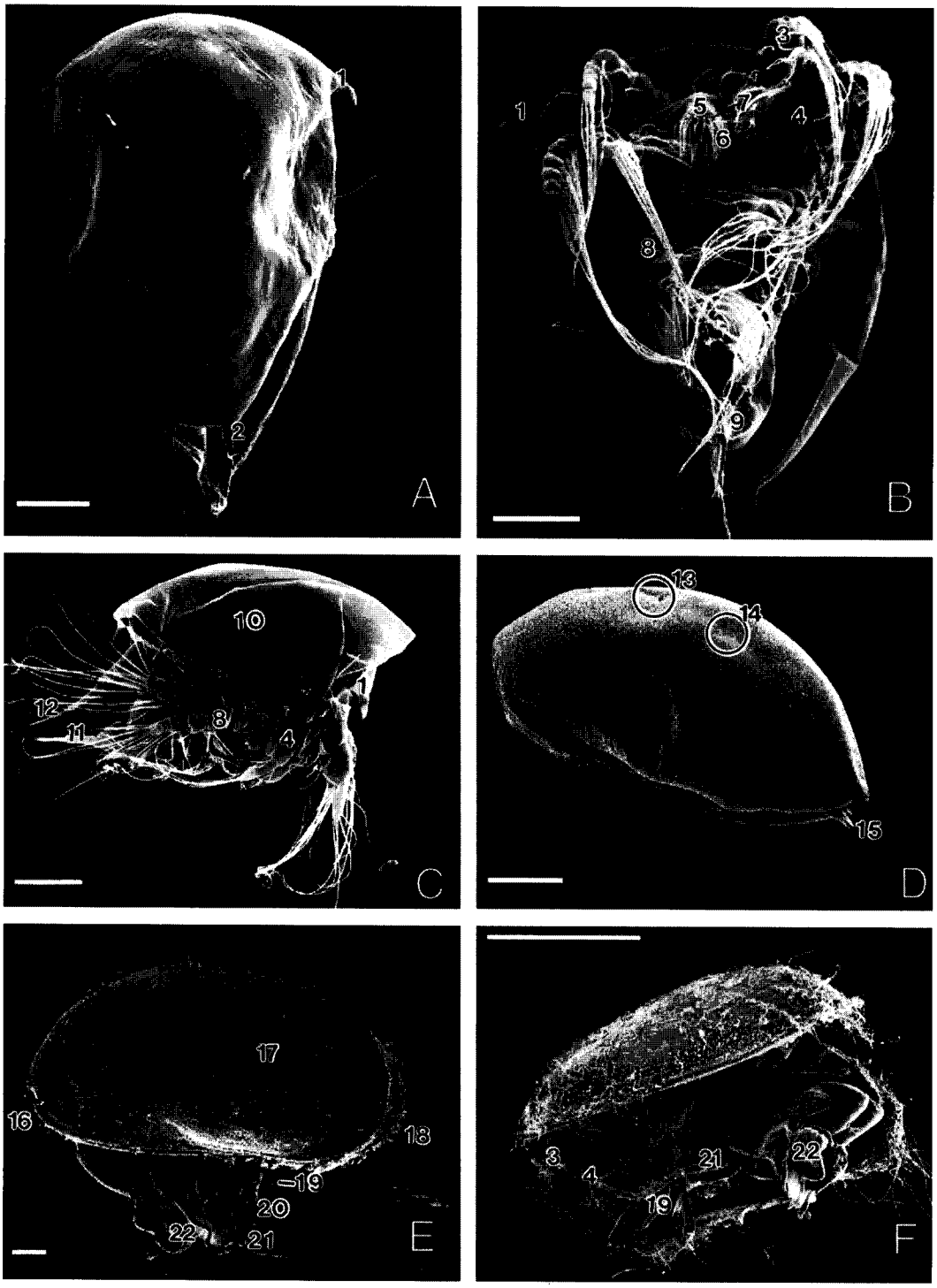


Figure 6. Salton Sea Cirripedia and Ostracoda. (A) Nauplius larva of barnacle *Balanus amphitrite,* dorsal view. (B) Nauplius larva of *B. amphitrite* (Stage V), ventral view. (C) Nauplius larva of *B. amphitrite,* lateral view, right side. (D) *B. amphitrite* cyprid larva, lateral view, left side. (E) Ostracod *Cyprideis beaconensis* Le Roy (male), lateral view, right side. (F) *Cyprideis beaconensis* (male), ventrolateral view, left side. Carapace is covered with bacteria. (1) Lateral horn; (2) posterior shield spine; (3) first antenna; (4) second antenna; (5) mouth; (6) mouth setae; (7) labrum; (8) mandible; (9) abdomen with six pair of thoracic limb primordiae; (10) cephalic shield; (11) caudal furca; (12) dorsal thoracic spine; (13) Anterior lattice; (14) Posterior lattice; (15) tips of thoracic limbs; (16) carapace setae; (17) carapace pits; (18) setae of first antenna; (19) first thoracic leg; (20) second thoracic leg; 21 third thoracic leg; (22) copulatory appendage. All scale bars = 100 μm.

differs from *T. gurwitschi* in the location of the spermathecae (Milligan, pers. comm.). The prostomium of *T. belli* is more pointed than that of *T. gurwitschi*, and appears to have fewer sense organs than that of *T. gurwitschi*.

Crustacea, Cirripedia

The barnacle *Balanus amphitrite*, Family Balanidae, dominates submerged hard substrates at the Salton Sea (Detwiler et al., 2002) and its larvae form a major component of the plankton (Tiffany et al., 2002). It has a cosmopolitan distribution, occurring in Europe, Mediterranean Sea, Indian Ocean, Pacific Oceania, and Southeast Asia (Newman & Ross, 1976), but it was introduced to the eastern Pacific.

The initial larval form is the nauplius larva (Fig. 6A–C) possessing three pairs of appendages (first and second antennae and mandibles). Only the first antennae are uniramous, the other appendages are biramous. All three are used in swimming, and the second and third appendages are used in feeding.

After six stages as a nauplius, the individual metamorphoses into the cyprid (Fig. 6D), the final larval stage, which superficially resembles an adult ostracod. The cyprid is enclosed in a bivalved smooth carapace and possesses all body appendages found in the benthic adult. The cyprid functions to locate the appropriate substrate for attachment; it does not feed. The dorsal anterior and posterior lattice are sensory structures (Newman, 1966). Its large first antennae have tactile and chemical sense organs to determine substrate suitability for settlement and cement glands which glue the cyprid to the substrate. The final molt results in a major change in orientation, and the appendages become feather-like for feeding.

Crustacea: Ostracoda

The ostracod *Cyprideis beaconensis* (Fig. 6E,F), (Order Podocopida: Family Cytherideidae) was identified by Richard Forester (U.S. Geological Survey). Podocopida is the only ostracod order that includes both marine and freshwater species. At the Salton Sea this species is found on the chlorophyte *Chaetomorpha linum* associated with rocky substrates, in shoreline barnacle shell substrates, and in muddy sediments at extremely shallow depths along the shoreline, especially between Red Hill Marina and Garst Road.

Cytherid ostracods possess a calcareous carapace covered with pits and setae (Fig. 6E). Some of the setae may be sensory (Yassini & Jones, 1995). The first antennae (Fig. 6F) are used to create a feeding current, and to assist in digging. *Cyprideis* is a selective feeder on benthic algae and organic matter found in the sediment. The second antennae are sensory and may also function in mating. Cytherids locomote along the substrate using their second antennae, maxillae, and the first, second, and third thoracic appendages (Maddocks, 1992). The male reproductive system is quite complex; the copulatory apparatus consists of a muscular base and copulatory organ, and includes sensory and clasping structures (Maddocks, 1992).

Crustacea: Copepoda

Apocyclops dengizicus (Order Cyclopoida) is the only planktonic copepod species in the Salton Sea and a major component of the zooplankton (Tiffany et al., 2002). The species is an active predator on microinvertebrates and algae (Hammer & Hurlbert, 1992). It is widely distributed in saline lakes on four continents and is tolerant of salinities ranging from 0.5 to 69 g l^{-1} (Dexter, 1993).

The first antennae (Fig. 7A,B) have mechanoreceptors to detect motion of their prey. Mature males can be easily recognized by the geniculate first antennae that are used to hold the female during mating. Swimming is accomplished with the first four thoracic legs (Fig. 7C). The first abdominal segment is the genital segment. In females, the genital complex is formed from the fusion of the genital segment and the following segment (Fig. 7B). The fifth abdominal segment is the anal segment.

Larval life begins with a nauplius larva, with three pairs of appendages (Fig. 7D). The nauplius larva has an anterior (upper) lip or labrum which appears as a round plate. The larva illustrated has four pairs of head appendages present, and is therefore technically a metanauplius larva. The sixth naupliar stage molts into a copepodite stage (not shown).

Cletocamptus deitersi (Order Harpacticoida, Family Cletodidae) (Fig. 8A,B) has a cosmopolitan distribution. This crustacean is found in freshwater to hypersaline habitats, and laboratory cultures of this species produced several generations at salinities from 0.5 to 90 g l^{-1}(Dexter, 1995). It has been collected from sand and muddy sediments at the Salton Sea, but is most abundant there on macroscopic algal mats (*Enteromorpha intestinalis* (L) Link and *Chaetomorpha linum* Müller) and on cyanobacterial mats. It feeds on benthic algae and organic detritus associated with

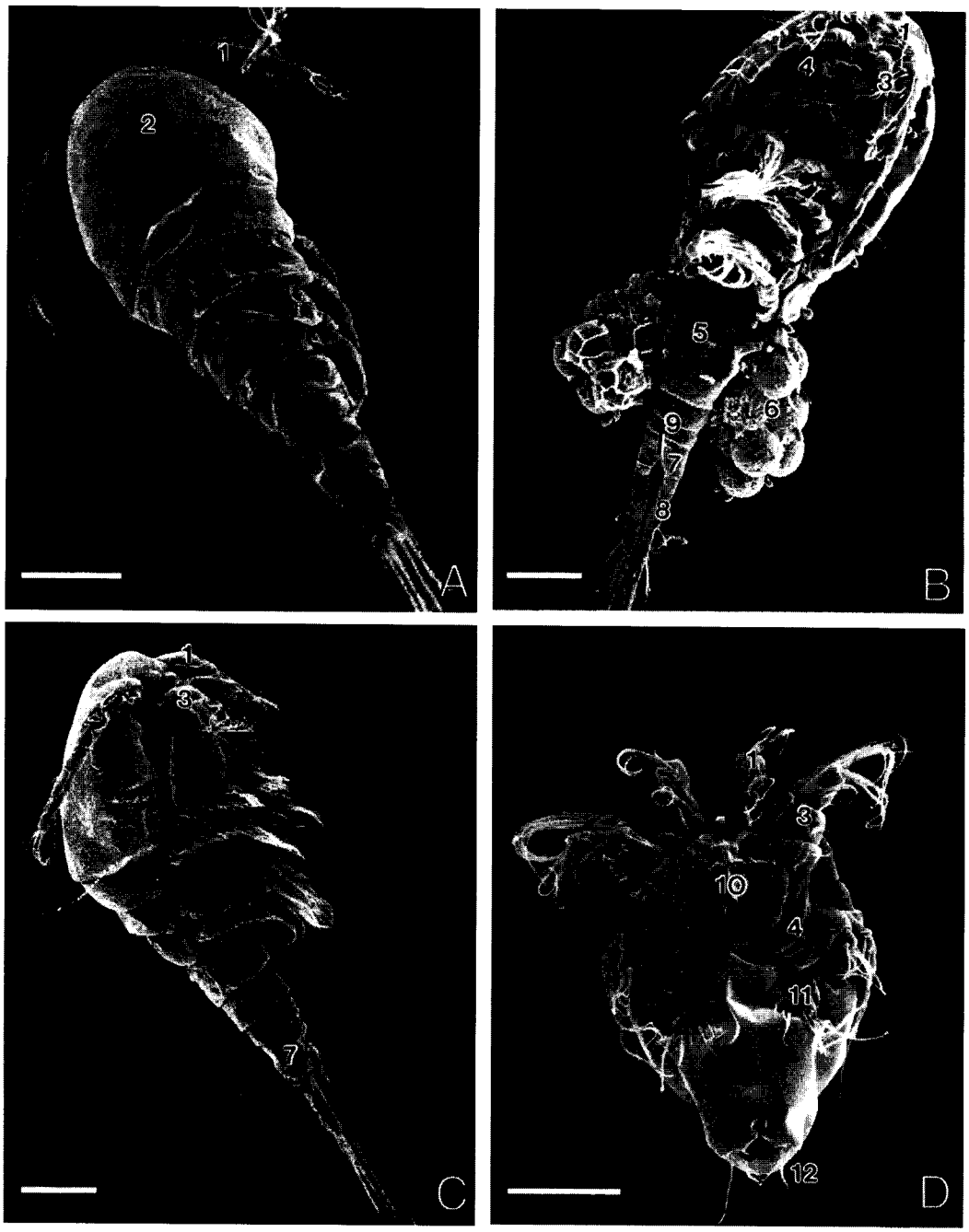


Figure 7. Cyclopoid copepod *Apocyclops dengizicus*. (A) Dorsal view. (B) Ventral view, female. (C) Lateral view. (D) Nauplius larva, ventral view. (1) First antenna; (2) cephalothorax; (3) second antenna; (4) mandible; (5) genital complex; (6) egg sac; (7) caudal furca; (8) caudal ramus; (9) anus; (10) labrum; (11) first maxilla; (12) furcal bristles. All scale bars = 100 μm.

substrates on which it lives using its mouthparts to scrape up food items. There are numerous spinules along the posterior margins of all 10 segments of *Cletocamptus* (Fig. 8A). Males are generally smaller than females and can be recognized by their geniculate first antennae (not shown).

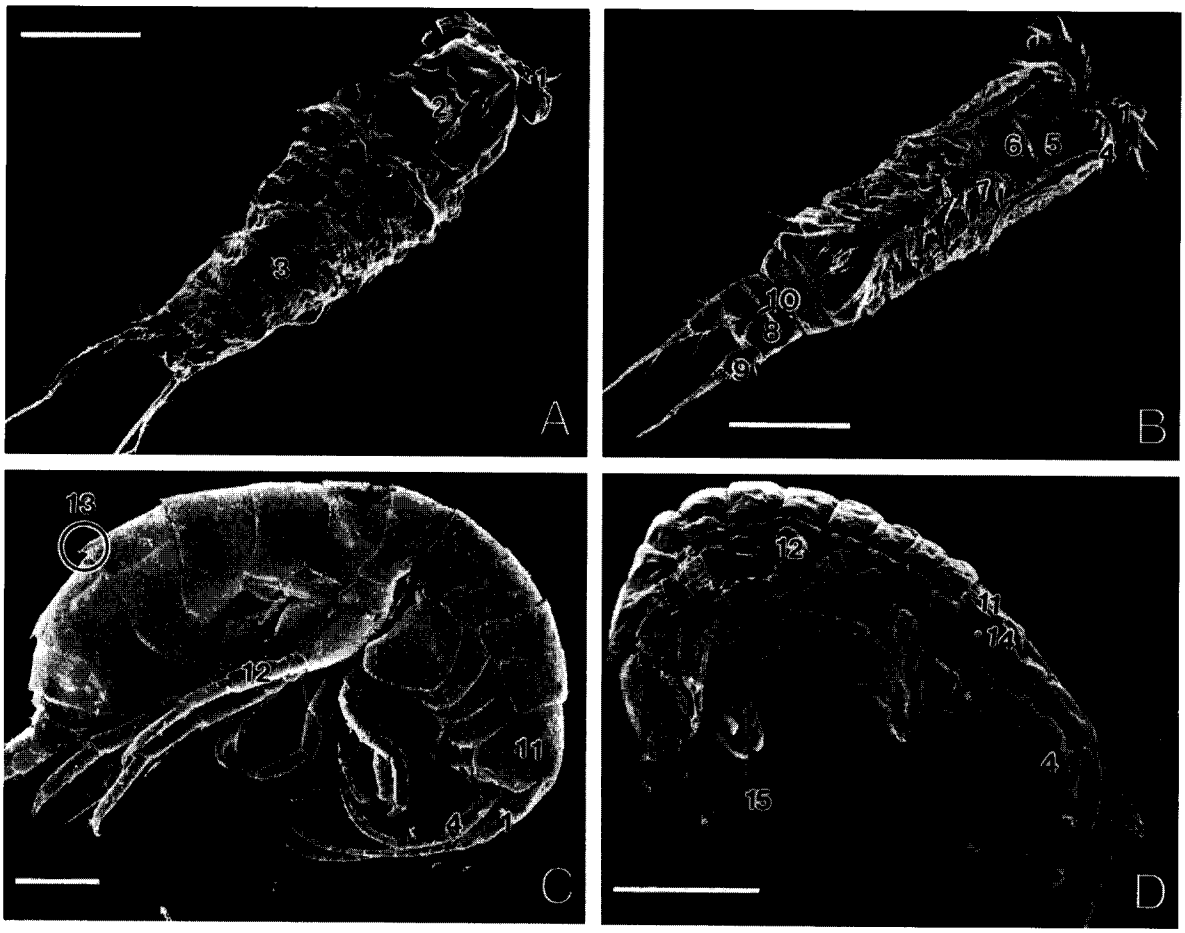


Figure 8. Salton Sea harpacticoid copepod and amphipods. (A) Harpacticoid copepod *Cletocamptus deitersi,* dorsal view. (B) *C. deitersi,* ventral view. (C) Gammarid amphipod *Gammarus mucronatus,* lateral view. (D) Corophiid amphipod *Corophium louisianum,* female, lateral view. (1) First antenna; (2) cephalothorax; (3) spinules; (4) second antenna; (5) mandible; (6) maxilla; (7) first thoracic appendage; (8) caudal furca; (9) caudal ramus with caudal setae; (10) anus; (11) cephalon; (12) fifth periopod; (13) mucronations on pleomeres 1–3; (14) compound eye; (15) second gnathopod. All scale bars =500 μm.

Crustacea: Amphipoda

Gammarus mucronatus, Family Gammaridae, is widely distributed along the Atlantic and Gulf coasts of the United States. It is extremely abundant within the algal mats attached to rocky substrates at the Salton Sea (Detwiler et al., 2002). Amplexing mating pairs are often seen in the water column at dusk along the shoreline. The sharp spines or mucronations along the dorsal surface of the first three pleosomal (abdominal) segments are the source of its specific name (Fig. 8C). The gnathopods are used to collect food including benthic detritus, macroscopic algae, and invertebrates (Simpson et al., 1998). The second antennae are sexually dimorphic, being much larger in males.

Corophium louisianum (Family Corophiidae), identified by James D. Thomas (Nova Southeastern University, Florida), is known from the U.S. Coast of the Gulf of Mexico (Hedgpeth, 1959). At the Salton Sea this species constructs a tube of mud and detritus attached to rocks, algae, the interiors of empty barnacle shells, or imbedded within the soft sediments (Detwiler et al., 2002). In common with other tubiculous amphipods, the body is more dorso-ventrally compressed than in many families of amphipods (Fig. 8D). The setae on the antennae are for sensory reception. The long setae on the second gnathopods are used to collect detritus, algae, and suspended matter brought in by currents generated by beating of the uropods. The first gnathopods comb the food off the second gnathopods and, along with the first maxilli-

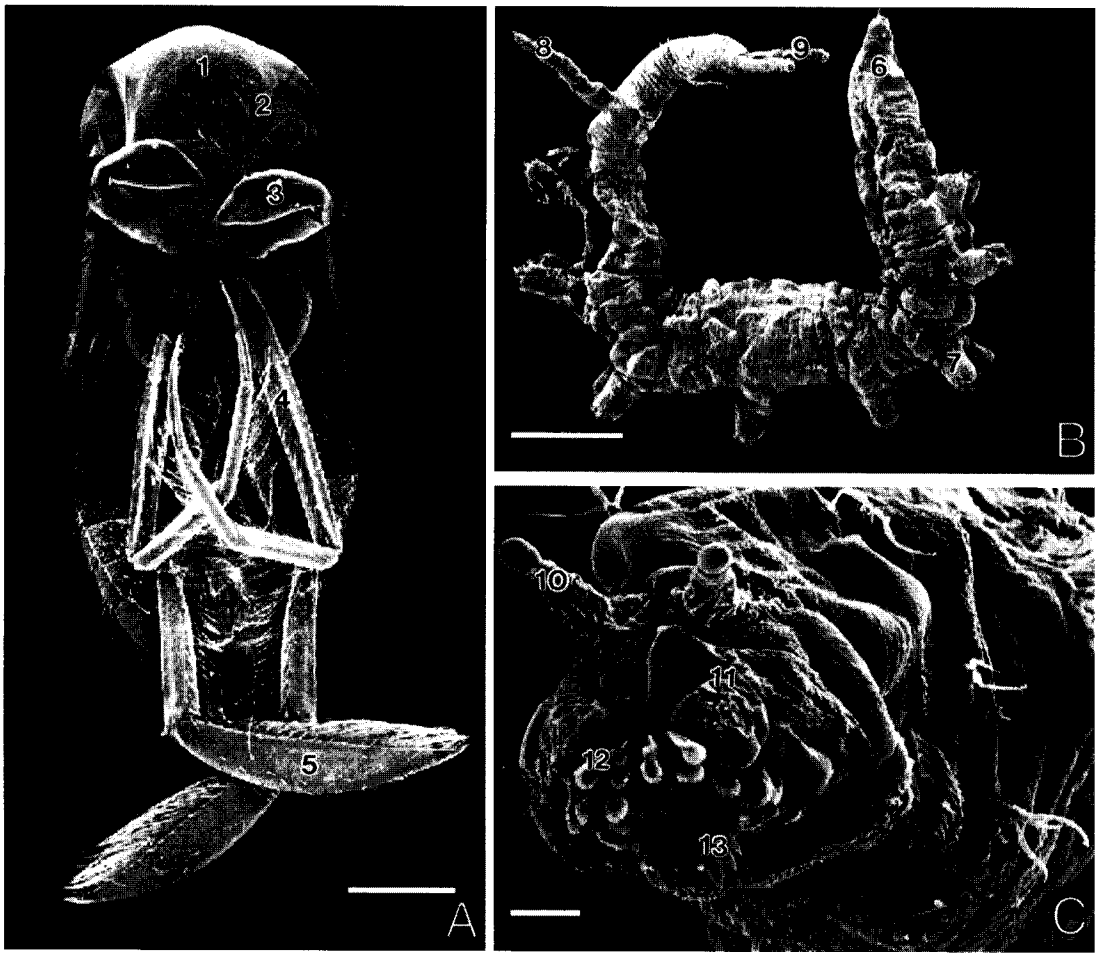


Figure 9. Salton Sea insects. (A) *Trichocorixa reticulata,* female, ventral view. (B) Larva of *Ephedra cinerea.* (C) Facial mask of larval *E. cinere.* (1) Frons; (2) compound eye; (3) first leg; (4) second leg; (5) third leg; (6) cephalic segment; (7) ventral prolegs (eight pairs); (8) spiracular tube; (9) respiratory tube; (10) antennae (2 segmented); (11) circular sensory plate; (12) comb-like structures; (13) mandibles with mandibular teeth. Scale bars: A=100 μm, B = 20 μm, C = 500 μm.

peds, direct food to the mouth. Sexual dimorphism is evident with the males having much larger second antennae and enlarged gnathopods. The fifth periopod (leg) is shortest and turned posteriorly.

Uniramia: Insecta

Trichocorixa reticulata (Order Hemiptera: Family Corixidae) occurs in the Caribbean Islands, the southern United States, and along the eastern Pacific from Peru to Arcata, California, and has been found in salinities ranging from 0 to 190 g l^{-1} (Balling & Resh, 1984). At the Salton Sea it occurs mainly in protected embayments or isolated pools at the fringe of the lake, where salinity is usually higher than the main body of the lake. Corixids feed on a variety of food from plant material (algae and aquatic vegetation), to microorganisms from the substrate (including protozoans, rotifers, diatoms), as well as amphipods, insect larvae, and planktonic crustaceans, and may be an important predator where they are abundant (Scudder, 1976). *T. reticulata* is present in the gut contents of earred grebes feeding at the Salton Sea (Dexter, pers. observ.).

Males and females can be distinguished by the frons; in males it is flat or concave, while in females the frons is convex (Scudder, 1976) (Fig. 9A). The legs of corixids are morphologically very different and have different functions. The first pair of legs is used to scoop organic detritus and associated organisms from the substrate toward the mouth. The terminal segment or pala of the first leg has many bristles which help

in retaining food items. Corixids store air they have gathered from the surface, and those air bubbles make them positively buoyant. The second pair of legs is quite long and the terminal segment on each leg is modified into a tong which grasps the vegetation or the substrate (Scudder, 1976). This is necessary because they need to anchor themselves in order to remain underwater. The third pair of legs is flattened and is used for swimming. The terminal segment is developed as an oar heavily bristled to aid in swimming.

Ephydra species (Order Diptera: Family Ephydridae) are commonly known as brine flies because of their abundance in highly saline aquatic habitats. *Ephydra cinerea* prefers highly saline water and is common in brine pools along the west coast and in saline lakes in southern and central California (Wirth & Stone, 1956). The larval form possesses eight pairs of ventral prolegs with terminal claws used in locomotion and a pair of elongated, retractable respiratory (Fig. 9B,C). Spiracles are located at the apex of these respiratory tubes and spiracular tubes are also present for air uptake (Fig. 9B).

The facial mask is distinctive (Fig. 9C). The antennae consist of two segments, the mandibles have serrated teeth, and there is a pair of circular sensory plates. Comb-like structures surround the mouth, and these are found on species whose larvae feed on a wide variety of microorganisms, especially algae (Foote, 1991).

Conclusion

This undertaking should prove useful to future investigators studying this and other saline lakes. Understanding of the microstructure of organisms is helpful in ecological and environmental studies. Scanning electron microscopy, although seldom used in ecological studies, can assist in the identification of small invertebrates inhabiting aquatic environments.

Acknowledgements

This research has been funded in part by the United States Environmental Protection Agency through grant # R826552-01-0 to the Salton Sea Authority. The research results have not been subjected to the Agency's required peer review and therefore do not necessarily reflect the views of the Agency. Therefore, no official endorsement should be inferred.

References

Arnal, R. E., 1958. Rhizopoda from the Salton Sea, California. Contrib. Cushman Found. foraminiferal Res. 9(2): 36–44.

Ax, P. & W. Armonies, 1990. Brackish water Plathelminthes from Alaska as evidence for the existence of a boreal brackish water community with circumpolar distribution. Microfauna Marina 6: 7–109.

Balling, S. S. & V. H. Resh, 1984. Life history variability in the water boatman, *Trichocorixa reticulata* (Hemiptera: Corixidae), in San Francisco Bay salt marsh ponds. Ann. entomological Society Am. 77: 14–19.

Carpelan, L. H. & R. H. Linsley, 1961. The pile worm, *Neanthes succinea* (Frey and Leuckart). In Walker, B. W. (ed.), The Ecology of the Salton Sea, California, in Relation to the Sportfishery. Calif. Fish Game Fish Bull. 112: 63–76.

Detwiler, P. M., M. F. Coe & D. M. Dexter, 2002. The benthic invertebrates of the Salton Sea: Distribution and seasonal dynamics. Hydrobiologia 473/Dev. Hydrobiol. 161: 139–160.

Dexter, D. M., 1993. Salinity tolerance of the copepod *Apocyclops dengizicus* (Lepeschkin, 1900), a key food chain organism in the Salton Sea, California. Hydrobiologia 267: 203–209.

Dexter, D. M., 1995. Salinity tolerance of *Cletocamptus deitersi* (Richard 1897) and its presence in the Salton Sea. Bull. southern Calif. Acad. Sci: 94(2): 169–171.

Donner, J., 1966. Rotifers. Frederick Warne and Co. Ltd., London, 80 pp.

Erséus, C., 1990. The marine Tubificidae (Oligochaeta) of the barrier reef ecosystems at Carrie Bow Cay, Belize, and other parts of the Caribbean Sea, with descriptions of twenty-seven new species and revision of *Heterodrilus*,*Thalassodrilides*, and *Smithsonidrilus*. Zool. Scripta 19: 243–303.

Faubel, A., 1974. Macrostomida (Turbellaria) von einem Sandstrand der Nordseeinsel Sylt. Mikrofauna Meeresbodens Akad. Wiss. Literatur. 45: 341–370.

Foote, B. A., 1991. Ephydridae (Ephydroidea). In Stehr, F. W. (ed.), Immature Insects, Volume 2. Kendall Hunt Pub. Co., Dubuque, IA: 843–846.

Hammer, U. T. & S. H. Hurlbert, 1992. Is the absence of *Artemia* determined by the presence of predators or by lower salinity in some saline waters? In Robarts, R. D. & M. L. Bothwell (eds), Aquatic Ecosystems in Semi-arid Regions: Implications for Resource Management. Nat. Hydrol. Res. Inst. Symposium Series 7, Environment, Canada, Saskatoon: 91–102.

Hedgpeth, J. W., 1959. Some preliminary considerations of the biology of inland mineral waters. Arch. Oceanogr. Limnol. Suppl. 11: 111–141.

Hedley, R. H. & C. G. Adams, 1978. Foraminifera. Academic Press, New York, 290 pp.

Levin, L. A., 1984. Multiple patterns of development in *Streblospio benedicti* Webster (Spionidae) from three coasts of North America. Biol. Bull. 166: 494–508.

Maddocks, R. F., 1992. Ostracoda. In Harrison, F. W. & A. G. Humes (eds), Microscopic Anatomy of Invertebrates, Vol. 9, Crustacea. Wiley-Liss, Toronto: 415–441.

Newman, W. A., 1966. Sous-classe de Cirripèdes (Cirripedia Burmeister, 1837) Super-orders des Thoraciques et des Acrothoraciques (Thoracica Darwin, 1854 – Acrothoracic Gruvel, 1905). In Grassé, P. (ed.), Traité de Zoologie, Tome VII. Masson, Paris, France: 453–540.

Newman, W. A. & A. Ross, 1976. Revision of the Balanomorpha Barnacles; including a catalog of the species. San Diego Soc. Nat. Hist. Mem. 9: 1–108.

Pettibone, M. H., 1963. Marine Polychaete worms of the New England region. U.S. National Mus. Bull. 227 (1): 1–356.

Risser, N. W. & M. P. Morse, 1974. Biology of the Turbellaria. McGraw-Hill Book Co., New York, 530 pp.

Rogerson, A. & G. Hauer, 2002. Naked amoebae (Protozoa) of the Salton Sea, California. Hydrobiologia 473/Dev. Hydrobiol. 161: 161–177

Scudder, G. G. E., 1976. Water-boatmen of saline waters (Hemiptera: Corixidae). In Cheng, L. (ed.), Marine Insects. North-Holland Publ. Co., Amsterdam: 263–289.

Simpson, E. P., M. R. González, C. M. Hart & S. H. Hurlbert, 1998. Salinity and fish effects on Salton Sea microecosystems: benthos. Hydrobiologia 381: 153–177.

Small, E. B., G. F. Gebler & J. C. Cole, 2002. A survey of the Ciliophora (Protista) of the Salton Sea, California: preliminary results. In press.

Tiffany, M. A., B. K. Swan, J. M. Watts & S. H. Hurlbert, 2002. Metazooplankton dynamics in the Salton Sea, California, 1997–1999. Hydrobiologia 473/Dev. Hydrobiol. 161: 103–120.

Walker, B. W. (ed.), 1961. The ecology of the Salton Sea, California, in relation to the sportfishery. Calif. Fish Game Fish Bull. 113: 1–204.

Watts, J. M., B. K. Swan, M. A. Tiffany & S. H. Hurlbert. 2001. Thermal, mixing, and oxygen regimes of the Salton Sea, California, 1997–1999. Hydrobiologia 466/Dev. Hydrobiol. 162: 159–176.

Wirth, W. W. & A. Stone, 1956. Aquatic Diptera. In Unsinger, R. L. (ed.), Aquatic Insects of California: with Keys to North American Genera and California Species. University of California Press, Berkeley, CA: 372–482.

Yassini, I. & B. G. Jones, 1995. Recent Foraminifera and Ostracoda from Estuarine and Shelf Environments on the Southeastern Coast of Australia. University of Wollongong Press, Wollongong, 484 pp.

Hydrobiologia **473:** 217–221, 2002.
D.A. Barnum, J.F. Elder, D. Stephens & M. Friend (eds), The Salton Sea.
© 2002 *Kluwer Academic Publishers. Printed in the Netherlands.*

Skeletal development in *Hermesinum adriaticum* Zacharias, a flagellate from the Salton Sea, California

M. A. Tiffany
Department of Biology, San Diego State University, U.S.A.

Key words: Ebriidians, phytoplankton, salt lake

Abstract

Hermesinum adriaticum is a rarely reported unicellular biflagellated organism with a solid siliceous skeleton. Live specimens were not observed but many skeletons were found in sediments and, in small numbers, in cyanobacterial mats and the water column of the Salton Sea, a salt lake in California, U.S.A. Stages of the developing skeleton were studied with scanning electron microscopy, and the progression from small tetraxial daughter skeletons to complete asymmetrical adult skeletons is presented. Some variability in the adult skeletons is illustrated.

Introduction

Ebriidians are a rare group of marine heterotrophic flagellates of uncertain classification. Corliss (1994) has tentatively placed them in his phylum Opalozoa, and Taylor (1990) put them as possibly related to the dinoflagellates. Ebriidians have two dissimilar flagella and solid internal siliceous skeletons in contrast to the external hollow skeletons of silicoflagellates. There are two extant genera validly described, *Ebria* Borgert and *Hermesinum* Zacharias, of these *Ebria* is the more commonly reported in plankton surveys.

Presently, *H.adriaticum* Zacharias and *H. platense* Frenguelli are the only two known extant species in the genus. Others have been recorded as fossils, mostly from the Miocene (Tappan, 1980). The type of *H. adriaticum* was from the Adriatic Sea (Zacharias, 1906). Occasional blooms of *H. adriaticum* have been recorded from the southern Mediterranean near the Nile River (Halim, 1960), the Black Sea (Bodeanu, 1969), the Pettaquamscutt River in Rhode Island (Hargraves & Miller, 1974), the lower Chesapeake Bay (Rhodes & Gibson 1981) and Lake Rogoznica, a salt lake near the eastern Adriatic coast (Vilicic et al., 1996/97). The greatest abundance of *H.adriaticum* found to date was in the Salton Sea, California in 1955 (Carpelan, 1961) at 450 cells/ml, although it was misidentified as "a silicoflagellate, possibly *Dictyocha* sp.?". For a photograph of a living cell of *H. adriaticum*, see Rhodes & Gibson (1981).

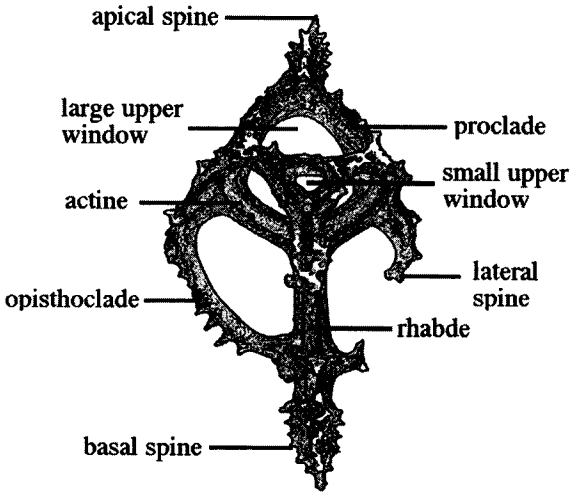


Figure 1. Diagram showing the terminology for parts of the *Hermesinum adriaticum* skeleton (after Deflandre, 1952).

Reproduction of the ebriidian cell has been little studied, and only asexual division is known (Tappan, 1980). Formation of the skeleton of the daughter cell is thought to begin before nuclear division and be nearly complete before cellular division. Rarely, double skeletons are formed by the accidental fusion of the daughter with the original skeleton (Hovasse, 1932). Skeletal parts are named using the traditional nomenclature of sponge spicules as proposed by Deflandre (1952) and are shown in Figure 1.

Study area

The Salton Sea is a saline lake in Imperial County, California that is below sea level and receives inflows from agricultural and municipal wastewaters. It began as a freshwater lake formed as a result of an accidental diversion of the Colorado River in 1905. Due to the lack of an outflow and the evaporation rates in its desert environment, the salinity rose gradually. When Carpelan (1961) reported high densities of *H. adriaticum* in 1955–1956, the lake had a salinity close to that of seawater. Presently it has a salinity of approximately 43 g l^{-1}. Scanning electron microscope images of adult skeletons of *H.adriaticum* from the Salton Sea, taken by A. R. Loeblich from 1967 to 1969, have previously been published (Tappan, 1980).

Marine micro-organisms were likely introduced accidentally along with marine fish that were stocked into the Salton Sea, mostly in the 1940s and 1950s. Many of these fish were from the Gulf of California, some from the Pacific Ocean and coastal Texas. Most of the organisms in the Sea are of marine origin,including *H. adriaticum*, possibly as a direct result of these introductions. Migratory birds are a less likely source of inoculation because the life cycle is not known to include a cyst form (Tappan, 1980).

H. adriaticum has an optimum temperature of 20–25 °C (Hargraves & Miller, 1974), well within the range for the Salton Sea of 12–35 °C. The salinity tolerance is unknown, but it has been reported at salinities as low as about 12 g l^{-1} (Hargraves & Miller 1974) and as high as 38 g l^{-1} (Vilicic et al., 1996/97).

Materials and methods

A study of diatoms was carried out as part of a larger bio-inventory of the Salton Sea during 1999. Skeletons of *H. adriaticum* were encountered during the SEM analysis of samples prepared for the determination of diatom species.

Surface sediment was sampled on January 20, 1999 from mid-lake stations by L. F. R. Levine-Fricke as part of a study of sediment contaminants using a modified Birge-Eckman dredge. One of these samples (GB64-46.2-12099), taken at 33° 23′ 23.9″ N, 115° 51′ 57.0″ W (about 4 km from the eastern shore in the northern basin) was donated to the author for study of diatoms and other microfossils. Depth at the site was 13 m.

Samples of floating cyanobacterial mats were taken from Varner Harbor at the headquarters of the Salton Sea State Recreational Area. A mid-lake water sample was taken by bucket from the surface (approximately the top 10 cm) from the northern basin (33° 23′ 23.9″ N, 115° 51′ 57.0″ W) on 4/7/99.

All samples were treated by the Van Stosch method (Hasle & Syvertsen, 1997) using HNO_3 and H_2SO_4 to remove organic material, dried on a coverslip, coated with Au/Pd, and examined with a Hitachi 5200 SEM using 10 KV accelerating voltage.

Results and discussion

H. adriaticum, previously known to be present in the Salton Sea, (Carpelan, 1961; Tappan, 1980) was found in several types of samples in 1998–1999. The largest numbers were found in the sediment sample. The sediment sample contained a great many individual skeletons of *H.adriaticum*. Both adult and daughter skeletons were found. The number of skeletons in the surficial sediments suggests a bloom occurred in the recent past.

Several adult and daughter skeletons from organisms that may have been alive when collected were found on SEM stubs of samples of cyanobacterial mats that had been processed with concentrated acids. These mats rise to the surface in summer and contain many entrained benthic diatoms as well as the much rarer *H.adriaticum*. *H. adriaticum* is thought to be herbivorous on diatoms (Tappan, 1980) or flagellates (Hargraves & Miller, 1974).

A single adult skeleton was found on a stub prepared from a mid-lake surface water sample. This may represent resuspension from the sediment or a living specimen at the time it was collected. No living specimens of *H. adriaticum* were observed during this study.

A complete progression of daughter skeletons was found in samples from small tetraxial daughter skeletons about 10 μm long to adult skeletons 37–54 μm long (mean=44.4 μm, n=29).

The young skeletons, called trianes, have four rays called the actines. Three of these are set at about 120° apart in a plane, the fourth projects at a 90° angle from that plane (Fig. 2A, B). The fourth actine is topped by a triangle of silica (Fig. 2B, C). The two anterior apices of the triangle grow extensions that close to become the small circular upper window (Fig. 2D–F). The posterior apex of the triangle lengthens but

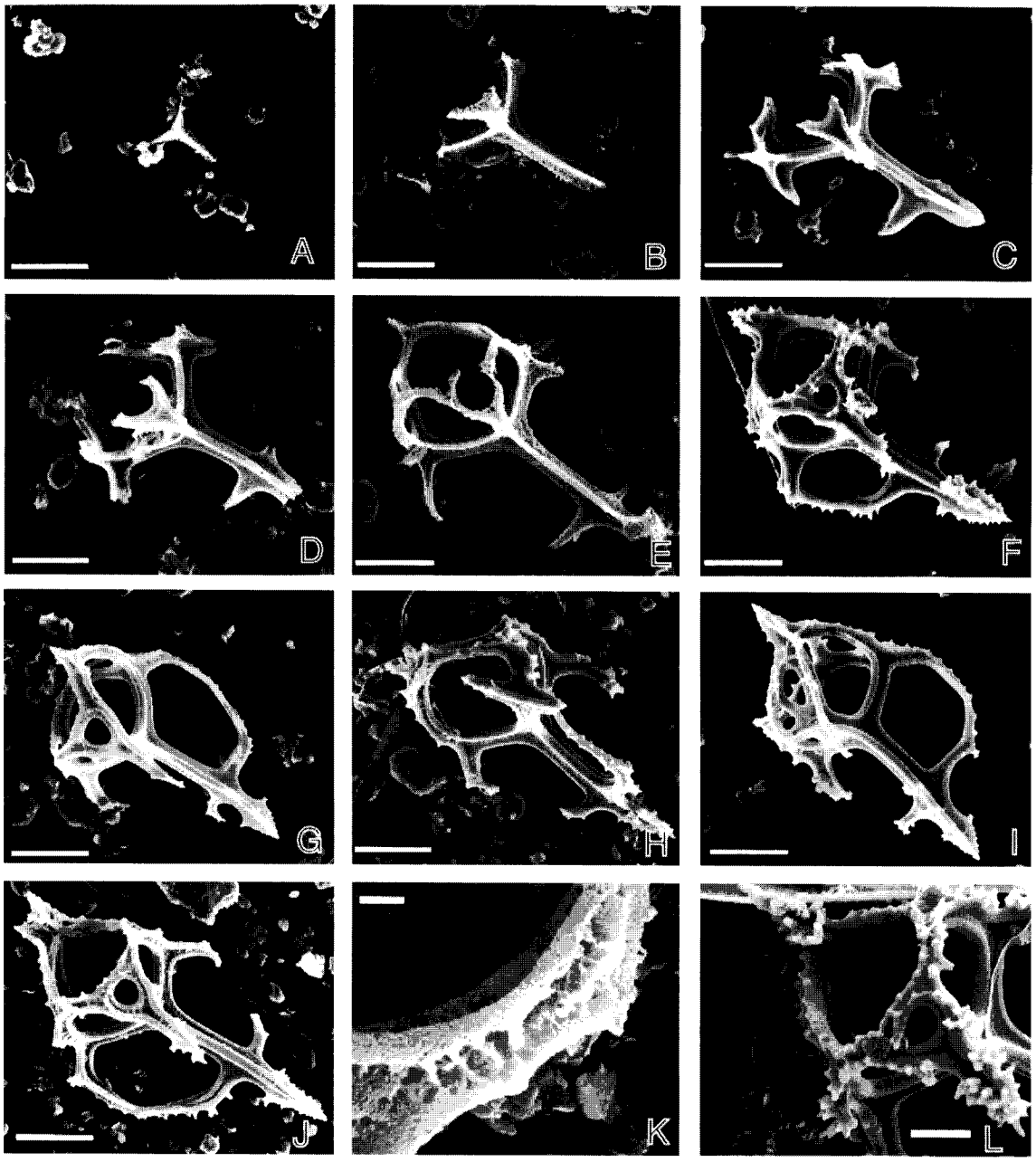


Figure 2. Stages in the development of and variability in skeletons of *Hermesinum adriaticum*. (A and B) very young skeletons showing the primary four-sided symmetry. (C and D) beginning of secondary development of the apices of the original skeleton. (E) small dorsal window beginning to form and continuation of apical growth with large upper window now fully formed. (F) adult left-handed skeleton with fully formed opisthoclade and spinose surface. (G) an adult right-handed skeleton showing smoother surface than the individual in F. (H) Error in skeleton formation with misplaced anterior apex and an extension to dorsal apex instead of an opisthoclade. (I and J) Double anterior apices. (K) illustration of rugose texture of skeleton at higher magnification. (L) spiny surface of adult skeleton. Scale bar for A–J=10 μm, for K=1 μm, and for L=5 μm.

normally does not connect further to the skeleton. The three bottom actines extend during development, the two anterior ones trifurcating (Fig. 2C). The third, posterior actine becomes the longer rhabde, forming the axis of the skeleton. It has three extensions, one of which becomes the posterior spine and one that

will help form the opisthoclade, an arch-like feature. The anterior extensions extend in a curved manner and fuse to form the large upper window (Fig. 2E). The anterior spine is formed at the forward end of this large window. The posterior extension of one of the anterior actines fuses with that of the rhabde to make the opisthoclade in the adult skeleton (Fig. 2E, F). The posterior extension of the other anterior actine forms the lateral spine.

The small upper window forms two bridges on either side to the lower anterior window forming a sort of siliceous basket in which the nucleus of the daughter cell will reside (Fig. 2E). At which point in the skeletal development the nucleus divides and exactly when the daughter nucleus enters the newly forming skeleton is not known, but Deflandre (1952) illustrated a cell undergoing cytokinesis with an incomplete daughter skeleton, the nuclear 'basket' of silicon not yet formed.

Skeletons of *Hermesinum* are always asymmetric with a completed arch only on one side of the skeleton. Assuming that Figure 1 illustrates the 'dorsal' view of the skeleton (after Hargraves & Miller, 1974), the right-handed skeleton is defined as one where the opisthoclade is on the right side of the skeleton. The illustration of a double skeleton given by Hovasse (1932) shows fused daughter skeletons that are mirror images. This suggests that after division one daughter is left-handed (Fig. 2F) and one is right-handed (Fig. 2G). This would imply that in a population of this species equal numbers of left and right-handed skeletons should be present. Of the 29 adult skeletons of *Hermesinum* examined, 15 had the arch on the left side and 14 on the right, in close agreement with this hypothesis.

Much variability in the development of the skeleton occurs in the ebriidians. The morphology of several skeletons in this study differed substantially from the diagram in Figure 1. For example, in Figure 2H the upper triangle of silica apparently extended to the posterior apex, forming a bridge; an 'error' observed in several specimens. In Figure 2I, there are two small upper windows instead of one and in Figure 2J two anterior apices were accidentally formed. In these samples, no double skeletons were observed but they are known to be common in the ebriidians (Tappan, 1980). It is not clear what, if any, effect this variability might have on the cell.

At high magnification, the texture of the skeleton is evident (Fig. 2K). In contrast to the relative smoothness seen in some silica secreting organisms, such as silicoflagellates and some diatoms, it is rather rugose. The skeleton is solid and internal to the cell. This is in contrast to silicoflagellates that have a hollow external skeleton. A ridge about 1.5–1.7 μm wide is central to the main rib which ranged from 2.5 to 4 μm wide. The apices and other projections are sometimes decorated with an extensive spiny surface (Fig. 2L) that may merely be a variable feature. It is also possible that these spines continue developing after the basic skeleton is completed (compare Fig. 2F, G).

The mechanism of silica deposition in ebriidians is unknown (Preisig, 1994). More is understood about diatom frustules (Schmid & Schultz, 1979) and chrysophycean cysts (Sandgren, 1989) which are formed with the SDV (silica depositional vesicle). Transmission electron microscope studies may elucidate the mechanism of skeleton formation in the asymmetric *Hermesinum* and determine if a similar membrane is used to make the daughter skeleton. This would require fixation of living material. It would also be of interest to determine the timing and mechanism of movement of the newly formed nucleus to the daughter cell. In addition, study of the cellular ultrastructure may help to determine the correct classification of this organism.

Acknowledgements

I would like to thank the staff of LFR Levine-Fricke, especially Richard Vogl and Ryan Henry, for the sediment sample; James Watts, Brandon Swan and Kristen Reifel for obtaining water samples; Joan Dainer for technical assistance; and Stuart Hurlbert for reviewing the manuscript. I would like to thank Steven Barlow for the generous use of the Electron Microscope Facility at San Diego State University. I also thank two anonymous reviewers.

References

Bodeanu, N., 1969. Ceretari asupra fitoplanctonului din zona de mica ad ncime de la litorialul românese al Mării Negre. Ecol. Mar. 3: 65–147.

Carpelan, L. H., 1961. Phytoplankton and plant productivity. In Walker, B. (ed.), The Ecology of the Salton Sea, California in Relation to the Sportfishery. Calif. Fish and Game, Fish Bull. 113: 33–43.

Corliss, J., 1994. An interim utilitarian ('user-friendly') hierarchical classification and characterization of the protists. Acta Protozool. 33: 1–51.

Deflandre, G., 1952. Classe des ébriédiens. In Grassé, P. (ed.), Traité de Zoologie: Anatomie, Systématique, Biologie. Masson et Cie, Paris: 407–424.

Halim, Y., 1960. Observations on the Nile bloom of phytoplankton in the Mediterranean. J. du Cons. 26: 57–67.

Hargraves, P. & B. Miller, 1974. The ebridian flagellate *Hermesinum adriaticum* Zach. Arch. Protist. 116: 280–284.

Hasle, G. R. & E. Syvertsen, 1997. Marine diatoms. In Identifying Marine Phytoplankton. Academic Press, Harcourt Brace & Co. San Diego, California.

Hovasse, R., 1932. Contribution à l'étude des silicoflagellés. Multiplication, variabilité, hérédité, affinités. Bull. biol. Fr. Belg. 66: 447–501.

Preisig, H., 1994. Siliceous structures and silification in flagellated protists. Protoplasma 181: 29–42.

Rhodes, R. & V. Gibson, 1981. An annual survey of *Hermesinum adriaticum* and *Ebria tripartita*, two ebridian algae in the lower Chesapeake Bay. Estuaries 4: 150–152.

Sandgren, C. D., 1989. SEM investigations of statospore (stomatocyst) development in diverse members of the Chrysophyceae and Synurophyceae. Beih. Nova Hedwigia 95: 45–69.

Schmid, A. & D. Schultz, 1979. Wall morphogenesis in diatoms: deposition of silica by cytoplasmic vesicles. Protoplasma 100: 267–288.

Taylor, F., 1990. Incertae Sedis Ebridians. In Margulis, L., J. Corliss, M. Melkonian & D. Chapman (eds), Handbook of Protoctista. Jones & Bartlett Publ., Boston: 720–721.

Tappan, H. N., 1980. The Paleobiology of Plant Protists. W. H. Freeman & Co., San Francisco: 1028 pp.

Vilicic, D., I. Marasovic & G. Kuspilic, 1996/97. The heterotrophic ebridian microflagellate *Hermesinum adriaticum* Zach. in the Adriatic Sea. Arch. Protist. 147: 373–379.

Zacharias, O., 1906. Eine neue Dictyochide aus dem Mittelmeer, *Hermesinum adriaticum* n. g., n. sp. Arch. Hydrobiol. und Planktonkunde, Stuttgart 1: 394–398.

Hydrobiologia **473:** 223–228, 2002.
D.A. Barnum, J.F. Elder, D. Stephens & M. Friend (eds), The Salton Sea.
© 2002 *Kluwer Academic Publishers. Printed in the Netherlands.*

Summer movements of desert pupfish among habitats at the Salton Sea

Ronald J. Sutton
U.S. Bureau of Reclamation, P.O. Box 25007 (D-8210), Denver, CO 80225, U.S.A.

Key words: desert pupfish, Salton Sea, movements, marking, recapture

Abstract

Summer movement behavior of native desert pupfish (*Cyprinodon macularius* Baird and Girard) was evaluated among various habitats around the Salton Sea, located in southern California. Agricultural drains, shoreline pools, and Salt Creek were sampled six times between June 28 and September 16, 1999. Collected pupfish were marked using fluorescent elastomer implants. Unique marks were used at each site. Movements were detected from locations of recaptured pupfish. Desert pupfish were found in 10 of 12 sites sampled. Of 3239 pupfish captured during the study, 278 were recaptures, including 27 recaptures at areas different from where they were initially marked. The best evidence of pupfish movements was in the southwestern area of the Salton Sea between a drain and a connected shoreline pool. Movements were also observed from lower Salt Creek into a shoreline pool at the mouth of the creek as the water level dropped. The use of the Salton Sea as a migration corridor between habitats was not documented during this short study. The marking technique was successful and showed promise for future mark and recapture studies of desert pupfish.

Introduction

The desert pupfish (*Cyprinodon macularius* Baird and Girard) is the only fish species endemic to the Salton Sink. This species was listed as a California endangered species in 1980; the U.S. Fish and Wildlife Service (FWS) listed the desert pupfish and its critical habitat as endangered in 1986 because of habitat alteration, the introduction of exotic species and contaminants, and other habitat impacts (FWS, 1986).

Recently, extreme annual variability in catch numbers has occurred at some agricultural drains around the Salton Sea (Sea). For example, at County Line Drain, the California Department of Fish and Game (CDFG) collected 490 pupfish in 1996. This was followed by catches of six and four pupfish in 1997 and 1998, respectively (CDFG, unpublished data). In 1993, 261 desert pupfish were collected in Trifolium 12 Drain (Remington & Hess, 1993), followed by 3 pupfish collected in 1994 (CDFG, unpublished data). Variability in catch has also occurred within a season. Nicol et al. (1991) found that some drains that did not yield pupfish during one trap set often produced pupfish in subsequent trappings. A variety of factors may have influenced trap results, including placement of traps, number of traps, bait types, timing, water level fluctuations, and vegetation removal (Nicol et al., 1991). Barlow (1958) described pupfish movement behavior within shoreline pools, but he did not evaluate movements among habitats.

In 1999, the U.S. Bureau of Reclamation (Reclamation) conducted a desert pupfish reconnaissance within shoreline pools of the Sea, agricultural drains, and in a natural tributary for the Salton Sea Restoration Project. The primary objectives were to (1) determine the movement of pupfish among various habitat types within one summer season and (2) address the purposes (i.e. feeding, spawning, dispersal, and avoidance of predators) for which pupfish were utilizing these areas. This information would help determine the importance of the Sea as a corridor to movements among various habitats and allow mixing of the gene pool. In addition, this study could be used to determine how various proposed Sea restoration actions might affect the desert pupfish, such as the construction of a desert pupfish channel around a series of concentration ponds to allow movements among habitats.

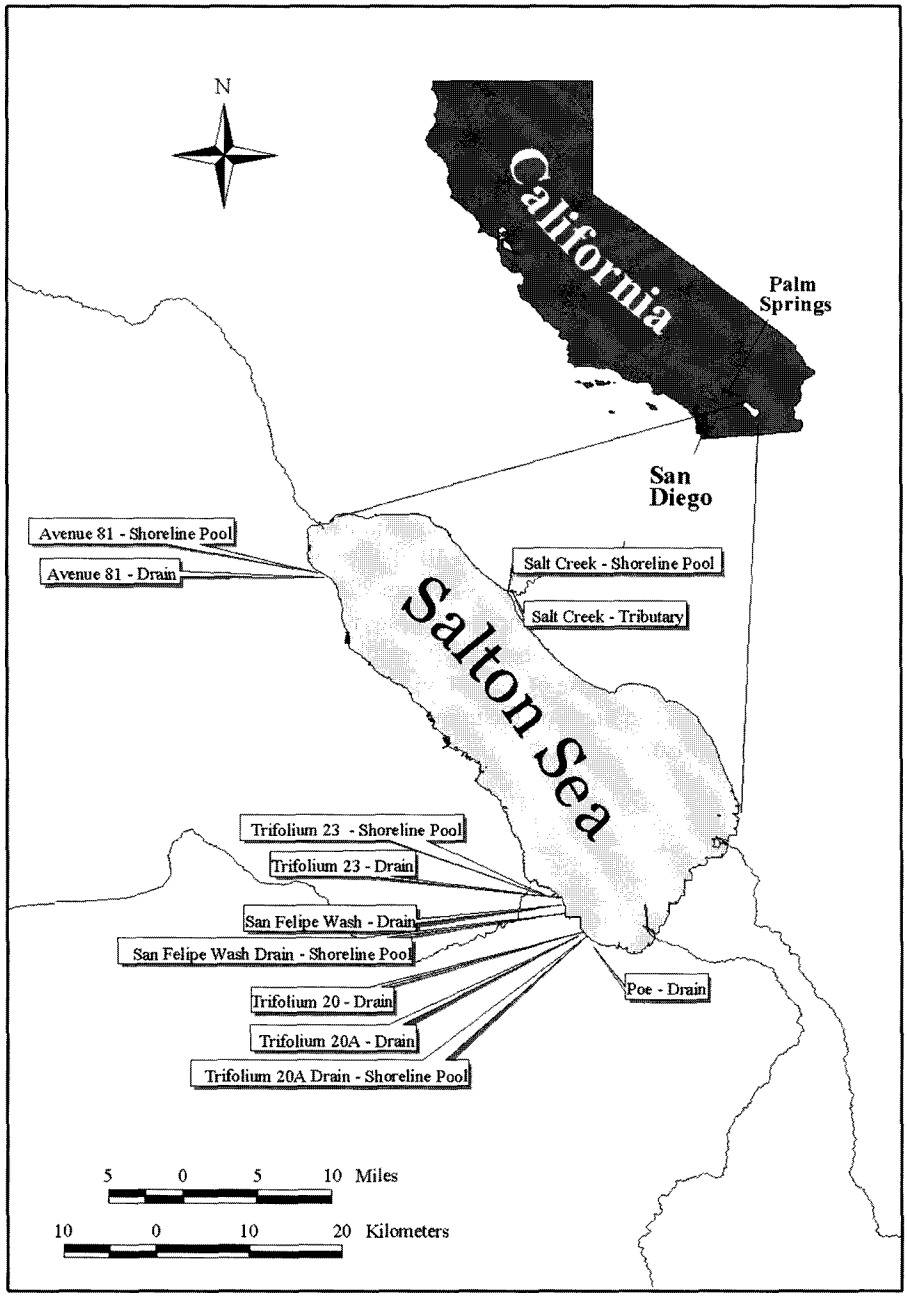


Figure 1. Map of Salton Sea with desert pupfish sample locations.

Study sites

Based on discussions and a field tour with CDFG, we decided to focus most of the sampling effort in the southwestern area of the Sea because of its close proximity to the proposed concentration ponds. Twelve sample sites were selected where desert pupfish had previously been collected and included shoreline pools, agricultural drains, and lower Salt Creek (west of Highway 111 bridge) (Fig. 1). Trifolium 20 Drain and Poe Drain were added after the fourth sample trip to help determine if pupfish were using the Sea to move between Trifolium 20A Drain and these nearby drains. San Felipe Creek, designated critical habitat for desert pupfish (FWS, 1986), was not selected because it was usually dry or flood-

Table 1. Desert pupfish captured at sites around the Salton Sea, 1999

Site	Total number captured	Total recaptured from this site	Total recaptured from other sites	
Drains:				
San Felipe Wash	1	0		0
Trifolium 23	2	0		0
Trifolium 20A	1441	214	North of Trifolium 20A Drain	19
Avenue 81	5	1		0
Trifolium 20	22	1		0
Poe	1	0		0
Shoreline Pools:				
North of Trifolium 23 Drain	1130	17		0
North of Trifolium 20A Drain	308	13	Trifolium 20A Drain	7
West of Salt Creek	214	1	Salt Creek	1
North of Avenue 81 Drain	0	0		0
South of San Felipe Wash Drain	0	0		0
Salt Creek	115	4		0
Total	3239	251		27

ing. Schoenherr (1990) observed that flash flooding in Salt Creek washed out large numbers of desert pupfish. Sampling sites were accurately located using a Rockwell HNV-560 PLGR global positioning system (GPS).

Methods and materials

Six sampling trips occurred about once every 2 weeks between June 28 and September 16, 1999, during the season when desert pupfish are most vulnerable to capture (Nicol et al., 1991). Sampling gear consisted of baited minnow traps with 0.6-cm mesh size and 3.8-cm opening size. Depending on location, $\leq$12 traps were set for 2–24 h during each sample period to obtain sufficient numbers of pupfish for marking and recapturing. All collected fish were held in a live well with an airstone and were handled using disposable gloves. Fish were identified, enumerated, and returned to their capture location. Personnel from CDFG provided training on fish identification.

Captured desert pupfish were marked with elastomer implants to track movements. Fluorescent elastomers have been used successfully to monitor movements of juvenile reef fishes (8–57 mm standard length) (Frederick, 1997). Reclamation staff practiced the marking technique on sheepshead minnows (*C. variegatus* Lacépède), a close relative of desert pupfish, prior to the field sampling. Unique marks were used at each site. Movements were detected from locations of recaptured fish.

Results

Of the 3239 desert pupfish captured at all sites during the study, 278 were recaptured, including 27 recaptures at sites different from where they were initially marked (Table 1). The best evidence of desert pupfish movements was between Trifolium 20A Drain and the connected shoreline pool adjacent to this drain (Fig. 2). A barnacle bar separated the Trifolium 20A Drain outlet from the Sea. This forced water in the drain to flow into the adjacent shoreline pool, which was always open to the Sea. Of the 1441 pupfish captured during the study in Trifolium 20A Drain, 214 were recaptured from this drain and 19 were recaptured which were originally marked in the shoreline pool (Table 1). In the shoreline pool, 308 desert pupfish were captured during the study. This included 13 recaptured from this pool and 7 recaptured that were initially marked in Trifolium 20A Drain (Table 1). The percentage of recaptures in Trifolium 20A Drain of those marked in this drain showed a steady increase from 2.5% on July 12 to 11.7% on September 14. Few pupfish were captured in the two drains closest

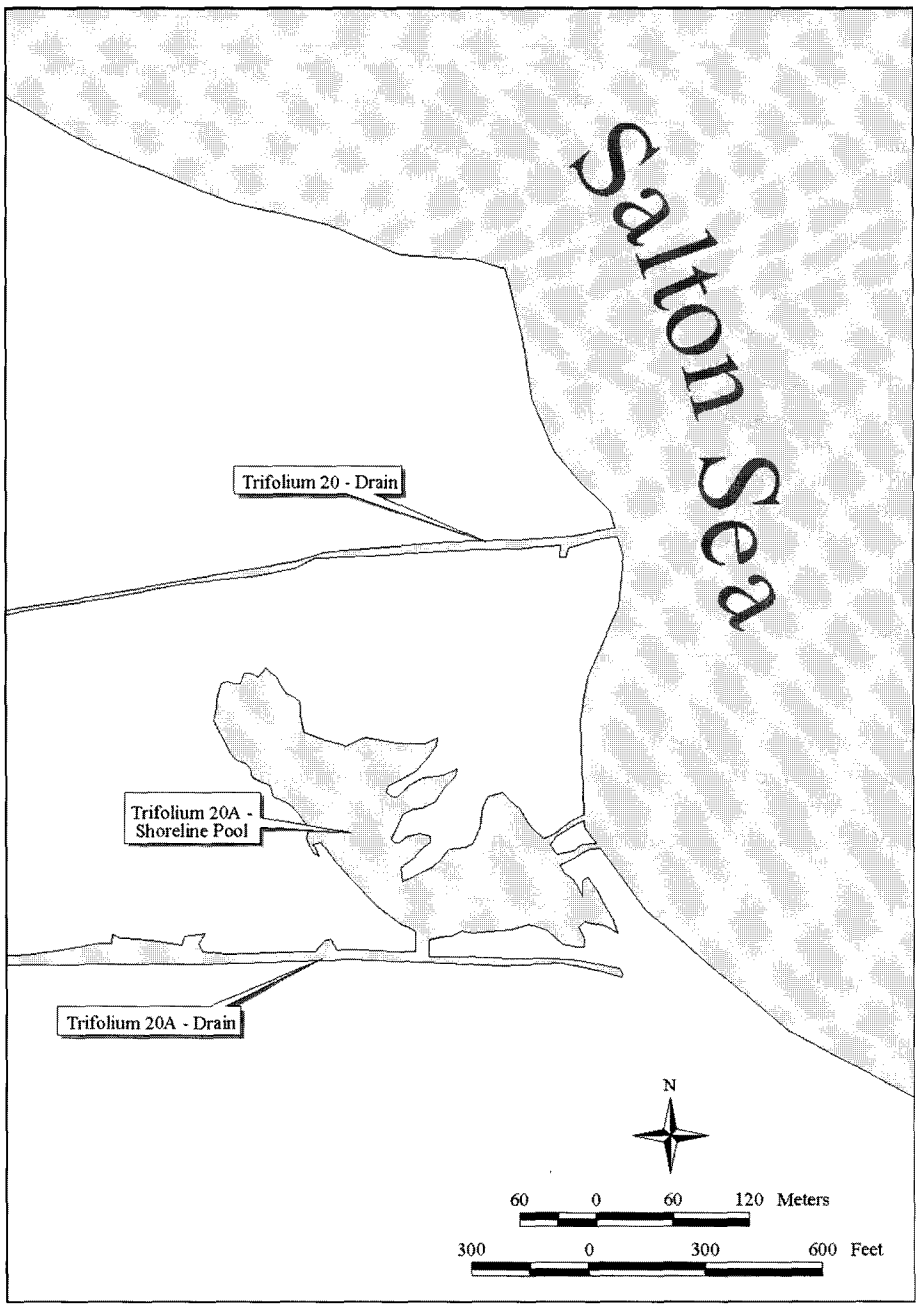


Figure 2. Irrigation drain (Trifolium 20A) and shoreline pool where desert pupfish movements were detected.

to Trifolium 20A Drain, Trifolium 20 Drain and Poe Drain (Table 1). No marked pupfish from Trifolium 20A Drain or the shoreline pool were recaptured in these drains.

Desert pupfish movements were also detected in lower Salt Creek. Salt Creek entered into a shoreline pool that was always separated from the Sea by a barnacle bar (Fig. 3). Although water was present at all times in lower Salt Creek, no water flow was observed and the dense aquatic vegetation at this site eventually died and matted as the water level dropped.

Of the 115 desert pupfish captured in lower Salt Creek during the study, 4 were recaptured from this location (Table 1). Capture data strongly suggested movements of desert pupfish from Salt Creek downstream into the shoreline pool, a distance of approxim-

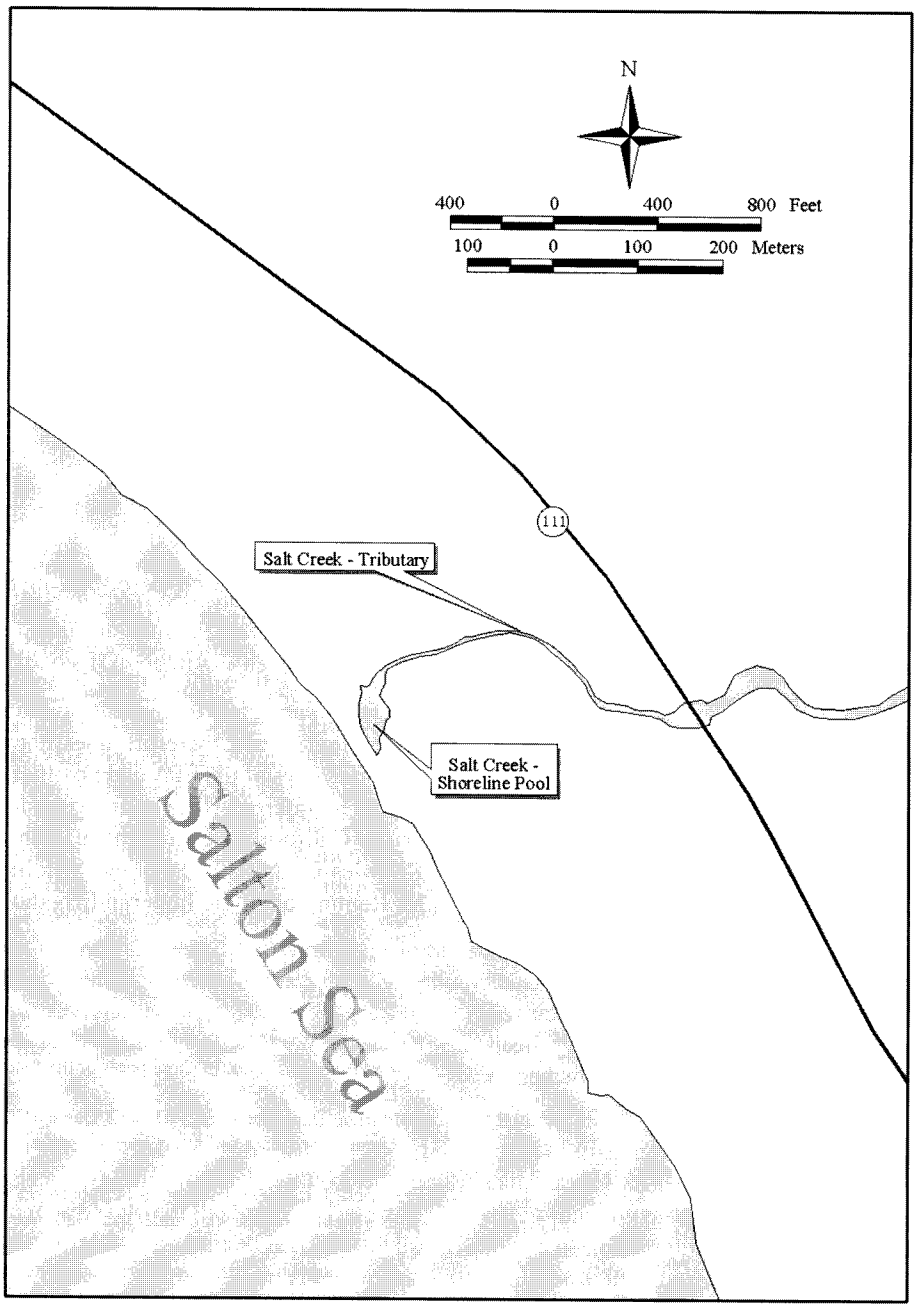


Figure 3. Lower Salt Creek and shoreline pool where desert pupfish movements were detected.

ately 0.5 km. Pupfish catch per unit effort (CPUE) declined from 2.9 fish/trap/h on July 15 to 0.0 fish/trap/h on September 15 in lower Salt Creek. This compared with an increase in pupfish CPUE from 0.5 fish/trap/h on July 1 to 2.3 fish/trap/h on September 15 in the shoreline pool. Movements were confirmed when one marked pupfish from Salt Creek was recaptured in the shoreline pool on August 19. No marked pupfish from other sites were recaptured in Salt Creek.

Discussion

The use of the Sea as a migration corridor for desert pupfish was not confirmed in this study. However, this

reconnaissance did show that desert pupfish moved short distances between agricultural drains or creeks and nearby shoreline pools.

The mark and recapture results indicated that although some pupfish were moving between Trifolium 20A Drain and the adjacent shoreline pool, a large proportion remained where they were initially marked. There was no clear reason why some pupfish moved and others remained. It appeared that small randomly scattered schools of pupfish broke away from the main population and dispersed into another area. Since the shoreline pool was always open to the Sea, it was possible that some of these small schools moved from the shoreline pool into the Sea where they migrated along the shoreline and into other habitats.

Movements from lower Salt Creek into the shoreline pool were likely due to the water level dropping between July and September, which forced desert pupfish to seek better habitat. A barnacle bar separated the shoreline pool from the Sea and effectively blocked access to the Sea.

The marking technique appeared successful based on the recapture data that showed fish movements. The elastomer implants were quickly and easily applied, were usually identified with the naked eye, and appeared to have long retention. Frederick (1997) reported that fish marked and held in the laboratory showed 100% tag visibility and retention for periods up to 76 days. Marks in the sheepshead minnows used in our study were visible after 7 months using ultraviolet light. Frederick (1997) found that mortalities of small fish related to this marking technique occurred within 24 hours of the procedure. The sheepshead minnows in our study showed no behavior or health problems related to the marking procedure.

Conclusions

Although use of the Sea as a migration corridor between habitats was not confirmed during this short study, desert pupfish movements were documented between different, adjacent habitat types. The best evidence of movements was observed in the southwestern area of the Sea between Trifolium 20A Drain and a connected shoreline pool. Since the shoreline pool was always open to the Sea, it was possible that some pupfish moved into other habitats via the Sea. A longer study concentrated in this area might confirm this theory.

Movements of desert pupfish from lower Salt Creek into the connected shoreline pool were possibly the result of dropping water level in the creek. A barnacle bar blocked access from the shoreline pool to the Sea. Seasonal fluctuations in water levels might affect fish health and/or force pupfish to seek other habitat. Thus, connectivity between habitat types could be necessary to prevent pupfish from becoming stranded within habitats that cannot sustain them for prolonged periods.

The marking technique was successful based on the recapture results. The elastomer implants showed promise for future mark and recapture studies of desert pupfish.

Acknowledgements

Although the research described in this paper was funded wholly or in part by the United States Environmental Protection Agency (EPA) through grant #R826552-01-0 to the Salton Sea Authority, it has not been subjected to the EPA's required peer and policy review and therefore does not necessarily reflect the views of the EPA and no official endorsement should be inferred. Thanks are extended to S. Keeney of the California Department of Fish and Game, G. Knowles of the U.S. Fish and Wildlife Service, and M. Remington of the Imperial Irrigation District.

References

Barlow, G. W., 1958. Daily movements of desert pupfish, *Cyprinodon macularius*, in shore pools of the Salton Sea, California. Ecology 39: 580–587.

California Department of Fish and Game (CDFG), 1996–1998. Unpublished data on desert pupfish surveys around the Salton Sea.

Frederick, J. L., 1997. Evaluation of fluorescent elastomer injecting as a method for marking small fish. Bull. mar. Sci. 61: 399-408.

Nicol, K., S. Lau & C. Boehm, 1991. A distribution survey of desert pupfish (*Cyprinodon macularius*) around the Salton Sea, California. Final Report for Section 6, Project No. EF90XII-1. California Department of Fish and Game Inland Fisheries Division.

Remington, M. D. & P. Hess, 1993. Results of desert pupfish trapping in Imperial Irrigation District Drains, August 8–September 21, 1993. Draft report. Environmental Compliance Section, Imperial Irrigation District.

Schoenherr, A. A., 1990. A comparison of two populations of the endangered desert pupfish (*Cyprinodon macularius*). First Annual Report. California Department of Fish and Game.

U.S. Fish and Wildlife Service (FWS), 1986. Endangered and threatened wildlife and plants; determination of endangered status and critical habitat for the desert pupfish. Federal Register 51: 10842–10851.

Hydrobiologia **473:** 229–244, 2002.
D.A. Barnum, J.F. Elder, D. Stephens & M. Friend (eds), The Salton Sea.
© 2002 *Kluwer Academic Publishers. Printed in the Netherlands.*

Fish biology and fisheries ecology of the Salton Sea, California

Ralf Riedel[1], Lucille Caskey[2] & Barry A. Costa-Pierce[3]
[1]*Gulf Coast Research Laboratory, College of Marine Sciences, University of Southern Mississippi, Ocean Springs, MS 39564, U.S.A.*
[2]*U.S. Fish and Wildlife Service, 2730 Loker Ave, West, Carlsbad, CA 92008, U.S.A.*
[3]*Rhode Island Sea Grant College Program, Department of Fisheries, Animal & Veterinary Science, University of Rhode Island, Narragansett Bay Campus, Narragansett, RI 02882-1197, U.S.A.*

Key words: tilapia, Sciaenidae, salt lakes, phi prime, restoration, growth

Abstract

Studies of the fisheries ecology and fish biology of the Salton Sea, California, were conducted in 1999 and 2000 using 50 m gill nets in river, nearshore, pelagic, and estuarine areas. Total lengths and weights were measured for all fish captured, and sub-samples were dissected for gonad weights and aging. Ten fish species were captured of which a hybrid tilapia (*Oreochromis mossambicus* x *O. urolepis hornorum*) was dominant by number and weight. Nearshore and estuarine areas had highest catch rates (over 11 kg h^{-1} net^{-1} for tilapia). Rivers were richest in the number of species (6 of 10 species were exclusively riverine), but lowest in fish abundance. Orangemouth corvina (*Cynoscion xanthulus*), bairdiella (*Bairdiella icistia*), sargo (*Anisotremus davidsoni*), and tilapia grew faster, but had shorter life spans than conspecifics elsewhere and Salton Sea conspecifics of 50 years ago. Reproduction occurred mostly in the nearshore and estuarine areas. Onset of reproduction of bairdiella and sargo was in the spring and extended through the beginning of summer. Reproduction of orangemouth corvina started in the summer and of tilapia in the spring. Reproduction of orangemouth corvina and tilapia extended through the fall. Gender ratios of tilapia were skewed toward males in all areas, except the rivers, where females predominated. All four species aggregated along the nearshore and estuarine areas in the summer when dissolved oxygen in the pelagic area was limited. Any restoration alternative for the Salton Sea should consider areas close to shore as primary areas for fish reproduction and survival.

Introduction

The Salton Sea is a 980 km^2 artificial salt lake of the Lower Colorado River Valley of the Sonoran Desert in southeastern California. It was created in 1904–05 by winter floods that broke through irrigation headworks, diverting water from the Colorado River into the Imperial Valley of California. The river flowed unabated for almost 2 years, filling the Salton Sink, an ancient, below sea level basin, resulting in the creation of California's largest lake – a desert sea – in the midst of a hot, alkaline desert.

The Salton Sea is designated by the state of California as a repository for nutrient-rich drainage waters from several commercial farms surrounding the lake. As a result, it has a high primary productivity, which in turn accounts for the high productivity of its fishery (Black, 1974, 1988). In 1971, the California Department of Fish and Game (CDFG) recorded recreational catches at 1.88 fish $angler^{-1}$ h^{-1}, one of the highest catch rates recorded in the state (CDFG, 1971). Due to the destruction of habitat in California, millions of birds now use the Salton Sea, which has become a vital link in the Pacific flyway, and one of the most important wildlife refuges in North America (Jehl, 1996; Kaiser, 1999).

Since 1992, massive deaths of fish and birds have occurred at the Salton Sea and captured the attention of scientists, the public, and the press (Kaiser, 1999). The salinity of the sea is currently 45 g l^{-1} and has been rising due to evaporation, dissolution of alkaline mineral deposits, and increased inputs of saline, nutrient-rich agricultural drainage water. High salinities, accelerated eutrophication, and outbreaks of

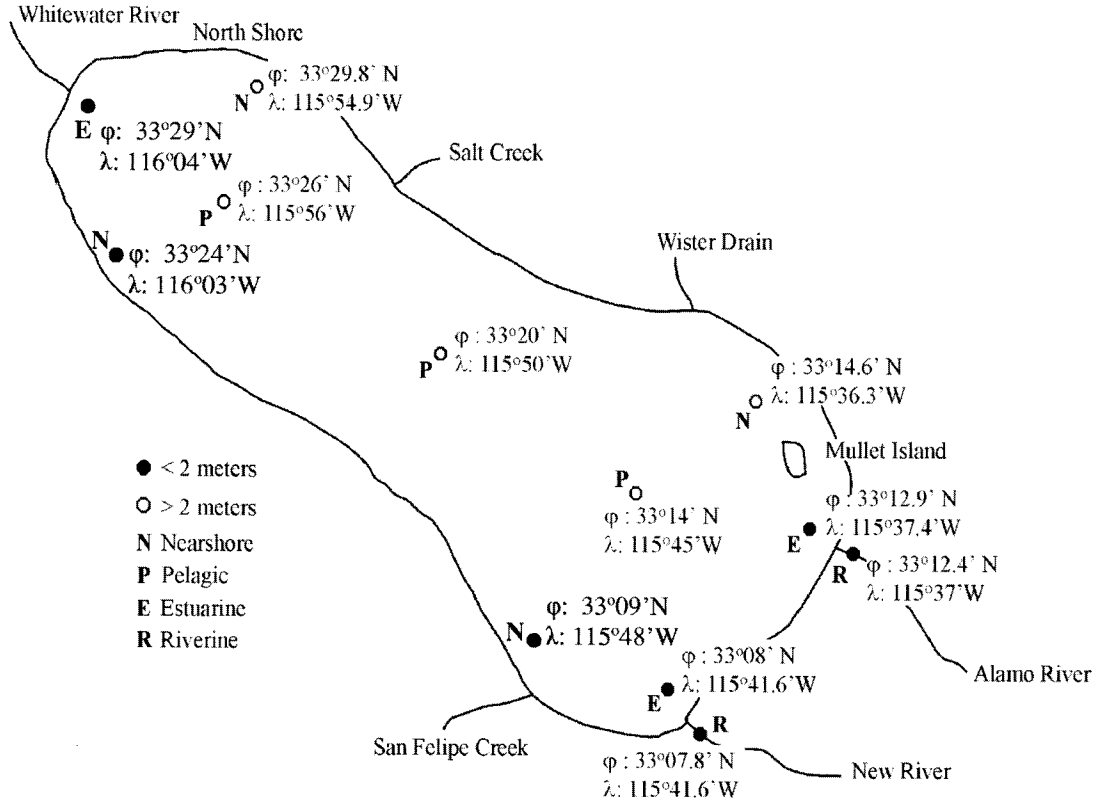


Figure 1. Station locations at the Salton Sea. Open circles are for stations deeper than 2 m, closed circles are for stations 2 meters or less; φ = latitude, λ = longitude. P = pelagic; N = nearshore; E = estuarine; R = riverine.

diseases have been blamed for reproductive failures and high larval mortalities of Salton Sea fish (Matusi et al., 1991a, b) and have been implicated in the recurrent fish and bird die offs (Jehl, 1996; Kaiser, 1999).

Starting in 1929, over 30 marine fish species were introduced into the Salton Sea mostly from the northern Gulf of California (Walker et al., 1961). Of these, only the orangemouth corvina (*Cynoscion xanthulus* Jordan and Gilbert), bairdiella (*Bairdiella icistia* Jordan and Gilbert) and sargo (*Anisotremus davidsoni* Steindachner) established and flourished. In 1964–65, tilapia (*Oreochromis mossambicus* x *O. urolepis hornorum* Linneaus) escaped to the Sea (Costa-Pierce & Doyle, 1997), and by the early 1970s dominated the fish community as the salinity rose above seawater levels (Dill & Cordone, 1997).

Salton Sea fish have wide salinity tolerances (Lasker et al., 1972; Prentice & Colura, 1984; Prentice et al., 1989; Costa-Pierce & Riedel, 2000), but a further increase in salinity may have adverse effects on reproduction (Hickling, 1963; Chervinski & Yashouv, 1971; Perry & Avault, 1972), recruitment (Hodgkiss & Man, 1977), and growth (Chervinski & Zorn, 1974; Payne, 1983; Payne & Collinson, 1983). Our study is the first comprehensive reconnaissance of Salton Sea fish since the pioneering study by Walker et al. (1961). An understanding of the Salton Sea fisheries is a first step in determining the importance of the fish resource in the modern lake ecosystem and a potential indicator for evaluating impacts on biota from restoration alternatives proposed for the lake (Cohen et al., 1999; Glenn et al., 1999; SSA, 2000).

Materials and methods

Field

Salton Sea fish were sampled bimonthly in 1999 (February 4th–16th; April 4th–12th; May 24th–31st; August 2nd–10th; October 2nd–23rd; November 27th–December 6th) and quarterly in 2000 (April 15th–21st; July 27th–August 1st; October 12th–21st; November 30th–December 4th) using multipanel gill nets at

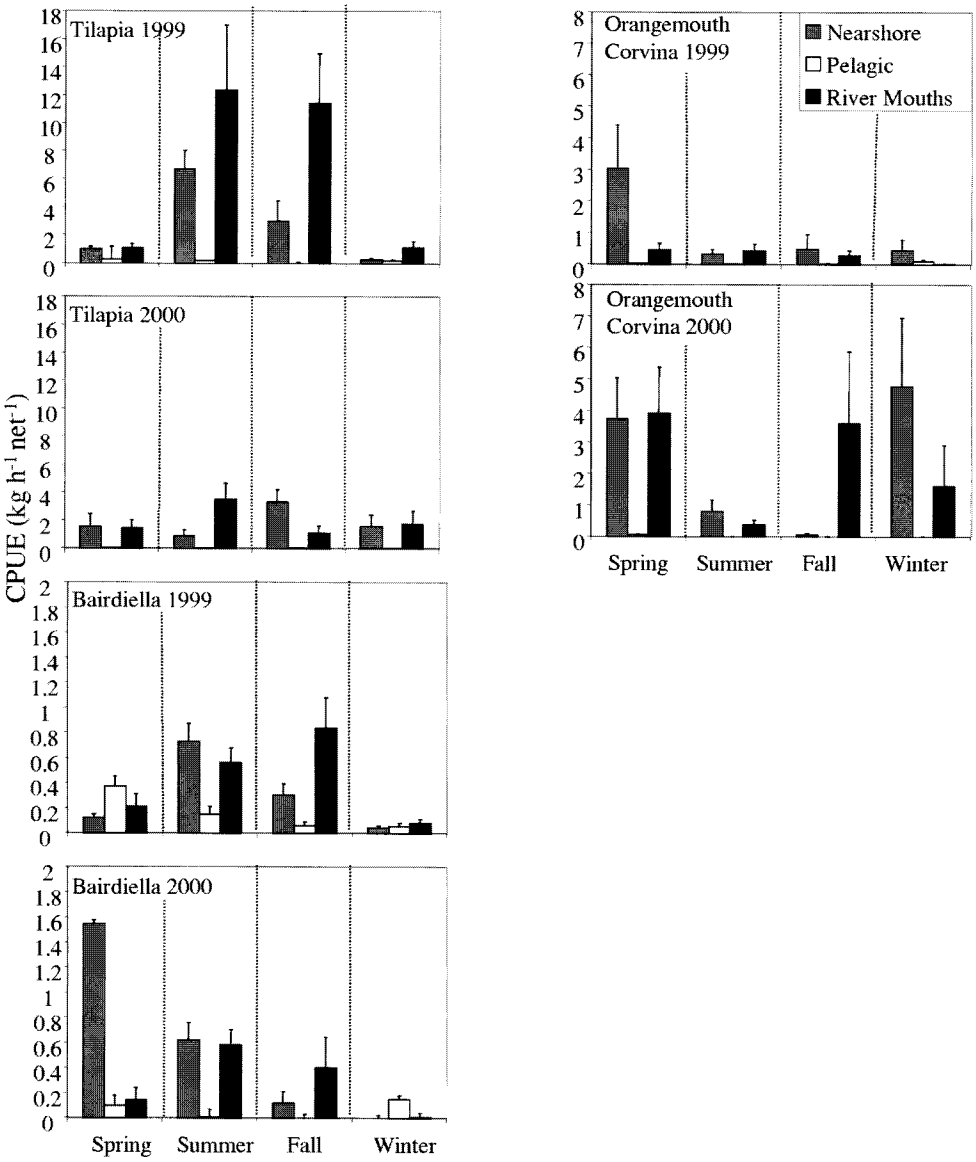


Figure 2. Back-transformed logarithm of catch-per-effort (kilograms $h^{-1}net^{-1}$) ± standard error of the mean for tilapia (*Oreochromis mossambicus* x *O. urolepis hornorum*), bairdiella (*Bairdiella icistia*), orangemouth corvina (*Cynoscion xanthulus*), and sargo (*Anisotremus davidsoni*) by area (excluding rivers), season, and year of the Salton Sea, California.

twelve stations covering rivers (1999 only), nearshore, pelagic, and estuarine areas (Fig. 1). Pelagic stations ranged between 10 and 15 m and all other stations were between 1 and 2 m. Multipanel gill nets were chosen to minimize biases from size selection (Lagler, 1978; Lott & Willis, 1991; Hubert, 1996). Gill nets consisted of five 10 m long × 2 m deep twisted nylon panels of 1, 2, 7, 10, and 12.5 cm stretched mesh sizes. Two surface gill nets were set at all stations. Two additional bottom nets were set at pelagic stations (Fig. 1) to infer fish preference between the surface and bottom of the lake. Gill net set time was used for calculating catch per unit effort (CPUE). Biomass-based CPUE (kg h^{-1} net^{-1}) was used as a proxy for production (Freon & Misund, 1999) and abundance-based CPUE (fish number h^{-1} net^{-1}) for assessing fish distribution, preference between lake surface and bottom, and mortality.

Fish were weighed to the nearest gram and total length measured to the nearest millimeter. A sub-

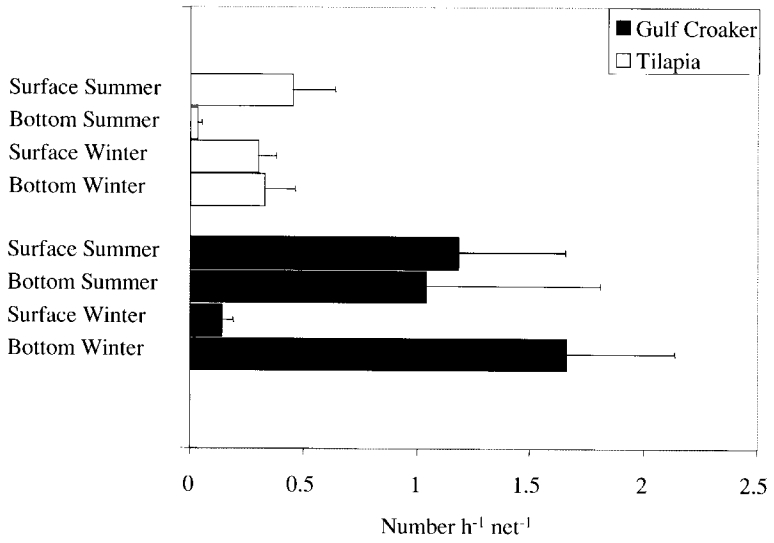


Figure 3. Vertical distribution of Salton Sea tilapia (*Oreochromis mossambicus* x *O. urolepis hornorum*) and bairdiella (*Bairdiella icistia*) catches during 1999 and 2000 in the Salton Sea. Numbers are average kg h^{-1} net^{-1} ± standard error of the mean, n = 18 for all bars.

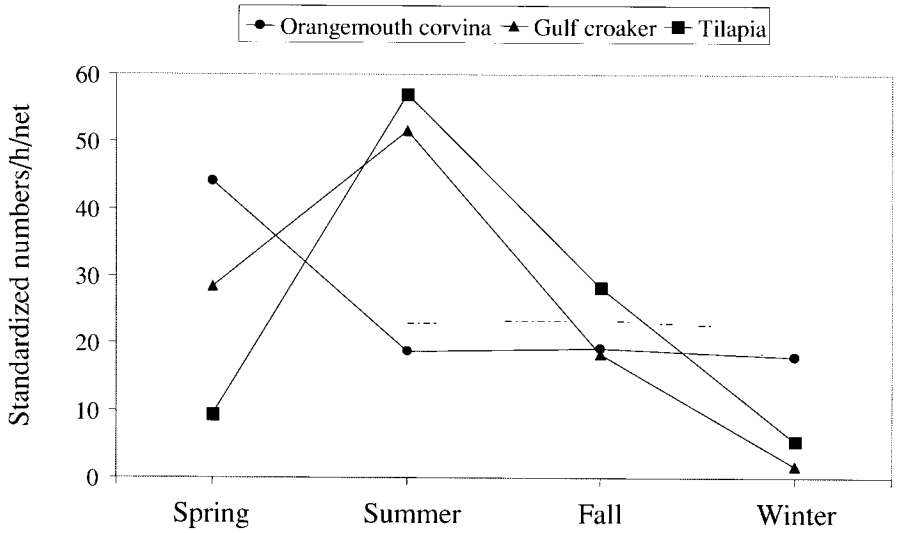


Figure 4. Standardized catch per unit effort (CPUE; fish numbers/50 m net/h) by season for three Salton Sea species sampled with multipanel gill net sets during 1999 and 2000 in the nearshore and estuarine areas combined. Percent CPUE was the fraction of a season's CPUE from the sum of the CPUEs of all seasons. Standardization was done by converting CPUEs for each species to percent values.

sample of approximately 50 fish per species per sampling period was dissected for gonad weights and otoliths taken from approximately 30 fish per species. Individual fish were dissected for determinations of gonadosomatic indices (GSIs). GSIs were calculated as the percentage of the gonad weight from the total weight of fish (Anderson & Neumann, 1996). Dissected fish were also sexed by examining gonads, weighed, and measured (total length).

Fish otoliths were used for age and growth determinations (DeVries & Frie, 1996) and viewed by two readers. Tilapia otoliths were viewed whole. Bairdiella and sargo otoliths were sectioned before viewing. Orangemouth corvina otoliths were broken at the focus and burned to aid in resolving annuli (Christensen, 1964; Chilton & Beamish, 1982). A simple light microscope with reflected light was used to examine whole otoliths, and transmitted light for sectioned and

broken otoliths. Each age ring consisted of a translucent zone and opaque zone. A translucent zone appeared clear under reflected light and white under transmitted light. An opaque zone appeared white under reflected light and dark brown or black under transmitted light. Annual deposition of rings was determined by observing the marginal increment pattern of otolith zones. Otolith readings were rejected if they disagreed, or the marks were faint or obscured by crystalline structures.

Analyses

Data were spatially and temporally grouped for analyses and the four major species, bairdiella, orangemouth corvina, sargo, and tilapia, analyzed independently. Catches of surface and bottom nets at the pelagic area were contrasted for tilapia and bairdiella to infer fish preference between the lake surface and bottom. Catches between surface and bottom nets were not assessed for the other species because of low sample size. Surface and bottom catches were analyzed with a two-sample Student *t*-test using the logarithm of CPUEs as the dependent variable. A *t*-test using data for the summer – low dissolved oxygen and high water temperature – and the winter – high dissolved oxygen and low water temperature – was conducted. Fish seasonal distribution was analyzed with a one-way analysis of variance (ANOVA). The logarithm of CPUE of stations at the lake shore (the nearshore and estuarine stations combined) was the dependent variable used and season was the factor. The sampling periods of February 4th–16th and November 27th–December 6th in 1999, and November 30th–December 4th in 2000 were winter; April 4th–12th and May 24th–31st in 1999, and April 15th–21st in 2000 were spring; August 2nd–10th in 1999 and July 27th-August 1st in 2000 were summer; October 2nd–23rd in 1999 and October 12th–21st in 2000 were fall. Seasonal patterns in female GSI were analyzed with a one-way ANOVA using GSI as the dependent variable and season as the factor. Fish gender ratios were expressed as percent female.

A von Bertalanffy growth function (VBGF) was used to describe fish growth for 1999 and 2000. If there was no convergence in parameter estimates using data for either year, data both years were combined. Growth performance was estimated using the phi prime index described in Moreau et al. (1986). The phi prime index was used over other indices (Gallucci & Quinn, 1979; Pauly, 1979; Munro & Pauly, 1983; Pauly & Munro, 1984) because it provided an unbiased growth estimator (Moreau et al., 1986). Phi prime indices were used to compare growth of the Salton Sea bairdiella and the orangemouth corvina populations described in Walker et al. (1961) to the populations sampled in this study. The phi prime indices from the fish populations in Walker et al. were derived using mean monthly lengths at age. The phi prime index of Salton Sea tilapia was compared with

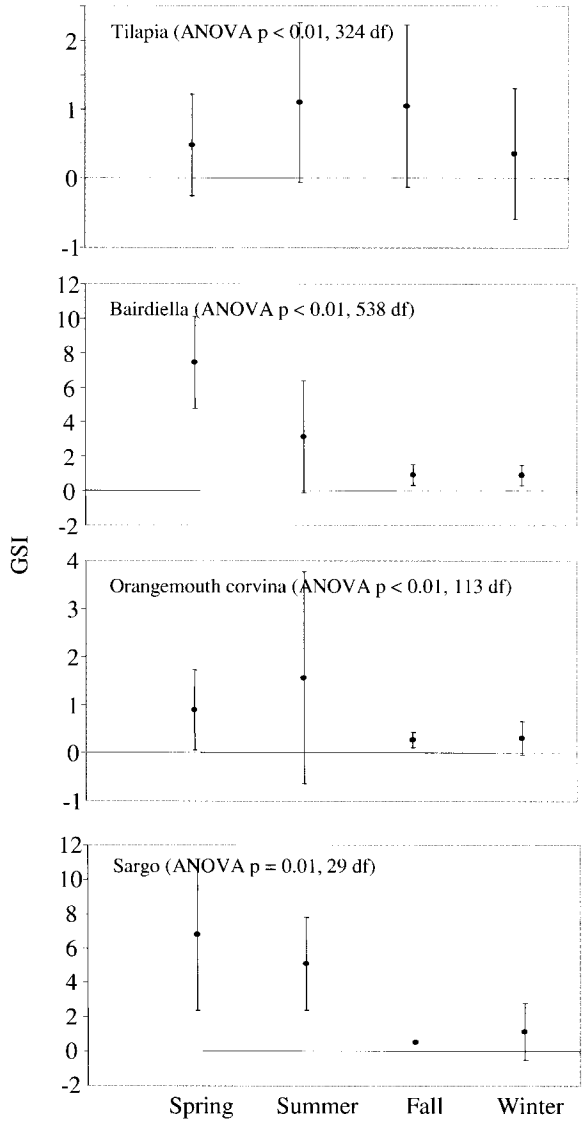


Figure 5. Gonadosomatic indices [(gonad weight/total body weight) × 100] ± SD by season and year for female tilapia (*Oreochromis mossambicus* x *O. urolepis hornorum*), bairdiella (*Bairdiella icistia*), orangemouth corvina (*Cynoscion xanthulus*), and sargo (*Anisotremus davidsoni*) captured in the Salton Sea, California during 1999 and 2000.

those from *O. mossambicus* provided by Moreau et al. (1986) for tropical and subtropical regions.

Because of the strong decline in tilapia numbers between 1999 and 2000, instantaneous total mortality estimates were determined for that species. Data for other species were too variable to offer any reliable mortality estimate. Mortality was estimated using the exponential decay model:

$$N_t = N_0 * e^{-Z},$$

where N_t is the number of fish during 2000, N_0 is the number of fish during 1999, and Z is the total mortality. Total mortality from 1999 to 2000 was calculated for the 1995 cohort. Tilapia not aged were assigned an age based on length using a log-likelihood function for multiple length-frequency data (Fournier et al., 1990, 1991).

Results

Ten fish species were captured between 1999 and 2000 from the Salton Sea (Table 1). Bairdiella and tilapia were the most abundant, followed by orangemouth corvina and sargo. Tilapia was the most important in weight, followed by orangemouth corvina, bairdiella, and sargo. All other species were of marginal importance in abundance and biomass.

Tilapia

Tilapia biomass-based CPUEs ranged from <1 in the rivers to over 11 kg h^{-1} net^{-1}in the estuarine areas (Fig. 2). Differences in CPUEs between the surface and bottom of the lake were not detected during the winter. Tilapia catches at the surface were higher in the summer (*t*-test, $p = 0.03$; Fig. 3). Tilapia CPUEs were higher in the summer and declined in the fall and winter at the nearshore and estuarine areas (ANOVA, $p < 0.01$; Fig. 4). GSIs showed an increase in the summer and fall (ANOVA, $p < 0.01$; Fig. 5), suggesting reproductive activity. Young of the year were observed along the shoreline of the lake in July and August 1999, but captured in gill nets only in December, 2000, suggesting a major recruitment failure of the 1999 year class. Tilapia percent females were of 17 (1752 fish caught) in the estuarine, 18 (1753 fish caught) in the nearshore, 25 (611 fish caught) in the pelagic, and 91 (83 fish caught) in the river area.

The 1995 tilapia cohort was dominant (89%) throughout the two-year sampling period. Fish older than 5+ years were not observed (Fig. 6). Data from 2000, which included juveniles (Fig. 6), was combined with 1999 data to describe growth (Fig. 7). The phi prime index for tilapia was 2.76. Tilapia length at age was consistently larger than conspecifics elsewhere (Table 2). Tilapia total instantaneous mortality for the 1995 cohort was estimated to be 0.51 (Fig. 6).

Bairdiella

The highest biomass-based CPUE for bairdiella was 1.6 kg $h^{-1}net^{-1}$ in the nearshore during the spring of 2000 (Fig. 2). Bairdiella CPUEs were higher at the bottom in the winter (*t*-test, $p < 0.01$) and showed no difference in the summer (Fig. 3). Bairdiella CPUEs were higher in the summer and declined in the fall and winter at the nearshore and estuarine areas (ANOVA, $p < 0.01$; Fig. 4). GSI was strongly dependent on season (ANOVA, $p < 0.01$) and increased in the spring during (Fig. 5), suggesting that spawning started during that season. The bairdiella spawning season in 2000 was less than two months long. Bairdiella percent females were of 80 (673 fish caught) in the estuarine, 58 (1753 fish caught) in the nearshore, and 31 (2772 fish caught) in the pelagic area.

Lower recruitment was observed for bairdiella in 1999 than in 2000 (Fig. 8). The majority of the bairdiella population was of the 1996 (38%) and 1997 (23%) cohorts (Fig. 8). Bairdiella grew faster in 2000 than in 1999, with a phi prime index of 2.61 in 1999 and 2.73 in 2000 (Fig. 7). The bairdiella population sampled by Walker et al. (1961) had a phi prime index of 1.86.

Orangemouth corvina

The highest biomass-based CPUE for orangemouth corvina was 4.8 kg h^{-1} net^{-1}in the nearshore in the winter 2000 (Fig. 2). Orangemouth corvina CPUEs increased in the spring at nearshore and estuarine areas (ANOVA; $p = 0.02$; Fig. 4). Few orangemouth corvina were caught in the rivers and pelagic areas, indicating strong site fidelity to areas close to shore (Table 1). GSI did indicate reproductive activity in the summer (Fig. 5). Orangemouth corvina percent females were of 53 (96 fish caught) in the estuarine, 43 (195 fish caught) in the nearshore, and 58 (22 fish caught) in the pelagic area.

The strongest recruitment for orangemouth corvina was observed in 1999 (Fig. 9). The orangemouth corvina population was mostly of the 1996 (50%) and 1997 (24%) cohorts (Fig. 9). Orangemouth corvina phi prime index from this study was 3.58 for 1999,

Table 1. Species, total catch by numbers, by weights, and catch per unit efforts (kg h^{-1} net^{-1}) by area for fish sampled from the Salton Sea, CA between 1999 and 2000. CPUEs are mean catch per hour per net. * indicates a CPUE less than 0.1. P = pelagic; N = nearshore; E = estuaries; R = riverine

Species	Total catch by number	Total catch by weight (kg)	CPUEs
Major Species Sampled			
Salton Sea tilapia (*Oreochromis mossambicus x O. urolepis hornorum*)	P (613), N (2072), E (2102), R (85)	P (223.9), N (746.0), E (934.7), R (28.6)	P (0.1), N (2.5), E (4.2), R (0.1)
Bairdiella (*Bairdiella icistia*)	P (2775), N (1339), E (767), R (0)	P (269.5), N (114.9), E (95.3), R (0)	P (0.1), N (0.4), E (0.3)
Orangemouth Corvina (*Cynoscion xanthulus*)	P (22), N (195), E (111), R (5)	P (28.8), N (514.9), E (201.7), R (0.2)	P (*), N (1.4), E (1.3), R (*)
Sargo (*Anisotremus davidsoni*)	P (82), N (15), E (0), R (0)	P (17.9), N (6.0), E (0), R (0)	P (*), N (*)
Other Species Sampled			
Threadfin shad (*Dorosoma petenense*)	P (0), N (15), E (116), R (5)	P (0), N (0.8), E (6.9), R (<0.1)	E (*)
Common carp (*Cyprinus carpio*)	P (0), N (0), E (0), R (2)	P (0), N (0), E (0), R (0.9)	R (*)
Channel catfish (*Ictalurus punctatus*)	P (0), N (0), E (0), R (6)	P (0), N (0), E (0), R (1.4)	R (*)
Flathead catfish (*Pylodictis olivaris*)	P (0), N (0), E (0), R (1)	P (0), N (0), E (0), R (<0.1)	R (*)
Western mosquitofish (*Gambusia affinis*)	P (0), N (0), E (0), R (6)	P (0), N (0), E (0), R (<0.1)	R (*)
Striped mullet (*Mugil cephalus*)	P (0), N (0), E (4), R (0)	P (0), N (0), E (6.8), R (0)	E (*)

3.41 for 2000, and 3.40 for the population studied by Walker et al. (1961; Fig. 7).

Sargo

Sargo were captured only in the nearshore and pelagic areas. Mean CPUE was 0.01 ± 0.004 kg h^{-1} net^{-1}, n = 248. No trend in CPUEs by sampling areas for sargo was detected. Sargo GSI was highest in the spring (Fig. 5). Sargo percent females were of 38 (15 fish caught) in the nearshore and 39 (82 fish caught) in the pelagic areas.

The sargo age distribution was distinctly bimodal, with peaks in the 1996 (36%) and 1998 (52%) cohorts (Fig. 10). Growth was estimated by combining 1999 and 2000 data because not enough fish were caught during either year. Sargo had the second fastest growth rate of all major fish species sampled (Fig. 7). No phi prime index was calculated for sargo because data for populations of conspecifics were not available for comparisons.

Discussion

Tilapia

The high tilapia CPUEs were expected due to the high primary productivity of the Salton Sea. Lake and reservoir tropical fisheries average 80 kg ha^{-1} (Oglesby, 1985), of which Sri Lankan reservoirs are among the most productive (De Silva, 1988). Amarasinghe (1987) and Amarasinghe & De Silva (1990) reported CPUEs ranging between 0.4 and 1.2 kg d^{-1} at four reservoirs with average *O. mossambicus* productivity of 63–918 kg ha^{-1} yr^{-1} in Sri Lanka (De Silva, 1988). Gill nets in Sri Lanka are 50–75 m long and 1.5–2 m deep, set for an average of 12 h d^{-1} (De Silva, 1991). Overnight gill net sets of 10–12 h conducted in this study yielded catches ranging from 50 to 112 kg in the nearshore and from 86 to 129 kg in the estuarine area, most of which were caught in a 10 m section of the 50 m long multipanel gill net. Higher productivities of tilapia (as per CPUE) were evident in areas closer to shore, especially the estuarine areas.

Tilapia dominance in the Salton Sea might also be due to the high adaptability of that fish to adverse environmental conditions and their ability to feed on a vast array of food items (Mironova, 1969; Trewavas, 1983). Tilapia are known for tolerating low dissolved oxygen and high salinities, and shift readily from a phytoplankton diet to alternate food sources (Trewavas, 1983; Suresh & Lin, 1992).

Maximum life span for tilapia has been reported to be between 8 (Mironova, 1969; De Silva, 1991) and 11 years (Fryer & Iles, 1972; James, 1989). Lower longevity (James, 1989) and slow growth (Hecht & Zway, 1984) have been observed in tilapia living in extreme environments. Even though the maximum observed age was 5 years old, Salton Sea tilapia grew fast, reaching adult size quickly. Moreover, Salton Sea tilapia length at age was higher than length at age for tilapia in other lakes and reservoirs (Table 2).

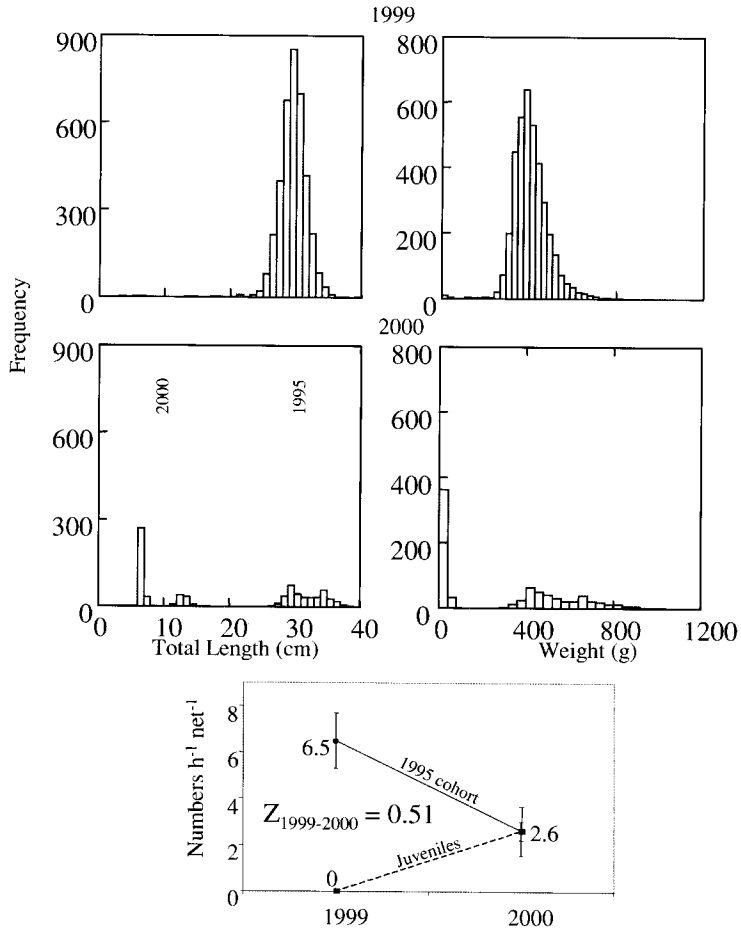


Figure 6. Salton Sea tilapia (*Oreochromis mossambicus* x *O. urolepis hornorum*) size distribution, juvenile recruitment, and adult mortality for 1999 and 2000. Fish less than 15 cm are less than a year old. Fish larger than 20 cm are 3 and 4 years old (in 1999), and 4 and 5 years old (in 2000). The broken line represents juvenile fish recruiting to the population and the solid line represents adult mortality estimates from gill net catch rates. Numbers associated with lines are catches per unit of effort (CPUEs, number of tilapia net^{-1} h^{-1}). Bars are standard errors of CPUEs averaged over seasons and Salton Sea habitats. Z is instantaneous mortality rate for the 1995 cohort.

Moreau et al. (1986) reported a range of phi prime indices of 2.05–2.80 for Mozambique tilapia (*O. mossambicus*) in Africa and west Asia. The phi prime index for Salton Sea tilapia was the second highest compared with those tilapia populations (Table 3). Tilapia have been reported to increase food consumption (Watanabe, 1989) and to lower routine metabolism (Ron et al., 1995) as salinity rises. A gradual salinity rise over the years in the Salton Sea might have led to the rapid adaptation of tilapia, rendering a unique strain of faster growing, short lived fish.

GSIs for female tilapia have been reported to range between 2.3 and 2.7 in freshwater lakes in Sri Lanka (De Silva, 1986). Tilapia GSIs from the Salton Sea were similar to those reported in De Silva (1986) during the reproductive season in spring and summer, indicating normal reproductive activity. Tilapia peak spawning occurred in the spring and continued throughout the summer. High densities of young fish were observed along the immediate nearshore area, up into the splash zone. The lack of juvenile fish sampled in 1999 suggests that there is large juvenile mortality before dispersal into the pelagic area.

Tilapia female to male gender ratio have been reported to vary between 0.4:1 and 7:1 in Sri Lankan freswater lakes (De Silva & Chandrasoma, 1980). The skewed sex ratio from Salton Sea tilapia – as high as 0.16:1 – might be due to temperature (Wang & Tsai, 2000) or the low number of founders, and possibly inbreeding (Costa-Pierce & Doyle, 1997).

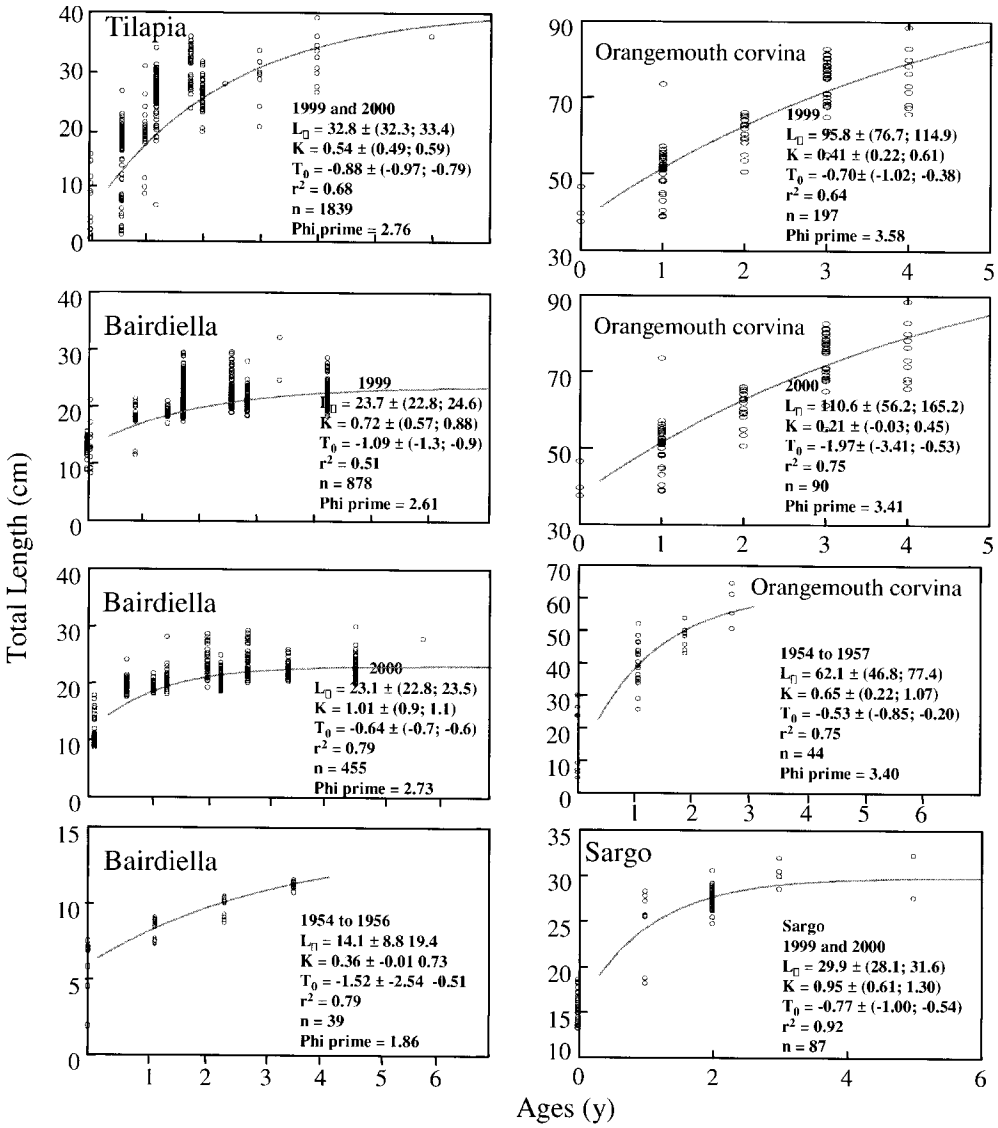


Figure 7. Von Bertalanffy growth function parameter estimates and phi prime growth performance index for tilapia (*Oreochromis mossambicus* x *O. urolepis hornorum*), bairdiella (*Bairdiella icistia*), orangemouth corvina (*Cynoscion xanthulus*), and sargo (*Anisotremus davidsoni*) captured in the Salton Sea, California during 1999 and 2000. Numbers in parenthesis are lower and upper 95% confidence intervals of parameter estimates.

Bairdiella

Based on the higher phi prime indices, the modern Salton Sea bairdiella is growing faster than conspecifics studied by Whitney (1961a). Additionally, there was evidence of faster growth in 2000 than in 1999, possibly due to the colder spring water temperatures in 1999. Higher growth rates for bairdiella might have come at the expense of life span. The oldest bairdiella sampled in this study was 5 years old. The bairdiella population sampled at the Salton Sea in the 1980s by Lattin (1986) had an age distribution ranging from 0 to 8 years old.

Bairdiella mature in 1–2 years, depending on environmental conditions (Whitney, 1961a). Maturation time may be related to the abundance of invertebrates (Walker et al., 1961). In the Salton Sea, Walker et al. (1961) found a peak spawning period in mid May, which agrees with our findings. Bairdiellas are annual spawners with peak spawning periods in the spring. For the closely related Atlantic croaker, Welsh

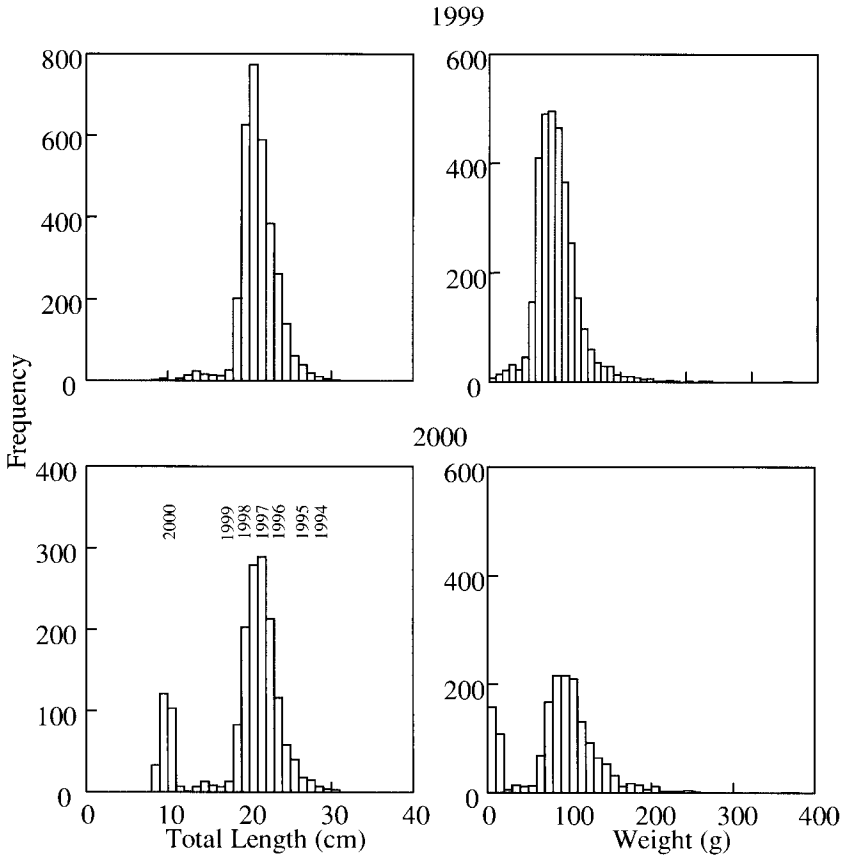


Figure 8. Length and weight distribution for the bairdiella (*Bairdiella icistia*) sampled at the Salton Sea between 1999 and 2000.

& Breder (1923) found a peak spawning time during May in North Carolina. Similarly, Haydock (1971) reported peak spawning based on GSIs during May and early June. GSIs were reported to average 10 and be as high as 12 (Haydock, 1971), which are similar to the GSIs reported herein for the Salton Sea bairdiella.

Based on the trend in GSIs observed in this study and on the higher catches in the nearshore areas during the summer months, the bairdiella moved to shallow waters to spawn. Atlantic croaker exhibit a strong nearshore schooling behavior, then migrate to deeper waters as adults. The inshore movement of Salton Sea bairdiella for spawning, unlike the movement pattern of the Atlantic croaker, may be driven by the low levels of dissolved oxygen and scarcity of food in the summer in the pelagic area (Carpelan & Linsley, 1961; Walker et al., 1961).

Orangemouth corvina

Orangemouth corvina was the third most abundant species and confined mostly to nearshore and estuarine areas. Orangemouth corvina catches in weight surpassed that of tilapia in the nearshore area during the spring of 1999 because of their larger individual sizes. Compared with the orangemouth corvina sampled by Whitney (1961b), the individuals sampled in 1999 and 2000 grew faster, which is evidence of adaptation to Salton Sea conditions.

Prentice et al. (1989) suggested two peaks of spawning for orangemouth corvina when fish were experimentally induced to spawn under summer and fall conditions. Fish & Cummings (1972) showed evidence of peak spawning for Salton Sea orangemouth corvina only once a year. Our data indicate an inshore movement pattern in the spring and reproduction starting in the summer, suggesting that inshore movement is unrelated with spawning due to a mismatch of reproduction and movement onset.

Sargo

Sargo was the least abundant of the four major species sampled. Many factors about this species in the

Table 2. Age (y) and mean total length (cm) ± one standard deviation for Salton Sea fish sampled in 1999 and 2000 compared with Salton Sea fish sampled in the mid 1950s and conspecifics sampled elsewhere. Dashes indicate no data

	N	Age	Mean total length ±	Mean total length from SD other studies	Reference
Bairdiella	52	0+	13.0 ± 2.2	-	
	36	1+	18.6 ± 2.0	13.1	Whitney (1961a)
	606	2+	21.2 ± 2.0	15.4	ditto
	184	3+	22.4 ± 2.3	17.2	ditto
	2	4+	28.5 ± 5.3	17.3	ditto
Orangemouth corvina	9	0+	28.4 ± 8.0	-	
	62	1+	46.1 ± 11.6	11.0	Whitney (1961b)
	115	2+	65.9 ± 6.0	40.0	ditto
	10	3+	69.6 ± 4.9	50.2	ditto
	-	4+			
	-	5+			
	1	6+	83.0	-	
Sargo	32	0+	15.6 ± 1.5	-	
	2	1+	18.5 ± 0.4	-	
	33	2+	27.5 ± 1.4	-	
	-	4+		25.0	Love (1996)
	-	12+		32.5	ditto
Tilapia	404	0+	8.0 ± 2.7	5.8	Khoo & Moreau (1990)
	-	1+			
	-	2+			
	2828	3+	29.2 ± 1.8	25.0	Khoo & Moreau (1990)
				25.0	Roux (1961)
				20.6	Hecht (1980)
				15.0	Koura & Bolock (1958)
	1314	4+	30.6 ± 2.5	26.0	Khoo & Moreau (1990)
				30.0	Roux (1961)
				25.5	Hecht (1980)
				18.0	Koura & Bolock (1958)
	292	5+	32.9 ± 2.9	28.5	Khoo & Moreau (1990)
				32.5	Roux (1961)
				23.4	Hecht (1980)

Salton Sea remain unanswered because of the few fish sampled. Sargo is an important sport fishery in the southern California Bight (Watson & Walker, 1992) and a target species for anglers at the Salton Sea. Walker et al. (1961) reported the presence of sargo in the Salton Sea, but did not provide any information about its abundance and potential for supporting a fishery. The increase in sargo GSIs during the summer (onset of spawning) is evidence that this species is still reproducing at the current Salton Sea salinity. There is some evidence that Salton Sea sargo are adopting the same adaptive mechanism as the other three major species investigated in this study. Salton Sea sargo grow faster than conspecifics in the Pacific coast of southern California, where four year old fish have been measured to be 25 cm long (Love, 1996), whereas two year old Salton Sea sargo measured 27.5 cm. The evidence should, however, be taken with caution because no measurement of dispersion was given for the length of Pacific sargo.

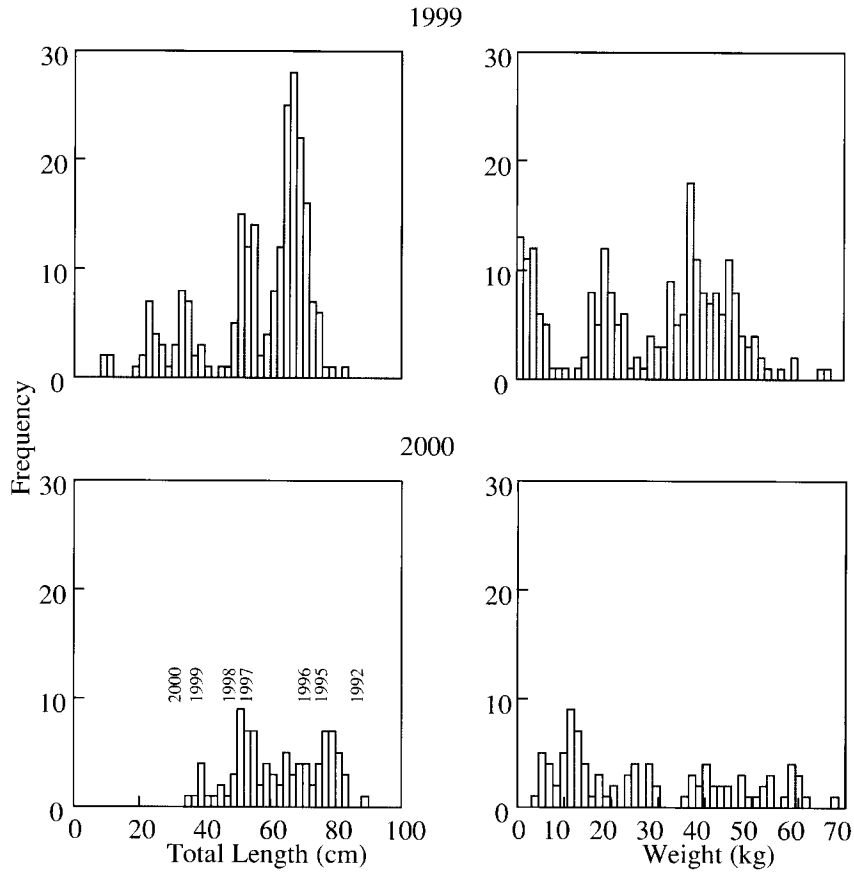


Figure 9. Length and weight distribution for the orangemouth corvina (*Cynoscion xanthulus*) sampled at the Salton Sea between 1999 and 2000.

Conclusions

The high catch rates are evidence for high production and the fast growth evidence for high tolerance of the Salton Sea fish community to stressful environmental conditions. The phi prime growth indices indicate that modern Salton Sea fish are growing faster than conspecifics elsewhere and present in the Salton Sea five decades ago, despite the stressful environment. There is also evidence that the modern fish have a shorter life span, possibly due to an increase in metabolic level leading to faster growth.

The fish community in the Salton Sea is not evenly distributed throughout the lake. Fish form a dense 'bathtub ring' all along the nearshore and estuarine areas in the summer when dissolved oxygen in the pelagic area is limited. Any restoration alternative should take this into account. Proposed water withdrawals could isolate critical nearshore spawning, nursery, and feeding areas. Because the nearshore and estuarine areas have the highest catch rates, any reduction in the extent of these areas may also negatively affect fish yield of a sport or potential commercial fishery. Additionally, because tilapia, bairdiella, and orangemouth corvina used the nearshore and estuarine areas for reproduction, they should be considered at least partly as essential fish habitats.

Due to the high salinity of the lake, the rivers were expected to serve as refugia for fish. This was not observed. Salinity may not be as important to the Salton Sea fish community now as is dissolved oxygen, especially during hot months. Tilapia and bairdiella in the Salton Sea seem to distribute in the water column partly according to oxygen levels. Similarly, seasonal distribution across the Salton Sea might be driven by oxygen for all fish. The estuarine areas were important habitats, yielding the highest catch rates, especially during the summer, providing an important refuge. The high levels of dissolved oxygen in these areas might have been a contributing factor for the high

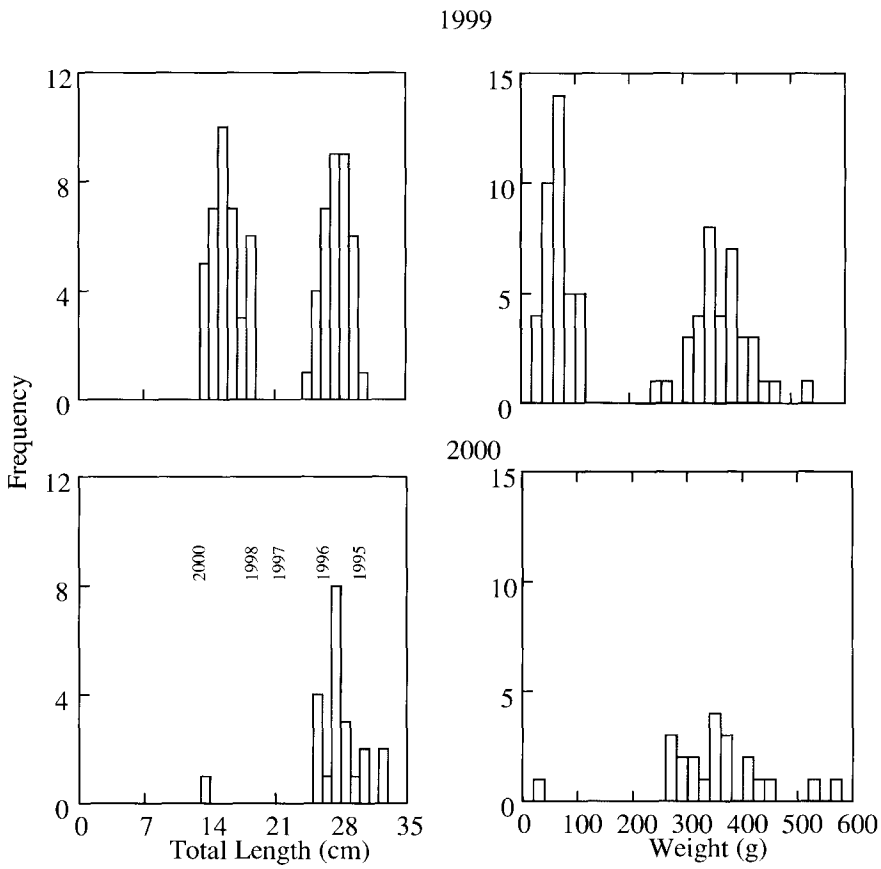


Figure 10. Length and weight distribution for sargo (*Anisotremus davidsoni*) sampled at the Salton Sea between 1999 and 2000.

catches. In contrast, the low oxygen levels prevailing in the pelagic area in the summer may be the strongest factor limiting fish abundance in that area.

Salinity will eventually become a factor limiting fish reproduction and survival if it continues to rise. *O. mossambicus* have been observed to reproduce at salinity as high as 49 g l^{-1} (Popper & Lichatowich, 1975) and tolerate up to 120 g l^{-1}(Whitefield & Blaber, 1979), whereas optimum growth has been reported to be between brackish and seawater salinity (Stickney, 1986). The Atlantic croaker tolerates salinities ranging from freshwater to 45 g l^{-1} (Simmons, 1957) and a related sciaenid, *Bairdiella chrysura*, has been found at 45 g l^{-1} in Laguna Madre, TX (Simmons, 1957). In a study of physiological responses of Salton Sea bairdiella, orangemouth corvina, and sargo, Brocksen & Cole (1972) reported an optimum range salinity of 33–37 g $l^{-1}$for food consumption and conversion, growth, and respiration. A salinity threshold may first affect reproduction (May, 1974, 1975, 1976; Matsui et al., 1991b), which may cause an abrupt collapse in the fishery. Efforts to curb the salinity increase of the Salton Sea are underway (SSA, 2000) and hopefully will occur before it is not late to prevent catastrophic declines of fish.

Implementation of a restricted commercial fishery may benefit many components of the Salton Sea fauna. When exploiting a virgin fish resource, younger, faster growing individuals benefit from the harvest of older, slower growing fish (Schaefer, 1954; Hilborn & Walters, 1992), and incidence of disease (and possibly periodic die offs) may be lowered. Given the high values of fish CPUEs, developing a commercial fishery may also benefit local communities on a sustained basis. The product of the fishery may be commercialized as meal, food, or fertilizer. The fast growth of Salton Sea fish may increase the likelihood of success of a commercial fishery. The Salton Sea may be the world's largest and most productive unfished water body, where a commercial fish harvest has promising results. Implementing a commercial fishery is the likely the most ecologically and economically

Table 3. Von Bertalanffy growth function parameters and phi prime growth performance indices for Salton Sea tilapia (*Oreochromis mossambicus* x *O. urolepis hornorum*) and the Mozambique tilapia (*O. mossambicus*) of Africa and West Asia. Data for Mozambique tilapia from Moreau et al. (1986)

Location	L_∞	K	Phi prime
Egypt Ponds	31.2	0.64	2.80
Salton Sea	32.8	0.54	2.76
Hong Kong	37.6	0.36	2.71
De Hoop Vlei Dam	28.2	0.62	2.70
Doorndrai Dam	26.0	0.68	2.67
Loskop Dam	32.0	0.41	2.63
Hong Kong	31.3	0.40	2.59
Loskop Dam	34.7	0.30	2.56
Loskop Dam	28.6	0.40	2.51
Luphephe Dam	27.0	0.42	2.48
Incomati Limpopo	38.7	0.20	2.47
Sheho Ngubu Dam	28.0	0.38	2.47
Hartseespoort Dam	33.0	0.27	2.46
Doorndrai Dam	25.8	0.44	2.46
Winter Dam	35.1	0.21	2.41
Luphephe Dam	25.8	0.37	2.39
Incomati Limpopo	30.7	0.25	2.37
Njele Dam	24.5	0.39	2.36
Zeeloei Vlei Dam	32.0	0.21	2.33
Lake Sibaya	21.6	0.36	2.22
Lake Sibaya	21.7	0.24	2.05

promising restoration strategy in the short term, while long-term strategies for controlling salinity and lake surface elevation are explored.

Acknowledgements

This research has been funded by the United States Environmental Protection Agency through Grant #R826552-01-0 to the Salton Sea Authority. The research results do not necessarily reflect the views of the Agency. No official endorsement should be inferred. We would like to thank the Salton Sea Authority for their generous support of this research, especially Tom Kirk; and the Salton Sea Science Subcommittee and Salton Sea Research Management Committee, especially Milt Friend, Barry Gump, Terri Foreman, and the late Rich Thiery. Special thanks are due to Stuart Hurlbert and the SDSU Center for Inland Waters for their support throughout this study. The technical assistance and expertise of John Butler and John Wagner are especially appreciated.

References

Amarasinghe, U., 1987. Growth overfishing: a potential danger in the Sri Lankan reservoir fishery. In De Silva, S. (ed.), Reservoir Fishery Management and Development in Asia. International Development Research Center, Katmandu, Nepal: 105–112.

Amarasinghe, U. & S. De Silva, 1990. Empirical approaches for evaluating efficiencies of different fishing methods in tropical, shallow reservoirs: a Sri Lankan case study. In De Silva, S. (ed.), Reservoir Fisheries of Asia Proc. 2nd Asian Res. Fish. Workshop, International Development Research Center, Hangzhou, People's Republic of China: 217–227.

Anderson, R. & R. Neumann, 1996. Length, weight, and associated structural indices. In Murphy, B. R. & D. W. Willis (eds), Fisheries Techniques. Am. Fish. Soc., Bethesda, Maryland: 447–482.

Black, G., 1974. The party boat fishery of the Salton Sea and the apparent effect of temperature and salinity on the catch of orangemouth corvina, *Cynoscion xanthulus*. Inland Fisheries Administrative Report 74–5, California Department of Fish and Game, Sacramento, CA.

Black, G., 1988. Description of the Salton Sea sportfishery 1982–83. Cal. Fish Game Adm. Rep.: 88–9.

Brocksen, R. W. & R. E. Cole, 1971. Physiological responses of three species of fishes to various salinities. J. Fish. Res. Bd Can. 29: 399–405.

Bruton, M. & B. Allanson, 1974. The growth of *Tilapia mossambicus* in Lake Sibaya, S. Afr. J. Fish Biol. 6: 701–715.

California Department of Fish and Game, 1971. Annual Report. Sacramento, CA.

Carpelan, L. & R. Linsley, 1961. The pile worm, *Neanthes succinea*. In Walker, B. (ed.), The Ecology of the Salton Sea, California, in Relation to the Sportfishery. Cal. Dep. Fish Game Bull. 113: 63–76.

Chervinski, J. & A. Yashouv, 1971. Preliminary experiments on the growth of *Tilapia aurea* in seawater ponds. Bamidgeh 23: 125–129.

Chervinski, J. & M. Zorn, 1974. Note on the growth of *Tilapia aurea* and *Tilapia zilii* in seawater ponds. Aquaculture 4: 249–255.

Chilton, D. & R. Beamish, 1982. Age determination methods for fishes studied by the groundfish program at the Pacific Biological Station. Can. Spec. Publ. Fish. aquat. Sci.: 60 pp.

Christensen & J. Burning, 1964. Otoliths, a technique for age determination of soles and other fish. J. Cons. 29: 73–81.

Cohen, M., J. Morrison & E. Glenn, 1999. Haven or Hazard: The Ecology and Future of the Salton Sea. Pacific Institute for Studies in Development, Environment, and Security.

Costa-Pierce, B. & R. Doyle, 1997. Genetic identification and status of tilapia regional strains in southern California. In Costa-Pierce, B. A. & J. Rakocy (eds), Tilapia Aquaculture in the Americas, 1. The World Aquaculture Society, Baton Rouge, Louisiana: 1–21.

Costa-Pierce, B. & R. Riedel, 2000. Fisheries ecology of the tilapias in subtropical lakes of the United States. In Costa-Pierce, B. A. & J. Rakocy (eds), Tilapia Aquaculture in the Americas, 2. The World Aquaculture Society, Baton Rouge, Louisiana: 1–20.

De Silva, S., 1986. Reproductive biology of *Oreochromis mossambicus* populations of man-made lakes in Sri Lanka: a comparative study. Aqu. Fish. Man. 17: 31–47.

De Silva, K., 1991. Growth rate and the role of *Oreochromis mossambicus* in the fishery of a tropical, upland, deep reservoir in Sri Lanka. Fish. Res. 12: 125–138.

De Silva, S., 1989. Reservoir of Sri Lanka and their fisheries. FAO Fish. Tech. Pap. 298.

De Silva, S. & J. Chandrasoma, 1980. Reproductive biology of *Sarotherodon mossambicus*, an introduced species, in an ancient man-made lake in Sri Lanka. Env. Biol. Fishes 5: 253–259.

DeVrie, D. & R. Frie, 1996. Determination of age and growth. In Murphy, B. R. & D. W. Willis (eds), Fisheries Techniques. Am. Fish. Sco., Bethesda, Maryland: 483–512.

Dill, W. A. & A. J. Cordone, 1997. History and status of introduced fishes in California, 1871–1996. Cal. Dept. Fish Game Bull 178.

Fish, J. & W. Cummings, 1972. A 50-dB increase in sustained ambient noise from fish (*Cynoscion xanthulus*). J. Acu. Soc. am. 52: 1266–1270.

Fournier, D., J. Sibert, J. Majkowski & J. Hampton, 1990. MULTIFAN, a likelihood-based method for estimating growth parameters and age composition for multiple length frequency data sets illustrated using data for southern bluefin tuna (*Thunnus maccoyii*). Can. J. Fish. aquat. Sci. 47: 301–317.

Fournier, D. J. Sibert & M. Terciero, 1991. Analysis of length frequency samples with relative abundance data for the Gulf of Maine northern shrimp (*Pandalus borealis*) by the MULTIFAN method. Can J. Fish. aquat. Sci. 48: 591–598.

Freon, P. & O. Misund, 1999. Dynamics of pelagic fish: effects on fisheries and stock assessment. Fishing News Books, Oxford, U.K.

Fryer, G. & T. D. Iles, 1972. The Cichlid Fishes of the Great Lakes of Africa. T. F. H., Neptune City, New Jersey.

Gallucci, V. & T. Quinn, 1979. Reparameterizing, fitting, and testing a simple growth model. Trans. am. fish. Soc. 108: 14–25.

Glenn, E., M. Cohen, J. Morrison, C. Valdés-Casillas & K. Fitzsimmons, 1999. Science and policy dilemmas in the management of agricultural waste waters: the case of the Salton Sea, CA, U.S.A. Env. Sci. Pol. 2: 413–423.

Haydock, I., 1971. Gonad maturation and hormone-induced spawning of the bairdiella, *Bairdiella icistia*. Fish. Bull. 69: 157–180.

Hecht, T., 1980. A comparison of the otolith and scale methods of ageing, and the growth of *Sarotherodon mossambicus* in a Venda impoundment (southern Africa). S. Afr. J. Zool. 15: 222–228.

Hecht, T. & P. Zway, 1984. On the stunted mocambique tilapia *Sarotherodon mossambicus* of the Matiovila Hot Spring, Kruger National Park. Koedoe 27: 25–38.

Hickling, C., 1963. The cultivation of tilapia. Sci. am. 208: 143–152.

Hilborn, R. & C. Walters, 1992. Quantitative Fisheries Stock Assessment. Chapman and Hall, New York.

Hodgkiss, J. & H. Man, 1977. Age composition, growth and body condition of the introduced *Sarotherodon mossambicus* (Cichlidae) in Plover Cove reservoir, Hong Kong. Environ. Biol. Fishes 2: 35–44.

Hubert, W., 1996. Passive capture techniques. In Murphy, B. R. & D. W. Willis (eds), Fisheries Techniques. Am. Fish. Sco., Bethesda, Maryland: 157–181.

James, E., 1988. A life-history approach to the biology of *Oreochromis mossambicus* in the Eastern Cape, South Africa. M. Sc. Publication, Rhodes University, Grahamstown, South Africa.

Jehl, J.R., 1996. Mass mortality events of eared grebes in North America. Am. J. field Ornith. 67: 471–476.

Johnson, G. D., 1978. Development of fishes of the mid-Atlantic Bight. Biol. Serv. Prog. Fish Wild. Serv. 4: 1–314.

Jubb, R., 1967. Freshwater Fishes of Southern Africa. Cape Town. Balkema, Johannesburg.

Kaiser, J., 1999. Battle over a dying sea. Science 284: 28–30.

Khoo, H. W. & J. Moreau, 1990. Population characteristics of *Oreochromis mossambicus* in the Seleter reservoir (Singapore) assessed through length-frequency analysis. In Hirano, R. & I. Hanyu (eds), The Second Asian Fisheries Forum Asian Fisheries Society, Manila, Philippines: 855–859.

Koura, R. & A. R. Bolock, 1958. Age, growth and survival of *Tilapia mossambica* in Egyptian ponds. Notes Mem. hydrobiol. Dep. U. A. R. 41: 1–18.

Lagler, K., 1978. Capture, sampling and examination of fishes. In Begenal, T. (ed.), Methods for Assessing Fish Production in Fresh Waters. Blackwell, Oxford, U.K.: 7–47.

Lasker, R., R. Tanaza & L. Chamberlain, 1972. The response of Salton Sea fish eggs and larvae to salinity stress. Cal. Fish Game 58: 58–66.

Lattin, G., 1986. Age and growth of the *Bairdiella icistia* in the Salton Sea using scales and otoliths. M. Sc. Publication, California State University, Long Beach.

Lott, J. & D. Willis, 1991. Gill net mesh size efficiency for yellow perch. Prairie Nat. 23: 139–144.

Love, M., 1996. Probably More Than You Want to Know About the Fishes of the Pacific Coast. Really Big Press, Santa Barbara, California.

May, R. C., 1974. Factors affecting buoyancy in the eggs of *Bairdiella icistia*. Mar. Biol. 28: 55–59.

May, R. C., 1975. Effects of temperature and salinity on fertilization, embryonic development, and hatching in *Bairdiella icistia*, and the effects of parental salinity acclimation on the embryonic and larval salinity tolerance. Fish. Bull. 73: 1–22.

May, R. C., 1976. Effects of Salton Sea water on the eggs and larvae of *Bairdiella icistia*. Calif. Fish Game 62: 119–131.

Matsui, M., A. Bond, G. Jordan, R. Moore, P. Garrahan, K. Iwanaga & S. Williams, 1991a. Abundance and distribution of ichthyoplankton in the Salton Sea, California in relation to water quality. California Fish and Game Report on Sport Fish Restoration Federal Aid Project F-51-R. California Department of Fish and Game, Sacramento, CA.

Matsui, M., G. Lattin, R. Moore, C. Mulski & A. Bond, 1991b. Salinity tolerance of *Cynoscion xanthulus*. California Fish and Game Report on Sport Fish Restoration Federal Aid Project F-51-R, Sacramento, CA.

Mironova, N., 1969. The biology of *Tilapia mossambica* under natural and laboratory conditions. Ichthyology 9: 506–514.

Moreau, J., C. Bambino & D. Pauly, 1986. Indices of overall growth performance of 100 tilapia (Cichlidae) populations. In Maclean, J., L. Dizon & L. Hosillos (eds), The First Asian Fisheries Forum. Asian Fisheries Society, Manila, Philippines: 201–206.

Munro, J. & D. Pauly, 1983. A simple method for comparing the growth of fishes and invertebrates. Fishbyte 1: 5–6.

Oglesby, R. T., 1985. Management of lacustrine fisheries in the tropics. Fisheries 10: 16–19.

Pauly, D., 1979. Gill size and temperature as governing factors in fish growth: a generalization of the von Bertalanffy's growth formula. Ber. Inst. Meeresk. Univ. Kiel 63.

Pauly, D. & J. Munro, 1984. Once more on growth comparisons in fish and invertebrates. Fishbyte 2: 21.

Payne, A., 1983. Estuarine and salt-tolerant tilapias. In Proceedings, International Symposium on Tilapia in Aquaculture. Tel-Aviv University, Tel-Aviv: 534–543.

Payne, A. & R. Collinson, 1983. A comparison of the biological characteristics of *Sarotherodon niloticus* with those of *S. aureus* and other tilapia of the delta and lower Nile. Aquaculture 30: 335–351.

Popper, D. & T. Lichatowich, 1975. Preliminary success in predator control of *Tilapia mossambica*. Aquaculture 5: 213–214.

Prentice, J. & R. Colura, 1984. Preliminary observations of orangemouth corvina spawn inducement using photoperiod, temperature, and salinity cycles. World Mar. Soc. J. 15: 162–171.

Prentice, J., R. Colura & B. Bumguardner, 1989. Observations on induced maturation and spawning of orangemouth corvina. Cal. Fish Game 75: 27–32.

Ron, B., S. K. Shimoda, G. K. Iwama & E. G. Grau, 1995. Relationships among ration, salinity, 17-alpha-methyltestosterone and growth in the euryhaline tilapia, *Oreochromis mossambicus*. Aquaculture 135: 185—193.

Roux, P. J., 1961. Growth of *Tilapia mossambica* in some Trasnvaal impoundments. Hydrobiologia 18: 165–175.

Schaefer, M., 1954. Some aspects of the dynamics of populations important to the management of commercial marine fisheries. Bull. inter-am. Trop. Tuna Com. 1: 27–56.

Simmons, E. G., 1957. An ecological survey of the upper Laguna Madre of Texas. Pub. Inst. mar. Sci. Texas 4: 156–200.

SSA (Salton Sea Authority), 2000. Guide to the Salton Sea Restoration Project Environmental Impact Statement/Environmental Impact Report. Department of the Interior-Bureau of Reclamation.

Stickney, R., 1986. Tilapia tolerance of saline waters: a review. Prog. Fish Cult. 48: 161–167.

Suresh, A. & C. Lin, 1992. Tilapia culture in saline waters: a review. Aquaculture 106: 201–226.

Trewavas, E., 1983. Tilipiine Fishes of the Genera *Sarotherodon*, *Oreochromis*, and *Danakila*. British Museum of Natural History, London.

Walker, B., R. Whitney & G. Barlow, 1961. Fishes of the Salton Sea. In Walker, B. (ed.), The Ecology of the Salton Sea, California, in Relation to the Sportfishery. Cal. Dep. Fish Game Bull. 113: 77–92.

Wang, L. & C. Tsai, 2000. Effects of temperature on the deformity and sex differentiation of tilapia, *Oreochromis mossambicus*. J. exp. Zool. 286: 534–537.

Watanabe, W., 1997. Saltwater culture of the Florida red and other saline-tolerant tilapias: a review. In Costa-Pierce, B. A. & J. Rakocy (eds), Tilapia Aquaculture in the Americas, 1. The World Aquaculture Society, Baton Rouge, Louisiana: 55–141

Watson, W. & H. Walker, Jr., 1992. Larval development of sargo (*Anisotremus davidsoni*) and salema (*Xenistius californiensis*) from the southern California Bight. Bull. mar. Sci. 51: 360–406.

Welsh, W. & C. Breder, 1924. Contributions to life histories of Sciaenidae of the eastern U. S. coast. Fish. Bull. 39: 141–201.

Whitfield, A. & S. Blaber, 1979. The distribution of the cichlid *Sarotherodon mossambicus* in estuarine systems. Environ. Biol. Fishes 4: 77–81.

Whitney, R., 1961(a). The bairdiella, *Bairdiella icistius*. In Walker, B. (ed.), The Ecology of the Salton Sea, California, in Relation to the Sportfishery. Cal. Dep. Fish Game Bull. 113: 105–152.

Whitney, R., 1961(b). The orangemouth corvina *Cynoscion xanthulus*. In Walker, B. (ed.), The Ecology of the Salton Sea, California, in Relation to the Sportfishery. Cal. Dep. Fish Game Bull. 113: 165–183.

Hydrobiologia **473:** 245–253, 2002.
D.A. Barnum, J.F. Elder, D. Stephens & M. Friend (eds), The Salton Sea.
© 2002 *Kluwer Academic Publishers. Printed in the Netherlands.*

Biology and migration of Eared Grebes at the Salton Sea

Joseph R. Jehl, Jr.[1] & Robert L. McKernan[2]
[1]*Hubbs-Sea World Research Institute, 2595 Ingraham Street, San Diego, CA 92109, U.S.A.*
Tel: 410-224-0728. E-mail: grebe5k@cs.com
[2]*San Bernardino County Museum of Natural History, 2024 Orange Tree Lane, Redlands, CA 92374, U.S.A.*

Key words: Eared Grebe, *Podiceps nigricollis*, Salton Sea, migration, monitoring, mortality

Abstract

The Eared Grebe (*Podiceps nigricollis* Brehm) is the North American bird species most closely associated with highly saline habitats, and in winter and early spring it is the most abundant waterbird at the Salton Sea. During the fall, the great majority of the North American population stages at hypersaline lakes in the Great Basin, departing in early winter for wintering areas in southern California and Mexico, principally in the central Gulf of California. On the northward return flight, nearly all the population passes through the Salton Sea, where concentrations of >1 million have been reported in February–March. After staging for several weeks, grebes leave in March–April and migrate toward breeding grounds in the northern United States and southern Canada. The Sea's development as the species' major spring staging area may be as recent as the 1960s, and presumably awaited the establishment of appropriate prey populations of marine worms. In the past decades, two major dieoffs at the Sea each resulted in the undiagnosed death of tens of thousands of birds. Whether the cause(s) are endemic to the Sea or involve the grebes' migration routes and stopover locations is unknown. Because of problems in estimating numbers, the significance of these mortality events is hard to evaluate. Population trends are better studied at fall staging areas, especially Mono Lake, where population turnover is inconsequential, grebes are virtually the only species present, and numbers can be ascertained by aerial photography.

Introduction

Despite its location in the hottest desert in the southwest, the Salton Sink for thousands of years has intermittently held significant bodies of water (Waters, 1981; Cohen et al., 1999; Patten et al., MS). In 1905–1907, 400 years after the drying of Lake Cahuilla, the overnight creation of a major freshwater lake to be known as the Salton Sea created habitats that were immediately discovered and exploited by waterbirds (Grinnell, 1908; van Rossem, 1911). High evaporation rates and low water influx quickly led to its increased salinization. The ecological changes that followed permitted the introduction/establishment of marine invertebrates and fish (Walker, 1961) that became the base for the food chain of an increasingly diverse avifauna, including species that prefer marine habitats. The attractiveness of the Salton Sink area was further enhanced by burgeoning commercial agriculture, the creation and management of extensive wetlands at the Salton Sea National Wildlife Refuge area (established 1930; renamed Sonny Bono Salton Sea National Wildlife Refuge in 1998) and, in the past decade or so, the establishment of a major aquaculture (catfish farming) industry, with its associated ponds that also supply food for fish-eating birds. By the 1960s, at the latest, the Sea had become an internationally recognized concentration point for well over 100 species of migrating and breeding waterbirds, dominated by grebes, waterfowl, gulls, shorebirds, and herons (McCaskie, 1970).

Currently, the Salton Sea is highly saline ($\approx$43 g l^{-1}), and the Eared Grebe is the most prominent waterbird in winter and spring. Although this grebe breeds in freshwater lakes and marshes through the western United States and southern Canada, for most of the year it is the North American bird species most closely tied to highly saline habitats, where it feeds mainly on small invertebrates. Starting in late July, most of the population leaves the breeding areas and

migrates directly to Mono Lake, California, and Great Salt Lake, Utah, to exploit the abundant brine shrimp (*Artemia* spp.) and alkali flies (*Ephedra* spp.). Grebes remain there until food resources are depleted, and then (usually November–December) make a non-stop flight across the deserts of southern Utah and California to wintering areas in Southern California and Mexico (Jehl, 1988, 1993; Jehl et al., 1999). Several tens of thousands move directly to the Salton Sea, and presumably remain there through the winter, but the great majority evidently bypass the area in favor of the mid-Gulf of California, where winter concentrations of hundreds of thousands have been reported persistently (R. Schreiber, S. Wilbur, D . Anderson, N. Roberts, pers. comm.; Jehl, 1988 and unpubl.). In fact, there seems to be little alternative to the Gulf's preeminence as a wintering site. Jehl (1988) was unable to find any evidence that substantial numbers currently wintered either in mainland Mexico or along the Pacific coast of Baja California, and there is no further information to the contrary. The population at the only other significant wintering location in Baja California – the salinas at Guerrero Negro (6000–9000, peak 13 790 in February–March; Carmona & Danemann, 1998) – is trivial compared to that in the Gulf.

In spring, wintering grebes reverse course and in late January–March congregate in large numbers (often >1million) at the Salton Sea (Fig. 1). They stage there for several weeks or longer and then depart in March–April, arriving at breeding areas in the northern United States and southern Canada in April–May (Jehl, 1988, 1993, 1997; Jehl et al., 1999; Cullen et al., 1999).

Despite its short history, the Salton Sea is probably the largest concentration point for Eared Grebes in North America and, indeed, the world, and on Christmas Bird Counts, the Sea routinely holds more Eared Grebes than are recorded over the entire rest of the censused winter range (Jehl, 1988 and unpubl.). The Sea's propensity to attract and concentrate migrants makes it potentially hazardous, as in recent years the Sea has experienced irregular and unexplained dieoffs of thousands of grebes (Jehl, 1996) and other waterbirds.

In this paper, we summarize information on the history and biology of the Eared Grebe at the Salton Sea and interpret it in light of extensive studies elsewhere in the western United States in the past two decades (e.g. Jehl, 1988; Cullen et al., 1999 and references therein).

Methods

Original data in this paper are mainly based on McKernan's >2 decades of studying bird life at the Salton Sea, and Jehl's winter/spring studies of Eared Grebes at the Sea since the mid-1980s. Jehl's work was designed to supplement information gathered at Mono Lake (1981–present) and other inland lakes on a broad range of studies concerning grebe natural history, physiology, migration, and mortality in the nonbreeding season.

A major goal of our studies was to document the number and schedule of grebes at the Sea. We used several methods to assess population size. Shore-based observations along the entire periphery of the Sea provide an overview of distributional patterns, and because grebes tend to be concentrated near shore in most seasons they can provide an index to population size. Although some proportion of birds in mid-Sea will be undetectable, omissions are unlikely to be important, except in spring, when large numbers assemble well offshore in preparation for migration.

To further study migration phenology and population size, McKernan conducted aerial surveys of the entire Sea, which were designed to encompass most of the fall , winter, and spring migration periods. Conducted intermittently, these surveys span the period 1982–83 to the fall of 1999, but are most complete for the 1990s. On each survey, data were gathered by two observers, usually from a Cessna 172 airplane flying at speeds of 55–65 mph and 100–200 m above the Sea. Although the Sea is large (roughly 56 × 16 km), it is also narrow, so that the majority of the surface can be scrutinized using three transect routes: (1) counterclockwise around the entire perimeter, starting at the north end, with the plane maintaining 1–2 km from shore; (2) north to south along the middle of the Sea, from the Whitewater River Delta to the mouth of the New River; and (3) south–north transect starting 3 km west of the New River ending 3 km west of the Whitewater River Delta. As needed, depending on the distribution and clumping patterns of migrants, surveys might be expanded to include replicate samples or supplement coverage. Flights were made at an altitude that was low enough to detect birds. Although these flights also elicited some diving behavior, it was largely restricted to birds seen directly under the flight path and did not contribute significantly to undercounting (Boyd & Jehl, 1998). On several occasions when grebes were concentrated offshore, McKernan used a small boat to access flocks and obtain an addi-

Figure 1. Huge numbers of Eared Grebes at the Salton Sea, February 1992.

tional estimate. In addition, we have each made dozens of trips to the Sea in November–April for various grebe-related studies.

Estimating numbers in flocks that may comprise thousands of birds is a major problem (Jehl, 1999). We think that our counts, including any errors resulting form diving birds, are probably accurate to within 30% when the population was small (<500 000) and dispersed, but could be greater during population highs and when birds were clumped. Although our independent estimates of flock size were similar, we had no ways of confirming accuracy. Aerial photography has been successful elsewhere (Boyd & Jehl, 1998), but is impractical at the Sea because images made from the required altitudes would not allow grebes to be differentiated from other waterbirds, especially Ruddy Ducks [*Oxyura jamaicensis* (Gmelin)]. However, because McKernan directed and took part in all the flights, we consider the data to be internally consistent and sufficiently accurate to show major trends.

We obtained data on the numbers of birds observed on Christmas Bird Counts from *Audubon Field Notes* (and its reincarnations *American Birds, Field Notes*), which should be consulted for precise locations. We used standard behavioral observations to study foraging. We obtained data on food habits from direct examination of the stomach contents of 40 grebes collected in conjunction with migration and disease studies, and of perhaps 100 more found freshly dead. While dead birds are usually of little value, the feather bolus in the gizzard of grebes entraps indigestible items and provides data on some kinds of prey that may have been taken days earlier.

We monitored Mono Lake to determine when grebes were leaving (Jehl, 1988 and unpubl.), and compared numbers and schedules of departing birds with arrival data from the Salton Sea. In 1982 and 1987–92, the Utah Division of Wildlife Resources carried out similar studies at Great Salt Lake (D. Paul, pers. comm.).

Results

A brief history

The Salton Sea was created in 1905–1907 and the Eared Grebe was one of the first species to be noted.

Joseph Grinnell (1908) saw several hundred that he considered transients (his description of small flocks is typical of birds in passage) on a "voyage" in mid-April 1908. Shortly thereafter, A. J. van Rossem (1911) spent eight weeks collecting around the Sea (1 December 1910–1 January 1911, 18–31 March 1911), which he thought was "rapidly drying up". Typical of collectors in that era, van Rossem was primarily interested in geographic variation in landbirds. Although he did visit the Sea itself, his sole mention of Eared Grebes was of "several individuals and sometimes small flocks from three to seven frequently seen..." in late March. Because March–April is the peak of spring migration, both Grinnell's and van Rosssem's findings indicate that grebes had no great affinity for the Sea in its early years. Neither Bent (1919) nor Dawson (1923) mention grebes there, and Grinnell & Miller's (1944) only mention was in passing and to establish this as a low altitude locality (−250 feet below sea level). By the late 1960s, however, McCaskie (1970) reported that Eared Grebes were "very abundant throughout the year". Subsequent authors (e.g. Small, 1974; Cogswell, 1977; Garrett & Dunn, 1981) also noted the species' general abundance, though almost casually and with little authority. But that is hardly surprising, as so little was known about biology in the nonbreeding season before the early 1980s, when studies were initiated at fall staging areas (e.g. Winkler & Cooper, 1986; Jehl, 1988).

Christmas Bird Counts

Evidence on when significant numbers of grebes began to use the Sea must be inferred from Christmas Bird Counts, which were started at the north end of the Sea in 1929 and at south end in 1940 (Fig. 2). That record is incomplete and difficult to evaluate because census localities were inconsistent prior to 1970, errors in estimating large numbers of birds are inevitable and, most importantly, phenology of migration is not constant; in some years grebes are still at staging areas at count time, whereas in others they left the lakes weeks earlier (Table 1), in which case they could have stayed at the Sea or continued south into Mexico. Nevertheless, those data and McCaskie's observations (1970) suggest that the large (>10 000) wintering populations became established in the 1960s. Why did this buildup occur so slowly, if the Sea had attained ocean salinity as early as 1920 (Fig. 2)? The most likely explanation is that its attraction for grebes awaited the development of appropriate food resources. This presumably occurred subsequent to 1935, when pile worms (*Neanthes succinea*, Frey and Leukart), the grebes' major current prey (see below), were first reported (evidently introduced in 1930; Carpelan & Linsley, 1961).

Population size, phenology of migration at the Salton Sea

When grebes leave staging lakes in fall, they make an overnight flight to the Salton Sea or Gulf of California (Jehl, 1988, 1993, 1997, 1999). Emigration takes place after food becomes too scarce to permit profitable foraging, and has occurred as early as late October or as late as early February (e.g. Jehl, 1988 and unpubl.; Table 1). In most years the number of potential emigrants from Mono Lake is probably 1–1.5 million (Boyd & Jehl, 1998; J. Jehl, S. Boyd, D. Paul & D. Anderson, unpubl.), and similar numbers are expected at Great Salt Lake (Jehl et al., 1999). Censuses at the Sea shortly after major departures from staging lakes have consistently failed to encounter anywhere near the number of potential immigrants that would be expected. For example (Table 1): in 1986 at least 745 000 grebes (and probably many more) left Mono Lake by the first days of November; on 11 November land-based observations around the entire Sea, conducted under ideal conditions, indicated that there were no more than 60 000 present. In 1999, over 2.5 million birds had left Mono Lake and Great Salt Lake by 8–10 December; a flight over the Sea on 17 December encountered 275 000. The only reasonable conclusion is that most southbound migrants bypass the Sea in favor of other wintering areas farther south (Jehl, 1988).

This is further indicated by aerial census data that establish general patterns of abundance. Thus (Fig. 3), numbers are trivial (usually <1000) until November–December, when grebes begin to leave staging areas. Late December counts average around 100 000, which is in accord with general Christmas Count estimates, once allowance is made for differences in the size of the areas surveyed. The population then increases quickly, and by February–March upwards of 1 million might be present. This influx must be from Mexico, as there is no other source for migrants at that season. Numbers subsequently drop off rapidly as the migrants move northward, with emigration from the Sea corresponding to the arrival of spring migrants at Great Salt Lake and the interior of the Great Basin (D. Paul, pers. comm.). By mid-April, nearly all migrants are gone. Lingering birds (a few of which summer) are rarely

Number of Grebes

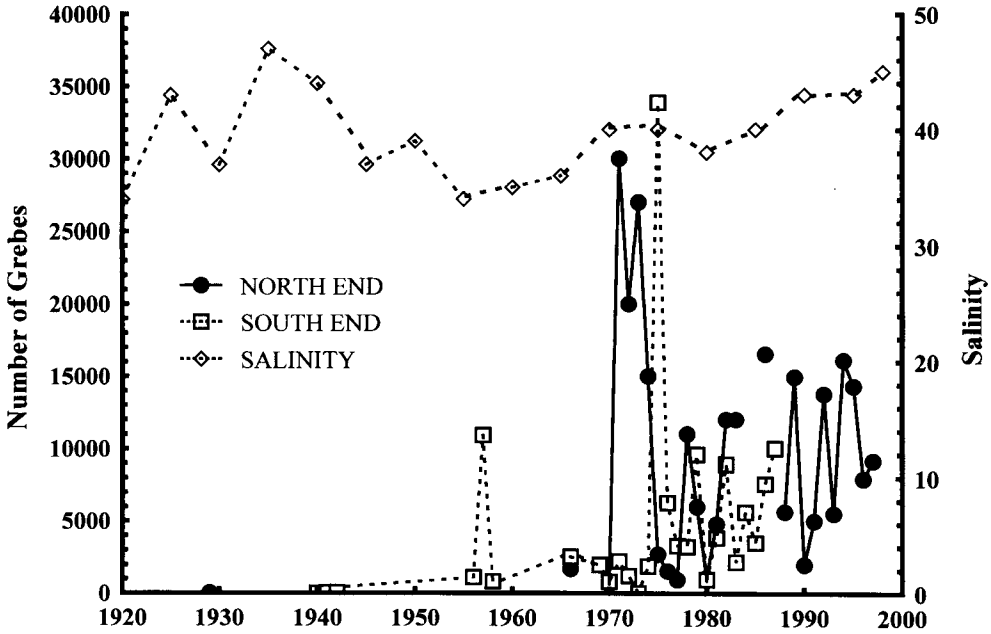


Figure 2. Salinity and Christmas Count data for Eared Grebes at the Salton Sea.

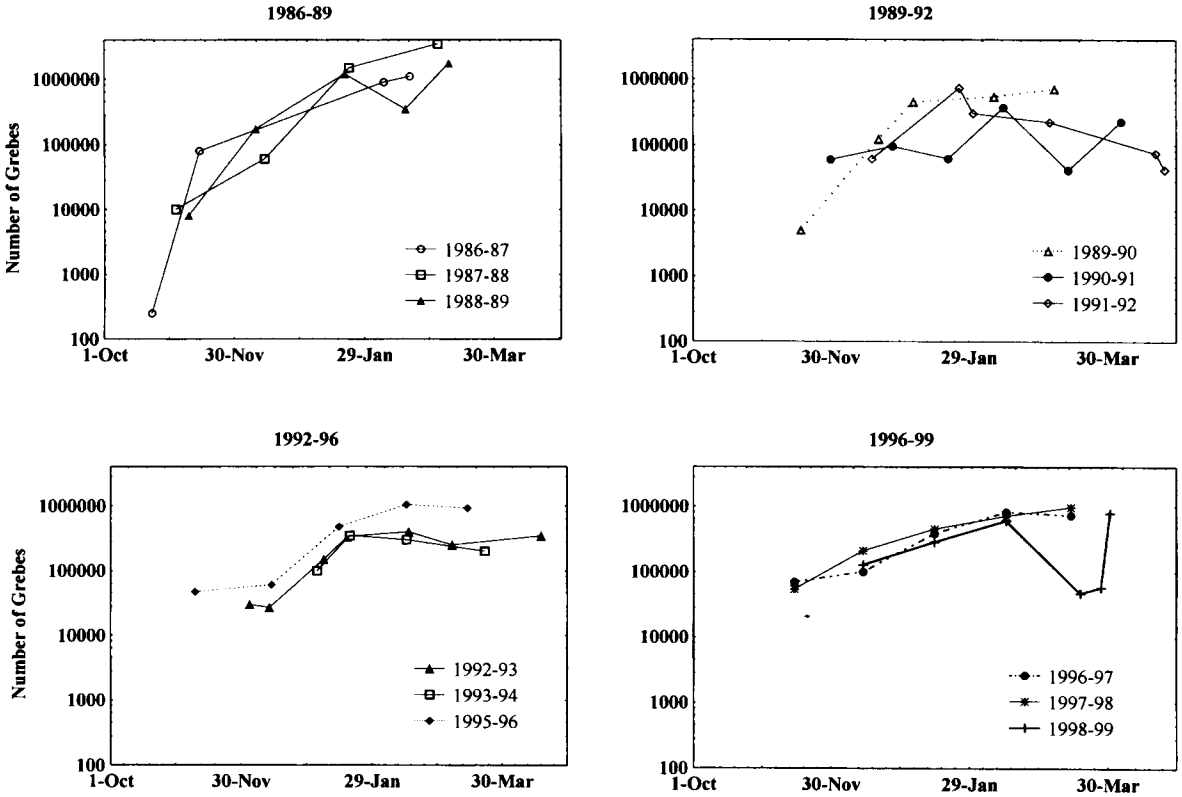


Figure 3. Aerial survey estimates of Eared Grebes at the Salton Sea.

Table 1. Estimates (in 1000s) of Eared Grebes at the Salton Sea based on aerial surveys. The dark bar indicates the departure periods of birds staging at Mono Lake, CA

Year	1982–83	1983–84	1986–87	1987–88	1988–89	1989–90	1990–91	1991–92	1992–93	1993–94	1995–96	1996–97	1997–98	1998–99	1999–00
Month															
Oct			(24)[a] 0.25												
Nov			(15) 80	(20) 10	(12) 8	(18) 5					(10) 47.3	(20) 71.1	(28) 55		(19) 173
Dec	250	310		(15) 60	(10) 175	(22) 125	1 (60) (28) 96	(19) 61	(5) 20–40 (14) 27		(14) 61	(10) 100	(27) 212	(15) 128	(17) 322
Jan	755	660		(23) 1500	(21) 1200	(6) 450	(21) 62	(26) 740	(8) 100–200 (19) 338	(5) 100 (16–20) 300–400	(22) 479	(28) 389	(19) 458	(24) 290	
Feb			(8) 900		(18) 325	(10) 550	(14) 375	(1) 305	(16) 400	(15) 300	(27) 1050	(22) 829	(25) 721	(10 611	
Mar			(20) 1100	(5) 3500	(11) 1750	(8) 715	(14) 41.5	(6) 175–250 (21) <80	(8) 250 (18) 346	(23) 200	(15) 920	(10) 740	(14) 984	(19) 47.5 (28) 58.4	
Apr							(6) 229	(25) 42						(1) >800[b]	

[a]Actual dates in parentheses.
[b]Shore based observation at northend only (JRJ).

in breeding plumage and are probably first-year birds or nonbreeders, which begin to arrive at Mono Lake in April–May and remain through the following fall (Jehl, 1988 and unpubl.).

In some years, however, we have observed different patterns, which are probably real because population estimates from successive censuses are too different to result solely from counting errors. We can only guess at their causes. In 1988–89 for example, the population dropped from an estimated 1.2 million in January to 325 000 in February, the decline coinciding with a large dieoff. It then rebounded to 1.75 million in March. (No similar pattern was detected in the 1991–92 die-off.) In 1990–91, the population dropped by more than half between February and March, then increased in April. A similar pattern appeared in 1998-99, when February numbers of 611 000 dropped to about 50 000 in March, then increased to >800 000 in early April. These examples probably signal turnover and the northward departure of some birds in early March, to be replaced later in the month or early April by arrivals from the Gulf.

Food and foraging

Eared Grebes feed on a variety of prey but specialize on invertebrates, which they may probe or glean from the substrate or capture as free-swimming prey in the water column (Jehl, 1988; Cullen et al., 1999). No exhaustive studies of food habits at the Sea have been conducted. Nevertheless, stomach contents obtained incidental to other work and bolstered by behavioral and distributional information (below) show that from January to April, pile worms (*Neanthes succinea*) comprise >95% of the diet, the remainder being small amphipods and fish, or occasionally corixids (for birds feeding in lagoonal situations). Stomach analyses are inherently skewed in favor of indigestible matter, and bias is extreme in grebes because the feather bolus in their gizzard entraps and retains hard parts. Even so, the importance of pile worms can hardly be exaggerated. These worms occur in tremendous numbers (Carpelan & Lindsey, 1961, Detwiler et al., 2002) and gizzards from the Sea are invariably packed with hundreds or thousands of worm "teeth". Only rarely does one encounter fresh tissue of any kind anywhere the digestive tract.

The distribution of grebes on the Sea strongly parallels that of the pile worms. That is, they occur mostly in relatively shallow areas within 1 km (200–300 m) of the beach where the substrate consists of organic mud or, along the shoreline, algae-covered rocks (Detwiler et al., 2002; D. Dexter, pers. comm; pers. obs.). The turbidity of the water makes it impossible to observe how grebes catch food, and in some areas must restrict their ability to hunt visually. Although they dive and presumably, as elsewhere, obtain most of their food during the day, some diving and surface-feeding also takes place after dark (JJ), at least in some seasons. We infer that nocturnal feeding is associated with worms becoming available in the water column, when they leave the mud or rock substrates to reproduce (D. Dexter, pers. comm.). Nocturnal feeding is interesting because it has not been observed at the fall staging lakes (Winkler & Cooper, 1986; Jehl, 1988; Cullen et al., 1999). In periods of apparent food scarcity, we have also seen grebes tipping up like dabbling ducks and probing into the mud like sandpipers.

Any grebes foraging well offshore are probably taking free-swimming prey, because worms are absent from the anoxic muds in the deep water zones. In some oceanic environments, Eared Grebes may engage in group foraging, presumably for free-swimming or schooling prey (Cullen et al., 1999). The fact that we have never seen this behavior at the Salton Sea is further suggestive of their reliance on pile worms.

Behavior

During their sojourn at the Sea, grebes do little but swim, dive, preen, sleep, and increase their body mass by about 100 g (ca. 30%) to accumulate the fat needed for the next phase of the migration. Except for those that have just arrived or are about to leave, they do not fly. In fact, adjustments in body composition in the staging or non-migratory periods make them incapable of flight for several weeks or more (Jehl, 1997).

As the time for northward departure nears, hordes of grebes tend to accumulate along the north shore of the Sea, at the same time that huge flocks form offshore. The groups appear to be on quite different schedules and in different physiological condition. The former dive and feed actively, whereas the latter are quiescent and probably have stopped feeding and are preparing to leave (Jehl, 1997). The preparation involves further changes in body composition, including rebuilding of flight muscles that have been allowed to atrophy. It is signaled by wing-flapping exercises, and birds (often in small groups) racing across the surface in short practice flights are conspicuous in the March emigration period (Fig. 4).

Figure 4. Eared Grebes engaging in practice flights before departing Salton Sea in March.

Mortality

In some years, the fall population of Eared Grebes in North America has reached nearly 4 million birds (Boyd & Jehl, 1998; unpubl.). Considering that there are several estimates of 1–3 million at the Sea in spring – and those figures do not include migrants that had already passed through or had yet to arrive it follows that nearly all of the North American population passes through at that season.

Recent dieoffs of grebes and other waterbirds at the Sea have elicited much attention. One in January–March 1992 was estimated by the U.S. Fish and Wildlife Service to have involved an estimated 150 000 grebes; another perhaps of similar magnitude occurred in January–March 1989 (Jehl, 1996). While these dieoffs are unlikely to have had significant consequences for the population (they would have involved 3–5% of the North American population), they are worrisome because so many grebes pass through, and because most deaths remain undiagnosed, despite much study. The prevailing assumption is that the problem is endemic to the Sea. Perhaps so, but in view of the species' ability to fly hundreds of miles overnight, the possibility that disease (if that is the cause) could be imported cannot yet be excluded. "Caught there, or brought there," that is the question. And to resolve it requires detailed knowledge of basic natural history, and especially migration routes, timing, and stopover points discussed above.

Population studies

Appraising the population status of birds that congregate at restricted habitats for long periods of time would seem to be relatively easy (but see Jehl, 1999), and the Salton Sea would seem to be the prime site for surveying Eared Grebes, because so large a fraction of the population occurs there. In practice, however, there are many difficulties, the most important being our inability to count tens to hundreds of thousands of birds with measurable precision. At the Sea this is not possible either from shore-based or aerial estimates surveys (can anyone really tell the difference between, say, 400 000 and 600 000 birds?) or, as noted above, by using aerial photography. A second challenge is that the spring movement is protracted, and the rate of turnover is unknown (and probably unknowable). It is even possible that in some years birds may be moving south while others are moving north. Finally,

migration schedules vary from year to year. Lacking information about the size and departure times of populations staging at Mono Lake, Great Salt Lake, and the Gulf of California, it would be impossible to determine the significance of the numbers at the Sea, and that would be true even if precise counts were forthcoming. It follows that current procedures – whether based on Christmas Counts or other surveys – are not useful for addressing year-to-year trends. If understanding trends in the North American population is the goal, efforts should be directed to Mono Lake in mid-late October, where the entire lake surface can be surveyed in few hours and photocensusing techniques can be applied. Because Eared Grebes make up >98% of the avifauna at that season, the population size can be determined with good accuracy (Boyd & Jehl, 1998). A further advantage is that the phenology of fall migration appears to be consistent (Jehl, 1988; Jehl & Johansson, 2002); because staging birds remain into late fall problems of turnover are insignificant. Accordingly, precise data can be generated from data gathered at the same time in different years (Boyd & Jehl, 1998; Jehl & Johansson, 2002), and this will allow for annual comparisons and trend analyses.

Acknowledgements

Many people helped us in gathering information about grebes, or in expanding our knowledge of the ecology of the Salton Sea. These include C. Bloom, M. Hunnicutt, W. Radke, D. Dexter, P. Detwiler, T. Johnson, M. Crook, D. Paul, S. Bond, S. Hurlburt, T. Evans, M. McCrary, K. Molina and W. Wagner. H. Ellis and G. McCaskie kindly commented on manuscript. Jehl's work was an outgrowth of studies on saline lakes and was supported, in part, by the Los Angeles, Department of Water and Power. Point Reyes Bird Observatory funded several of the 1999 flights. Additional support to McKernan was provided by Southern California Edison and the San Bernaradino County Museum Association.

References

Bent, A. C., 1919. Life histories of North American birds. U.S. Natl. Mus. Bull: 107 pp.

Boyd, W. S. & J. R. Jehl, Jr., 1998. Estimating the abundance of Eared Grebes on Mono Lake, California, by aerial photography. Colonial Waterbirds 21: 236–241.

Carmona, R. & G. D. Danemann, 1998. Distribución espaciotemporal de aves in la salina de Guerrero Negro, Baja California Sur, México. Ciencias Marinas 24: 389–408.

Carpelan, L. H. & R. H. Linsley, 1961. The pile worm *Neanthes succinea* (Frey and Leukart). In Walker, B. W. (ed.), The Ecology of the Salton Sea, California, in Relation to the Sportfishery. Calif. Dept. of Fish and Game, Fish Bull. No. 113: 63–76.

Cohen, M. J., J. I. Morrison & E. P Glenn, 1999. Haven or Hazard: the ecology and future of the Salton Sea. Pacific Inst. for Studies in Development, Environment and Security, Oakland, CA. 63 p.

Cogswell, H., 1977. Water birds of California. U. Calif. Press, Berkeley, Los Angeles, London.

Cullen, S. A., J. R. Jehl, Jr. & G. Nuechterlein, 1999. Eared Grebe (*Podiceps nigricollis*). In Poole, A. & F. Gill (eds), The Birds of North America, No. 433 (A. Poole and F. Gill, eds.). The Birds of North America, Inc., Philadelphia, PA.

Detwiler, P. M., M. F. Coe & D. M. Dexter, 2002. The benthic invertebrates of the Salton Sea: distribution and seasonal dynamics. Hydrobiologia 473/Dev. Hydrobiol. 161: 139–160.

Dawson, W. L., 1923. The birds of California. South Moulton, San Diego, CA.

Garrett, K. & J. Dunn, 1981. Birds of Southern California. Artisan Press, Los Angeles, CA.

Grinnell, J., 1908. Birds of a voyage on the Salton Sea. Condor 10: 185–191.

Grinnell, J. & A. H. Miller, 1944. The distribution of the birds of California. Pacific Coast Avifauna No. 27.

Jehl, J. R., Jr., 1988. Biology of the Eared Grebe and Wilson's Phalarope in the nonbreeding season: a study of adaptations to saline lakes. Stud. Avian Biol: No. 12.

Jehl, J. R., Jr., 1993. Observations on the fall migration of Eared Grebes, based on the evidence from a mass downing in Utah. Condor 95: 470–473.

Jehl, J. R., Jr., 1996. Mass mortality events of Eared Grebes in North America. J. Field Ornithol. 67: 471–476.

Jehl. J. R., Jr., 1997. Cyclical changes in body composition in the annual cycle and migration of the Eared Grebe *Podiceps nigricollis*. J. Avian Biol. 28: 132–142.

Jehl, J. R., Jr., 1999. Population studies of Wilson's Phalaropes at Fall staging areas, 1980–1997: A challenge for monitoring. Waterbirds 22: 37–46.

Jehl, J. R., Jr. & C. Johansson, 2002. The autumnal migration of Eared Grebes through southwestern Wyoming: a key to assessing the size of the North American population. Western North American Naturalist, In press.

Jehl, J. R., Jr., A. E. Henry & S. I. Bond, 1999. Flying the gantlet: population characteristics, flight energetics, sampling bias, and migration routes of Eared Grebes downed in the Utah desert. Auk 116: 178–183.

McCaskie, G., 1970. Shorebird and waterbird use of the Salton Sea. Calif. Fish and Game 56: 87–95.

Small, A., 1974. The birds of California. Winchester Press, New York.

Tershy, B. E. Van Gelder & D. Breese, 1993. Relative abundance and seasonal distribution of seabirds in the Canal de Ballenas, Gulf of California. Condor 95: 458–464.

Van Rossem, A. J., 1911. Winter birds of the Salton Sea region. Condor 13: 129–137.

Walker, B. (ed.), 1961. The ecology of the Salton Sea, California, in relation to the Sportfishery. Calif. Dept. of Fish and Game, Fish Bull: 113 pp.

Waters, M., 1981. Lake Holocene lacustrine chronology and archaeology of Ancient Lake Cahuilla, California. M. S. Thesis, Univ. Arizona, Dept. of Geosciences.

Winkler, D. W. & S. D. Cooper, 1986. Ecology of migrant Black-necked Grebes *Podiceps nigricollis* at Mono Lake, California. Ibis 128: 483–491.

Hydrobiologia **473:** 255–274, 2002.
D.A. Barnum, J.F. Elder, D. Stephens & M. Friend (eds), The Salton Sea.
© 2002 *Kluwer Academic Publishers. Printed in the Netherlands.*

The Salton Sea as critical habitat to migratory and resident waterbirds

W. David Shuford[1], Nils Warnock[1], Kathy C. Molina[1,2] & Kenneth K. Sturm[3,4]
[1]*Point Reyes Bird Observatory, 4990 Shoreline Highway, Stinson Beach, CA 94970, U.S.A.*
[2]*Current address: Section of Ornithology, Natural History Museum of Los Angeles County, 900 Exposition Blvd., Los Angeles, CA 90007, U.S.A.*
[3] *Sonny Bono Salton Sea National Wildlife Refuge, 906 West Sinclair Road, Calipatria, CA 92233, U.S.A.*
[4]*Current address: Canaan Valley National Wildlife Refuge, HC 70, Box 200, Davis, WV 26260, U.S.A.*

Key words: conservation concerns, nesting colonies, migratory stopover, Pacific Flyway, wetland connectivity, wintering area

Abstract

Concern about the Salton Sea ecosystem, based on potential impacts of increasing salinity, contaminants, disease outbreaks, and large die-offs of birds, is heightened because of tremendous prior loss and degradation of wetland habitat in western North America. In 1999, we used a variety of survey methods to describe patterns of abundance of birds at the Salton Sea and in adjacent habitats. Our results further documented the great importance of the Salton Sea within the Pacific Flyway to wintering, migratory, and breeding waterbirds. Exclusive of Eared Grebes, we estimated about 187 000 individual waterbirds at the Salton Sea in January, 88 000 in April, 170 000 in August, and 261 000 in November. Additional surveys of Eared Grebes in November and December suggested the total population of all waterbirds was about 434 000 to 583 000 in those months, respectively. We also documented breeding by about 14 000 pairs of colonial waterbirds. Waterbirds were particularly concentrated along the northern, southwestern, southern, and southeastern shorelines and river deltas. By contrast, some species of wading birds (Cattle Egret, White-faced Ibis, Sandhill Crane) and shorebirds (Mountain Plover, Whimbrel, Long-billed Curlew) were much more numerous in agricultural fields of the Imperial Valley than in wetland habitats at the Sea. Various studies indicate the Salton Sea is of regional or national importance to pelicans and cormorants, wading birds, waterfowl, shorebirds, and gulls and terns. Important taxa are the Eared Grebe, American White Pelican, Double-crested Cormorant, Cattle Egret, White-faced Ibis, Ruddy Duck, Yuma Clapper Rail, Snowy Plover, Mountain Plover, Gull-billed, Caspian, and Black terns, and Black Skimmer. Proposed restoration projects should be carefully assessed to ensure they do not have unintended impacts and are not placed where large numbers of breeding, roosting, or foraging birds concentrate. Similarly, plans to enhance opportunities for recreation or commerce at the Sea should aim to avoid or minimize disturbance to birds. Future research should focus on filling gaps in knowledge needed to effectively conserve birds at the Salton Sea.

Introduction

The Salton Sea, as an integral part of the Río Colorado Delta region, supports large numbers and a great variety of avian species and is one of the most important wetlands to birds in North America (e.g. Jehl, 1994). A number of bird species have populations in the Salton Sea area that are of regional or continental importance in size or are highly vulnerable. Also, the Salton Sea serves as a vital migratory stopover and wintering area for species that breed elsewhere in western North America. Because of this connectivity, the health of populations of many species of waterbirds is linked to that of the Salton Sea. Great concern recently has been expressed about the future of the Salton Sea ecosystem because of historically increasing salinity, contamination from agricultural and urban sources, disease outbreaks, and large die-offs of waterbirds (e.g. USFWS, 1997; Tetra Tech, 2000). This concern is heightened by the tremendous prior loss and degradation of wetland habitat in western North America (Dahl et al., 1997) and ongoing threats to other large saline lakes in the region (Jehl, 1994).

Although key previous information on the avifauna of the Salton Sea has been summarized (Shuford et al., 1999; Patten et al., in press), various proposals to deal with problems of ecosystem health are hampered by the limited quantitative data available on the current status and ecology of birds using this area. As part of a multi-disciplinary reconnaissance survey coordinated by the Salton Sea Science Subcommittee (papers this volume), we conducted a year-long study to document the abundance, distribution, annual phenology, and broadscale habitat associations of birds using the Salton Sea and adjacent habitats. Here we report the patterns of abundance of waterbirds at the Salton Sea in 1999, compare them with prior data, and discuss both the regional and continental importance of bird populations at the Salton Sea. We also interpret the relevance of our findings to plans for restoration at the Sea and make recommendations for further research.

Study area and methods

The study area was the saline Salton Sea and adjacent areas in Riverside and Imperial counties, California, U.S.A. Aspects of the physical characteristics, limnology, and aquatic life of the Sea are described elsewhere in this volume. Habitats surveyed included the shoreline and open water of the Salton Sea; adjacent fresh or brackish marshes and freshwater impoundments; and isolated freshwater marshes, lakes, ponds, and the extensive irrigated agricultural fields of the Imperial Valley (Figs 1–3). To obtain data on bird use of this area, we used a suite of survey methods and protocols described below. Scientific names of all birds recorded on surveys are listed in Table 1.

Comprehensive waterbird surveys

We used comprehensive surveys to document the overall abundance, distribution, and broadscale habitat associations of most waterbirds using the Salton Sea and nearby wetlands and marshes. These surveys were conducted over four short periods during mid-winter (22 January–5 February), spring migration (17–18 April), fall migration (13–16 August), and early winter (11–15 November). In contrast to the other three, the 22 January to 5 February survey involved two separate surveys of the Sea, one to cover shorebirds (22–30 [mostly 22–27] January) and another to cover all other waterbirds (29 January–5 February). On each census, a team of observers surveyed the entire Salton Sea shoreline and open water zone within 0.5 km of shore, adjacent marshes and impoundments, and various sites in the Imperial Valley, including the Finney-Ramer Unit of Imperial Wildlife Area (WA) south of Calipatria and private duck clubs near Brawley. For a detailed description of the areas and area boundaries (and additional maps), see Shuford et al. (2000). The number of observers (project staff and skilled volunteers) ranged from 7 to 19 per survey. Observers counted birds with the aid of binoculars and spotting scopes, generally traveling by vehicle or on foot. During summer months, surveys of the shoreline from Iberia Wash at Salton City south to, and including, the New River (Fig. 1) were accomplished with the aid of an airboat to reduce the risk of heat exhaustion while covering this long, isolated stretch.

On these surveys, we recorded all shorebirds and other waterbirds except Eared Grebes, American White Pelicans, Brown Pelicans, Double-crested Cormorants, American Coots, and waterfowl, which were counted on aerial surveys as described below. On the January comprehensive survey, Western and Clark's grebes were not surveyed in all areas, and the Pied-billed Grebe and all rails, gulls, and terns were not surveyed in areas 3–5.

We instructed observers, when possible, to identify all birds to species. Groups of unidentified waterbirds fell mostly into seven categories: large grebes of the genus *Aechmophorus*, either Western or Clark's grebes; white egrets, mostly Snowy and Cattle egrets; yellowlegs, either Greater or Lesser yellowlegs; small sandpipers of the genus *Calidris*, primarily Western Sandpipers, Least Sandpipers, and Dunlins; dowitchers, either Short-billed or (primarily) Long-billed dowitchers; phalaropes, either Wilson's or Red-necked phalaropes; and various gulls of the genus *Larus*. For analytical purposes we grouped all dowitchers as dowitcher spp. owing to the difficulty of identifying most individuals to species. We assigned other unidentified waterbirds to species using methods described in Page et al. (1999), leaving some in unidentified categories when the ratio of unidentified–identified was high.

Aerial surveys for various waterbirds

Pelicans and cormorants

Mostly in tandem with photographic surveys of nesting colonies, K. Molina and D. Shuford conducted aerial surveys of American White and Brown pelicans and Double-crested Cormorants around the periphery

Table 1. List of 107 species of native waterbirds recorded on surveys of the Salton Sea, California, in 1999. Taxonomy follows AOU (1998)

Common Loon *Gavia immer*
Pied-billed Grebe *Podilymbus podiceps*
Eared Grebe *Podiceps nigricollis*
Western Grebe *Aechmophorus occidentalis*
Clark's Grebe *Aechmophorus clarkii*
Black Storm-Petrel *Oceanodroma melania*
American White Pelican *Pelecanus erythrorhynchos*
Brown Pelican *Pelecanus occidentalis*
Double-crested Cormorant *Phalacrocorax auritus*
American Bittern *Botaurus lentiginosus*
Least Bittern *Ixobrychus exilis*
Great Blue Heron *Ardea herodias*
Great Egret *Ardea alba*
Snowy Egret *Egretta thula*
Tricolored Heron *Egretta tricolor*
Cattle Egret *Bubulcus ibis*
Green Heron *Butorides virescens*
Black-crowned Night-Heron *Nycticorax nycticorax*
White-faced Ibis *Plegadis chihi*
Wood Stork *Mycteria americana*
Fulvous Whistling-Duck *Dendrocygna bicolor*
Greater White-fronted Goose *Anser albifrons*
Snow Goose *Chen caerulescens*
Ross's Goose *Chen rossii*
Canada Goose *Branta canadensis*
Brant *Branta bernicla*
Wood Duck *Aix sponsa*
Gadwall *Anas strepera*
American Wigeon *Anas americana*
Mallard *Anas platyrhynchos*
Blue-winged Teal *Anas discors*
Cinnamon Teal *Anas cyanoptera*
Northern Shoveler *Anas clypeata*
Northern Pintail *Anas acuta*
Green-winged Teal *Anas crecca*
Canvasback *Aythya valisineria*
Redhead *Aythya americana*
Ring-necked Duck *Aythya collaris*
Greater Scaup *Aythya marila*
Lesser Scaup *Aythya affinis*
Surf Scoter *Melanitta perspicillata*
White-winged Scoter *Melanitta fusca*
Black Scoter *Melanitta nigra*
Bufflehead *Bucephala albeola*
Common Goldeneye *Bucephala clangula*
Common Merganser *Mergus merganser*
Red-breasted Merganser *Mergus serrator*
Ruddy Duck *Oxyura jamaicensis*
Yuma Clapper Rail *Rallus longirostris yumanensis*
Virginia Rail *Rallus limicola*
Sora *Porzana carolina*
Common Moorhen *Gallinula chloropus*
American Coot *Fulica americana*
Sandhill Crane *Grus canadensis*
Pacific Golden-Plover *Pluvialis fulva*
Snowy Plover *Charadrius alexandrinus*
Semipalmated Plover *Charadrius semipalmatus*
Killdeer *Charadrius vociferus*
Mountain Plover *Charadrius montanus*
Black-necked Stilt *Himantopus mexicanus*
American Avocet *Recurvirostra americana*
Greater Yellowlegs *Tringa melanoleuca*
Lesser Yellowlegs *Tringa flavipes*
Solitary Sandpiper *Tringa solitaria*
Willet *Catoptrophorus semipalmatus*
Spotted Sandpiper *Actitis macularia*
Whimbrel *Numenius phaeopus*
Long-billed Curlew *Numenius americanus*
Marbled Godwit *Limosa fedoa*
Ruddy Turnstone *Arenaria interpres*
Black Turnstone *Arenaria melanocephala*
Red Knot *Calidris canutus*
Sanderling *Calidris alba*
Western Sandpiper *Calidris mauri*
Least Sandpiper *Calidris minutilla*
Baird's Sandpiper *Calidris bairdii*
Dunlin *Calidris alpina*
Stilt Sandpiper *Calidris himantopus*
Ruff *Philomachus pugnax*
Short-billed Dowitcher *Limnodromus griseus*
Long-billed Dowitcher *Limnodromus scolopaceus*
Common Snipe *Gallinago gallinago*
Wilson's Phalarope *Phalaropus tricolor*
Red-necked Phalarope *Phalaropus lobatus*
Red Phalarope *Phalaropus fulicaria*
Laughing Gull *Larus atricilla*
Franklin's Gull *Larus pipixcan*
Bonaparte's Gull *Larus philadelphia*
Heermann's Gull *Larus heermanni*
Mew Gull *Larus canus*
Ring-billed Gull *Larus delawarensis*
California Gull *Larus californicus*
Herring Gull *Larus argentatus*
Thayer's Gull *Larus thayeri*
Lesser Black-backed Gull *Larus fuscus*
Yellow-footed Gull *Larus livens*
Western Gull *Larus occidentalis*
Glaucous-winged Gull *Larus glaucescens*
Gull-billed Tern *Sterna nilotica*
Caspian Tern *Sterna caspia*
Common Tern *Sterna hirundo*
Forster's Tern *Sterna forsteri*
Least Tern *Sterna antillarum*
Black Tern *Chlidonias niger*
Black Skimmer *Rynchops niger*
American Golden-Plover *Pluvialis dominica*
Black-bellied Plover *Pluvialis squatarola*

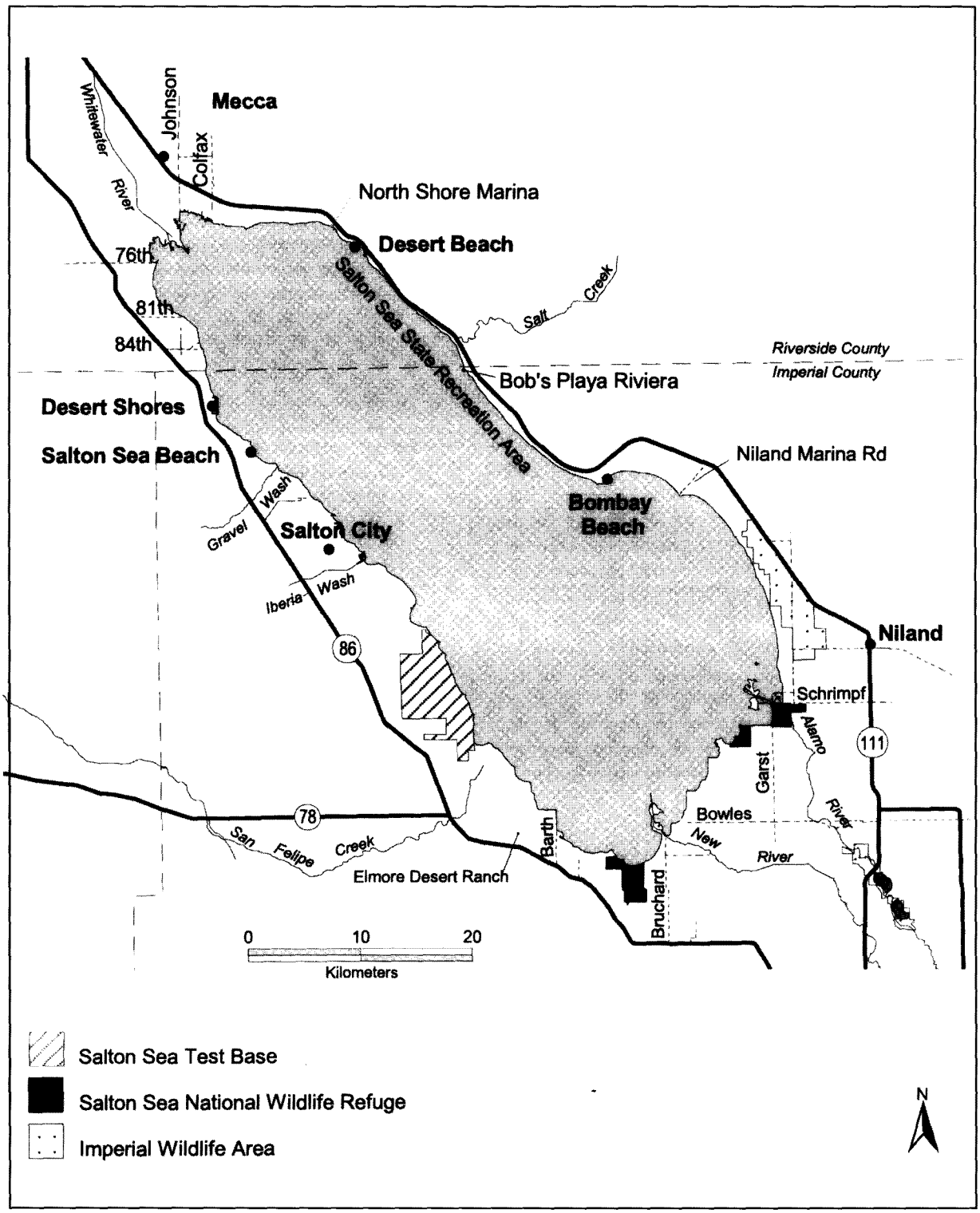


Figure 1. Overview map of the Salton Sea, California, and vicinity.

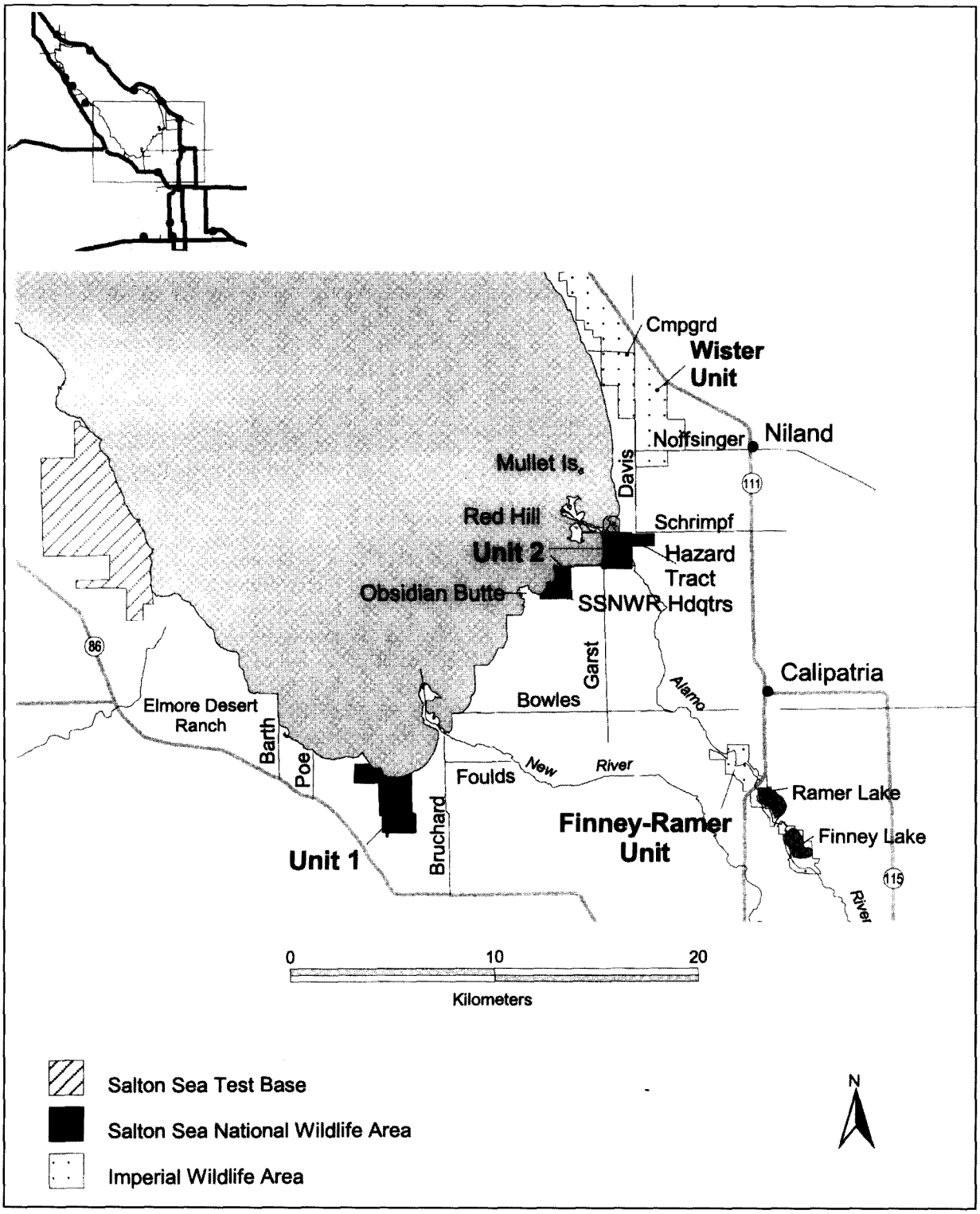


Figure 2. Map detail of the south end of the Salton Sea and adjacent portion of the Imperial Valley, California.

of the Salton Sea from a fixed-wing Cessna aircraft. We began all surveys at the southern shoreline at the end of Garst Road and conducted one or two counterclockwise circumnavigations of the Sea (Figs 1 and 2). We maintained a course parallel to and about 0.5 km from the shoreline, flying at heights from 60 to 90 m and at speeds of 70–100 knots. All individuals of the above species were counted off both sides of the plane. In addition, we also counted birds while flying multiple parallel transects across various pond complexes adjacent to the Sea. Aerial survey dates were: 28 January, 12 February, 5 March, 16 April, 28 May, and 16 August.

Eared Grebes, Aechmophorus *Grebes, and Ruddy Ducks*

We initially attempted to count Eared Grebes using new aerial photographic techniques pioneered at Mono Lake, California (Boyd & Jehl, 1998), but abandoned that effort because of an inability to distinguish on photographs among Eared Grebes and relatively large numbers of Ruddy Ducks, other waterfowl, and, particularly, dead or dying fish floating on the Sea's surface. Instead, R. McKernan and K. Molina conducted aerial surveys for this and other species on 19 March, 28 March, 29 November, and 17 December. They counted birds from a Cessna 172 high-wing airplane flying at speeds of 70–90 knots at altitudes varying between 60 and 90 m above the water. The survey route for each flight included: (1) transect one, which covered the entire inshore zone of the Sea by flying a route parallel to and about 0.5 km out from the shoreline, (2) transect two, which traversed a north-south track over the open water zone about 6–8 km out from the west shoreline, and (3) transect three, which traversed a south–north track over the open water zone about 8–10 km out from the eastern shoreline. Observers viewed from opposite sides of the aircraft and counted birds out to the distance at which species could be readily identified, which usually was about 0.5 km. Only birds positively identified were included in totals. Although surveys focused on Eared Grebes and Ruddy Ducks, observers also counted large grebes (*Aechmophorus* spp.), American White and Brown pelicans, and Double-crested Cormorants. On the 19 March survey, all species but the Eared Grebe were counted only from the inshore side of the plane.

Waterfowl

Salton Sea National Wildlife Refuge (SSNWR) biologists conducted aerial waterfowl surveys of the Salton Sea shoreline, adjacent marshes and impoundments, and Imperial Valley duck clubs and reservoirs on 8 January, 9 March, 3 April, 27 May, and 18 November 1999 using techniques established in prior years. Observers counted from a fixed-wing aircraft flying at heights varying from 75 to 90 m above the land and water's surface at speeds of 70–100 knots. All observations were made by a single observer (aided at times by the pilot) looking off the right (shoreward) side of the plane. Surveys began with impoundments in the Imperial Valley then shifted to a counterclockwise circumnavigation of the Salton Sea on which the plane followed a course parallel to and about 0.4 km from shore. The circumnavigation was periodically broken to fly multiple parallel transects over complexes of marshes and freshwater impoundments adjacent to the shoreline. Observers focused on counting all geese, ducks, and American Coots, but also tallied Eared Grebes and American White and Brown pelicans.

Roost counts

To obtain data on the population sizes of certain waterbirds that forage primarily in irrigated agricultural fields in the Imperial Valley rather than at the Salton Sea, we conducted eight roost counts on the following dates in fall and winter: 27 January, 13 February, 13 March, 14 August, 15 September, 21 October, 11 November, and 16 December. Counts were conducted at most known nighttime roosting sites for these species in the Imperial Valley. Counts were taken simultaneously at three to six sites on each survey. Observers (at least 2 at each site) were asked to be in place about 1.5 h before dusk and to count the number of Great Blue Herons, Great, Snowy and Cattle egrets, White-faced Ibis, and Sandhill Cranes that arrived at, or departed from, a site before nightfall. To guard against double-counting birds that left sites before dark to eventually roost at another site, we subtracted the departures from the sum of the arrivals and those present at the onset of the count to arrive at a net total. Observers terminated counts when birds stopped arriving or when it became too dark to see.

Agricultural transects

To assess occurrence patterns of birds in agricultural fields, we conducted monthly surveys of five roadside transects, each 8.05 km (5 mi) long, located in the northern Imperial Valley just south of the Salton Sea (Fig. 3). Project staff conducted surveys on 15 January, 6 February, 6 March, 2 April, 16 May, 7 June, 8 July,

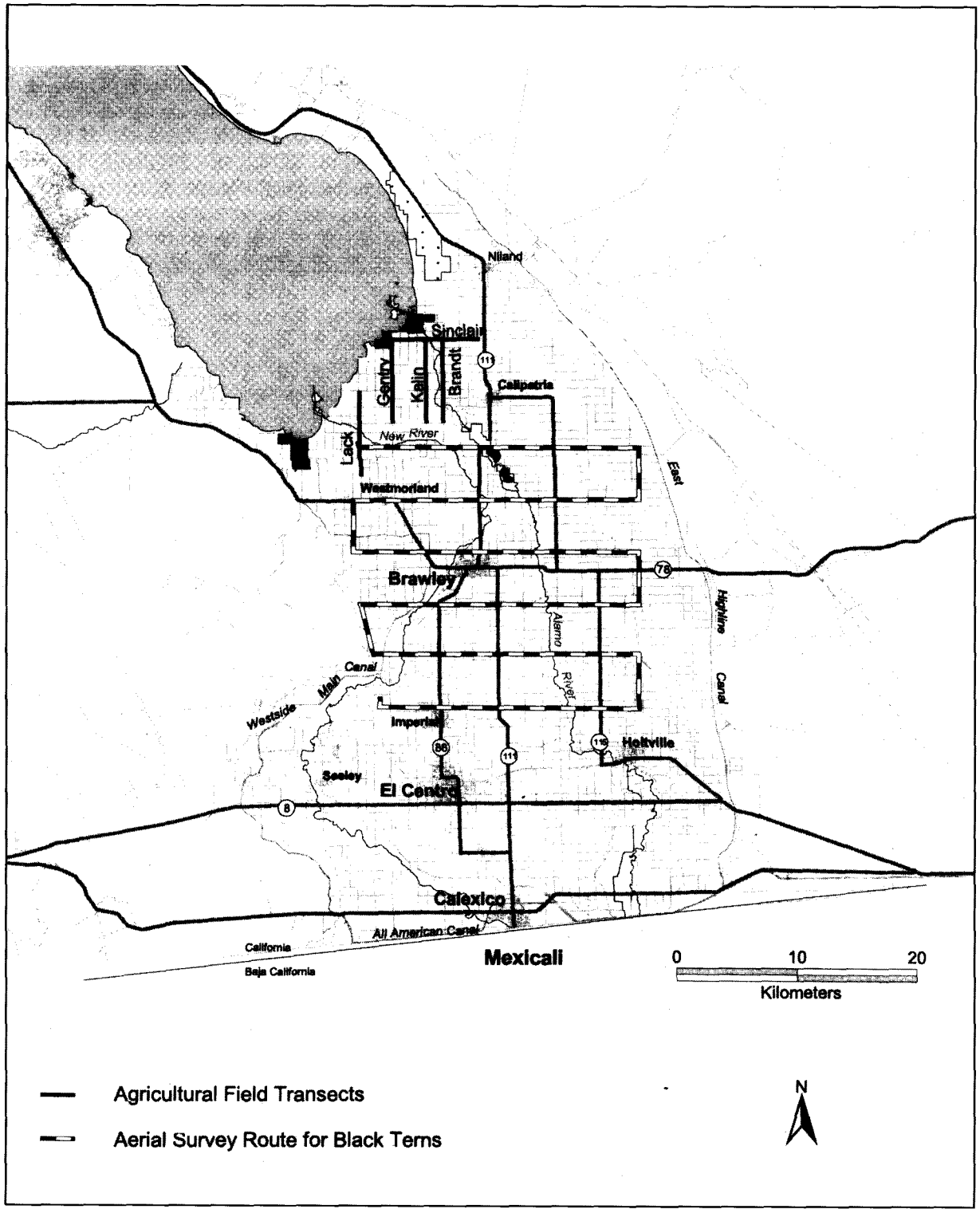


Figure 3. Overview map of the Imperial Valley, California, showing the location of roadside transects of agricultural fields (Lack, Gentry, Kalin, Brandt and Sinclair roads) and aerial survey route for Black Terns in 1999.

11 August, 9 September, 14 October, 10 November, and 10 December. To reduce sampling bias, observers alternated the order in which they surveyed transects and the starting point of individual transects between successive survey periods. They recorded the numbers of all species of birds found in agricultural fields adjacent to both sides of each roadside transect.

Colonial nesting waterbird surveys

We used airboat surveys of the entire Salton Sea shoreline as the primary method to document the distribution and abundance of all major cormorant and ardeid (heron, egret, night-heron) colonies. K. Sturm and associates conducted shoreline airboat surveys on 40 dates between 22 January and 16 July, but not all colonies were visited on a particular date. Surveys of some of the smaller colonies continued only through April. Airboat surveys were supplemented by vehicular visits by K. Sturm or project staff to additional colonies at Ramer Lake (6 & 14 May) and the Westmorland eucalyptus grove (8 July) away from the Salton Sea shoreline. On each survey, observers recorded the number of active nests and the general stage of nesting for each species at each site. Descriptions of the colony sites surveyed and their nesting substrates can be found in Shuford et al. (2000).

We used aerial photographic surveys to avoid disturbance and maximize the accuracy of nest counts for some of the larger colonies or for ones that were least visible from a boat. We used a fixed-wing aircraft to conduct photographic surveys of colonies of the Double-crested Cormorant and Great Blue Heron nesting on bare ground and rocks at Mullet Island at the south end of the Salton Sea (Fig. 2) on 1 February, 19 February, 25 March, and 16 April. While the plane slowed to about 70–90 knots and circled at 130–160 m over the island, D. Shuford shot multiple rolls of overlapping photographs of the nesting colonies using a Canon EOS single-lens reflex camera with a 300 mm lens and ASA 200 color film. J. Roth used standardized methods developed for surveying coastal seabird colonies (G. J. McChesney & H. R. Carter, in litt.) to count the numbers of cormorant and heron nests. She sorted the photographs (slides) to obtain a subset of overlapping reference photos of the highest resolution and contrast, projected these on a large sheet of white paper (69 × 86 cm easel), and marked nests and birds with a fine marker using identifiable landmarks as reference points to avoid double-counting. We defined active nests as those in which incubating or brooding adults, eggs, or chicks were visible.

Using the same field methods, K. Sturm or D. Shuford photographed aggregations of herons, egrets, and cormorants nesting in trees and marsh vegetation at the New and Alamo river mouths on 25 March, 3 April, 16 April, 27 May, and 28 May. Subsequently, we converted slides to 10 × 15 cm glossy prints, which we first sorted to obtain a subset of reference photos of the highest resolution and contrast. We then overlapped and taped together the prints to provide a composite photo of the colonies, or sub-colonies, from which we counted adults and nests directly. Great Blue Heron and Double-crested Cormorant nests and adults were readily identifiable on prints, but it was difficult to identify Great, Snowy, and Cattle egrets to species or to distinguish their nests. Consequently, for the latter species we estimated the number of active nests by first adjusting the counts of adult white egrets from 28 May aerial photographs by the following ratios derived from a 16 June boat survey – Great Egret (2%), Snowy Egret (4%), and Cattle Egret (94%). We then divided these numbers by two (adults/nest) to obtain a minimum estimate of nesting pairs of these species. Finally, we combined the data from aerial surveys of these colonies with that from other survey methods described elsewhere to estimate the total numbers of nesting pairs at the Sea.

As part of an independent long-term study, K. Molina and associates collected data on the size and productivity of larid (gull, tern, skimmer) colonies via foot or kayak surveys conducted at weekly to semi-monthly intervals from 7 March to 8 September and generally from a distance.

Estimating total nesting pairs

Estimating the total number of nesting pairs for each species of colonial waterbird at the Salton Sea was complicated by a lack of marked nests and individuals, our inability to survey all sites on a single day, and a high level of intra- and inter-colony nesting asynchrony exacerbated by several complete colony desertions by some species. The latter resulted in failed breeders moving to other colony sites. For each species at each colony site, we estimated the peak number of nesting pairs as the greatest number of nests recorded on a single colony visit. To avoid double-counting any renesting pairs that changed colony sites after failing in their initial attempts, we excluded high counts that occurred shortly after colony failures at nearby sites. We then summed the remaining high counts for

each site to obtain an estimate of the total number of nesting pairs at the Salton Sea. Although we knew of no complete colony failures for the Double-crested Cormorant, we used the peak count from Mullet Island as the estimate of the total number of nesting pairs of that species for the Salton Sea. This seems justified as the vast majority of cormorants had initiated nests on Mullet Island by early January, and the relatively small number of nests established elsewhere on the Sea after 28 February may have represented the relocation of some adults that failed in initial attempts at Mullet.

We believe our combined methodology for surveying nesting colonies produced reasonable, minimum estimates of nesting pairs for most species. We maintained aerial coverage of the entire shoreline and adjacent habitats throughout the breeding season, minimizing the possibility that significant colonies went undetected. Still we may have missed small colonies of the more secretive species, such as the Black-crowned Night-Heron and Snowy Egret, which might have nested within dense marshes away from the Salton Sea proper. We likely underestimated peak numbers of nest attempts for arboreal nesters because of the difficulty of viewing dense aggregations of nests stratified within three dimensional and, sometimes, dense habitats. Count accuracy was greatest for the Double-crested Cormorant on Mullet Island and for all larids, which nested on the ground in the open.

Additional survey methods

We used several other methods to survey target species. To document occurrence patterns of various rails and other marsh birds, we conducted breeding season surveys using tape playbacks. These focused primarily on the federally endangered Yuma Clapper Rail and the state threatened Black Rail. As part of the annual survey of the former taxa, we conducted censuses in a variety of marsh habitats around the periphery of the Salton Sea using methods developed by the Yuma Clapper Rail Recovery Team. We focused survey efforts at previously known Clapper Rail areas, particularly the Wister Unit of Imperial WA and the SSNWR, and explored new sites, particularly at the north end of the Sea. See Shuford et al. (2000) for a list and map of sites surveyed. Refuge personnel and project staff surveyed all Clapper Rail transects twice between 24 April and 15 May. On each transect, observers picked listening stations within appropriate marsh habitat. At each station, they played a tape for 2 min, stopped to listen for responses for 2 min, and then played the tape again for 2 min. Observers recorded birds responding to the tapes as well as incidental sightings of rails.

We also surveyed Black Rails (*Laterallus jamaicensis*) in marshes around the Salton Sea using methods developed by Evens et al. (1991) to detect birds responding to taped vocalizations ("*grr*" and "*kic-kic-kerr*" calls). Within appropriate habitat, observers selected transects with a set of listening stations, totaling 42 stations in 18 areas. From 24 April to 15 May, we surveyed each transect twice with the exception of three areas that we surveyed only once. Tape playback protocol was identical to that for the Clapper Rail as described above.

For comparison to prior surveys (Shuford et al., 1995), we conducted three surveys of the entire shoreline of the Salton Sea for Snowy Plovers. The winter surveys from 22 to 30 January and 11 to 14 November, when plovers flock and are easiest to detect, were conducted as part of the comprehensive surveys described above. The breeding season survey from 21 to 31 May was a separate survey focusing entirely on Snowy Plovers. At that season, surveying is made more difficult by adults sitting cryptically on nests and by adults with chicks sometimes moving long distances to mob observers. To minimize these problems, we instructed the five observers involved to follow a more stringent protocol in May than in winter. They used both binoculars and spotting scopes to repeatedly scan long distances up and down beaches and alkali flats to try to detect incubating adults before the plovers snuck off nests and scattered. We also asked observers to zig-zag back and forth across beaches and alkali flats to try to detect roosting or incubating plovers or those foraging behind shoreline berms where they otherwise might not be visible from the upper beach. On very wide beaches and alkali flats, two observers worked in tandem, one covering the upper beach or alkali flats and the other the immediate shoreline, zig-zagging as needed.

We estimated the winter population size of the Mountain Plover by conducting three comprehensive surveys of most (80–90%) of the agricultural lands in the Imperial Valley on 14–15 February, 13–14 November, and 11–12 December (Fig. 3). Adjusting for individuals participating on both days of two-day survey periods, the number of observers ranged from a low of 11 observers in 8 parties on the 14–15 February survey to a high of 26 observers in 15 parties on the 11–12 December survey. Observers drove all accessible roads and used binoculars and spotting scopes to

Table 2. Numbers of native waterbirds recorded on four comprehensive surveys of the Salton Sea, California, and adjacent wetlands in 1999 (see 'Methods'). Waterfowl and Eared Grebes were counted on aerial surveys at intervals that often did not coincide with comprehensive surveys (see Tables 4 and 5)

Species	22 January–5 February[a]	17–18 April	13–16 August	11–15 November
Pied-billed Grebe	25	15	47	56
Western Grebe	0[b]	379	363	714
Clark's Grebe	0[b]	340	371	222
Black Storm-Petrel	0	0	1	0
Am. White Pelican[c]	16 697	3738	554	19 197
Brown Pelican	16	0	1995	38
Double-crested Cormorant	18 504	11 160	3023	15 179
American Bittern	0	1	2	5
Least Bittern	2	0	7	7
Great Blue Heron	1566	925	1741	1380
Great Egret	275	229	1027	958
Snowy Egret	107	350	1103	759
Cattle Egret	42	238	1213	54
Green Heron	6	8	53	8
Black-crowned Night-Heron	116	69	608	114
White-faced Ibis	361	434	205	826
Wood Stork	0	0	6	0
Clapper Rail	8	12	16	7
Virginia Rail	5	0	6	3
Sora	10	8	2	17
Common Moorhen	12	18	62	62
Black-bellied Plover	1310	575	253	1381
Pacific Golden-Plover	0	1	0	0
Snowy Plover	275	285	351	170
Semipalmated Plover	73	131	139	122
Killdeer	277	215	259	228
Black-necked Stilt	3941	3465	15 857	5938
American Avocet	7318	7001	10 037	18 800
Greater Yellowlegs	81	14	113	82
Lesser Yellowlegs	62	12	28	69
Solitary Sandpiper	0	0	1	0
Willet	1162	682	582	1531
Spotted Sandpiper	7	7	19	11
Whimbrel	0	43	31	0
Long-billed Curlew	373	33	394	1380
Marbled Godwit	1297	928	1036	1205
Ruddy Turnstone	17	44	10	0
Red Knot	0	371	1	20
Sanderling	52	249	39	37
Western Sandpiper	1573	14 700	34 394	22 526
Least Sandpiper	2006	1226	942	3773
Baird's Sandpiper	0	0	1	0
Dunlin	799	141	1	964
Stilt Sandpiper	164	1	15	206
Ruff	1	0	3	0
dowitcher spp.	6356	6492	7153	11 589
Common Snipe	24	1	2	5

Continued on p. 265

Table 2. contd.

Wilson's Phalarope	1	23	3065	2
Red-necked Phalarope	0	32	32	20
Red Phalarope	0	3	0	0
Laughing Gull	0	0	7	1
Franklin's Gull	0	5	0	0
Bonaparte's Gull	297	403	27	626
Heermann's Gull	0	0	1	0
Mew Gull	2	0	0	0
Ring-billed Gull	28 523	5049	4800	22 833
California Gull	6987	3293	5730	11 313
Herring Gull	7026	291	1	6900
Thayer's Gull	0	0	0	2
Lesser Black-backed Gull	0	0	0	1
Yellow-footed Gull	1	1	789	15
Western Gull	4	0	3	3
Glaucous-winged Gull	6	1	0	0
Western × Glacous-winged Gull	1	0	0	0
Gull-billed Tern	0	69	11	0
Caspian Tern	22	269	2404	44
Common Tern	0	0	6	0
Forster's Tern	0	19	1402	172
Black Tern	0	2	4011	0
Black Skimmer	0	6	777	38
Total individuals	107 790	64 007	107 132	151 613
Total species[d]	49	55	63	54

[a] On this survey, Western and Clark's grebes were not counted in all areas and the Pied-billed Grebe, all rails, and all gulls and terns were not counted in areas 3–5.
[b] Although not counted, present and included in species total for this survey.
[c] An additional aerial survey in December tallied 24 974 pelicans.
[d] Species totals for April, August, and November include both Short- and Long-billed dowitchers.

carefully scan fields with appropriate plover habitat, i.e. those with barren ground or sparse low growth. On all surveys, observers recorded and mapped the location of all flocks and described the types of fields on which plovers occurred.

In conjunction with the August comprehensive ground survey, we also counted all Black Terns on a 16 August aerial survey, which followed the same protocol described above for pelicans and cormorants. In addition, we conducted aerial surveys for Black Terns over irrigated agricultural fields in the Imperial Valley by flying six parallel transects about 240 km long and spaced 5 km apart (Fig. 3).

Results

Species richness and abundance

In 1999, we recorded a total of 107 species of native waterbirds on our various surveys (Table 1). On the four comprehensive surveys of the Salton Sea and nearby wetlands, we recorded a total of 70 species of waterbirds: 49 in January, 55 in April, 63 in August, and 54 in November (Table 2). We recorded a total 107 790 individuals on the January comprehensive, 64 007 in April, 107 132 in August, and 151 613 in November. Additional counts or estimates of waterfowl and coots at the Salton Sea and of herons, egrets, ibis, and cranes coming to roosts after foraging in Imperial Valley fields swelled the seasonal totals to about 186 913 in January, 88 431 in April, 169 809 in August, and 261 499 in November (Table 3). These totals do not include Eared Grebes, surveyed in 1999 only in

March, November, and December (Table 4). Adding the Eared Grebe count for November provides an estimate of about 434 049 waterbirds at the Salton Sea that month. If numbers of other waterbirds remained relatively constant from November to December and the Eared Grebe count for the latter month were added, there probably were about 583 000 waterbirds at the Salton Sea in December.

Pelecaniformes (pelicans and cormorants), wading birds (herons, egrets, ibis, storks), shorebirds, and larids (gulls, terns, skimmers) were the groups that together accounted for ≥99% of the individuals on our comprehensive surveys. Three species of fish-eating pelecaniformes were among the most numerous birds at the Salton Sea in 1999. Of these, the American White Pelican and the Double-crested Cormorant reached highest numbers in winter with peak counts, respectively, of 24 974 individuals in December and 18 504 in January (Table 2). Of the 10 native species of long-legged wading birds recorded on comprehensive surveys, 8 were ardeids and the others were the White-faced Ibis and the Wood Stork (Table 2). Wader numbers totaled 2475 individuals in January, 2254 in April, 5965 in August, and 4111 in November (Table 2). Of the ardeids, the Great Blue Heron, Great Egret, Snowy Egret, and Cattle Egret each exceeded 1000 individuals on at least one comprehensive survey of the Salton Sea and adjacent wetlands (Table 2). Three species of waders were much more numerous in agricultural lands in the Imperial Valley than at the Salton Sea. Peak counts of birds coming to nighttime roosts after foraging in irrigated fields in the Imperial Valley were 40 000 Cattle Egrets in August, 37 438 White-faced Ibis in October, and 320 Sandhill Cranes in October. The latter species occurred only in agricultural areas of the Imperial Valley. Monthly counts at roost sites there in January and February and from October to December ranged from 255 to 320 cranes, except for an anomalous count of 37 birds in November, when we probably overlooked a roost site.

We detected 29 species of shorebirds on 4 comprehensive surveys of the Salton Sea area in 1999. Shorebird totals were 27 169 individuals in January, 36 675 in April, 74 758 in August, and 70 059 in November (Table 2). The ten taxa that exceeded 1000 individuals on at least one survey in 1999 were the Black-bellied Plover, Black-necked Stilt, American Avocet, Willet, Long-billed Curlew, Marbled Godwit, Western Sandpiper, Least Sandpiper, dowitchers, and Wilson's Phalarope. During three seasons three taxa accounted for at least 75% of the totals: American Avocet, Western Sandpiper, and dowitchers in April and November and Black-necked Stilt, American Avocet, and Western Sandpiper in August. In January it took five taxa to exceed 75% of the shorebird total.

Table 3. Total numbers of waterbirds on various surveys at the Salton Sea, California, in 1999. Numbers in parentheses estimated because of a lack of surveys during particular months. See 'Methods' for descriptions of survey protocols

Survey type	January	April	August	November
Comprehensive surveys[a]	107 790	64 007	107 132	151 613
Waterfowl and Coot surveys[b]	59 436	16 924	(5000)	67 341
Roost counts[c]	19 687	(7500)	57 677	42 545
Totals	186 913	88 431	169 809	261 499

[a] See Table 2 for details.
[b] See Table 5 for details.
[c] Largely reflects the abundance of the Cattle Egret and White-faced Ibis, which comprise the vast majority of birds at Imperial Valley roost sites in all seasons.

Table 4. Numbers of Eared Grebes, Western/Clark's *(Aechmophorus)* grebes, and Ruddy Ducks counted on three aerial survey transects of inshore and offshore zones of the Salton Sea, California, in 1999 (see 'Methods')

Species	19 March	28 March	29 November	17 December
Eared Grebe	47 561	58 412	172 550	321 575
Aechmophorus spp.	8620	7123	1508	3830
Ruddy Duck	5120	3924	26 584	32 680

Several species of shorebirds were much more numerous in agricultural fields in the Imperial Valley than in shoreline or other wetland habitats at or near the Salton Sea. In 1999, we counted about 2486 Mountain Plovers in the Imperial Valley in February, 2790 in November, and 3758 in December. The increase in numbers across surveys may reflect a parallel increase in observer coverage. Although we did not conduct comprehensive surveys for the Whimbrel and Long-billed Curlew, prior anecdotal information indicate that thousands of individuals of these species use agricultural fields seasonally (PRBO and R. McKernan, unpubl. data).

We recorded a total of 13 species of gulls on comprehensive surveys of the Salton Sea. Totals for all species were 42 847 individuals in January, 9043 in April, 11 358 in August, and 41 694 in November (Table 2). The Ring-billed, California, and Herring gulls accounted for >98% of all individuals in January and November, whereas just the Ring-billed and California gulls accounted for >92% in April and August. The Ring-billed Gull alone accounted for 55–65% of

Table 5. Numbers of waterfowl and other waterbirds counted on five aerial surveys of the Salton Sea, California, and surrounding wetlands in 1999 (see 'Methods'). Data for 1999 courtesy of SSNWR; data for mid-winter counts 1978–1987 from Heitmeyer et al. (1989)

Species	Survey dates 1999					Mid-winter average 1978–1987
	8 January	9 March	3 April	27 May	18 November	
Gr. White-fronted Goose	16	0	0	0	0	0
Snow/Ross's goose	22 550	1303	30	0	4400	16 835
Canada Goose	76	0	0	0	17	3296
Gadwall	109	45	31	12	244	465
American Wigeon	1873	1997	4	0	1422	5623
Mallard	76	43	44	23	1938	389
Blue-winged/Cinnamon teal	204	239	61	51	48	242
Northern Shoveler	11 732	10 790	5404	22	13 264	12 670
Northern Pintail	5465	502	5	3	7465	14 091
Green-winged Teal	3759	4488	441	77	4227	3092
Unidentified dabbling ducks	3212	1482	440	39	0	0
Canvasback	256	111	6	0	379	1691
Redhead	117	24	10	7	266	336
Ring-necked Duck	2	4	0	0	0	110
Scaup spp.	557	3189	752	10	242	1760
Scoter spp.	0	1	0	0	10	0
Bufflehead	50	41	0	0	22	49
Common Goldeneye	5	2	0	0	0	0
Ruddy Duck	4828	15 213	7904	1493	14 655	16 269
Unidentified diving ducks	175	65	27	5	0	0
Total waterfowl	55 062	39 539	15 159	1742	48 599	76 918
Other waterbirds						
Eared Grebe	13 798	34 810	38 767	0	3370	-
Am. White Pelican	12 203	13 512	2674	0	22 706	-
Brown Pelican	415	0	0	23	154	-
American Coot	4374	4841	1765	735	18 742	-

all gulls at the Salton Sea in November and January, respectively. However, many thousands of Ring-billed Gulls also winter in agricultural fields of the Imperial Valley, where the species is proportionately even more dominant than on the shoreline of the Sea. Ring-billed Gulls accounted for 99.4% of the 6616 gulls identified on monthly agricultural field transects in the northern Imperial Valley just south of the Salton Sea.

We recorded five species of terns and the Black Skimmer on comprehensive surveys of the Salton Sea (Table 2). These species totaled 22 individuals in January, 365 in April, 8611 in August, and 254 in November. Numbers of Gull-billed and Black Terns probably were slightly underestimated because some individuals forage over irrigated agricultural fields. For example, we recorded totals of 31 and 539 Black Terns on 5 agricultural field transects in the northern Imperial Valley on 16 May and 11 August, respectively. By contrast, we did not see any Black Terns on a 16 August aerial survey of agricultural fields further south in the Imperial Valley (Fig. 3), suggesting that Black Terns forage over fields primarily near the Salton Sea.

Various other surveys provided additional data on the occurrence and abundance of other groups of birds. Numbers of waterfowl on five aerial surveys of the Salton Sea area in 1999 ranged from a high of about 55 062 individuals of 17 taxa in January to a low

of 1742 individuals of 9 taxa in late May (Table 5). On the January survey, dabbling ducks comprised 48% of all waterfowl, geese 41%, and diving ducks 11%. Geese were almost exclusively Snow or Ross's geese; ground observations indicate the former species typically predominates at the Sea. In January, dabbling ducks were dominated by the Northern Shoveler (50%), Northern Pintail (24%), Green-winged Teal (16%), and American Wigeon (8%), whereas diving ducks were dominated by the Ruddy Duck (83%).

The proportion of waterfowl comprised by diving ducks, and the proportion of Ruddy Ducks within that group, appear to be underestimated by the standard refuge surveys for waterfowl. The latter focus on inshore waters of the Sea and adjacent freshwater impoundments and do not cover offshore waters where substantial numbers of Ruddy Ducks can be found. Additional aerial surveys for various diving waterbirds also included estimates of Ruddy Duck numbers, which ranged from 3924 to 5120 in March, to 26 584 in November, and 32 680 in December (Table 4).

Data were collected on several taxa of high conservation concern. Observers detected a total of 279 Yuma Clapper Rails in the Salton Sea area in 1999: 271 in marshes immediately around the Salton Sea and 3 at Lower Finney Lake and 5 at Holtville Main Drain in the northern Imperial Valley. We did not detect any Black Rails on our surveys in 1999, perhaps because of their irregular occurrence in the area. Snowy Plover numbers ranged seasonally from 170 to 351 individuals (Table 2), and the estimated breeding population in late May was 221 adults.

In 1999, the Salton Sea supported over 14 000 pairs of colonial breeders comprised of 11 species representing three families (Table 6). Together the Cattle Egret, Double-crested Cormorant, Great Blue Heron, and Black Skimmer accounted for 94% of all nesting pairs. Colonial nesters bred at 21 sites on or near the shoreline of the Sea and at Ramer Lake and near Westmorland in the Imperial Valley. The Great Blue Heron, Double-crested Cormorant, and Great Egret nested at 18, 8, and 6 sites, respectively, whereas all other species nested at 1–4 sites (Table 6).

Table 6. Total numbers of nesting pairs and sites occupied by colonial breeding waterbirds at the Salton Sea, California, in 1999. Totals based on peak numbers of nesting attempts adjusted for colony desertions (see 'Methods')

Species	Total nesting pairs	Number of sites occupied
Cormorants		
Double-crested Cormorant	5425	8
Ardeids		
Great Blue Heron	888	18
Great Egret	165	6
Snowy Egret	170	4
Black-crowned Night-Heron	102	3
Cattle Egret	6660	2
Larids		
Laughing Gull	1	1
California Gull	40	1
Gull-billed Tern	101	2
Caspian Tern	211	1
Black Skimmer	377	3
Total	14 140	

Discussion

Importance of the Salton Sea to Pacific Flyway waterbirds

Our snapshot of bird use in 1999 further documented the great importance of the Salton Sea to birds in the Pacific Flyway of western North America, though such a short-term study necessarily underestimates the number of birds using a site. The Salton Sea is an important part of the Río Colorado Delta region, including the northern Gulf of California, and contains some of the highest biological diversity in the southwestern United States. This is especially true for birds. To date, 402 native and 5 non-native bird species have been recorded in the Salton Sea area, including about 100 breeding species (Patten in Shuford et al., 1999). In addition, the sheer number of birds using the Salton Sea at various times of the year is particularly noteworthy. Our surveys in 1999 suggest that a minimum of half a million waterbirds inhabited the Salton Sea in winter. While this number is impressive, in prior years the Eared Grebe population at the Sea alone has reached an estimated 3.5 million birds (R. McKernan, pers. comm. in Jehl, 1988).

As well as holding large numbers of birds, the Salton Sea also hosts populations of various species that are of continental or regional importance. For example, 90% or more of the entire North American population of the Eared Grebe may pass through the Sea in some years (J. R. Jehl, Jr., in litt.). Our peak count of about 25 000 American White Pelicans at the

Salton Sea in 1999 was similar to the range of about 26 500 to 33 000 in recent years (Setmire et al., 1990; McCaskie, 1999). These numbers represent about 23–30% of the entire North American breeding population and actually exceed the estimate of about 18 600 for the western population, which breeds and winters west of the continental divide (Johnsgard, 1993). Counts of 16 000–19 000 White-faced Ibis in the Imperial Valley further documented that area as one of the most important wintering sites for these birds in western North America (Shuford et al., 1996). Average October to April counts of Ruddy Ducks at the Salton Sea from 1984 to 1999 by R. McKernan (unpubl. data) ranged from 91 905 to 202 123 individuals (mean of means [Oct–Apr] = 150 515, SE = 8293, n = 16 yrs). What percentage of the Pacific Flyway population of the Ruddy Duck these numbers represent is unknown, but it must be large. Surveys of the endangered Yuma Clapper Rail indicate that the Salton Sea holds about 40% of the taxa's entire population in the United States (Yuma Clapper Rail Recovery Team, unpubl. data.). The total of 55 000 waterfowl in January 1999 was below the average of about 77 000 on mid-winter counts from 1978 to 1987 (Heitmeyer et al., 1989), but it is unclear if the 1999 numbers fall within the range of variation of prior years. Although the 1978–1987 average represents only about 2% of the wintering population of California's Central Valley (Heitmeyer et al., 1989), the premier waterfowl wintering area in the Pacific Flyway, the Salton Sea is still the most important site for waterfowl in the interior of southern California.

Shorebird totals at the Salton Sea in some years have exceeded 100 000 individuals in both spring and fall (PRBO and R. McKernan, unpubl. data) indicating it qualifies for designation as a site of international importance to shorebirds under criteria of the Western Hemisphere Shorebird Reserve Network (Harrington & Perry, 1995). Regional comparisons indicate the Salton Sea is one of only eight sites in the interior of western North America that holds over 10 000 shorebirds in fall and one of five such sites in spring (PRBO, unpubl. data). In terms of overall shorebird numbers, the Salton Sea is the most important area in the Intermountain and Desert region of the West in spring and the second most important, after Great Salt Lake, in fall. Shorebird populations at the Salton Sea from 1989 to 1995 averaged 24 000 in December, 90 000 in April, and about 85 000 individuals in August. Shorebird surveys in 1999 provided additional documentation for these patterns and added a total of about 70 000 shorebirds in November, a month for which prior thorough surveys were lacking. The relatively low numbers in April 1999 compared with prior years may have represented a lack of coincidence of the 1999 survey dates with the peak passage of Western Sandpipers, which can move through very rapidly in large numbers (e.g. >65 000 in 1992, PRBO, unpubl. data). Surveys in 1999 confirmed that the Salton Sea supports the largest population of wintering Snowy Plovers in the interior of western North America (Shuford et al., 1995) and is one of a handful of key breeding areas in the interior of California (Page et al., 1991).

Although California's Central and Imperial valleys are widely considered the primary wintering areas for the Mountain Plover (Knopf & Rupert, 1995), our surveys suggest the latter valley may be of more crucial importance than previously thought. The mean number for our three surveys represents about 30–38% of the species' total estimated population of 8000 to 10 000 individuals (Anonymous, 1999). On prior surveys across the California wintering range, the 2072 and 755 Mountain Plovers recorded in the Imperial Valley in 1994 and 1998, respectively, represented 61% and 35% of the totals of 3390 and 2179 individuals found statewide (B. Barnes, in litt.; CDFG, unpubl. data; K. Hunting, in litt.). The higher totals in the Imperial Valley in 1999 almost surely reflect an increase in observer coverage there over prior years rather than a population increase. Counts of Mountain Plovers on the Salton Sea (south) Christmas Bird Count, covering only part of the northern Imperial Valley, have ranged from 1 to 1003 birds (median = 180 birds) from 1979 to 1998.

In 1999, we estimated a total gull population of over 40 000 individuals at the Salton Sea, not including many additional thousands using agricultural lands in the adjacent Imperial Valley. Although data are lacking for quantitative comparisons, these numbers suggest that the Salton Sea is one of, if not the, most important area in the interior of western North America for wintering gulls. A count of over 4000 Black Terns at the Salton Sea in August 1999 appears to be the only comprehensive count at that site, although Small (1994) reported "tens of thousands" there during the period of peak occurrence in July and August. Regardless, the Salton Sea in one of the most important sites in western North America for migrating Black Terns (Shuford, 1999).

The number of species and the abundance of colonial nesting waterbirds at the Salton Sea rivals or

exceeds that at many coastal and interior colonies in western North America (Parnell et al., 1988; Price et al., 1995). Population reviews of the Double-crested Cormorant (Carter et al., 1995), Gull-billed Tern (Parnell et al., 1995), Caspian Tern (Cuthbert & Wires, 1999), and Black Skimmer (Collins & Garrett, 1996) suggest that Salton Sea populations are among the largest anywhere in western North America in recent years. For the Gull-billed Tern, the Salton Sea is one of only a few sites at which the western subspecies (*S. n. vanrossemi*) breeds (Parnell et al., 1995). Although comparative nesting numbers are not readily available for other areas, the breeding population of the Cattle Egret at the Salton Sea (up to 30 000 pairs in 1992; SSNWR files) is surely among the largest in western North America. The wintering population of Cattle Egrets at the Salton Sea is considered the third densest in all of North America (Telfair, 1994).

Population dynamics

Since its inception in 1905, the composition of the Salton Sea's avifauna has been dynamic with populations of various species of breeding and non-breeding birds fluctuating dramatically. Although it is beyond the scope of this paper to review population trends or fluctuations at the Salton Sea, it is clear that this dynamic flux has continued through the last few decades. For example, nesting Double-crested Cormorants began their explosive growth in 1996 with the colonization of Mullet Island (SSNWR files). This population continued to increase to over 5000 pairs in 1999 and now forms one of the largest concentrations of breeding cormorants in the Pacific coast states north of Mexico (Carter et al., 1995). Similarly, Brown Pelicans increased greatly at the Sea in the 1990s, and since 1996 small numbers have bred there irregularly (Sturm, 1998). By contrast, the Caspian Tern population in 1999 represented only about 30% of the average numbers at the Salton Sea in recent years (K. Molina, unpubl. data). The relatively low numbers of Eared Grebes in winter 1999 and of shorebirds in April 1999 compared with prior years suggest that populations of some non-breeding birds at the Salton Sea fluctuate greatly over time. Future detailed examinations of population trends at the Salton Sea should investigate whether patterns at the Salton Sea reflect changing local conditions or simply parallel those for the Pacific Flyway as a whole.

Connectivity with the Gulf of California

Although birds that use the Salton Sea come from widely scattered areas in western North America, many that pass through the Sea appear to do so via the Salton Trough and the Gulf of California. For shorebirds, anecdotal evidence suggests there is a strong migrant connection with the west coast of Mexico, the Gulf of California, and the Pacific Coast of the United States, particularly in spring. Butler et al. (1996) reported a Western Sandpiper banded in Panama was found at the Salton Sea in spring. The Salton Sea is also strongly linked to the Gulf of California by northward post-breeding dispersal of species such as the Brown Pelican, Wood Stork, Laughing Gull, and Yellow-footed Gull (Patten et al. in press). Further study is likely to greatly expand our knowledge of the extent of bird movement between the Sea and the Gulf of California.

Conservation concerns

The Salton Sea hosts 19 species of waterbirds of high conservation concern (Table 7), but many other species that concentrate there potentially are at great risk from disease, contaminants, or human encroachment. Birds at the Sea particularly hard hit by disease and other factors during the 1990s include the Eared Grebe (150 000 dead in 1992, unknown causes); American White Pelican (9000 dead in 1996, botulism); Brown Pelican (1200 dead in 1996, botulism); and waterfowl, shorebirds, and waders (>11 000 dead in 1998, avian cholera) (see summary in Shuford et al., 1999). Although die-offs occur sporadically at many other Pacific Flyway wetlands, the magnitude of those at the Salton Sea and the species affected, particularly diving and fish-eating birds, make them of special concern. Setmire et al. (1990, 1993) and the Imperial Irrigation District (1994) have reviewed the results of bird contaminant studies at the Salton Sea, which indicate birds are at risk from selenium, boron, and DDE. Although birds appear to be at greatest risk from agricultural drain waters in the Imperial Valley, many species that use the Salton Sea move to and from irrigated agricultural lands of the Imperial Valley and the Sea.

Additionally, human activities potentially could impact birds at sites where they concentrate at the Sea. Nesting waterbirds, which occur at the Salton Sea in large numbers, are sensitive to colony intrusions (Carney & Sydeman, 1999 and references therein), which may expose unattended eggs and young to extreme

Table 7. Seasonal status and significance of waterbirds of high conservation concern at the Salton Sea, California. FT = federally threatened, FE = federally endangered, ST = state threatened, ST = state endangered, MNMC = U.S. Migratory Nongame Bird of Management Concern (USFWS 1995), BSSC = Calif. Dept. of Fish and Game Bird Species of Special Concern[a] (CDFG, 1992)

Species	Special status designation	Seasonal status and significance
Brown Pelican	FE	Large non-breeding population and recent small and irregular breeding population. About 1200 died of botulism in 1996.
American White Pelican	BSSC, MNMC	Wintering population represents up to 30% of the entire North American breeding population and may exceed the size of the western breeding population. About 9000 died of botulism in 1996.
Double-crested Cormorant	BSSC	Large wintering and breeding population. Mullet Island colony one of largest in western North America.
American Bittern	MNMC	Small wintering and, perhaps, breeding population.
Least Bittern[b]	BSSC, MNMC	Resident population of unknown size.
White-faced Ibis	BSSC, MNMC	Large wintering and small irregular breeding population. A primary wintering area in western North America.
Wood Stork	BSSC	Small and declining post-breeding population.
Fulvous Whistling-Duck	BSSC	Small and declining breeding and wintering population.
Black Rail	ST, MNMC	Small irregular breeding population.
Yuma Clapper Rail	FE	Relatively small breeding population represents about 40% of entire U.S. population.
Greater Sandhill Crane	ST	Modest wintering population in Imperial Valley.
Snowy Plover	BSSC, MNMC	Year-round resident. Largest wintering population in the interior of the U.S. and one of a handful of key breeding areas in the interior of California.
Mountain Plover	BSSC, MNMC	Winter resident. Imperial Valley population represents about 30–40% of the species' entire population.
Long-billed Curlew	BSSC, MNMC	Relatively large wintering population, particularly in the Imperial Valley.
Laughing Gull	BSSC	Breeder and post-breeding visitor. Breeding population has declined, now very small and irregular.
California Gull	BSSC	Primarily a winter resident and non-breeding summer resident; recently established small breeding population.
Gull-billed Tern	BSSC	Breeder and summer resident. Hosts one of few breeding populations of western subspecies.
Black Tern	BSSC, MNMC	Migrant and non-breeding summer resident. One of key migratory stopover sites in western North America.
Black Skimmer	BSSC	Breeder and summer resident. Population among the largest in western North America in recent years.

[a] List currently outdated and under revision.
[b] A population estimate of 550 individuals around the Salton Sea (Setmire et al., 1993) is unsubstantiated.

thermal conditions and result in overheating and death in a short period of time (Grant, 1982; Molina, 1999). Hence, the nesting success of these populations, particularly of ground nesters, may be closely linked to the degree of colony disturbances (Molina, 1996).

Rising salinity and lowered water levels could profoundly affect the future composition of the Salton Sea's avifauna. Current models predict that within 13–22 years, depending on inflow regimes, salinities will reach 50 000 mg/l and severely affect invertebrate and fish populations and, by extension, the Sea's fish-eating bird populations (Tetra Tech, 2000). Shortly thereafter prey resources for birds likely would be dominated by brine shrimp *(Artemia franciscana)* and brine flies *(Ephydra* spp.), favoring species, such as the Eared Grebe and Wilson's and Red-necked phalaropes, that are numerous on hypersaline lakes. Various future water management projects that likely will reduce inflows to the Sea not only would accelerate the increase in salinity but also would lower water levels. The latter might reduce shoreline wetlands used by many species and would form landbridges to nearshore snags and islands, making them unsuitable as nesting sites for colonial waterbirds.

The current Salton Sea Restoration Project (Tetra Tech, 2000) addresses most of the aforementioned issues, but the solutions proposed to date focus primarily on various engineering alternatives for reducing salinity and maintaining the level of the Sea. Although reducing salinity may stave off the collapse of the Sea's fish populations and, by extension, those of fish-eating birds, it is unclear what affect, if any, a decrease in salinity will have in reducing bird mortality from diseases or other agents that may be triggered by perhaps unrelated factors. Nevertheless, any proposed projects to reduce salinity should be carefully evaluated and implemented only if they can provide substantial habitat improvements without negatively impacting the suitability of current habitats. Any proposed benefits should be weighed against the potential for concentrating contaminants and predators where large numbers of birds forage or nest and for killing large numbers of nocturnal migrants via collisions with project structures.

Research needs

Despite the studies to date, there are still large gaps in the knowledge needed to effectively solve the problems facing birds at the Salton Sea. Little quantitative information is available on the within-Sea distribution and habitat needs of most species of waterbirds, data that will be crucial to ensure that any large scale projects designed to solve problems, such as increasing salinity, will not harm important species or habitats. Time series studies are needed to see how birds use the Sea at different water elevations both on a seasonal and long-term basis. Research is needed on the effects of investigator and recreational disturbances on nesting colonies, isolated roosting sites, and areas that regularly concentrate large numbers of birds

Ongoing work should be continued to identify the causes of large scale die-offs, mechanisms of disease transmission, and factors that trigger these events before solutions can be implemented to reduce their effects. Likewise, additional studies are needed to understand the sources, mechanisms of uptake, and effect of contaminants on survival and reproduction of birds. Crucial to both disease and contaminant work will be more collaborative research on the diet of key species of birds, an area of study that has been particularly poorly represented in the past. A focus on seasonal changes in bird diets would make an important contribution to understanding the dynamics of the Salton Sea ecosystem. Long-term studies are needed of the reproductive success and demographics of colonial nesting waterbirds, which may be linked to disease, contaminant, and dietary research.

Research is needed on the daily and seasonal use patterns and movements of birds between agricultural fields in the Imperial and Coachella valleys and the Sea and movements among various portions of the Sea. Collection of data on turnover rates of migratory species would provide better estimates of the number of birds using the Sea. On a larger scale, research is needed on the dispersal patterns and migratory movements of birds between the Salton Sea and various Pacific Flyway wetlands, particularly the Río Colorado Delta and the Gulf of California. Finally, ongoing research and monitoring are needed to understand seasonal and long-term population dynamics and to assess the effectiveness of any large scale projects implemented to resolve the Sea's ecological problems.

Acknowledgements

Financial support for this project was provided by the Salton Sea Authority through U.S. Environmental Protection Agency grant # R826552-01-0 administered by Tom Kirk. We thank the following individuals and organizations for advice, logistical support, un-

published data, or other help essential to conducting our field studies or preparing this document: California Department of Fish and Game staff (Pam Cherny and associates, Tom Evans, and Kevin Hunting), Phil Capitolo, Moe Flannery, Kimball Garrett, Sue Geurs, Anne King, Chet McGaugh, Robert McKernan, Steve Meyers, Jon Parkinson, Michael Patten, Jennifer Roth, Zack Smith, and the University of Redlands' Salton Sea Database Program staff (Ken Althiser, Tim Krantz, and Doug Mende). Project biologist Brennan Mulrooney played a crucial role in data collection at the Salton Sea in 1999, and Anne Black prepared the map figures. Milt Friend, Barry Gump, Dick Zembal, and the entire Salton Sea Science Subcommittee provided oversight and guidance of our project as but one facet of the multi-disciplinary Salton Sea Reconnaissance Survey. We are extremely, and particularly, grateful to Clark Bloom, Steve Johnson, and other staff of the Sonny Bono Salton Sea NWR for providing access to refuge lands for our research, supplying airboat support for shoreline surveys, sharing their extensive data on populations of colonial nesting birds, Yuma Clapper Rails, and waterfowl, and otherwise cooperating to ensure the success of our work. We are also deeply appreciative of the help of over 50 volunteers without which this project would not have been possible. Comments by Dan Anderson improved an earlier draft of the manuscript. This is Contribution No. 932 of Point Reyes Bird Observatory.

References

American Ornithologists' Union, 1998. Check-list of North American Birds. 7th edn. American Ornithologists' Union, Washington (DC).

Anonymous, 1999. Endangered and threatened wildlife and plants: proposed threatened status for the Mountain Plover. Federal Register 64: 7587–7601.

Boyd, W. S. & J. R. Jehl, Jr., 1998. Estimating the abundance of Eared Grebes on Mono Lake, California, by aerial photography. Colonial Waterbirds 21: 236–241.

Butler, R. W., F. S. Delgado, H. de la Cueva, V. Pulido & B. K. Sandercock, 1996. Migration routes of the Western Sandpiper. Wilson Bulletin 108: 662–672.

California Department of Fish and Game, 1992. Bird species of special concern. Unpublished list, Calif. Dept. Fish Game, Sacramento (CA).

Carney, K. M. & W. J. Sydeman, 1999. A review of human disturbance effects on nesting colonial waterbirds. Waterbirds 22: 68–79.

Carter, H. R., A. L. Sowls, M. S. Rodway, U. W. Wilson, R. W. Lowe, G. J. McChesney, F. Gress & D. W. Anderson, 1995. Population size, trends, and conservation problems of the Double-crested Cormorant on the Pacific Coast of North America. Colonial Waterbirds 18 (Special Publ. 1): 189–215.

Collins, C. T. & K. L. Garrett, 1996. The Black Skimmer in California: an overview. W. Birds 27: 127–135.

Cuthbert, F. J. & L. R. Wires, 1999. Caspian Tern (*Sterna caspia*). In Poole, A. & F. Gill (eds), The Birds of North America, No. 403. The Birds of North America, Inc., Philadelphia (PA).

Dahl, T. E., R. D. Young, & M. C. Caldwell, 1997. Status and trends of wetlands in the conterminous United States: projected trends 1985–1995. U.S. Dept. Interior, Fish and Wildl. Serv., Washington (DC).

Evens, J. G., G. W. Page, S. A. Laymon & R. W. Stallcup, 1991. Distribution, relative abundance and status of the Black Rail in western North America. Condor 93: 952–966.

Grant, G. S., 1982. Avian incubation: egg temperature, nest humidity, and behavioral thermoregulation in a hot environment. Ornithol. Monogr. 30.

Harrington, B. & E. Perry, 1995. Important shorebird staging sites meeting Western Hemisphere Shorebird Reserve Network criteria in the United States. U.S. Dept. Inter., Fish and Wildl. Serv., Washington (DC).

Heitmeyer, M. E., D. P. Connelly & R. L. Pederson, 1989. The Central, Imperial, and Coachella valleys of California. In Smith, L. M., R. L. Pederson & R. M. Kiminski (eds), Habitat management for migrating and wintering waterfowl in North America. Texas Univ. Press, Lubbock (TX): 475–505.

Imperial Irrigation District, 1994. Final Environmental Impact Report for modified East Lowline and Trifolium interceptors, and completion projects, Volume 1. Imperial Irrigation District, May 1994.

Jehl, J. R., Jr., 1988. Biology of the Eared Grebe and Wilson's Phalarope in the nonbreeding season; a study of adaptations of saline lakes. Studies avian Biol. 12: 1–74.

Jehl, J. R., Jr., 1994. Changes in saline and alkaline lake avifaunas in western North America in the past 150 years. Studies avian Biol. 15: 258–272.

Johnsgard, P. A., 1993. Cormorants, Darters, and Pelicans of the World. Smithsonian Institution Press, Washington (DC).

Knopf, F. L. & J. R. Rupert, 1995. Habits and habitats of Mountain Plovers in California. Condor 97: 743–751.

McCaskie, G., 1999. Spring migration. Southern Pacific Coast region. Field Notes 52: 390.

Molina, K. C., 1996. Population status and breeding biology of Black Skimmers at the Salton Sea, California. W. Birds 27: 143–158.

Molina, K. C., 1999. An evaluation of hypotheses using Gull-billed Terns and Black Skimmers (Aves: Laridae) at the Salton Sea, California. M.S. Thesis, Calif. State Univ., Northridge.

Page, G. W., L. E. Stenzel & J. E. Kjelmyr, 1999. Overview of shorebird abundance and distribution in wetlands of the Pacific coast of the contiguous United States. Condor 101: 461–471.

Page, G. W., L. E. Stenzel, W. D. Shuford & C. R. Bruce, 1991. Distribution and abundance of the Snowy Plover on its western North American breeding grounds. J. field Ornithol. 62: 245–255.

Parnell, J. F., D. G. Ainley, H. Blokpoel, B. Cain, T. W. Custer, J. L. Dusi, S. Kress, J. A. Kushlan, W. E. Southern, L. E. Stenzel & B. C. Thompson, 1988. Colonial waterbird management in North America. Colonial Waterbirds 11: 129–169.

Parnell, J. F., R. M. Erwin & K. C. Molina, 1995. Gull-billed Tern (*Sterna nilotica*). In Poole, A. & F. Gill (eds), The Birds of North America, No. 140. The Academy of Natural Sciences, Philadelphia (PA), and The American Ornithologists' Union, Washington (DC).

Patten, M. A., G. McCaskie & P. Unitt, in press. Birds of the Salton Sea: status, biogeography, and ecology. Univ. California Press, Berkeley (CA).

Price, J., S. Droege & A. Price, 1995. The Summer Atlas of North American birds. Academic Press, San Diego (CA).

Setmire, J. G., R. A. Schroeder, J. N. Densmore, S. L. Goodbred, D. J. Audet & W. R. Radke, 1993. Detailed study of water quality, bottom sediment, and biota associated with irrigation drainage in the Salton Sea area, California, 1988–90. U.S. Geol. Surv. Water-Resources Invest. Rep. 93-4014. U.S. Geol. Surv., Federal Bldg., Rm. W-2233, 2800 Cottage Way, Sacramento, CA.

Setmire, J. G., J. C. Wolfe & R. K. Stroud, 1990. Reconnaissance investigation of water quality, bottom sediment, and biota associated with irrigation drainage in the Salton Sea area, California, 1986–87. U.S. Geol. Surv. Water-Resources Invest. Rep. 89-4102. U.S. Geol. Surv., Federal Bldg., Rm. W-2233, 2800 Cottage Way, Sacramento, CA.

Shuford, W. D., 1999. Status assessment and conservation plan for the Black Tern *(Chlidonias niger surinamensis)* in North America. U.S. Dept. of the Interior, Fish and Wildl. Serv., Denver (CO).

Shuford, W. D., C. M. Hickey, R. J. Safran & G. W. Page, 1996. A review of the status of the White-faced Ibis in winter in California. W. Birds 27: 169–196.

Shuford, W. D., G. W. Page & C. M. Hickey, 1995. Distribution and abundance of Snowy Plovers wintering in the interior of California and adjacent states. W. Birds 26: 82–98.

Shuford, W. D., N. Warnock & K. C. Molina, 1999. The avifauna of the Salton Sea: a synthesis. Report to the Salton Sea Science Subcommittee and Salton Sea Authority. Point Reyes Bird Observatory, 4990 Shoreline Highway, Stinson Beach, CA 94970.

Shuford, W. D., N. Warnock, K. C. Molina, B. Mulrooney & A. E. Black, 2000. Avifauna of the Salton Sea: abundance, distribution, and annual phenology. Contribution No. 931 of Point Reyes Bird Observatory. Final report for EPA Contract No. R826552-01-0 to the Salton Sea Authority, 78401 Highway 111, Suite T, La Quinta, CA 92253.

Small, A., 1994. California Birds: their Status and Distribution. Ibis Publishing, Vista (CA).

Sturm, K., 1998. From summer range to home range? Endangered Species Bulletin 23(5): 22–23.

Telfair, R. C. II, 1994. Cattle Egret *(Bubulcus ibis)*. In Poole, A. & F. Gill (eds), The Birds of North America, No. 113. The Academy of Natural Sciences, Philadelphia (PA), and The American Ornithologists' Union, Washington (DC).

Tetra Tech, Inc., 2000. Draft Salton Sea Restoration Project Environmental Impact Statement/Environmental Impact Report. Prepared for the Salton Sea Authority and U.S. Dept. of Interior Bureau of Reclamation.

U.S. Fish and Wildlife Service, 1995. Migratory nongame birds of the United States: the 1995 list. Office of Migratory Bird Management, U.S. Fish and Wildlife Service, Washington (DC).

U.S. Fish and Wildlife Service, 1997. Saving the Salton Sea: a research needs assessment. U.S. Dept. Interior Fish and Wildlife Service.

Hydrobiologia **473:** 275–292, 2002.
D.A. Barnum, J.F. Elder, D. Stephens & M. Friend (eds), The Salton Sea.
© 2002 *Kluwer Academic Publishers. Printed in the Netherlands.*

Possible importance of algal toxins in the Salton Sea, California

Kristen M. Reifel[1], Michael P. McCoy[2], Tonie E. Rocke[3], Mary Ann Tiffany[1], Stuart H. Hurlbert[1] & D. John Faulkner[2]
[1]*Department of Biology and Center for Inland Waters, San Diego State University, San Diego, CA 92182-4614, U.S.A.*
[2]*Scripps Institution of Oceanography, University of California at San Diego, La Jolla, CA 92093-0212, U.S.A.*
[3]*National Wildlife Health Center, U. S. Geological Survey, Biological Resources Division, 6006 Schroeder Road, Madison, WI 53711, U.S.A.*

Key words: dinoflagellate, raphidophyte, prymnesiophyte, *Gyrodinium uncatenum*, *Prorocentrum minimum*, *Protoceratium reticulatum*, *Gymnodinium* sp., *Chattonella marina*, *Pleurochrysis pseudoroscoffensis*, red tides, eared grebe, *Podiceps nigricollis*, saline lake, algal blooms

Abstract

In response to wildlife mortality including unexplained eared grebe (*Podiceps nigricollis*) die-off events in 1992 and 1994 and other mortality events including large fish kills, a survey was conducted for the presence of algal toxins in the Salton Sea. Goals of this survey were to determine if and when algal toxins are present in the Salton Sea and to describe the phytoplankton composition during those times. A total of 29 samples was collected for toxicity analysis from both nearshore and midlake sites visited biweekly from January to December 1999. Dinoflagellates and diatoms dominated most samples, but some were dominated by a prymnesiophyte (*Pleurochrysis pseudoroscoffensis*) or a raphidophyte (*Chattonella marina*). Several types of blooms were observed and sampled. The dinoflagellate *Gyrodinium uncatenum* formed an extensive, dense (up to 310 000 cells ml^{-1}) and long-lasting bloom during the winter in 1999. A coccolithophorid, *Pleurochrysis pseudoroscoffensis*, occurred at high densities in surface films and nearshore areas during the spring and summer of 1999. These surface films also contained high densities of one or two other species (an unidentified scrippsielloid, *Heterocapsa niei*, *Chattonella marina*). Localized blooms were also observed in the Salton Sea. An unknown small dinoflagellate reached high densities (110 000 cells ml^{-1}) inside Varner Harbor, and an unidentified species of *Gymnodinium* formed a dense (270 000 cells ml^{-1}) band along part of the southern shoreline during the summer. Three species known to produce toxins in other systems were found. *Protoceratium reticulatum* (=*Gonyaulax grindleyi*) and *Chattonella marina* were found in several samples taken during summer months, and *Prorocentrum minimum* was found in low densities in several samples. Extracts of most samples, including those containing known toxic species, showed a low level ($<10\%$ mortality across all concentrations) of activity in the brine shrimp lethality assay and were not considered toxic. All sample extracts tested in the mouse bioassay showed no activity. One sample extract taken from the bloom of the small dinoflagellate was highly active (100% mortality across all concentrations) in the brine shrimp lethality assay, but the active material could not be isolated. While dense algal blooms are common at the Salton Sea, no evidence gathered in this study suggests that algal toxins are present within phytoplankton cells; however, toxins actively excreted by cells may have been missed. Blooms of phytoplankton likely contribute to wildlife mortality at the Salton Sea. Possible mechanisms including intoxication due to ingestion of feathers in grebes and waterlogging caused by changes in surface tension are discussed.

Introduction

Saline and alkaline lakes of the western United States and southwestern Canada constitute an important, although overlooked, resource for migratory birds (Behle, 1958; Winkler, 1977; Jehl, 1988; Jehl, 1994). The Salton Sea is a 980 km^2, saline (43 g l^{-1}) lake located in southeastern California, U.S.A. (see Hart et al., 1998 or Watts et al., 2001 for maps of the Salton Sea). It is a shallow, closed-basin lake with a mean depth of 8 m and a maximum depth of 15 m (Ferrari & Weghorst, 1997). The lake is eutrophic largely because it is in a closed basin and receives most of its input from agricultural and municipal wastewaters (Bain et al., 1970; Cohen et al., 1999). Over 380 species of birds, some endangered, winter or live permanently at the Salton Sea (Jehl, 1994). The lake is a very important stopover and wintering ground for the eared grebe (*Podiceps nigricollis* Brehm). During the fall and spring migrations, the majority of the North American population of this species passes through the Salton Sea area en route to or from wintering areas in the Gulf of California. Additionally, tens or hundreds of thousands of individuals winter at the Salton Sea (Jehl, 1988; Jehl, 1996).

Between January and April 1992, approximately 150 000 eared grebes were found dead at the Salton Sea, and the principal cause is still unknown (Jehl, 1996). Prior to death, the birds were observed performing abnormal behaviors such as heavy preening and coming onto shore, and many appeared waterlogged, i.e. with wet plumage. Similar grebe dieoffs with mortalities numbering in the thousands also occurred during winter months of 1989, 1994, 1995 and 1997 (Jehl, 1996; NWHC, unpublished data). Large-scale mortality among eared grebes is not uncommon, but most mortality events are due to mass downings during migration and to common bird diseases (Jehl, 1983, 1996). During and after the 1992 mortality event, extensive studies were done by the National Wildlife Health Center to determine the cause of death. Although avian botulism and avian cholera were found in a small number of individuals, no significant viruses or bacteria were isolated from the majority of the eared grebes collected (Audet, 1992; Jehl, 1996). Also ruled out as causes of the dieoffs were organochlorine, organophosphorus and carbamate insecticides and salt toxicosis (Audet, 1992; Conference call notes, eared grebe dieoff 1994, unpublished memo, 25 February 1994, U.S. Fish and Wildlife Service). Some contaminants (e.g. selenium, mercury and chromium) were found in individuals collected from both the 1992 and 1994 events, but none were considered to be the causative agent (Conference call notes, eared grebe dieoff 1994, unpublished memo, 25 February 1994, U. S. Fish and Wildlife Service; Jehl, 1996). On the basis of a 1990 Salton Sea microcosm experiment in which very high densities of an unidentified species of *Prymnesium* occurred (M. Gonzalez, pers. com.), one of us suggested algal toxins as a possible cause (S. H. Hurlbert, discussion at U. S. Fish and Wildlife Service Salton Sea eared grebe die-off project status meeting, July 21–22, 1992, San Diego, California). This possibility eventually led to funding of several pilot projects of which the present study was one.

Algal toxins have been implicated in mortality events involving birds (Fritz et al., 1992; Beltrán et al., 1997; Henriksen et al., 1997), fish (Tangen, 1977; Roberts et al., 1983; Rosenberg et al., 1988; Burkholder et al., 1992; Montoya et al., 1996; Steidinger et al., 1998) and mammals (Anderson & White, 1989; Geraci et al., 1989; Hernandez et al., 1998). Several species of phytoplankton found in the Salton Sea have the potential to form toxic blooms. These include dinoflagellates, raphidophytes, and prymnesiophytes (Table 1). The species listed have either been implicated in mortality events in other systems (*Chattonella marina*, *Prorocentrum minimum*, and *Protoceratium reticulatum*) or are closely related to toxin-producing species (e.g. *Gymnodinium* sp., *Gyrodinium uncatenum*, *Heterocapsa niei*, *Prymnesium* sp., and *Chrysochromulina* sp.). Several of these species can be found in high densities (>1000 cells ml^{-1}) during particular times of the year at the Salton Sea. *Chattonella marina* (Raphidophyceae), a species that may be involved in mortality events at the Salton Sea, has been recorded at densities up to 600 cells ml^{-1} during summer months (Tiffany et al., 2001). This species was identified using scanning and transmission electron microscopy studies and was distinguished from *C. subsalsa* by its lack of mucocysts (see Tiffany et al., 2001). In a 1994 preliminary study, a sample dominated by an unarmored gymnodinioid dinoflagellate with some *Protoceratium reticulatum* (=*Gonyaulax grindleyi*) also present showed high activity in a mouse bioassay indicating the presence of a toxin (K. Steidinger, D. J. Faulkner, R. Dickey, unpublished data). The toxicity of phytoplankton at the Salton Sea, however, has not been fully investigated.

A survey of algal toxins in the Salton Sea was initiated in 1999. The goals of this study were to determine

Table 1. List of algal species found in the Salton Sea that produce toxins or are closely related to toxic species

Species found in the Salton Sea	Known toxic species	Toxin/type of toxin produced	Organism(s) affected	References
DINOPHYCEAE				
Gymnodinium sp.	*G. breve* Davis	brevetoxin	fish, molluscs, humans	Husain et al. (1996)
	G. catenatum Graham	PSP toxins	humans	Hallegraeff et al. (1989); Ikeda et al. (1989)
	G. galatheanum Braarud	not discussed	mussels, fish	Nielsen (1993)
	G. mikimotoi Adachi et Fukuyo	not discussed	shellfish, fish	Takayama & Adachi (1984); Matsuyama et al. (1999)
	G. pulchellum Larsen	neurotoxic, hemolytic, and hemagglutinative fractions	invertebrates, fish, humans	Steidinger et al. (1998) Onoue & Nozawa (1989)
	Gymnodinium sp., *G.* cf. *mikimotoi*	gymnodimine	fish	Seki et al. (1995); Mackenzie et al. (1996)
Gyrodinium uncatenum Hulburt	*G. aureolum* Hulburt	unknown	invertebrates, fish	Tangen (1977); Widdows et al. (1979); Jones et al. (1982); Dahl & Tangen (1993)
Heterocapsa niei Loeblich	*H. circularisquama* Horiguchi	unknown cell-surface protein	invertebrates, bivalves	Horiguchi (1995); Kamiyama & Arima (1997); Matsuyama et al. (1997, 1999)
Pfiesteria -like organism	*P. piscicida* Steidinger et Burkholder	unknown	fish, humans	Burkholder et al. (1992, 1995)
Prorocentrum minimum Schiller	*P. concavum* Fukuyo	DSP toxins	humans	Hu et al. (1993)
	P. lima (Ehrenberg) Dodge	DSP toxins	humans	Jackson et al. (1993); Hu et al. (1993); Quilliam et al. (1996)
	P. minimum	two unknown substances	bivalves, humans	Okaichi & Imatomi (1979); Lukenbach et al. (1993); Wikfors & Smolowitz (1993)
Protoceratium reticulatum (Claparede et Lachmann) Butschli[a]	*P. reticulatum*	yessotoxin	unknown	Mackenzie et al. (1998); Yasumoto & Satake (1998)
	G. polyedra Stein	homoyessotoxin	unknown	Tubaro et al. (1998)
RAPHIDOPHYCEAE				
Chattonella marina (Subrahmanyan) Hara et Chihara	*C. antiqua* (Hada) Ono	neurotoxins, superoxide radicals	fish	Tanaka et al. (1994); Kahn et al. (1996)
	C. marina	brevetoxin, superoxide radicals	fish	Onoue et al. (1990); Nakamura et al. (1998)
PRYMNESIOPHYCEAE				
Prymnesium sp.	*P. calathiferum* Chang et Ryan	unknown	shellfish, fish	Moestrup (1994); Moestrup & Thomsen (1995)
	P. parvum Carter	hemolytic compounds	tadpoles, fish, invertebrates	Shilo (1981); Moestrup (1994)
Chrysochromulina sp.	*C. leadbeateri* Estep, Davis, Hargraves et Sieburth	unknown	fish	Moestrup (1994); Moestrup & Thomsen (1995)
	C. polylepis Manton et Parke	hemolytic compounds	invertebrates, fish	Rosenberg et al. (1988); Yasumoto et al. (1990); Moestrup (1994)

[a]=*Gonyaulax grindleyi* Reinecke.

if and when algal toxins are present in the lake, and to document the composition of the phytoplankton at those times.

Methods

Five midlake stations (S-1, S-2, S-3, S-4 and S-5; see Watts et al., 2001) and three shoreline sites (North Shore, Bombay Beach and Red Hill) were visited biweekly from January to December 1999. Samples for taxonomic and toxicity analyses were collected when dense or unusual blooms were encountered or particular species were observed (Table 2). Five additional samples were collected when blooms were absent (Samples 11–14 and 16). Samples were also taken opportunistically at several other sites (Table 2). Measurements of temperature, specific conductance and dissolved oxygen concentration were taken in surface waters for nine of the samples collected (Samples 5, 6, 11, 14–16, 18, 19 and 27) using a YSI model UPG6000 Sonde. A factory-calibrated probe (accuracy: ±0.15 °C) was used for temperature measurements. Measurements of dissolved oxygen (accuracy: ±0.2 mg l^{-1}) were made using a probe that was calibrated using barometric pressure measured in the field and internally corrected for salinity using measurements of specific conductance (accuracy: ±5%).

In order to collect large samples of a wide variety of phytoplankton species, water samples were collected using four methods. In method 1, samples (10–13 l) were taken from algal films present on the lake surface using a film-concentrating device (Samples 5, 18, 19 and 29). This device consisted of 2 m-long thin strips of wood with polystyrene floats attached to either side of each wood strip. The device was floated on the surface and acted as a barrier allowing surface film to be concentrated. This method was used mainly to collect concentrated samples of a coccolithophore (*Pleurochrysis pseudoroscoffensis* Gayral et Fresnel) that occasionally was abundant on the surface of the Sea. In method 2, water samples (10–13 l) were collected from the top 50–100 cm of the water column (Samples 2, 4, 6–13, 17 and 25–28). This method was useful for collecting samples from dense blooms. All samples collected using methods 1 and 2 were centrifuged using an HN-SII (International Equipment Company) centrifuge at 2400 rpm to remove most of the water. The final concentrates were immediately frozen and stored at −80 °C until analyzed. Toxins have been recovered from cell samples of *Gymnodinium breve* concentrated in a similar manner, although complete recovery of the toxin was not possible due to the fragility of these cells (Sasner et al., 1972). Supernatants of several samples (Samples 17, 19, 25 and 26) were saved and also tested for toxicity. In method 3, large phytoplankton species were concentrated by filtering large amounts of water (50–450 l) through a 19–21 μm wire mesh filter (Samples 20–24). Because these concentrates contained large amounts of water, ethyl acetate was added to prevent bacterial growth. Samples were stored at 4 °C until analyzed. In method 4, water samples were taken from the top 50–100 cm of the lake and were not concentrated (Samples 14–16). Ethyl acetate was also added to these samples. This method was used to collect samples when blooms were absent. A foam fractionator was tested as an additional method (method 5) to concentrate algae (Samples 1 and 3), but it proved to be inefficient at separating algae from water and was no longer used.

Subsamples for enumeration were taken from each sample collected prior to centrifugation (methods 1 and 2) or addition of ethyl acetate (methods 3 and 4), preserved in 1% Lugol's solution and stored in the dark until analyzed.

Taxonomic analysis

Lugol's preserved phytoplankton samples were enumerated using the Utermöhl method (Lund et al., 1958). Preserved samples were settled in 25 ml settling chambers for at least 24 h before analysis (Hasle, 1978). Cells in two crossed diameters were enumerated using a Leitz inverted microscope at a total magnification of 400×. This represented the equivalent of 0.92 ml of unconcentrated lake water. When any given form was exceptionally abundant, 10–15 fields of view were enumerated. All cells larger than 5 μm in length were counted and identified to genus or species. Cell biovolumes were calculated by measuring at least 25 individuals of each species and using simple formulas for geometric shapes. Mean biovolume of each species is listed in Table 3.

Toxicity assessment

Sample extracts were first screened using a brine shrimp (*Artemia salina* Leach) lethality assay. This is a simple assay that is used as a surrogate to follow other properties such as cytotoxicity, toxicity, and antifungal activity. This assay is typically only used for screening purposes, and additional tests are needed

Table 2. Dates and locations of samples collected for toxicity analysis

Sample number	Date	Location[a]	Collection method	Geographic coordinates (N lat, W long)	Sample vol/wt[b]
1	1/7/99	GR	5	115° 35.73′; 33° 11.91′	450 mg
2	1/13/99	GR	2	115° 35.73′; 33° 11.91′	11 g
3	1/18/99	NS	5	115° 54.87′; 33° 30.11′	1.1 g
4	1/19/99	GR	2	115° 35.73′; 33° 11.91′	5.4 g
5[c]	2/28/99	west of S-4	1	115° 38.61′; 33° 16.21′	1.8 g
6	2/28/99	south of S-1	2	not taken	13 l/290 mg
7	2/28/99	S-4	2	115° 38.50′; 33° 16.30′	13 l/254 mg
8	2/28/99	NS	2	115° 54.87′; 33° 30.11′	13 l/350 mg
9	3/15/99	RH	2	115° 36.83′; 33° 11.72′	13 l
10	3/15/99	GR	2	115° 35.73′; 33° 11.91′	13 l
11	4/25/99	S-4	2	115° 38.50′; 33° 16.30′	13 l/125 mg
12	4/26/99	NS	2	115° 54.87′; 33° 30.11′	13 l/297 mg
13	4/26/99	BB	2	115° 43.99′; 33° 20.88′	13 l/220 mg
14	5/10/99	S-1	4	115° 55.00′; 33° 25.00′	16 l
15	5/10/99	S-3	4	115° 48.00′; 33° 18.00′	16 l
16	5/25/99	south of S-1	4	115° 53.79′; 33° 23.62′	16 l
17	5/26/99	GR	2[d]	115° 35.73′; 33° 11.91′	13 l/349 mg
18	6/20/99	near BB	1	115° 47.99′; 33° 23.04′	13 l
19	7/5/99	btwn S-3 & S-4	1[d]	115° 45.32′; 33° 17.48′	13 l
20	7/31/99	S-1	3	115° 55.00′; 33° 25.00′	57 l
21	8/1/99	BB	3	115° 43.99′; 33° 20.88′	450 l
22	8/8/99	RH	3	115° 36.83′; 33° 11.72′	3,000 l
23	8/8/99	BB	3	115° 43.99′; 33° 20.88′	3,000 l
24	8/8/99	NS	3	115° 54.87′; 33° 30.11′	1,500 l
25	8/17/99	NS	2[d]	115° 54.87′; 33° 30.11′	13 l
26	8/17/99	VH	2[d]	115° 54.87′; 33° 30.11′	13 l
27	8/29/99	RH	2	115° 36.83′; 33° 11.72′	16 l
28	10/19/99	east of S-4	2	115° 39.39′; 33° 17.22′	13 l
29	12/7/99	near S-4	1	115° 38.5′; 33° 16.3′	13 l

[a]NS North shore; BB Bombay Beach; RH Red Hill; GR Garst Road; VH Varner Harbor.
[b]Values for volume indicate volume of water processed; those for weight indicate dry weight of concentrated plankton sample.
[c]Sample for count analysis not collected.
[d]Supernatant from these samples was also tested for toxicity.

to determine the types and activities of any toxins that may be present. Therefore, extracts from some samples were also tested using a mouse bioassay. The mouse (*Mus musculus* Linnaeus) is one of the most widely used species in toxicology and is particularly suitable for acute toxicity studies when many animals may be needed (Gad & Chengelis, 1988). The principal advantage of using a mammalian bioassay is that the toxicity determination more directly relates to humans or other mammals (Fernandez & Cembella, 1995).

Extracts were prepared in the following manner at Scripps Institution of Oceanography (SIO). Frozen centrifuged algal samples were lyophilized and the dry residue subsequently weighed. The dried sample was triturated in methanol (ca. 100 ml g sample^{-1}) and the resulting suspension was filtered and then washed with methanol (ca. 200 ml g sample^{-1}). The filter plug was dried and washed with water (ca. 300 ml g sample^{-1}) and the filtrate was lyophilized. The methanol extracts were evaporated to dryness. The resulting residue was partitioned between ethyl acetate (ca. 200 ml g sample^{-1}) and water (ca. 200 ml g

Table 3. Mean biovolume for each taxa encountered in samples assayed for toxins

Species	Mean biovolume (μm^3)
Dinophyceae	
Gymnodinium sp. 1	8260
Gymnodinium sp. 2	9430
Gyrodinium uncatenum	17 500
Heterocapsa niei	656
Oxyrrhis marina	2550
Prorocentrum minimum	1120
Protoceratium reticulatum	44 700
Protoperidinum sp.	4570
scrippsielloids	8350
medium dinoflagellate	970
small dinoflagellates	562
Bacillariophyceae	
Chaetoceros muelleri var *subsalsum*	158
Cyclotella spp.	618
Cylindrotheca closterium	107
Entomoneis sp.	15 100
Fallacia sp.	1350
Navicula sp.	974
Pleurosigma ambrosianum	1210
Thalassionema sp.	337
Prymnesiophyceae	
Pleurochrysis pseudoroscoffensis	840
Raphidophyceae	
Chattonella marina	13 100
Prasinophyceae	
Tetraselmis sp.	741
Cryptophyta	
small cryptomonads	247
large cryptomonads	1010

sample^{-1}). The ethyl acetate partition was dried over sodium sulfate and the solvent evaporated to obtain the crude ethyl acetate extract. After evaporation of the residual ethyl acetate, the aqueous fraction was lyophilized. The combined aqueous extracts were placed on a freshly prepared Amberlite^{TM} XAD-2 column (ca. 10 cm^2 packing material g extract^{-1}) and desalted by washing with water (ca. 80 ml g extract^{-1}). The organic compounds were then washed from the column with methanol. Bulk water samples were extracted with ethyl acetate (typically 2 l ethyl acetate per 16 l water) and the extracts were treated in the manner described above. After weighing, each extract was assayed for brine shrimp lethality, and a ^{1}H NMR spectrum was recorded using a Varian Inova 300 MHz NMR spectrometer.

Brine shrimp lethality assays were performed at SIO using a modification of the methods of Meyer et al. (1982) and Solis et al. (1993). Extracts were dissolved in a 15% aqueous dimethyl sulfoxide (DMSO) or methanol solution to obtain a final concentration of 1.33 mg ml^{-1}. Replicates (2) were diluted to 400, 200, 100, or 50 μg ml^{-1} in the wells of a 96 well micro titer plate. Negative control sample wells (8) were created by duplicating the solvent system. Approximately 15 shrimp nauplii were added to each well. Mortality was monitored at intervals of 2, 4, 6, 12 and 24 h and was reported as percent mortality at 24 h. The activity of samples was labeled 'high' if they showed 100% mortality across all concentrations in at least one fraction. The activity of samples was considered 'low' if at least one concentration showed greater than 10% mortality. Samples with less than 10% mortality across all concentrations were considered inactive.

Mouse bioassays were performed at the National Wildlife Health Center (NWHC). Sample extracts were diluted to 1 mg ml^{-1} in DMSO for inoculation into ICR female mice (15–20 g) purchased from Harlan Sprague Dawley. Using a 1cc syringe and 25 g needle, 0.1 ml of each of the diluted extracts were inoculated intraperitoneally into each of three mice. Control mice were inoculated with 0.1 ml of DMSO. The mice were observed for signs of morbidity for 30 min post-inoculation and daily thereafter for 5 days. Samples were considered toxic if all three mice became sick or died. Samples, which resulted in mouse death, were diluted and re-tested in mice to approximate the total toxicity of the sample.

Results

Provenance and nature of samples

A total of 29 samples was collected for toxicity analysis (Tables 2 and 4). Dinoflagellates and diatoms were the dominant phytoplankton groups in 69% and 21% of these samples, respectively (Table 4). Other samples were dominated by a prymnesiophyte (*Pleurochrysis pseudoroscoffensis*, 7%) and a raphidophyte

Table 4. Taxonomic composition and activity of samples collected for toxicity analysis. NT not tested; ND no data

Sample number and dominant species		Percent of total biovol.	Subdominant species	Percent of total biovol.	Phytoplankton biovolume (10^6 μm^3 ml^{-1})	Toxicity to: brine shrimp	Mice
DINOPHYCEAE (69%)							
8	*Gymnodinium* sp. 1	35	*Heterocapsa niei*	13	11	low	NT
	G. uncatenum	33	*P. ambrosianum*	9			
27	*Gymnodinium* sp. 2	>99			2500	low	NT
1	*G. uncatenum*	99			390	none	NT
2	*G. uncatenum*	>99			2400	low	none
3	*G. uncatenum*	59	*Heterocapsa niei*	18	34	low	none
			Gymnodinium sp. 1	13			
			P. minimum	1			
4	*G. uncatenum*	>99			1100	NT	NT
6	*G. uncatenum*	82	*Gymnodinium* sp. 1	10	14	low	NT
7	*G. uncatenum*	94	*Cyclotella* spp.	4	80	low	NT
9	*G. uncatenum*	96			97	low	NT
10	*G. uncatenum*	99			600	NT	NT
13	*G. uncatenum*	90	*P. minimum*	1.0	22	low	NT
14	*G. uncatenum*	32	*Cyclotella* spp.	17	1.1	low	NT
			C. closterium	12			
			Thalassionema sp.	12			
			P. minimum	6			
15	*G. uncatenum*	56	*C. closterium*	12	2.2	low	NT
			Thalassionema sp.	10			
			P. minimum	2			
17	*G. uncatenum*	31	*P. reticulatum*	20	14	low	NT
			Fallacia sp.	19			
			Thalassionema sp.	17			
20	*P. reticulatum*	87	*Chattonella marina*	6	200[a]	low	NT
21	*P. reticulatum*	74	*Chattonella marina*	19	20[a]	low	NT
23	*P. reticulatum*	84	*Entomoneis* sp.	4	50	sample	lost
			scrippsielloids	3			
24	*P. reticulatum*	92	*Navicula* sp.	4	340	sample	lost
26	small dinoflagellates	82	*Chattonella marina*	14	130	high	none
19	scrippsielloids	90	*P. pseudoroscoffensis*	9	210[a]	low	none
BACILLARIOPHYCEAE (21%)							
22	*Entomoneis* sp.	70	*Fallacia* sp.	12	87	sample	lost
			P. reticulatum	8			
29	*Gyrosigma balticum*	38	*G. uncatenum*	26	28	NT	NT
			Entomoneis sp.	17			
28	*P. ambrosianum*	52	*G. uncatenum*	25	15	NT	NT
			Thalassionema sp.	9			
11	*Thalassionema* sp.	41	*G. uncatenum*	19	3.9	NT	NT
			P. ambrosianum	16			
			Cyclotella spp.	11			
12	*Thalassionema* sp.	44	*Cyclotella* spp.	14	0.7	low	NT
			C. closterium	11			
16	*Thalassionema* sp.	38	*Oxyrrhis marina*	11	8.4	low	NT
	G. uncatenum	31	*C. closterium*	6			
PRYMNESIOPHYCEAE (7%)							
5[b]	*P. pseudoroscoffensis*	ND	ND	ND	ND	low	none
18	*P. pseudoroscoffensis*	90	scrippsielloids	10	960[a]	low	none
RAPHIDOPHYCEAE (3%)							
25	*Chattonella marina*	79	*P. pseudoroscoffensis*	7	190	low	none
			Heterocapsa niei	6			

[a]These samples were concentrated during collection and do not represent densities present in lakewater.
[b]*P. pseudoroscoffensis* was determined to be the dominant species in a qualitative analysis.

Table 5. Surface water measurements of physical parameters at locations where samples for analysis of algal toxins were taken

Dominant group and sample number	Approx. time of collection (PST)	Temp. (°C)	Dissolved oxygen (mg l^{-1})	Estimated oxygen % saturation[a]	Salinity (g l^{-1})	pH
Dinophyceae						
6	1000	17	16	210	41.4	8.8
14	0900	20	4	48	40.7	8.4
15	1100	20	7	93	40.8	8.4
19	1100	31	13	210	41.3	8.8
27	1300	35	10	180	42.6	8.4
Bacillariophyceae						
11	1300	21	10	130	39.8	8.5
16	0900	24	8	120	41.7	8.4
Prymnesiophyceae						
5	1400	21	18	240	39.3	8.8
18	1400	34	11	190	42.1	8.5

[a]Estimated with UPG6000 Sonde calibrated using temperature, salinity and barometric pressure.

(*Chattonella marina*, 3%). Temperature, pH and specific conductance were within typical ranges for the location and time of year each sample was collected (Table 5; Watts et al., 2001). The surface water of most areas sampled, however, contained high concentrations of dissolved oxygen and was often supersaturated (Table 5).

Several types of blooms were observed throughout the year at the Salton Sea. An extensive (along at least 10.5 km of the shoreline) and long-lived (approximately three months) bloom of *Gyrodinium uncatenum* occurred along the southeastern shoreline during 1999. Samples taken during these three months (January, February and March) from one location a few kilometers from the mouth of the Alamo River (Garst Road) ranged in density from 6500 to 260 000 cells ml^{-1}. Samples taken in January at other locations along the southern shoreline ranged in density from 1000 to 310 000 cells ml^{-1} (Reifel, 2001). Although all samples were dominated by *G. uncatenum*, high numbers of diatoms (*Cylindrotheca closterium* [Ehrenberg] Lewin et Reimann and *Cyclotella* sp.) were also present in several samples. These diatoms are small in size and do not contribute substantially to total phytoplankton biovolume. The bloom of *G. uncatenum* was also present at Garst Road in January 2000 and January 2001 at densities ranging from 14 000 to 17 000 cells ml^{-1}. Annual blooms of this species have also been documented in other systems (Tyler et al., 1982). Because this bloom occurred over a large area during winter months when eared grebes and other migratory birds are present at the Salton Sea, samples were collected on several dates in January and March 1999 for toxicity analysis (Samples 1, 2, 4, 9 and 10). These samples were dense (up to 2400 × 10^6 μm^3 ml^{-1}), and *Gyrodinium uncatenum* made up 96–99% of total phytoplankton biovolume (Table 4).

Surface films containing high densities of the coccolithophore *Pleurochrysis pseudoroscoffensis* were observed between February and August (Reifel et al., 2001). These films were predominantly present on calm days, and during these blooms, surface waters contained high amounts of dissolved oxygen and were usually supersaturated (Table 5). Densities from two samples (Samples 18 and 19; Table 4) represent densities of artificially concentrated surface samples. Densities of the species present were certainly lower in the water column. Values for Sample 25 represent natural densities in the top portion of the water column. Samples from these surface films typically contained high densities of one or two other species (scrippsielloid dinoflagellates, *Heterocapsa niei*, *Chattonella marina*), and in some samples these species outnumbered *P. pseudoroscoffensis*. Because cells

of this species are small (10–14 μm in diameter), on a biovolume basis some samples were dominated by other species (Table 4).

Localized blooms, characterized by their small areal extent, have also been documented at the Salton Sea both in this study and in past studies (Carpelan, 1961). These blooms typically occur in the sheltered harbors and embayments around the shore of the Salton Sea. In August 1999, for example, a small dinoflagellate reached a density of 110 000 cells ml^{-1} inside Varner Harbor making up 82% of the total biovolume density of $130 \times 10^6 \mu m^3$ ml^{-1} (Sample 26, Table 4). It was not, however, observed in a sample collected just outside the mouth of the harbor (Sample 25). Localized blooms also occur in thin bands along the shoreline. An unidentified species of *Gymnodinium* (*Gymnodinium* sp. 2) formed a red band approximately 0.5 m wide along the shoreline of Red Hill Marina in August 1999. Within this band, greater than 99% of the total phytoplankton biovolume consisted of this species, and it reached a numerical density of 270 000 cells ml^{-1} (Sample 27, Table 4). Water in this band was supersaturated with oxygen (Table 5).

Although the identity of the small dinoflagellate, *Gymnodinium* sp. 2 and the scrippsielloid dinoflagellates are currently unknown, the morphological characteristics of these species can be compared with species that have been identified from the Salton Sea allowing speculations on the identity of these unknown dinoflagellates. In a recent survey of dinoflagellates in the Salton Sea, 22 different species were identified (K. Steidinger, pers. com.). Several scrippsielloid dinoflagellates including *Scrippsiella trochoidea* (Stein) Loeblich, *Bysmatrum* sp. and *Pentapharsodinium* sp. were identified during the study. It is difficult, however, to distinguish these species under the light microscope during count analysis; therefore, scrippsielloid dinoflagellates were combined during enumeration. Cells of the small dinoflagellate average 20 μm in length, 16 μm in width and are flattened dorsoventrally. Cells of *Gymnodinium* sp. 2 are unarmored and average 29 μm in length and 25 μm in width. In both species, morphological characteristics include an equatorial cingulum with little or no displacement and rounded epitheca and hypotheca. Of the species identified from the Salton Sea, *Kryptoperidinium* cf. *foliaceum* (Stein) Lindermann is most similar in morphology to the small dinoflagellate, but the identity of this dinoflagellate has not been confirmed. Several *Gymnodinium* species have been identified from the Salton Sea including *G. sanguineum* and at least three new species. Descriptions of most of these species, however, do not match that of *Gymnodinium* sp. 2. *Gymnodinium* sp. 2 may be one of the new species noted by Steidinger. It is also possible that this species was not present in samples examined by her.

Three known toxic species were observed in several samples. Four samples were dominated by or contained high densities of *Protoceratium reticulatum*, *Chattonella marina* or both (Samples 17, 20, 21 and 25; Table 4). Another species known to produce toxins, *Prorocentrum minimum*, was present in several samples (Samples 3, 13, 14 and 15). High densities of this species, however, were not observed, and when it was present, it made up very small proportions of the total phytoplankton biovolume (Table 4).

Toxicity analyses

All samples tested except one (Sample 1) were active in the brine shrimp lethality assay, although the level of activity varied (Table 4). Several samples were not tested in the brine shrimp lethality assay either because they were dominated by species that had already been tested (Samples 4 and 10), were dominated by species that are not considered to be potentially toxic (Samples 28 and 29) or because not enough material was collected (Sample 11). Also, three samples (Samples 22, 23 and 24) were discarded due to bacterial growth. Most samples tested showed a low level of activity, and ^{1}H NMR spectra from these samples contained mainly fats and sterols, and did not indicate the presence of compounds with structures that resemble known algal toxins such as NSP toxins (brevetoxins), PSP toxins or ASP toxins (domoic acid). Only Sample 26 had a high level of activity when tested in this assay. The ^{1}H NMR spectrum of this sample was extremely complex; however, during fractionation, the active material was lost probably through polymerization. No sample tested using the mouse bioassay showed activity (Table 4).

The cause of the low level of activity is at this point unknown. ^{1}H NMR spectra of most samples contained signals in the aromatic region of the spectrum. Although conclusions based on these data are only speculative, some of these unidentified aromatics could have been pesticides that potentially enter the Sea through agricultural wastewater. Brine shrimp are sensitive to minute concentrations of pesticides, reacting within 2–18 h to concentrations of 0.01 parts per million (Anonymous, 1955; Michael et al., 1956;

Tarpley, 1958; Areekul & Harwood, 1960). Low levels of pesticides potentially present in the water column may be responsible for the consistent low level of activity in the brine shrimp lethality assay.

Discussion

Toxicity of algal blooms

These results suggest that, in general, the dominant phytoplankters at the Salton Sea do not produce toxins. Both the brine shrimp lethality assay and mouse bioassay have been used to detect toxins of many phytoplankton species including dinoflagellates, raphidophytes and prymnesiophytes. The brine shrimp assay can detect a wide range of compounds with diverse structures and modes of activity, and is a more general test than other assays that have been used to detect plant extracts (Meyer et al., 1982). In addition, brine shrimp are not affected by high salinity such as that found in the Salton Sea. The mortality of brine shrimp is greatly increased when exposed to toxic phytoplankton species but not when exposed to non-toxic species, and this effect is more pronounced in larvae (Edvardsen, 1993; Demaret et al., 1995; Lush & Hallegraeff, 1996). Behavioral changes such as swimming upside down, uncoordinated swimming and cessation of swimming have also been noted in brine shrimp exposed to toxic algal species or extracts of algal toxins (Trieff et al., 1973; Demaret et al., 1995; Lush & Hallegraeff, 1996).

Methods to detect ciguatera from fish tissue extracts and whole cells of *Gymnodinium breve* with a brine shrimp assay were put forth in the 1970s (Trieff et al., 1973; Granade et al., 1976), and variations of this assay continue to be used to detect algal toxins (Edvardsen, 1993; Demaret et al., 1995; Lush & Hallegraeff, 1996). The effect of algal toxins on brine shrimp is more rapid than on other zooplankton species such as ciliates or copepods (White, 1981), and Demaret et al. (1995) suggested the use of brine shrimp as an easy, sensitive and cost effective ecotoxicological test for monitoring algal toxins. Although activity in this assay may have been influenced by the presence of other compounds such as pesticides present in samples, the presence or absence of algal toxins can be clarified by using additional assays and by examining ^{1}H NMR spectra of the samples.

Mammalian bioassays are still the most common methods used for analysis of algal toxins and are useful for detecting unknown or poorly defined toxic components (Fernandez & Cembella, 1995). The mouse bioassay has been used to detect paralytic shellfish poisoning (PSP) toxins in extracts from shellfish since the 1930s (Sommer & Meyer, 1937; Fernandez & Cembella, 1995), and the procedure was first published as an official method of the Association of Official Agricultural Chemists in 1960 (Erwin, 1970). A mouse bioassay of toxins from *Gymnodinium breve* was also developed in the 1960s (McFarren et al., 1965; Erwin, 1970). When injected with extracts containing PSP toxins, diarrhetic shellfish poisoning (DSP) toxins, amnesic shellfish poisoning (ASP) toxins (domoic acid) or neurotoxic shellfish poisoning (NSP) toxins (brevetoxins), mice typically undergo certain defined behavioral changes before death, and the effects of many of these toxins on the physiology and internal organs of mice have been described (Sommer & Meyer, 1937; McFarren et al., 1965; Sasner et al., 1972; Iverson et al., 1989; Terao et al., 1990; Work et al., 1993; Fernandez & Cembella, 1995).

High levels of certain metals and low pH can induce mouse death and lead to artifacts in the PSP bioassay, and interference by free fatty acids can yield false positive reactions in assays for DSP toxins (Takagi et al., 1984; McCulloch et al., 1989; Fernandez & Cembella, 1995). These problems, however, were not apparent in the current study due to the fact that behavioral changes or mortality were not observed in the mice. High amounts of salts (mainly Na^{+} ions) dissolved in extracts can decrease apparent toxicity in the mouse bioassay (Shantz et al., 1958). Water washing steps during the extraction process, however, can remove salts (Fernandez & Cembella, 1995), and most salts were likely removed in the desalting step during extraction of Salton Sea samples. Although common algal toxins such as those listed above are routinely detected using mouse bioassays, it is possible that one or more toxins were present and were not detected in the mouse bioassay. Ogata & Kodama (1986) found evidence of an icthyotoxic cytotoxin in the cultured media of *Protogonyaulax* sp. that caused death in fish but was not detected in a mouse bioassay. Also, Beltrán et al. (1997) were unable to detect domoic acid in many of their samples using mouse bioassay due to the low concentrations present. It is unlikely that algal toxins went undetected in the brine shrimp lethality assay due to its high sensitivity to a wide range of compounds, and the ^{1}H NMR spectra of most samples collected showed no indications of the presence of algal toxins. Although the whole water samples and supernatants

tested did not show evidence of containing toxins, water-soluble toxins produced by algae and actively excreted into the surrounding water may not have been detected in this study.

Throughout the current study, only one bloom occurred that might have been toxic (Sample 26, Table 4). This bloom was dominated by a small dinoflagellate possibly *Kryptoperidinium* cf. *foliaceum*. The bloom was localized and was observed during the summer when the majority of migratory birds are not present at the Salton Sea. The samples taken during this study are indicative of both bloom and non-bloom conditions and of all seasons throughout the year. Other toxic blooms may have occurred, but these types of blooms would have to have been present only rarely, if at all, to be missed by the sampling regime. Thus we find no evidence that algal toxins were likely to have caused the eared grebe mass mortality events or other large dieoffs of fish or birds at the Salton Sea.

Three species known to produce toxins in other systems (*Prorocentrum minimum, Protoceratium reticulatum,* and *Chattonella marina*) were observed in several samples. These samples, however, showed no evidence of containing toxins in both the mouse and brine shrimp assays and in analysis of their ^{1}H NMR spectra. Toxins produced by both *P. minimum* and *P. reticulatum* have affected humans by accumulating in shellfish (Kat, 1979; MacKenzie, 1998; MacKenzie et al., 1998). Because no shellfish are present in the Salton Sea, any toxins produced could not be accumulated in this manner. Also, not all strains of *P. minimum* are toxic (Grzebyk et al., 1997). Although *P. reticulatum* was observed in the 1994 toxic sample, all samples containing this species collected during the present study were inactive. The toxicity in the 1994 sample was most likely due to the unidentified gymnodinioid, based on the results of this study.

P. minimum has also directly been responsible for fish kills at high cell concentrations (8000–45 000 cells ml^{-1}) when it composed over 90% of the phytoplankters (Rabbani et al., 1990). Although this species has been observed in high densities (up to 6700 cells ml^{-1}; Reifel, 2001), it is generally present in much smaller concentrations in the Salton Sea (up to 370 cells ml^{-1}) and only rarely composed more than 10% of the total phytoplankton biovolume (Table 4, unpublished data). If *P. minimum* in the Salton Sea is producing toxins, they may not be detectable at such low cell concentrations.

Chattonella marina is present during most of the summer at densities ranging from 10 to 600 cells ml^{-1} (Tiffany et al., 2001) and was observed at densities up to 12 000 cells ml^{-1} in this study. This species has been responsible for major fish kills in other systems (Imai & Itoh, 1987; Marshall & Hallegraeff, 1999). Though it has been shown to produce toxins (Onoue et al., 1990; Endo et al., 1992; Ahmed et al., 1995), the mechanism by which it kills fish is poorly understood and may involve the production of superoxide radicals (Hallegraeff, 1993; Hallegraeff & Hara, 1995; Nakamura et al., 1998).

Future blooms?

These results are not easily extrapolated into the future. The Salton Sea is changing, and the composition of its microflora will change, subtly or dramatically, with it. The best-documented and easily predictable environmental change is an increase in salinity. For constant lake level conditions, this is likely to be about 0.3 g l^{-1} y^{-1} (S. Hurlbert & P. Detwiler, unpublished data). In general, a large salinity increase could be expected to reduce the number of algal taxa capable of thriving in the Salton Sea and hence the number of potentially toxic taxa. Toxic algal blooms are virtually unknown from highly saline (>50–60 g l^{-1}) lagoons or lakes.

But in any predicted scenario, the results are unpredictable given our present state of knowledge. For example, in a microcosm experiment with Salton Sea water and plankton assemblages, the experimental elevation of salinity from 39 to 48 g l^{-1} resulted in a 10–100-fold increase in the density of an unidentified species of *Prymnesium* (M. Gonzalez, pers. com.). *Prymnesium* is now scarce in the Salton Sea, where the current salinity is 40–44 g l^{-1} (Watts et al., 2001; Tiffany et al., unpublished data), but clearly we cannot be sure it will remain so after salinity has risen by another 4 g l^{-1}. Phytoplankton blooms may also be altered by salinity-induced changes in the upper levels of the food web. As increasing salinity alters abundances or eliminates fish and zooplankton species that feed on phytoplankton or each other, phytoplankton composition and abundance are likely to be affected in consequence.

Algal toxins and eared grebe mortality

It is unlikely that any known algal toxin was responsible for mortality in eared grebes at the Salton Sea. There are a few references to bird mortality during red tides (e.g. Rowan, 1962; McFarren et al., 1965), but only one algal toxin, domoic acid, has been implicated

in mortality events of birds. Diatoms in the genera *Nitzschia* and *Pseudonitzschia* are capable of producing domoic acid, which has not only caused mortality of brown pelicans and cormorants (Fritz et al., 1992; Work et al., 1993; Beltrán et al., 1997), but has been implicated in human illness as well (Perl et al., 1987; Wright et al., 1989; Perl et al., 1990; Teitelbaum et al., 1990; Horner et al., 1996). No *Pseudonitzschia* species have been identified from the Salton Sea. Several species of *Nitzschia* have been observed in samples, but they are not common members of the planktonic community and none are known to produce domoic acid in other systems (Lange & Tiffany, 2002). Birds affected by domoic acid show characteristic central nervous system abnormalities including unusual head movements, scratching, disorientation, difficulty in swimming and eventually the loss of their righting reflex (Work et al., 1993; Beltrán et al., 1997). Although the intense preening behavior observed in eared grebes during the Salton Sea mortality events may correlate to the scratching behavior noted in bird mortality due to intoxication of domoic acid, eared grebes did not exhibit any other behaviors characteristic of central nervous system damage. The preening behavior of eared grebes is likely a function of other factors described below.

Several cyanobacterial toxins, the neurotoxic anatoxin-a and anatoxin-a(s) and the hepatotoxic microcystins and nodularins, have also been implicated in bird mortality. Anatoxin-a and anatoxin-a(s) have been detected in blooms of cyanobacteria including species in the genera *Anabaena, Aphanizomenon* and *Oscillatoria*, and have been associated with poisonings of fish, dogs, sheep, birds and humans (Cook et al., 1989; Carmichael, 1994; Henriksen et al., 1997). Hepatotoxic peptides can be produced by species in the genera *Anabaena, Microcystis, Nodularia, Nostoc* and *Oscillatoria* and have also been involved in mortality of dogs, sheep, cattle, fish and birds (Carmichael, 1995). Cyanobacterial species capable of producing toxic blooms typically occur in warm (15–30 °C), freshwater habitats (Carmichael, 1994, 1995). Of these potentially toxic genera, only *Oscillatoria* has been identified from the Salton Sea (Wood et al., 2002).

Typical symptoms of intoxication by anatoxin-a include muscle twitching and cramping and eventually death by paralysis of the respiratory muscles. In addition to these symptoms, anatoxin-a(s) can cause excessive salivation in vertebrates (Carmichael, 1994; Henriksen et al., 1997). Clinical signs of anatoxin poisonings in ducks include diarrhea, muscle tremors, leaning, labored or difficult respiration and wing and leg paralysis (Cook et al., 1989). Symptoms of intoxication by hepatotoxins produced by cyanobacteria in birds include eye blinking, restlessness and defecation (Carmichael, 1995). None of these symptoms was noted during the eared grebe dieoffs. It is, therefore, unlikely that cyanobacterial toxins were involved in these mortality events.

Toxins produced by several species found in the Salton Sea such as *Protoceratium reticulatum* and *Prorocentrum minimum*, and toxins that affect birds such as domoic acid typically affect other organisms by accumulating in shellfish such as mussels and oysters. Although shellfish are not found in the Salton Sea, the transfer of toxins to eared grebes through other organisms is possible. Herbivorous zooplankters, including copepods, cladocerans and barnacle nauplii, are capable of ingesting toxic phytoplankton species and retaining algal toxins, and transfer of toxins through zooplankton has been suggested as a possible cause of mortality of zooplanktivorous fish (White, 1980; White, 1981; Robineau et al., 1991). Domoic acid, transferred to humans through shellfish, is most likely transferred to birds through accumulation in planktivorous fish such as anchovy and mackerel (Work et al., 1993; Beltrán et al., 1997). Eared grebes typically feed on bottom-dwelling invertebrates (Cramp & Simmons, 1977; Jehl, 1988) and feed primarily on the polychaete worm *Neanthes succinea* Frey et Leukart at the Salton Sea. Extracts of samples of *N. succinea*, however, were inactive in the brine shrimp lethality assay, and ^{1}H NMR spectra showed no indication of the presence of toxins. Several other bird species and species of fish also feed heavily on *N. succinea*, and these species were not involved in the eared grebe mortality events. It is therefore unlikely that algal toxins were transferred to eared grebes through their food source.

Possible roles of phytoplankton blooms in eared grebe mortality

Although known algal toxins were likely not at the root of the 1992 and 1994 eared grebe dieoffs and toxins did not appear to accumulate in their major food source, phytoplankton blooms may have been involved in these events. Other possible mechanisms of phytoplankton involvement include (1) ingestion of toxins excreted by algae into the water and adsorbed onto feathers and (2) reduction of surface tension resulting in waterlogging and hypothermia.

Grebes are noted for plucking and ingesting their own feathers, and the amount of feathers in the stomach can vary with changes in body mass and food intake (Simmons, 1956; Jehl, 1988). The function of feather ingestion in grebes is not well understood (Jehl, 1988), but many theories have been suggested (e.g. Lawrence, 1950; Madsen, 1957; Storer, 1961; Fjeldsä, 1973). Although correlations between duration and intensity of preening with the amount of feathers ingested have not been explored, feathers tend to be swallowed during self-preening (Simmons, 1956; Fjeldsä, 1973; Cramp & Simmons, 1977). If toxins were involved in the Salton Sea eared grebe mortality events, feathers, rather than a food source, may have acted as the vector. Algal toxins present in the surface layer could be adsorbed onto feathers that may then have been swallowed during preening behaviors resulting in intoxication.

Eared grebes may also have been affected by changes in surface tension caused by algal blooms. Phytoplankton release a large number of organic compounds extracellularly into water, including ones of low molecular weight such as organic acids and organic phosphates, and others of high molecular weight such as carbohydrates, peptides, and a number of growth-inducing and growth-inhibiting compounds (Wetzel, 1983). Species in all major algal groups have been shown to exude compounds of high molecular weight into their environments that cause a reduction in surface tension (Hoyt, 1970). In calm waters, algal blooms or dissolved organic compounds released by phytoplankton can form surface slicks where surface tension is reduced (Sieburth & Conover, 1965; Williams, 1967). Extracts of algal concentrates dominated by dinoflagellates such as *Gyrodinium uncatenum, Gymnodinium* sp. and scrippsielloid dinoflagellates, the raphidophyte *Chattonella marina*, the prymnesiophyte *Pleurochrysis pseudoroscoffensis* and mixed samples containing several dinoflagellate species consisted mostly of fats. Extracts of whole water samples that were not concentrated also consisted mainly of fats. If released into the surrounding water, these compounds could cause reductions in surface tension.

The ability of aquatic birds to waterproof their feathers is only partly due to natural oils. Feathers themselves, which are made of keratin, repel water (Stephenson, 1997). Elder (1954) showed that natural oils are not critical for water-repellency and probably function to keep feathers supple and structurally intact. Surface tension, however, is a critical factor to the waterproofing properties of avian plumage (Swennen, 1978; Stephenson, 1997). If the surface tension of a body of water is reduced to a critical level (38–50 mN m^{-1}), the natural spacing of the barbs on the feathers will no longer be optimal, and the feathers will admit water (Stephenson, 1997; Stephenson & Andrews, 1997). Also, once water has penetrated the feathers, birds must leave the water long enough for the feathers to dry out; removal of water by preening will only temporarily restore the insulating air layer (Stephenson, 1997). Mortality of birds has been observed during blooms of particular diatom species that produce an oily film on the water surface and adhere to feathers (Grøntved, 1952; Hasle & Fryxell, 1995).

Grebes would be particularly susceptible to changes in surface tension for several reasons. Many diving and swimming birds propel themselves underwater with large feet attached to short legs situated far back on the body (Ehrlich et al., 1988). The position of their legs makes grebes powerful swimmers but virtually unable to walk or move quickly on land (Proctor & Lynch, 1993). Eared grebes also rarely fly and tend to escape danger by diving or running over the surface of the water (Jehl, 1997). Most birds immediately leave the water after becoming wetted (Swennen, 1978). If, however, a large algal bloom in the Salton Sea caused a change in surface tension, grebes would remain in the water much longer than other birds because of their poor ability to move on land. Increased preening activity is also required to dry and maintain the wetted feathers (Fabricius, 1956). A change in surface tension causing grebes to become wetted would explain why many birds appeared to be waterlogged, why they engaged in heavy preening and why they eventually came onto shore during the 1992 and 1994 die-off events. Intense preening was also observed during mortality events in 1997 and 1998 involving Clark's and western grebes in Tulare Lake Basin, California possibly as a result of changes in surface tension due to oils released by decaying fish (R. Hansen, pers. com.).

Although the cause of death during these mortality events was not initially determined, we now suspect the eared grebes died from hypothermia (NWHC, unpublished data). From January to March, when the dieoffs took place, mean water temperatures in the Salton Sea range from 12–18 °C (Watts et al., 2001), and mid-lake surface water (0–3 m) phytoplankton is abundant (5–73 μg chl *a* l^{-1}; Tiffany et al., unpublished data), and even denser blooms are observed nearshore (see above). When birds become wetted, they lose their plumage air layer and the ensuing el-

evated rate of heat loss can cause hypothermia (Stephenson & Andrews, 1997). Death due to hypothermia could be explained if grebes became waterlogged after experiencing a reduction in surface tension and remained in cold water long enough for their body temperatures to drop to a critical level.

Non-involvement of other species

Between 65 000 and 700 000 eared grebes visit the Salton Sea each year making it the most numerous waterbird during winter months (Jehl, 1988; Ogden, 1996; Jehl, 1996). Other swimming and diving waterbirds including cormorants, pelicans and ducks and other grebe species including the western grebe (*Aechmophorus occidentalis* Lawrence) and Clark's grebe (*Aechmophorus clarkii* Lawrence) are also present at the Salton Sea during the winter (McCaskie, 1970; Shuford et al., 1999). Significant mortality in these species, however, was not noted during the eared grebe mortality events. Eared grebes may be more susceptible to ingestion of toxins adsorbed onto feathers or changes in surface tension due to their behavior and habitat use. And although many of these other species are quite common at the Salton Sea during winter, none reaches densities noted for the eared grebe. Die-offs of these waterbirds would thus be less noticeable.

Waterbirds such as cormorants, ducks and pelicans, who are also unable to move well on land, may have avoided the effects of large phytoplankton blooms in several ways. Cormorants have 'wettable' feathers and regularly leave the water and engage in wing-spreading behaviors thought to aid in drying the feathers once they are wet (Ehrlich et al., 1988). Large numbers of cormorants are regularly observed perched in dead trees nearshore many with their wings spread (K. Reifel., pers. observ.). Changes in surface tension would not affect these common members of the Salton Sea bird community. At least 16 species of diving ducks have been identified from the Salton Sea, and over 30 000 white pelicans are present during the winter (Shuford et al., 1999). Although these species may be at risk when changes in surface tension occur, they also regularly use the wetlands and small freshwater lakes near the Salton Sea. These areas may serve as refuges allowing these species to escape the effects of a change in surface tension.

It is possible that only eared grebes were involved in the mortality events due to their size, behavior or habitat use. Although both Clark's and western grebes are also common during winter months (Shuford et al., 1999), the impact of phytoplankton blooms may not be as great on these species. Both are considerably larger than the eared grebe and would, therefore, not succumb to hypothermia as quickly. The horned grebe (*Podiceps auritus* Linnaeus) prefers shallow feeding areas (0.3–1.5 m; Fjeldsä, 1973), and eared grebes likely have the same preference. They are generally concentrated nearshore (within 0–2 km) during the day where they engage in diving and foraging behaviors. Large numbers of western and Clark's grebes, which are largely piscivorous, however, have been observed farther offshore (K. Reifel, pers. observ.). These species may be able to escape nearshore phytoplankton blooms by utilizing offshore habitats making them less susceptible to waterlogging and hypothermia or ingestion of toxins while swallowing feathers.

Conclusions

Although phytoplankton blooms in the Salton Sea do not at present seem to produce toxins in significant quantities, they are likely involved in large mortality events such as the eared grebe dieoffs. Before algal toxins can be ruled out as a major cause of the eared grebe mortality events, several factors including the possible toxicity of species that did show activity both in this study and in past studies, the potential of species known to produce toxins in other systems to produce toxic blooms in the Salton Sea, and the potential for phytoplankton to produce and actively excrete water-soluble toxins must be investigated. Several potential mechanisms for the transfer of toxins from phytoplankton to fish and birds including accumulation of toxins in organisms such as zooplankton and ingestion of toxins adsorbed onto feathers have been suggested and require further exploration. These mechanisms, however, become impossible if phytoplankton species in the Salton Sea do not produce toxins. The large dieoffs of eared grebes can also be explained if dissolved organic compounds released by algal blooms present in late winter caused changes in surface tension.

Acknowledgements

The authors would like to thank Brandon Swan, James Watts, and Paul Detwiler for their assistance in field collections. This project was made possible in part

by a grant from Sigma Xi and supported by the Salton Sea Research Management Committee and the Salton Sea Science Subcommittee. The research described in this article has been funded in part by the United States Environmental Protection Agency through grant #R826552-01-0 to the Salton Sea Authority. The research results have not been subjected, however, to the Agency's required peer review and do not necessarily reflect the views of the Agency. Therefore, no official endorsement should be inferred.

References

Ahmed, M. S., O. Arakawa & Y. Onoue, 1995. Toxicity of cultured *Chattonella marina*. In Lassus, P., G. Arzul, E. Erard, P. Gentien & C. Marcaillou (eds), Harmful Algal Blooms. Lavoisier, Intercept Ltd., New York: 499–504.

Anderson, D. M. & A. W. White, 1989. Toxic dinoflagellates and marine mammal mortalities. Woods Hole Oceanographic Institute, Technical Report WHOI-89-36 (CRC-89-6): 65 pp.

Anonymous, 1955. Brine shrimp used in residue tests. Farm Chem. 118: 26.

Areekul, S. & R. F. Harwood, 1960. Two organisms suitable for bioassaying specific acaricides. J. Agric. Food Chem. 8: 32–36.

Audet, D., 1992. Salton Sea eared grebe dieoff project status meeting, July 21–22, 1992, San Diego, California. U.S. Fish and Wildlife Service, Carlsbad, California: 3 pp.

Bain, R. C., A. M. Caldwell, R. H. Clawson, H. L. Scotten & R. G. Willis, 1970. Salton Sea California: water quality and ecological management considerations. U.S. Dept. Interior, Fed. Wat. Qual. Administration, Pacific Southwest Region: 54 pp.

Behle, W. H., 1958. The bird life of the Great Salt Lake. University of Utah Press, Salt Lake City, Utah: 203 pp.

Beltrán, A. S., M. Palafox-Uribe, J. Grajales-Montiel, A. Cruz-Villacorta & J. L. Ochoa, 1997. Sea bird mortality at Cabo San Lucas, Mexico: evidence that toxic diatom blooms are spreading. Toxicon 35: 447–453.

Burkholder, J. M., H. B. Glasgow Jr. & C. W. Hobbs, 1992. New 'phantom' dinoflagellate is the causative agent of major estuarine fish kills. Nature 358: 407–410.

Burkholder, J., H. Glasgow Jr. & C. Hobbs, 1995. Fish kills linked to a toxic ambush-predator dinoflagellate: distribution and environmental conditions. Mar. Ecol. Prog. Ser. 124: 43–61.

Carmichael, W. W., 1994. The toxins of cyanobacteria. Sci. am: 78–86.

Carmichael, W. W., 1995. Cyanobacterial toxins. In Hallegraeff, G. M., D. M. Anderson & A. D. Cembella (eds), Manual on Harmful Microalgae. IOC Manuals & Guides no. 33. UNESCO Publishing, Paris: 163–175.

Carpelan, L. H., 1961. Phytoplankton. In Walker, B. W. (ed.), The Ecology of the Salton Sea, California in Relation to the Sportfishery. Calif. Dept. Fish. Game, Fish Bull. 113: 33–42.

Cohen, M. J., J. I. Morrison & E. P. Glenn, 1999. Haven or Hazard: the Ecology and Future of the Salton Sea. Pacific Institute, Oakland, California: 64 pp.

Cook, W. O., V. R. Beasley, R. A. Lovell, A. M. Dahlem & S. B. Hooser, 1989. Consistent inhibition of peripheral cholinesterases by neurotoxins from the freshwater cyanobacterium *Anabaena flos-aquae*: studies of ducks, swine, mice and a steer. Envir. Toxic. Chem. 8: 915–922.

Cramp, S. & K. E. L. Simmons, 1977. Handbook of the Birds of Europe, the Middle East and North Africa, Vol. 1. Oxford University Press: 722 pp.

Dahl, E. & K. Tangen, 1993. Twenty five years experience with *Gyrodinium aureolum* in Norwegian waters. In Smayda, T. J. & Y. Shimizu (eds), Toxic Phytoplankton Blooms in the Sea. Elsevier Science Publishers: 15–21.

Demaret, A., K. Sohet & G. Houvenaghel, 1995. Effects of toxic dinoflagellates on the feeding and mortality of *Artemia franciscana* larvae. In Lasssus, P., G. Arzul, E. Erard, P. Gentien & C. Marcaillou (eds), Harmful Marine Algal Blooms. Lavoisier, Intercept Ltd: 427–432.

Edvardsen, B., 1993. Toxicity of *Chrysochromulina* species (Prymnesiophyceae) to the brine shrimp *Artemia salina*. In Smayda, T. J. & Y. Shimizu (eds), Toxic Phytoplankton Blooms in the Sea. Elsevier, Amsterdam: 681–686.

Ehrlich, P. R., D. S. Dobkin & D. Wheye, 1988. The Birder's Handbook: a Field Guide to the Natural History of North American Birds. Simon & Schuster, Inc., New York: 785 pp.

Elder, W. H., 1954. The oil gland of birds. Wilson Bull. 66: 6–31.

Endo, M., Y. Onoue & A. Kuroki, 1992. Neurotoxin-induced cardiac disorder and its role in the death of fish exposed to *Chattonella marina*. Mar. Biol. 112: 371–376.

Erwin, N., 1970. Recommended procedures for the examination of seawater and shellfish. American Public Health Association, Inc., New York: 105 pp.

Fabricius, E., 1956. What makes plumage waterproof? Zoologisk Revy 18: 71–83.

Fernandez, M. L. & A. D. Cembella, 1995. Mammalian bioassays. In Hallegraeff, G. M., D. M Anderson & A. D. Cembella (eds), Manual on Harmful Microalgae. IOC Manuals & Guides no. 33. UNESCO Publishing, Paris: 213–228.

Ferrari, R. L. & P. Weghorst, 1997. Salton Sea 1995 hydrographic GPS survey. U.S. Bureau of Reclamation, Water Resources Services. Denver, Colorado: 23 pp.

Fjeldsä, J., 1973. Feeding and habitat selection of the horned grebe, *Podiceps auritus* (Aves), in the breeding season. Vidensk. Meddr dansk naturh. Foren. 136: 57–95.

Fritz, L., M. A. Quilliam & J. L. C. Wright, 1992. An outbreak of domoic acid poisoning attributed to the pennate diatom *Pseudonitzschia australis*. J. Phycol. 28: 439–442.

Gad, S. C. & C. P. Chengelis, 1988. Acute Toxicology Testing Perspectives and Horizons. The Telford Press, New Jersey: 530 pp.

Geraci, J. R., D. M. Anderson, F. J. Jimperi, D. J. St. Aubin, G. A. Early, J. H. Prescott & C. A. Mayo, 1989. Humpback whales (*Megaptera novaeangliae*) fatally poisoned by dinoflagellate toxin. Can. J. Fish. aquat. Sci. 46: 1895–1898.

Granade, H. R., P. C. Cheng & N. J. Doorenbos, 1976. Ciguatera I: brine shrimp (*Artemia salina* L.) larval assay for ciguatera toxins. J. Pharm. Sci. 65: 1414–1415.

Grøntved, J., 1952. Investigations on the phytoplankton in the Southern North Sea in May 1947. Medd. Komm. Danm. Fiskeri- og Havundersøgelser Ser. Plankton 5: 1–56.

Grzebyk, D., A. Đenardou, B. Berland & Y. F. Pouchus, 1997. Evidence of a new toxin in the red-tide dinoflagellate *Prorocentrum minimum*. J. Plankton Res. 19: 1111–1124.

Hallegraeff, G. M., 1993. A review of harmful algal blooms and their apparent global increase. Phycologia 32: 79–99.

Hallegraeff, G. M. & Y. Hara, 1995. Taxonomy of harmful marine raphidophytes. In Hallegraeff, G. M., D. M. Anderson & A. D. Cembella (eds), Manual on Harmful Microalgae. IOC Manuals and Guides no. 33. UNESCO, Paris: 365–371.

Hallegraeff, G. M., S. O. Stanley, C. J. Bolch & S. I. Blackburn, 1989. *Gymnodinium catenatum* blooms and shellfish toxicity in southern Tasmania, Australia. In Okaichi, T., D. M. Anderson & T. Nemoto (eds), Red Tides, Biology, Environmental Science, and Toxicology. Elsevier Science Publishing, New York: 77–80.

Hart, C. M., M. R. Gonzalez, E. P. Simpson & S. H. Hurlbert, 1998. Salinity and fish effects on Salton Sea microecosystems: zooplankton and nekton. Hydrobiologia 381: 129–152.

Hasle, G. R., 1978. Settling: the inverted-microscope method. In Sournia, A. (ed.), Phytoplankton Manual. UNESCO Publishing, Paris: 88–96.

Hasle, G. R. & G. A. Fryxell, 1995. Taxonomy of diatoms. In Hallegraeff, G. M., D. M. Anderson & A. D. Cembella (eds), Manual on Harmful Microalgae. IOC Manuals and Guides no. 33. UNESCO Publishing, Paris: 339–364.

Henriksen, P., W. W. Carmichael, J. An & Ø. Moestrup, 1997. Detection of an anatoxin-a(s)-like anticholinesterase in natural blooms and cultures of cyanobacteria/blue-green algae from Danish lakes and in the stomach contents of poisoned birds. Toxicon 35: 901–913.

Hernandez, M., I. Robinson, A. Aguilar, L. M. González, L. F. López–Jurado, M. I. Reyero, E. Cacho, J. Franco, V. López–Rodas & E. Costas, 1998. Did algal toxins cause monk seal mortality? Nature 393: 28–29.

Horiguchi, T., 1995. *Heterocapsa circularisquama* sp. nov. (Peridiniales, Dinophyceae): a new marine dinoflagellate causing mass mortality of bivalves in Japan. Phycol. Res. 43: 129–136.

Horner, R. A., L. Hanson, C. L. Hatfield & J. A. Newton, 1996. Domoic acid in Hood Canal, Washington, U.S.A. In Yasumoto, T., Y. Oshima & Y. Fukuyo (eds), Harmful and Toxic Algal Blooms. Intergovernmental Oceanographic Commission of UNESCO: 127–129.

Hoyt, J. W., 1970. High molecular weight algal substances in the sea. Mar. Biol. 7: 93–99.

Hu, T., A. S. W. deFreitas, J. Doyle, D. Jackson, J. Marr, E. Nixon, S. Pleasance, M. A. Quilliam, J. A. Walter & J. L. C. Wright, 1993. New DSP toxin derivatives isolated from toxic mussels and the dinoflagellates *Prorocentrum lima* and *Prorocentrum concavum*. In Smayda, T. J. & Y. Shimizu (eds), Toxic Phytoplankton Blooms in the Sea. Elsevier Science Publishers: 507–512.

Husain, K., R. Singh, M. P. Kaushik & A. K. Gupta, 1996. Acute toxicity of synthetic *Gymnodinium breve* toxin metabolite and its analogues in mice. Ecotox. Envir. Safety 35: 77–80.

Ikeda, T., S. Matsuno, S. Sato, T. Ogata, M. Kodama, Y. Fukuyo & H. Takayama, 1989. First report of paralytic shellfish poisoning caused by *Gymnodinium catenatum* Graham (Dinophyceae) in Japan. In Okaichi, T., D. M. Anderson & T. Nemoto (eds), Red Tides, Biology, Environmental Science, and Toxicology. Elsevier Science Publishing, New York: 411–414.

Imai, I. & K. Itoh, 1987. Annual life cycle of *Chattonella* spp., causative flagellates of noxious red tides in the Inland Sea of Japan. Mar. Biol. 94: 287–292.

Iverson, F., J. Truelove, E. Nera, L. Tryphonas, J. Campbell & E. Lok, 1989. Domoic acid poisoning and mussel-associated intoxication: preliminary investigations into the response of mice and rats to toxic mussel extract. Food Chem. Toxicol. 27: 377–384.

Jackson, A. E., J. C. Marr & J. L. McLachlan, 1993. The production of diarrhetic shellfish toxins by an isolate of *Prorocentrum lima* from Nova Scotia, Canada. In Smayda, T. J. & Y. Shimizu (eds), Toxic Phytoplankton Blooms in the Sea. Elsevier Science Publishers: 513–518.

Jehl, J. R. Jr., 1983. Mortality of eared grebes in winter of 1982–1983. Am. Birds 37: 832–835.

Jehl, J. R. Jr., 1988. Biology of the eared grebe and Wilson's phalarope in the nonbreeding season: a study of adaptations to saline lakes. Studies in avian biology, no. 12. Cooper Ornithological Society, Los Angeles, California: 74 pp.

Jehl, J. R. Jr., 1994. Changes in saline and alkaline lake avifaunas in western North America in the past 150 years. In Jehl, J.R. Jr. & N. K. Johnson (eds), Studies in Avian Biology, no. 15. Cooper Ornithological Society, Los Angeles, California: 258–272.

Jehl, J. R. Jr., 1996. Mass mortality events of eared grebes in North America. J. Field Ornithol. 67: 471–476.

Jehl, J. R. Jr., 1997. Cyclical changes in body composition in the annual cycle and migration of the eared grebe *Podiceps nigricollis*. J. Avian Biol. 28: 132–142.

Jones, K. J., P. Ayres, A. M. Bullock, R. J. Roberts & P. Tett, 1982. A red tide of *Gyrodinium aureolum* in sea lochs of the Firth of Clyde and associated mortality of pond-reared salmon. J. mar. biol. Ass. U. K. 62: 771–782.

Kahn, S., O. Arakawa & Y. Onoue, 1996. A toxicological study of the marine phytoflagellate *Chattonella antiqua* (Raphidophyceae). Phycologia 35: 239–244.

Kamiyama, T. & S. Arima, 1997. Lethal effect of the dinoflagellate *Heterocapsa circularisquama* upon the tintinnid ciliate *Favella taraikaensis*. Mar. Ecol. Prog. Ser. 160: 27–33.

Kat, M., 1979. The occurrence of *Prorocentrum* species and coincidental gastrointestinal illness of mussel consumers. In Taylor, D. L. & H. H. Seliger (eds), Toxic Dinoflagellate Blooms. Elsevier North Holland, New York: 215–220.

Lange, C. B. & M. A. Tiffany, 2002. The diatom flora of the Salton Sea, California. Hydrobiologia 473/Dev. Hydrobiol. 161: 179–201.

Lawrence, G. E., 1950. The diving and feeding activity of the Western Grebe on the breeding grounds. Condor 52: 3–16.

Lukenbach, M. W., K. G. Sellner, S. E. Shumway & K. Greene, 1993. Effects of two bloom-forming dinoflagellates, *Prorocentrum minimum* and *Gyrodinium uncatenum*, on the growth and survival of the eastern oyster, *Crassostrea virginica* (Gmelin 1791). J. Shell. Res. 12: 411–415.

Lund, J. W. G., C. Kilpling & E. D. LeCren, 1958. The inverted microscope method of estimating algal numbers, and the statistical basis of estimation by counting. Hydrobiologia 11: 143–170.

Lush, G. J. & G. M. Hallegraeff, 1996. High toxicity of the red tide dinoflagellate *Alexandrium minutum* to the brine shrimp *Artemia salina*. In Yasumoto, T., Y. Oshima & Y. Fukuyo (eds), Harmful and Toxic Algal Blooms. Intergovernmental Oceanographic Commission of UNESCO: 389–392.

MacKenzie, L., 1998. Examination of mussel stomach contents as a method of diagnosing the potential for DSP-toxin contamination. In Reguera, B., J. Blanco, M. L. Fernandez & T. Wyatt (eds), Harmful Algae. Xunta de Galicia and Intergovernmental Oceanographic Commission of UNESCO, Spain: 237–238.

MacKenzie, L., A. Haywood, J. Adamson, P. Truman, D. Till, T. Seki, M. Satake & T. Yasumoto, 1996. Gymnodimine contamination of shellfish in New Zealand. In Yasumoto, T., Y. Oshima & Y. Fukuyo (eds), Harmful and Toxic Algal Blooms. Intergovernmental Oceanographic Commission of UNESCO: 97–100.

MacKenzie, L., P. Truman, M. Satake, T. Yasumoto, J. Adamson, D. Mountfort & D. White, 1998. Dinoflagellate blooms and associated DSP-toxicity in shellfish in New Zealand. In Reguera, B., J. Blanco, M. L. Fernandez & T. Wyatt (eds), Harmful Algae. Xunta de Galicia and Intergovernmental Oceanographic Commission of UNESCO, Spain: 74–77.

Madsen, F. J., 1957. On the food habits of some fish-eating birds in Denmark. Dan. Game Biol. 3: 19–83.

Marshall, J. A. & G. M. Hallegraeff, 1999. Comparative ecophysiology of the harmful alga *Chattonella marina* (Raphidophyceae) from South Australian and Japanese waters. J. Plankton Res. 21: 1809–1822.

Matsuyama, Y., T. Uchida & T. Honjo, 1997. Toxic effects of the dinoflagellate *Heterocapsa circularisquama* on clearance rate of the blue mussel *Mytilus galloprovincialis*. Mar. Ecol. Prog. Ser. 146: 73–80.

Matsuyama, Y., T. Uchida & T. Honjo, 1999. Effects of harmful dinoflagellates, *Gymnodinium mikimotoi* and *Heterocapsa circularisquama*, red-tide on filtering rate of bivalve molluscs. Fish. Sci. 65: 248–253.

McCaskie, G., 1970. Shorebird and waterbird use of the Salton Sea. Calif. Fish Game 56: 87–95.

McCulloch, A. W., R. K. Boyd, A. S. W. de Freitas, R. A. Foxall, W. D. Jamieson, M. V. Laycock, M. A. Quilliam & J. L. C. Wright, 1989. Zinc from oyster tissue as a causative factor in mouse deaths in official bioassay for paralytic shellfish poison. J. Ass. Off. Anal. Chem. 72: 384–386.

McFarren, E. F., H. Tanabe, F. J. Silva, W. B. Wilson, J. E. Campbell & K. H. Lewis, 1965. The occurrence of a ciguatera-like poison in oysters, clams and *Gymnodinium breve* cultures. Toxicon 3: 111–123.

Meyer, B. N., N. R. Ferrigni, J. E. Putman, L. B. Jacobsen, D. E. Nichols & J. L. MacLaughlin, 1982. Brine shrimp: a convenient general bioassay for active plant constituents. Pl. Med. 45: 31–34.

Michael, A. S., C. G. Thompson & M. Abramovitz, 1956. *Artemia salina* as a test organism for bioassay. Science 123: 464.

Moestrup, Ø., 1994. Economic aspects: 'blooms', nuisance species, and toxins. In Green, J. C. & B. S. C. Leadbeater (eds), The Haptophyte Algae. Clarendon Press, Oxford: 265–285.

Moestrup, Ø. & H. A. Thomsen, 1995. Taxonomy of toxic haptophytes (Prymnesiophytes). In Hallegraeff, G. M., D. M. Anderson & A. D. Cembella (eds), Manual on Harmful Microalgae. IOC Manuals and Guides no. 33. UNESCO Publishing, Paris: 319–338.

Montoya, N. G., R. Akselman, J. Franco & J. I. Carreto, 1996. Paralytic shellfish toxins and mackerel (*Scomber japonicus*) mortality in the Argentine sea. In Yasumoto, T., Y. Oshima & Y. Fukuyo (eds), Harmful and Toxic Algal Blooms. UNESCO Publishing, Paris: 417–420.

Nakamura, A., T. Okamoto, N. Komatsu, S. Ooka, T. Oda, A. Ishimatsu & T. Muramatsu, 1998. Fish mucus stimulates the generation of superoxide anion by *Chattonella marina* and *Heterosigma akashiwo*. Fish. Sci. 64: 866–869.

Nielsen, M. V., 1993. Toxic effect of the marine dinoflagellate *Gymnodinium galatheanum* on juvenile cod *Gadus morhua*. Mar. Ecol. Prog. Ser. 95: 273–277.

Ogata, T. & M. Kodama, 1986. Icthyotoxicity found in cultured media of *Protogonyaulax* spp. Mar. Biol. 92: 31–34.

Ogden, 1996. Salton Sea management project evaluation of salinity and elevation management alternatives. Ogden Environmental and Energy Services, San Diego, California: 235 pp.

Okaichi, T. & Y. Imatomi, 1979. Toxicity of *Prorocentrum minimum* var. *mariae-lebouriae* assumed to be a causative agent of short-necked clam poisoning. In Taylor, D. L. & H. H. Seliger (eds), Toxic Dinoflagellate Blooms. Elsevier North Holland, New York: 385–388.

Onoue, Y. & K. Nozawa, 1989. Separation of toxins from harmful red tides occurring along the coast of Kagoshima Prefecture. In Okaichi, T., D. M. Anderson & T. Nemoto (eds), Red Tides, Biology, Environmental Science, and Toxicology. Elsevier Science Publishing, New York: 371–374.

Onoue, Y., M. S. Haq & K. Nozawa, 1990. Separation of neurotoxins from *Chattonella marina*. Nippon Suisan Gakk. 56: 695.

Perl, T., L. Bédard, R. Remis, T. Kosatssky, J. Hoey & R. Massé, 1987. Intoxication following mussel ingestion in Montreal. Can. Dis. Week Rep. 13: 224–226.

Perl, T. M., L. Bédard, T. Kosatsky, J. C. Hockin, E. C. D. Todd & R. S. Remis, 1990. An outbreak of toxic encephalopathy caused by eating mussels contaminated with domoic acid. New Engl. J. Med. 322: 1775–1780.

Proctor, N. S. & P. J. Lynch, 1993. Manual of Ornithology. Yale University Press: 340 pp.

Quilliam, M. A., W. R. Hardstaff, N. Ishida, J. L. McLachlan, A. R. Reeves, N. W. Ross & A. J. Windust, 1996. Production of diarrhetic shellfish poisoning (DSP) toxins by *Prorocentrum lima* in culture and development of analytical methods. In Yasumoto, T., Y. Oshina & Y. Fukuyo (eds), Harmful and Toxic Algal Blooms. Intergovernmental Oceanographic Commission of UNESCO, Paris: 289–292.

Rabbani, M. M., A. U. Rehman & C. E. Harms, 1990. Mass mortality of fishes caused by dinoflagellate bloom in Gwadar Bay, southwestern Pakistan. In Granéli, E., B. Sundstrom, L. Edler & D. M. Anderson (eds), Toxic Mmarine Phytoplankton. Elsevier Science Publishing, New York: 209–214.

Reifel, K. M., 2001. Spatial variation and toxicity of phytoplankton in the Salton Sea. Master's Thesis, San Diego State University: 115 pp.

Reifel, K. M., M. P. McCoy, M. A. Tiffany, T. E. Rocke, C. C. Trees, S. B. Barlow, S. H. Hurlbert & D. J. Faulkner, 2001. *Pleurochrysis pseudoroscoffensis* (Prymnesiophyceae) blooms on the surface of the Salton Sea, California. Hydrobiologia 466: 177–185.

Roberts, R. J., A. M. Bullock, M. Turner, K. Jones & P. Tett, 1983. Mortalities of *Salmo gairdneri* exposed to cultures of *Gyrodinium aureolum*. J. mar. biol. Ass. U. K. 63: 741–743.

Robineau, B., J. A. Gagné, L. Fortier & A. D. Cembella, 1991. Potential impact of a toxic dinoflagellate (*Alexandrium excavatum*) bloom on survival of fish and crustacean larvae. Mar. Biol. 108: 293–301.

Rosenberg, R., O. Lindahl & H. Blanck, 1988. Silent spring in the sea. Ambio 17: 289–290.

Rowan, M. K., 1962. Mass mortality among European common terns in South Africa in April–May 1961. Brit. Birds 55: 103–114.

Sasner, J. J. Jr., M. Ikawa, F. Thurbert & M. Alam, 1972. Physiological and chemical studies on *Gymnodinium breve* Davis toxin. Toxicon 10: 163–172.

Seki, T., M. Satake, L. Mackenzie, H. R. Kaspar & T. Yasumoto, 1995. Gymnodimine, a new marine toxin of unprecedented structure isolated from New Zealand oysters and the dinoflagellate *Gymnodinium* sp. Tetrahedron Lett. 36: 7093–7096.

Shantz, E. J., E. F. McFarren, M. L. Schafer & K. H. Lewis, 1958. Purified shellfish poison for bioassay standardization. J. Ass. Off. Anal. Chem. 41: 160–168.

Shilo, M., 1981. The toxic principles of *Prymnesium parvum*. In Carmichael, W. W. (ed.), The Water Environment. Plenum Press, New York: 37–47.

Shuford, W. D., N. Warnock & K. C. Molina, 1999. The avifauna of the Salton Sea: a synthesis. Synthesis report, Salton Sea Authority: 35 pp.

Sieburth, J. M. & J. T. Conover, 1965. Slicks associated with *Trichodesmium* blooms in the Sargasso Sea. Nature 205: 830–831.

Simmons, K. E. L., 1956. Feather-eating and pellet-formation in the great crested grebe. Br. Birds 49: 432–435.

Solis, P. N., C. W. Wright, M. M. Anderson, M. P. Gupta & J. D. Phillipson, 1993. A microwell cytotoxicity assay using *Artemia salina* (brine shrimp). Pl. Med. 59: 250–252.

Sommer, H. & K. F. Meyer, 1937. Paralytic shell-fish poisoning. Arch. Path. 24: 560–598.

Steidinger, K. A., J. H. Landsberg, E. W. Truby & B. S. Roberts, 1998. First report of *Gymnodinium pulchellum* (Dinophyceae) in North America and associated fish kills in the Indian River, Florida. J. Phycol. 34: 431–437.

Stephenson, R., 1997. Effects of oil and other surface-active organic pollutants on aquatic birds. Envir. Conserv. 24: 121–129.

Stephenson, R. & C. A. Andrews, 1997. The effect of water surface tension on feather wettability in aquatic birds. Can. J. Zool. 75: 288–294.

Storer, R. W., 1961. Observations of pellet-casting by horned and pied-billed grebes. Auk 78: 90–92.

Swennen, C., 1978. Keeping pelagic seabirds in captivity. Ibis 120: 112–113.

Takagi, T., K. Hayshi & Y. Itabashi, 1984. Toxic effect of free unsaturated fatty acids in the mouse assay of diarrhetic shellfish toxin by intraperitoneal injection. Bull. Japanese Soc. Sci. Fish. 50: 1413–1418.

Takayama, H. & R. Adachi, 1984. *Gymnodinium nagasakiense* sp. nov., a red-tide forming dinophyte in the adjacent waters of Japan. Bull. Pl. Soc. Japan 31: 7–14.

Tanaka, K., Y. Muto & M. Shimada, 1994. Generation of superoxide anion radicals by the marine phytoplankton organism, *Chattonella antiqua*. J. Plankton Res. 16: 161–169.

Tangen, K., 1977. Blooms of *Gyrodinium aureolum* (Dinophyceae) in north European waters, accompanied by mortality in marine organisms. Sarsia 63(2): 123–133.

Tarpley, W. A., 1958. Studies on the use of brine shrimp *Artemia salina* (Leach) as a test organism for bioassay. J. Econ. Entomol. 51: 780–783.

Teitelbaum, J. S., R. J. Zatorre, S. Carpenter, D. Gendron, A. C. Evans, A. Gjedde & N. R. Cashman, 1990. Neurologic sequelae of domoic acid intoxication due to the ingestion of contaminated mussels. New Engl. J. Med. 322: 1781–1787.

Terao, K., E. Ito, M. Oarada, M. Murata & T. Yasumoto, 1990. Histopathological studies on experimental marine toxin poisoning. 5. The effects in mice of yessotoxin isolated from *Patinopectenn yessoensis* and of a desulfated derivative. Toxicon 28: 1095–1104.

Tiffany, M. A., S. B. Barlow, V. E. Matey & S. H. Hurlbert, 2001. *Chattonella marina* (Raphidophyceae) a potentially toxic alga in the Salton Sea, California. Hydrobiologia 466/Dev. Hydrobiol. 162: 187–194.

Tiffany, M. A., M. R. González, B. K. Swan & S. H. Hurlbert. Phytoplankton dynamics in the Salton Sea, California, 1997–1999 (in preparation).

Trieff, N. M., M. McShan, D. Grajcer & M. Alam, 1973. Biological assay of *Gymnodinium breve* toxin using brine shrimp. Texas Rep. Biol. Med. 31: 409–422.

Tubaro, A., L. Sidari, R. D. Loggia & T. Yasumoto, 1998. Occurrence of yessotoxin-like toxins in phytoplankton and mussels from northern Adriatic Sea. In Reguera, B., J. Blanco, M. L. Fernández & T. Wyatt (eds), Harmful Algae. Xunta de Galicia and Intergovernmental Oceanographic Commission of UNESCO: 470–472.

Tyler, M. A., D. W. Coats & D. M. Anderson, 1982. Encystment in a dynamic environment: deposition of dinoflagellate cysts by a frontal convergence. Mar. Ecol. Prog. Ser. 7: 163–178.

Watts, J. M., B. K. Swan, M. A. Tiffany & S. H. Hurlbert, 2001. Thermal, mixing and oxygen regimes of the Salton Sea, California, 1997–1999. Hydrobiologia 466/Dev. Hydrobiol. 162: 159–176.

Wetzel, R. G., 1983. Limnology, second edition. Saunders College Publishing: 767 pp.

White, A. W., 1980. Recurrence of kills of Atlantic herring (*Clupea harengus harengus*) caused by dinoflagellate toxins transferred through herbivorous zooplankton. Can. J. Fish. aquat. Sci. 37: 2262–2265.

White, A. W., 1981. Marine zooplankton can accumulate and retain dinoflagellate toxins and cause fish kills. Limnol. Oceanogr. 26: 103–109.

Widdows, J., M. N. Moore, D. M. Lowe & P. N. Salkeld, 1979. Some effects of a dinoflagellate bloom (*Gyrodinium aureolum*) on the mussel, *Mytilus edulis*. J. mar. biol. Ass. U. K. 59: 522–524.

Wikfors, G. H. & R. M. Smolowitz, 1993. Detrimental effects of a *Prorocentrum* isolate upon hard clams and bay scallops in laboratory feeding studies. In Smayda, T. J. & Y. Shimizu (eds), Toxic Phytoplankton Blooms in the Sea. Elsevier Science Publishers: 447–452.

Williams, P. M., 1967. Sea surface chemistry: organic carbon and organic and inorganic nitrogen and phosphorus in surface films and subsurface waters. Deep Sea Res. 14: 791–800.

Winkler, D. W. (ed.), 1977. An Ecological Study of Mono Lake, California. Institute of Ecology Publ. No. 12. Univ. Calif. Press, Davis, California: 190 pp.

Wood, A. M., S. R. Miller, W. K. W. Li & R. W. Castenholz, 2002. Preliminary studies of cyanobacteria, picoplankton, and virioplankton in the Salton Sea with special attention to phylogenetic diversity among eight strains of filamentous cyanobacteria. Hydrobiologia 473/Dev. Hydrobiol. 161: 77–92.

Work, T. M., A. M. Beale, L. Fritz, M. A. Quilliam, M. Silver, K. Buck & J. L. C. Wright, 1993. Domoic acid intoxication of brown pelicans and cormorants in Santa Cruz, California. In Smayda, T. J. & Y. Shimizu (eds), Toxic Phytoplankton Blooms in the Sea. Elsevier Science Publishers: 643–649.

Wright, J. L. C., R. K. Boyd, A. S. W. de Freitas, M. Falk, R. A. Foxall, W. D. Jamieson, M. V. Laycock, A. W. McCulloch, A. G. McInnes, P. Odense, V. P. Pathak, M. A. Quillam, M. A. Ragan, P. G. Sim, P. Thibault, J. A. Walter, M. Gilgan, D. J. A. Richard & D. Dewar, 1989. Identification of domoic acid, a neuroexcitatory amino acid, in toxic mussels from eastern Prince Edward Island. Can. J. Chem. 67: 481–490.

Yasumoto, T. & M. Satake, 1998. New toxins and their toxicological evaluations. In Reguera, B., J. Blanco, M. L. Fernandez & T. Wyatt (eds), Harmful Algae. Xunta de Galicia and Intergovernmental Oceanographic Commission of UNESCO, Spain: 461–464.

Yasumoto, T., B. Underdal, T. Aune, V. Hormazabal, O. Skulberg & Y. Oshima, 1990. Screening for hemolytic and ichthyotoxic components of *Chrysochromulina polylepis* and *Gyrodinium aureolum* from Norwegian coastal waters. In Granéli, E., B. Sundström, L. Edler & D. M. Anderson (eds), Toxic Marine Phytoplankton. Elsevier Science Publishing, New York: 436–440.

Hydrobiologia **473:** 293–306, 2002.
D.A. Barnum, J.F. Elder, D. Stephens & M. Friend (eds), The Salton Sea.
© 2002 *Kluwer Academic Publishers. Printed in the Netherlands.*

Avian disease at the Salton Sea

Milton Friend
Salton Sea Science Office, La Quinta, CA 92253, U.S.A.

Key words: Avian disease, Salton Sea, avian botulism, avian cholera, salmonellosis, Newcastle disease, waterfowl, shorebirds, pelicans, cormorants, grebes, *Clostridium botulinum*, *Pasteurella multocidia*, *Salmonella typhimurium*, Sonny Bono National Wildlife Refuge, pesticides

Abstract

A review of existing records and the scientific literature was conducted for occurrences of avian diseases affecting free-ranging avifauna within the Salton Sea ecosystem. The period for evaluation was 1907 through 1999. Records of the U.S. Department of Agriculture, Bureau of Biological Survey and the scientific literature were the data sources for the period of 1907–1939. The narrative reports of the U.S. Fish and Wildlife Service's Sonny Bono National Wildlife Refuge Complex and the epizootic database of the U.S. Geological Survey's National Wildlife Health Center were the primary data sources for the remainder of the evaluation. The pattern of avian disease at the Salton Sea has changed greatly over time. Relative to past decades, there was a greater frequency of major outbreaks of avian disease at the Salton Sea during the 1990s than in previous decades, a greater variety of disease agents causing epizootics, and apparent chronic increases in the attrition of birds from disease. Avian mortality was high for about a decade beginning during the mid-1920s, diminished substantially by the 1940s and was at low to moderate levels until the 1990s when it reached the highest levels reported. Avian botulism (*Clostridium botulinum* type C) was the only major cause of avian disease until 1979 when the first major epizootic of avian cholera (*Pasteurella multocidia*) was documented. Waterfowl and shorebirds were the primary species affected by avian botulism. A broader spectrum of species have been killed by avian cholera but waterfowl have suffered the greatest losses. Avian cholera reappeared in 1983 and has joined avian botulism as a recurring cause of avian mortality. In 1989, avian salmonellosis (*Salmonella typhimurium*) was first diagnosed as a major cause of avian disease within the Salton Sea ecosystem and has since reappeared several times, primarily among cattle egrets (*Bubulcus ibis*). The largest loss from a single epizootic occurred in 1992, when an estimated 155 000 birds, primarily eared grebes (*Podiceps nigricollis*), died from an undiagnosed cause. Reoccurrences of that unknown malady have continued to kill substantial numbers of eared grebes throughout the 1990s. The first major epizootic of type C avian botulism in fish-eating birds occurred in 1996 and killed large numbers of pelicans (*Pelecanus occidentalis* & *P. erythrorhynchos*). Avian botulism has remained as a major annual cause of disease in pelicans. In contrast, the chronic on-Sea occurrence of avian botulism in waterfowl and shorebirds of previous decades was seldom seen during the 1990s. Newcastle disease became the first viral disease to cause major bird losses at the Salton Sea when it appeared in the Mullet Island cormorant (*Phalacrocorax auritus)* breeding colony during 1997 and again during 1998.

Introduction

Disease is rarely a random event and does not just happen. Instead, the occurrence of disease is an outcome involving susceptible hosts, agents capable of causing disease and suitable environmental factors that facilitate host-agent interactions in a manner that results in disease (Friend, 1995a). Disease processes are effected by a variety of factors. In addition to genetics (Read et al., 1995), factors that stress the host in various ways can predispose the host to disease agents that may be encountered (Friend & Trainer, 1970, 1974a, b; Wobeser 1981; Zapata & Cooper, 1990; Ficken, 1991; Lloyd, 1995; Haschek & Rousseaux, 1998). Also, the environmental persistence of disease agents at levels capable of initiating disease may be

greatly affected by environmental conditions (Price & Brand, 1984; Metcalf et al., 1994). There also must be adequate pathways for disease agents to reach the host and cause disease (Atkinson & Van Riper, 1991; Ewald, 1995; Lockhart et al., 1996; Gratz, 1999; Rocke & Friend, 1999; Hillis, 2000). The factors just noted are important forces driving the changing pattern of avian disease at the Salton Sea.

A wide variety of avian species have been affected by disease at the Salton Sea. The array and frequency of disease outbreaks (epizootics) involving migratory birds within that ecosystem has increased dramatically within the 1990s. Disease outbreaks now occur annually, often killing thousands of birds. Mortality has exceeded 150 000 during a single event (Salton Sea National Wildlife Refuge Narrative Reports; National Wildlife Health Center Epizootic Database). The increased frequency of occurrence, magnitude of losses and variety of diseases occurring at the Salton Sea (Table 1; Fig. 1) are indicative of an ecosystem under severe stress (Rapport & Whitford, 1999).

Environmental change as a factor for disease emergence

The Salton Sea is a young ecosystem initially formed during the period of 1905–7 by floodwaters of the Colorado River (Kennan, 1917). The resulting freshwater lake became nearly as salty as ocean water by 1929 (Arnal, 1961). Salinity now exceeds ocean water by about 25% (González et al., 1998). The fauna of the Salton Sea has changed from freshwater to marine species in response to increasing salinity and introductions of salt tolerant species (Arnal, 1961; Walker, 1961; Black, 1988). Thus, considering the time-frame for the major transition that has occurred, the physical environment and biota of the Salton Sea have been subject to dynamic change.

Environmental change is commonly associated with disease emergence, maintenance and spread (Friend, 1992; May, 1993; Schrag & Wiener, 1995; Epstein et al., 1998; DaSilva & Iaccarino 1999). Important factors include environmental quality as a function of organism health, and species associations and interactions as opportunities for transfer of disease agents. The environmental quality of the Salton Sea is degrading due to increasing salinity, excess nutrients that result in the Sea being hypereutrophic, and other factors. In combination with the harsh physical conditions present, those factors place stress on much of the Sea's fauna. In addition, biotic relations within this ecosystem are still evolving due to the young age of the Salton Sea and the unique species associations within this waterbody.

The Salton Sea has become an attractant for birds because of habitat losses within California, an abundant food base, and a minimum of disturbance factors for the birds using the Sea. California leads the United States in wetland losses (more than 90% of the inland wetland acreage present at the time of settlement [Dahl, 1990]). The abundant fishery of the Salton Sea provides a reliable food base for fish-eating birds, while other wetland-dependant avian species feed on the invertebrates present and other species heavily utilize the surrounding agricultural fields, another part of the changing landscape of the California Desert. Isolation from disturbance is provided by the large size of the Salton Sea (surface area of 980 km^2) and low human density surrounding the Sea. The physical location of this waterbody along the Pacific Flyway is another factor contributing to the high bird use during migration and wintering periods.

The pattern of bird-use at the Salton Sea is more than just a transient stop-over for migratory birds. In addition to resident species, a high percentage of the populations for some other species are present for prolonged periods of time. Increased vulnerability to epizootic disease has been an outcome. The causes for disease emergence are multiple, complex, different for different diseases and are currently under investigation. Disease carriers among the birds using the Sea may be contributing to the infectious diseases present (Brand, 1984; Samuel et al., 1997; Friend & Franson, 1999). Novel species interactions within the evolving environment of the Salton Sea are another likely factor. This article reports the changing pattern of avian disease at the Salton Sea as an initial compendium against which other evaluations of avian disease can be made.

Methods

Narrative reports of the U.S. Fish and Wildlife Service National Wildlife Refuge System and the U.S. Geological Survey's National Wildlife Health Center Epizootic Database are the primary data sources utilized for the evaluations made. Those data were supplemented by correspondence obtained from a search of records in the National Archives and by published literature and government agency reports.

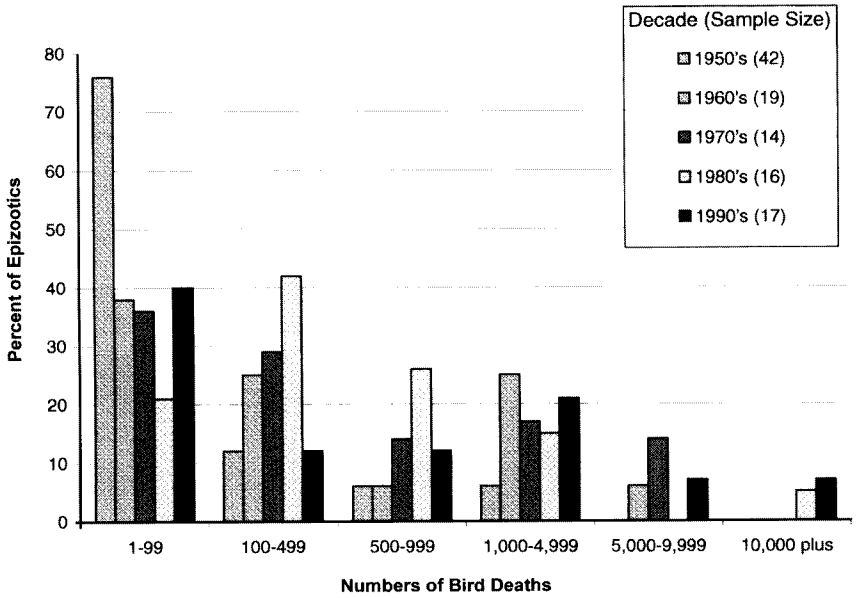


Figure 1. Reported avian mortality events within the Salton Sea ecosystem, 1950–2000.

Table 1. Reported causes of avian mortality within the Salton Sea ecosystem, 1907 through 1999[a,b]

Disease [c]	Causative agent	Agent type	Year of first report	Frequency of subsequent reports[d]
Avian botulism	*Clostridium botulinum*, type C	Bacterial toxin	1917	Common
Avian cholera	*Pasteurella multocida*	Bacteria	1978	Common
Salmonellosis	*Salmonella typhimurium*	Bacteria	1989	Frequent
Staphylococcosis	*Staphylococcus aureus*	Bacteria	1997	Rare
Pseudomoniasis	*Pseudomonas sp*	Bacteria	1992	Rare
Avian tuberculosis	*Mycobacterium avium*	Bacteria	1999	Rare
Aspergillosis	*Aspergillus fumigatus*	Fungus	1992	Occasional
Newcastle disease	Newcastle disease virus (PMV-3)	Virus	1997	Common
Parmyxovirus infection	Avian paramyxovirus type 3 (PMV-3)	Virus	1997	Rare
Hepatitis	Not identified	Unknown	1991	Rare
Neoplasia	Not identified	Unknown	1999	Rare
Lead poisoning	Spent lead shot	Heavy metal	1920s[e]	Occasional
Pesticides	Diamethoate, phorate, parathion	Organophosphates	1978	Occasional
	Carbofuran	Carbamate	1974	Occasional
	Strychnine	Poison	1991	Rare

[a]National Wildlife Health Center diagnostic cases database primary data source (1975–2000).
[b]Does not include hunting or predation.
[c]Does not include diagnoses lacking supporting information, trauma, emaciation, drowning or secondary findings associated with primary cause of death (such as parasites).
[d]Common = numerous diagnosis with occurrence in most years; Frequent = numerous diagnoses with occurrence more years than not; Occasional = periodic appearance; Rare = seldom observed.
[e]Estimated occurrence based on descriptions of sick birds and history of disease in waterfowl.

Table 2. Data sources used for Salton Sea avian disease synopsis

Time period	Bureau of Biological Survey records	Salton Sea[a] National Wildlife Refuge Narrative Reports	National Wildlife[b] Health Center Databases		Scientific literature	Miscellaneous reports
			Epizootic	Diagnostic		
1907–29	X				X	
1930–39	X				X	
1940–49		X[c]			X	
1950–59		X[d]			X	
1960–69		X[e]			X	
1970–79		X[f]	X	X	X	X
1980–89		X[g]	X	X	X	X
1990–99		X[h]	X	X	X	X

[a]Refuge initiated in 1930, first report available was 1939.
[b]Center came into existence in 1975.
[c]Reports found only for 1940, 1941, 1947–49.
[d]Reports found for all years.
[e]Reports found for all years.
[f]No report found for 1977.
[g]No reports found for 1981 or 1982.
[h]Reports found for all years.

National Wildlife Refuge System narrative reports

The National Wildlife Refuge System has narrative reports for each of its holdings. Those reports provide a mixture of data, anecdotal comments and other information that serves as a chronicle for that refuge, as well as the Salton Sea ecosystem as a whole. Disease occurrence is one of the items regularly commented on and recorded in those reports. The Salton Sea Migratory Bird Refuge was established in 1930, later became the Salton Sea National Wildlife Refuge and then the Sonny Bono Salton Sea National Wildlife Refuge. Narrative reports for that refuge were individually reviewed for information on avian mortality. Information found often lead to other sources where greater detail or questions about the information could be resolved. The format and frequency for the narrative reports varied over time and reports could not be located for all years (Table 2). Tables and comments in some reports filled in some of the data gaps for years when reports were missing. In other instances, there is no information for years for which reports could not be found. Photographs found in reports showing field conditions and clinical signs of affected birds were of value in reaching judgments about diseases involved (Friend & Franson, 1999).

National Wildlife Health Center epizootic database

The National Wildlife Health Center began in January, 1975 as a research center within the U.S. Fish and Wildlife Service (FWS). Along with the other FWS research centers, it was placed within the National Biological Survey in 1993 (Friend, 1995b) and in 1996 became part of the U.S. Geological Survey during the continuing Department of the Interior reorganizations of the 1990s. Major activities of the Center include disease diagnosis and field investigations of wildlife mortality events on U.S. Department of Interior holdings. The great majority of those activities are associated with the National Wildlife Refuge System. The Center maintains an epizootic database that has records of wildlife mortality events from across the United States. The epizootic database contains a broad spectrum of information associated with each epizootic. Computer searches were utilized to obtain basic information and where needed, individual case files were examined to resolve questions. The author founded the National Wildlife Health Center and served as its Director from 1975–98. As a result, data evaluation for this paper was facilitated by the personal knowledge of Center operation, data acquisition processes and the databases.

Data evaluations

Epizootic events were assigned to specific diseases on the basis of laboratory confirmed diagnoses when such data were available. In other instances, narrative descriptions of clinical signs, field observations, photographs that were part of the record and other information provided or present in other reports of the same event were used to exercise professional judgment regarding the validity of the stated cause of the mortality and to infer cause where none was stated and it was reasonable to make such judgments.

Results

1907–1919

In 1917, duck sickness, now known to be type C avian botulism, was reported from the Salton Sea (Kalmbach & Gunderson, 1934). No other reports of avian mortality at the Salton Sea were found for that time period.

1920–1929

Correspondence between a Westmoreland resident and the U.S. Bureau of Biological Survey focused on large-scale avian mortality events the resident had been observing annually since 1926, with the exception of 1932 (Holmes, 1933a,b). Based on descriptive information from a 1933 field investigation of the area of the Salton Sea referred to by the resident (Tonkin, 1933) and disease diagnostic evaluations of other events at the Salton Sea by the leading avian botulism investigators of that time (Hobmaier, 1930a,b, 1932; Kalmbach, 1934a,b) it is likely that the 1926–29 mortality events (Holmes, 1933a,b) were due to type C avian botulism. The deltas of the New and Alamo Rivers were identified as the locations for those events.

1930–1939

Hobmaier (1932) reported avian botulism at the Salton Sea and noted a major epizootic occurred in 1931. Two years later, a field investigation was conducted at the southeastern shore of the Salton Sea in response to the claim, "... that several *hundred thousand* ducks have been lost this season from this cause" (Holmes, 1933a). Although that level of mortality is highly suspect based on Bureau of Biological Survey file correspondence it is clear that a major epizootic did occur. The field report states:

> "On the mud flats between the mouths of the Alamo and New Rivers there were hundreds of sick ducks and gulls and others out in the soup, where the boat could barely run. Out in the muddy water there were still fewer birds. Probably the number of birds lost by sickness since the hunting season opened will equal the number killed by hunters in that area, or on all the Sea, during the same period" (Tonkin, 1933).

The field situation and clinical signs described strongly suggest avian botulism as the cause of the 1933 epizootic. This evaluation is further supported by reference to an unavailable 1934 report by E.R. Kalmbach titled, "The Salton Sea Refuge With Respect to Possible Future Outbreaks of Duck Sickness and their Control". That missing report was referenced in a response to considerations for enlargement of the Salton Sea Migratory Bird Refuge and as further support for his position that:

> "... I am convinced that one of the most valuable features of the improvement works on the Salton Sea Refuge will be those that will curb botulism and thus save many waterfowl. Without adequate provisions for disease control, an enlarged refuge might become simply an aggravated death trap" (Kalmbach, 1935a).

Kalmbach (1938) reported 800 dead birds per linear mile on some sections of the Salton Sea shoreline during the late summer 1933 epizootic. He also reported a recurring outbreak at the same locations the following spring. The only other reported epizootic for the 1930s occurred in 1939. An estimated 3000 birds, primarily waterfowl and shorebirds, died from avian botulism in the vicinity of Mullet Island. It was noted in the 1939 Narrative Report that, "... This is a small number when compared with some of the estimated figures of past outbreaks in the Salton Sea area".

1940–1949

There were no reports of major epizootics at the Salton Sea during the 1940s. A few cases of avian botulism were reported during 1940 and the November–January Narrative Report contains the statement, "The season in which botulism ordinarily breaks out passed without its occurrence in the area, only a few sick gulls were found". An accompanying photograph of a sick gull was consistent with avian botulism. Reports in 1942 of disease in waterfowl resulted in a visit to the Salton Sea National Wildlife Refuge that year by

a high level FWS administrator (O'Neill, 1999). The September–December 1947 Narrative Report documents an estimated loss of 250 waterfowl from avian botulism at the Imperial Waterfowl Management Area. An undocumented number of dead eared grebes were also noted along the east shore of the Salton Sea during 1947 (O'Neill, 1999). The 1948 report noted that no avian disease was detected in the general vicinity of the Salton Sea. Less than 10 sick and dead birds were observed during 1949, none of which were submitted for diagnostic evaluations.

1950–1959

Avian botulism was again the only disease reported to be affecting birds at the Salton Sea during the 1950s. The 1950 Narrative Reports indicated no disease occurrence at the Salton Sea but note an outbreak of botulism that killed 4600 pheasants (*Phasianus colchicus*) at the State's game farm near Calipatria. Approximately 300 waterfowl and an equal number of shorebirds died at the Salton Sea during 1951 and between 4000 and 5000 waterfowl and 1000 shorebirds during 1952. That epizootic appears to be the same event referred to by O'Neil (1999) as occurring during 1953. Very few botulism affected birds were seen during 1953 but the Narrative Report noted continued observations of large numbers of flightless ruddy ducks (*Oxyura jamaicensis*) along the Sea. No cause was postulated for what was reported to be a recurring situation. No specimens were submitted for diagnostic evaluations. A 1953 serologic survey for Newcastle disease disclosed five pintails (*Anas acuta*) and two wigeon (*A. americana*) from among 313 waterfowl tested to have antibody titers between 1:64 and 1:128 or greater. One hundred and seventy-six coots (*Fulica americana*) tested were negative. Follow-up sampling during 1954 resulted in 1 of 338 waterfowl having a positive antibody titer to Newcastle disease. None of the five additional coots tested positive.

A few shorebirds, egrets and eared grebes were noted sick in the January–April 1954 Narrative Report; the May–August report for that year indicated no disease among waterfowl, two sick snowy egrets (*Egretta thula*) and a few sick sandpipers.

Observations and documentation of avian botulism were absent from the 1955 Narrative Reports, but reports of sick birds included approximately 300 flightless coots seen on the Sea. Those birds were reported to be emaciated and to have ink-black watery feces. At that same time period, a few sick white pelicans unable to fly and in a weakened condition were also seen. Other notations of disease during 1955 were 20 dead egrets due to unknown causes and additional small numbers of sick and dead white pelicans and egrets.

Small numbers of sick and dead birds were also reported for 1956. Avian botulism affected unspecified small numbers of black-necked stilts (*Himantopus mexicanus*). Mortality of egrets and mourning doves (*Zenaida macroura*) from unknown causes was also reported along with several cases of lead poisoning among pintail ducks. Similar reports involving small numbers of birds dying from avian botulism and from unknown causes appear in the 1957–9 reports. Avian botulism was diagnosed as the cause of mortality (number of affected birds not given) on the State's Finney-Ramer Unit of the Imperial Waterfowl Management Area near Calipatria.

1960–1969

In 1962, following two years of reports of no disease occurrence, several thousand birds died at the Salton Sea. Avian botulism killed an estimated 4000 ducks and 2000 shorebirds during one event. An additional 1000 shorebirds died from unknown causes during another event. Other undiagnosed mortality events reported during the year included the loss of 2000 shorebirds and 500 ducks, a considerable die-off of sandpipers (numbers not given), and the deaths of 4 white pelicans. During 1963, avian botulism killed 2000 waterfowl and 4000 shorebirds during one event and 2000 shorebirds and 500 waterfowl during an additional event. An estimated 2000–3000 shorebirds and a few white pelicans also died during another event for which the cause was not determined. Reported losses for 1964 were 300 ducks and 500 shorebirds dying from avian botulism. Parathion was diagnosed as the cause of death for 13 Canada geese (*Branta canadensis*) found dead in an alfalfa field a few miles from the Salton Sea near Brawley. Losses of approximately 400 waterfowl but only a small number (30) of shorebirds from avian botulism were reported for 1965.

Reported bird losses from disease continued to decline during the remainder of the 1960s. An estimated 30 waterfowl and 50 shorebirds died from avian botulism during 1966. Estimated losses from avian botulism were approximately 100 per year during 1967–9 with waterfowl and shorebirds being the primary species affected. No other diseases were reported during those years.

1970–1979

The low levels of avian mortality for the latter half of the 1960s persisted through 1970 and 1971. Two outbreaks of avian botulism were recorded for 1970, the first killing an estimated 25 waterfowl and 50 shorebirds and the other an estimated 450 waterfowl and 200 shorebirds. Losses from avian botulism during 1971 were estimated at 150 waterfowl and 100 shorebirds. An epizootic of avian botulism causing substantial but unspecified losses occurred during the spring of 1972 on the Wister Unit of the Imperial Waterfowl Management Area (Hosier, 1975). That event was followed by a major avian botulism epizootic during the winter of 1972 at the Alamo River delta that resulted in a total carcass pick up of 4325 waterfowl, 465 other dead birds and 199 sick birds during a 3 week disease response effort. Total losses were not estimated. Small numbers of botulism affected birds were reported during 1973. During 1974, botulism resulted in the collection of over 1000 shorebirds of 10 different species in addition to coots, grebes and ruddy ducks. Less than 200 dead ducks were found. A major mortality event involving wigeon due to the pesticide carbofuran also occurred during 1974, but not at the Salton Sea. That event occurred in Riverside County agricultural fields and killed 2400 birds.

Several mortality events were reported during 1975. About 400 ducks died from avian botulism during one event, and approximately 200 ducks and a few shorebirds during another event. In addition, about 200 eared grebes were found dead of unknown causes. The death of more than 100 soft-shelled turtles (*Trionyx spiniferus*) was also reported from a drainage canal that runs through one of the refuge units. The California Department of Fish and Game examined specimens and issued a diagnosis of pesticide poisoning from applications farther south in the Imperial Valley. The pesticide involved was not identified in the Narrative Report.

Disease is not reported to have occurred during 1976 and the Narrative Report for 1977 could not be found. There are no records of any specimens from the Salton Sea being submitted to the National Wildlife Health Center during 1976–77. Disease outbreaks are absent from the 1978 Narrative Report. However, several events were recorded for 1978. A total of 10 (waterfowl and shorebirds), for which no diagnosis was made, were found on the Salton Sea. Phorate was diagnosed as the cause of poisoning of 20 ring-billed gulls (*Larus delawarensis*) from agricultural fields in Calipatria. The most significant event was the first appearance of avian cholera in waterfowl in Imperial County. A total of 261 carcasses were retrieved from the Imperial Wildlife Area due to avian cholera, gunshot (hunting season birds not retrieved) and unknown causes. At the start of 1979, the first major epizootic of avian cholera appeared at the Salton Sea. Mortality was reported by Brand & Duncan (1983) to be 3800 waterfowl, shorebirds and wading birds. However, other records indicate that event killed more than 9000 birds, primarily waterfowl. Avian botulism also occurred during 1979. A total of 795 carcasses were collected in association with that event.

1980–1989

Disease occurrence is not prominent in the Narrative Reports for most of the 1980s. The National Wildlife Health Center established nine wildlife mortality transects at the Salton Sea during 1980, but those transects were only run during that year. None of the 10 bird carcasses found were suitable for necropsy. Avian cholera was diagnosed for 12 carcasses (waterfowl, coots, an eared grebe and a gull) found incidental to conducting the transects; type C avian botulism was diagnosed for two white pelicans; and gunshot for a snow goose (*Chen caerulescens*) and a yellow-headed blackbird (*Xanthocephalus xanthocephalus*) (Brand, 1981). The National Wildlife Health Center epizootic database contains an entry of avian botulism killing 200 birds at the Salton Sea during 1980 and an avian cholera outbreak killing 250 birds during 1981. There are no reports of disease for 1982. Another small avian cholera event that occurred during 1983 resulted in a tally of 235 carcasses. Avian botulism resulted in 312 carcasses during 1984. There are no reports of disease at the Salton Sea during 1985 or 1986. Carbofuran killed 32 Canada geese in agricultural fields at El Centro during 1986.

As estimated 500 waterfowl and other species died from avian cholera at the Salton Sea during 1987. Avian cholera reappeared during 1988, killing an estimated 600 birds, primarily ruddy ducks and eared grebes. Several outbreaks of avian botulism also occurred during that year. Estimated total losses were 2000 birds. An additional botulism epizootic resulted in 595 waterfowl and shorebird carcasses being disposed of from a private hunting club in the immediate vicinity of the Salton Sea.

Several different mortality events were recorded during 1989. A total of 215 waterfowl and shorebird

caresses were collected during an outbreak of avian botulism. Avian cholera resulted in an estimated 750 bird loss during one event and 56 carcasses being recovered from another event. Lead poisoning was diagnosed as the cause of death for 4 pintail ducks found dead on the Sea and as the cause of an estimated 200 ducks found dead at the Brawley Gun Club. In addition, 4515 cattle egrets died from salmonellosis during an epizootic at Brawley. Dimethoate was diagnosed as the cause of mortality for 5 snow geese and 1 Ross' goose (*C. rossii*). Also, Jehl (1996) reported an estimated 40 000 bird die-off of eared grebes to unknown causes.

1990–1999

Disease outbreaks at the Salton Sea were reported for each year of the 1990s. The magnitude of bird losses recorded during the 1990s exceeds the totals reported for all other years combined since 1930. Judgments cannot be made relative to losses prior to 1930. The frequency of reported large-scale epizootics was greater during the 1990s than for any other decade (Fig. 1) as was the frequency of reported disease events (Fig. 2) and the variety of disease conditions diagnosed (Table 1). The most notable epizootics of the decade are those killing an estimated 155 000 birds during 1992; 20 000 birds during 1994 and 1996; 8000 birds during 1997; 6000 birds during 1998; and 7000 birds during 1999 (Table 4).

The great majority of birds lost during the 1992 epizootic were eared grebes. Other than ruddy ducks, no other species suffered major losses. The primary cause for the event was not determined despite extensive diagnostic efforts by the National Wildlife Health Center. Jehl (1996) reported similar field signs for the 1989 grebe mortality event and postulated that the loss during that year may have equaled that for 1992. Algal toxins were suspected but that diagnosis could not be confirmed. Avian cholera was diagnosed as the cause of some of the bird deaths but was considered to be a secondary mortality factor. The primary cause of the 20 000 bird loss in 1994 also was not determined. Once again, the eared grebe was the primary species affected, and avian cholera was determined to be a secondary cause of mortality associated with the die-off.

The 20 000 bird loss in 1996 was a unique event. That was the first reported occurrence of type C botulism involving major losses of fish-eating birds. More than 8500 white pelicans and more than 1100 endangered California brown pelicans died during that event. Another unique event took place during 1997 when Newcastle disease killed approximately 2500 double-crested cormorants nesting on Mullet Island. That event was the first diagnosis within the United States in wild birds of a lethal strain of Newcastle disease west of the Rocky Mountains. Avian cholera was responsible for the deaths of nearly 8000 birds collected during a late 1997 epizootic that extended well into 1998. The great majority of birds killed were ruddy ducks. A repeat Newcastle disease epizootic at Mullet Island during 1998 killed an estimated 6000 cormorants.

In comparison with the other Salton Sea major epizootics of the 1990s, the 1999 avian cholera epizootic is almost mundane. A total of 6921 carcasses was collected for disposal, the majority of those being ruddy ducks and northern shovelers (*A. clypeata*). Seventy-four white pelican carcasses were also among the wide variety of species affected.

Discussion

The primary variables effecting the quality of the information obtained are the probability for disease detection, the availability of records for disease events, the quality of disease diagnosis, and the accuracy of numbers of birds affected. Major events that have bearing on those variables are the 1930 development of the Salton Sea Migratory Bird Refuge, the 1975 development of the National Wildlife Health Center and the 1998 initiation of the Salton Sea Restoration Project.

Disease surveillance prior to the development of the Salton Sea Migratory Bird Refuge was limited to random observations by local residents and visitors to the Sea. Records of observations those individuals may have made generally do not appear as public documents. However, notification and requests for government actions do result in a record of the event (Holmes, 1939a,b). Major disease events commonly result in such requests and subsequent response by government agencies (Tokin, 1933; National Wildlife Health Center Epizootic Database). The early focus on the Salton Sea for recreational activities and for shoreline development (Laflin, 1995; du Boyes & Myers, 1999; Horvitz, 1999) resulted in considerable on-Sea presence by humans prior to the presence of government natural resources agencies having on-Sea programs. Also, the focus for developing the Salton

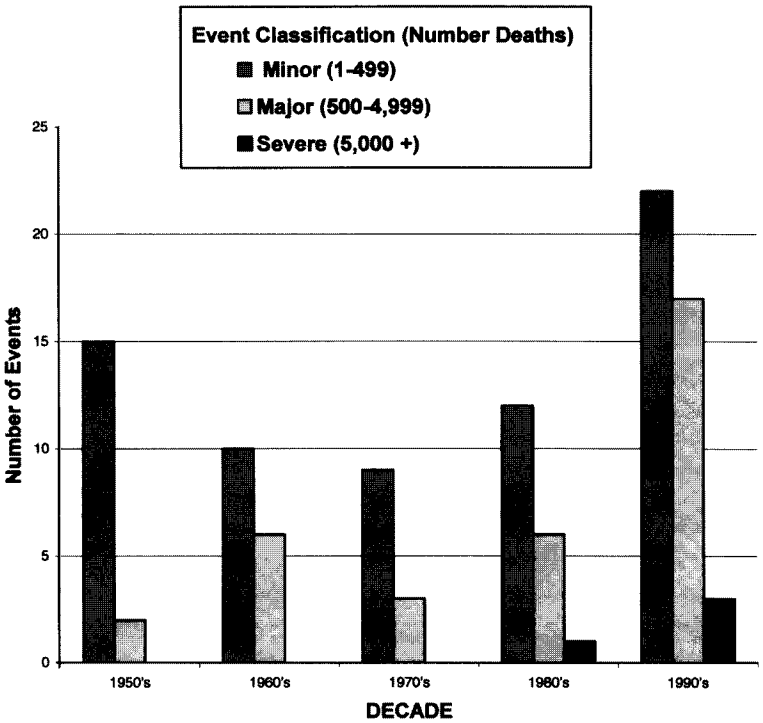


Figure 2. Number and severity over time of avian mortality events within the Salton Sea ecosystem, 1950–2000.

Sea as California's Riviera made it likely that major avian mortality events would have been detected and government agencies notified.

The development of on-Sea natural resources facilities provided for enhanced probability for detection and recording of avian mortality events of all magnitudes. The Salton Sea Migratory Bird Refuge (1930), the Wister Unit of the Imperial Waterfowl Management Area (1954) and the Salton Sea State Park (1955) are the primary programs with staff that are frequently on the Sea and interact with the public that use the Sea. The most intensive disease surveillance activities at the Salton Sea have been those carried out by personnel of the Sonny Bono Salton Sea National Wildlife Refuge. Those efforts were further enhanced as a result of the 1996 avian botulism epizootic and by the initiation of the Salton Sea restoration project.

The greatest Narrative Report data gaps are for the 1930s and during the World War II years of the 1940s. Some coverage for those years is provided by the records of the Bureau of Biological Survey and by the scientific literature. Also, it is noteworthy that O'Neill (1999) does not highlight disease in his coverage of the early history and development of the Salton Sea Migratory Bird Refuge despite considerable focus on disease for some of the other refuges included in his presentation of personal experiences on nine western state and federal wildlife refuges. However, he does provide support for disease being a major problem during the 1930s by citing comments from the 75th Congress (1937) about the Salton Sea Wildlife Refuge "... and the control of the diseases that take such a great toll of the bird life of the region".

The quality of avian disease evaluations at the Salton Sea is also influenced by such factors as the quality of field observations, the selection and quality of specimens provided to diagnostic laboratories (Friend & Franson, 1999), the use of diagnostic laboratories, completeness of diagnostic work, how familiar the laboratory is with the types of diseases likely to affect wild bird populations, technology available and other factors.

A continuum of highly competent wildlife disease investigators and programs have been associated with avian disease evaluations at the Salton Sea. Included are the wildlife disease investigation laboratories of the Bureau of Biological Survey, California Department of Fish and Game and the U.S. Fish and

Table 3. Primary recurring diseases causing major losses of Salton Sea avifauna

Disease/causative agent	First documented occurrence in wild birds	Identification of the causative agent	First documented at the Salton Sea
Avian botulism *Clostridium botulinum*, type C	1890s (Hobmaier, 1932; Kalmbach, 1968; Kalmbach & Gunderson, 1934)	1930 (Giltner & Couch, 1930; Hobmaier 1930a,b; Kalmbach, 1930)	1917 (Kalmbach & Gunderson, 1934)
Avian cholera *Pasteurella multocida*	1940[a] (Rosen, 1971)	1879–1880 (Rosen, 1971)	1978[b]
Avian salmonellosis *Salmonella typhimurium*	1930s (Steele & Galton, 1971)	1895 (Williams, 1965)	1989[c]
Newcastle disease Newcastle disease virus	1950 (Blaxland, 1951; Brandly & Hanson, 1965; Wilson, 1950)	1926 (Hanson, 1964)	1997[c]

[a]First epizootic in free-ranging waterfowl; similar events first occurred in the United States in 1944. Small numbers of wild birds closely associated with poultry rearing operations have previously died from avian cholera.
[b]Salton Sea National Wildlife Refuge Narrative Report.
[c]National Wildlife Health Center Epizootic Database.

Wildlife Service (subsequently, the National Biological Survey and then the U.S. Geological Survey). Also, the primary diseases diagnosed at the Salton Sea have been recognized elsewhere as distinct diseases for many years prior to their diagnosis at the Salton Sea. They are all diseases routinely diagnosed by commonly applied technology and methods (Table 3).

The ease and speed for getting specimens to diagnostic laboratories has improved over time, as has the amount of on-site mortality event involvement by wildlife disease specialists. Nevertheless, continued weaknesses result from the limited numbers of specimens submitted to diagnostic laboratories and the small percentage of disease events for which on-site investigations are carried out by wildlife disease specialists. Despite those inherent weaknesses, the quality of disease diagnostic evaluations at the Salton Sea has been consistently good over time based on the composite of information available for evaluation.

The amount of laboratory evaluations in support of field observations is as good as that for most other geographic areas and better than for many areas. Also, the clinical and field signs associated with the diseases diagnosed at the Salton Sea, while not pathognomonic, have distinctive differences from one another, but not all other avian diseases (Friend & Franson, 1999). Those differences help to make informed field evaluations. Some diseases may not have been diagnosed. However, with the exception of the recurring unknown cause(s) of eared grebe mortality, it is likely that any major disease affecting the avifauna of the Salton Sea has been identified.

Data relative to the numbers of birds lost during disease events must be interpreted with caution. Carcass counts provide the best information but search effort can be highly variable and carcasses found are minimum numbers of the actual loss. Estimates of total losses can either underestimate or overestimate the actual losses. Light conditions, bird size and color, habitat, methods of search and numerous other factors can effect field estimates for numbers of birds lost and the number of carcasses retrieved (Wobeser, 1994). Therefore, comparisons between numbers of birds lost to disease during different events and times at the Salton Sea can only be based on subjective evaluations because no corrective factor can be applied to enhance interpretations for the data reported.

Pesticide-related deaths of birds documented within the Salton Sea ecosystem have been associated with agricultural fields of the surrounding area. With the exception of the 1974 loss from carbofuran of approximately 2400 American wigeon, pesticide

Table 4. Mortality events within the Salton Sea ecosystem causing severe losses of avifauna, 1930 through 1999[a]

Year	Location	Disease	Mortality	Primary species affected
1930	Alamo & New River deltas	Avian botulism	Large-scale[b]	Waterfowl
1931	Alamo & New River deltas	Avian botulism	Large-scale[c]	Waterfowl
1933	Alamo & New River deltas	Avian botulism	'Thousands'[d]	Waterfowl
1952	Salton Sea shoreline & impoundments	Avian botulism	4–5000	Waterfowl
1963	Shallow muddy areas of Salton Sea shoreline	Avian botulism	4000 2000	Ducks Shorebirds
1972	Alamo & New River deltas	Avian botulism	6000	Waterfowl & shorebirds
1979	East side of Salton Sea	Avian cholera	9037	Waterfowl
1989	Imperial County breeding colonies, Brawley[f]	Salmonellosis	4515[g]	Cattle egrets
1989	Salton Sea[h]	Not determined	40 000[i]	Eared grebes
1992	Salton Sea-Sea wide	Not determined;[j] avian cholera secondary problem	150 000 45 000	Eared grebes Ruddy ducks
1994	Salton Sea – Sea wide	Not determined;[j] avian cholera secondary problem	20 000	Mostly eared grebes, also ruddy ducks & gulls as lesser numbers of primary species
1996	Alamo & New River deltas primary area	Avian botulism[k]	20 000[l]	White pelican, brown pelican, great egret, gulls
1997	Wister Unit, southern areas of the Sea, impoundments	Avian cholera	7952[e]	Ruddy duck, northern shoveler, coot
1998	Mullet Island	Newcastle disease	6000[m]	Double-crested cormorant
1999	Alamo & New River deltas, Unit 1	Avian cholera	6921[e]	Ruddy duck northern shoveler, gulls

[a]Severe losses are arbitrarily considered to be approximately 5000 birds or greater based on estimated losses and 4000 birds or greater based on carcass counts.
[b]The actual severity cannot be determined; Holmes (1933a, b) reported annual large-scale mortalities at those locations starting in 1926. [c]The actual severity cannot be determined; Hobmair (1932) reported a major epizootic.
[d]The actual severity cannot be determined; Holmes (1933a) reported several hundered thousand but field investigations by Tonkin (1933), while confirming a major epizootic, do not support the magnitude of loss reported by Holmes (1933a).
[e]Carcass count, actual mortality greater.
[f]Two breeding colonies at separate locations.
[g]Based on field investigation of affected colonies.
[h]Carcasses found along west and north shores but mortality extended across the Sea.
[i]Jehl (1996) speculated that mortality may have equaled the 1992 event.
[j]Avian cholera was responsible for much of the ruddy duck mortality.
[k]First epizootic of type C avian botulism in fish-eating birds.
[l]Largest documented die-off of an endangered species (over 1100 brown pelicans); an estimated 15–20% loss of the western population of white pelicans (over 8500 carcasses).
[m]Estimated on basis of number of nests and the total loss of nestling produced.

mortalities have involved small numbers of birds and have only been sporadically reported. On some occasions when the causes for bird mortalities have not been diagnosed, the reports for those events contain speculation that pesticides may have been the cause. In those instances, no chemical residue analyses or associations with the timing of pesticide applications were provided as supporting data for pesticides as a probable cause. Instead, the context typically appeared to be speculation based on enhanced awareness of pesticide-wildlife problems during the years following the publication of 'Silent Spring' (Carson, 1962) and other scientific findings documenting pesticide impacts (Anderson et al., 1969; Stickel et al., 1969).

Another cause for mortality for which there is even greater speculation is that of algal toxins. This is not a new area for speculation. Statements of algal toxins being the suspected cause of disease in birds appear in Narrative Reports from the 1950s and 1960s. A current hypothesis is that algal toxins are the primary cause for the large-scale losses of eared grebes that have been occurring at the Salton Sea since at least 1989. Algae that are known to produce toxins are present at the Sea (Salton Sea Science Office database; Wood et al., 2001) algal toxins have been isolated from water samples collected at the Sea and algal toxins were recovered from the tissues of dead grebes during the 1992 epizootic, but not at levels that are known to cause avian mortality. Algal toxins isolated at the Salton Sea have been lethal for invertebrates but not for mice when evaluated in the laboratory (National Wildlife Health Center records). Avian cholera and avian botulism have both been diagnosed as causes of eared grebe mortality at the Sea (Salton Sea National Wildlife Refuge Narrative Reports; National Wildlife Health Center Epizootic Database) and both must still be considered as possible causes for the deaths of grebes for which no other etiologic agent has been identified.

An especially noteworthy change in the disease patterns of the Salton Sea during the 1990s is the general absence of the classical type C avian botulism events affecting shorebirds and waterfowl at the deltas of the Alamo and New Rivers. The large scale avian botulism epizootics of the past were not present. Instead, avian botulism is now primarily occurring in off-Sea freshwater impoundments except for the events involving pelicans and other fish-eating birds. The ecology of avian botulism in pelicans has not yet been elucidated but differs from the classical ecology of type C epizootics (Rocke & Friend, 1999). The diminished occurrence of classical outbreaks, typically involving dabbling ducks and shorebirds, on-Sea may be related to increased salinity and other water quality changes (Rocke & Samuel, 1999).

Conclusions

The information presented here is an annotated synopsis of the records for avian disease within the Salton Sea ecosystem. It is likely that additional information exists that was not found during the search for data, that in some instances the reported cause for events may be in error, and that there has been an increasing probability for detecting disease events over the timeframe considered. It is far less likely that major disease events have been missed or that the cause for major events have been misdiagnosed.

It is reasonable to conclude that the frequency for disease occurrence, variety of diseases causing avian mortality and magnitude of bird loses have changed greatly over time. Based on information available, more birds may have died from disease at the Salton Sea since 1989 than during the previous 82 years.

Avian botulism was the only major cause of bird mortality at the Sea until the 1979 epizootic of avian cholera. There are now four major diseases affecting Salton Sea avifauna; avian botulism, avian cholera, salmonellosis (1989) and Newcastle disease (1997); plus recurring mortality of eared grebes (1989) that is recognized on the basis of field signs, but for which the etiologic agent remains elusive. The 1996 epizootic of avian botulism in pelicans was an unprecedented event. The continued recurrence of type C toxin as a cause of mortality in fish-eating birds represents a unique expression of avian botulism that appears to be related to the live fish food base rather than to the typical maggot cycle for that disease.

All diagnosed major causes of avian mortality at the Salton Sea involve microbes as the disease agent. Those findings provide a clear indication of where attention should be focused to minimize avian losses not associated with predation and hunting. Pesticides have not been documented as a cause of on-Sea bird deaths. Several minor and one moderate pesticide mortality event have been documented in nearby agricultural fields. Those events have been sporadic and of low impact relative to numbers of birds lost to infectious disease and avian botulism.

Acknowledgements

I thank Salton Sea National Wildlife Refuge Manager C. Bloom for making the Refuge Narrative Reports available for review and Refuge biologist K. Sturm for his insights relative to those records and disease events at the Salton Sea. I also thank the National Wildlife Health Center for access to their databases, K. Cunningham and K. Cleary for computer assistance and data compilation, K. Wesenberg for literature searches and other library assistance, and C. Brand and S. Wright for their technical reviews and helpful suggestions. In addition, I thank the U.S. Fish and Wildlife Service Division of Refuges for providing a search of National Archives records for historic accounts of disease at the Salton Sea.

References

Anderson, D. W., J. J. Hickey, R. W. Risebrough, D. F. Hughes & R. E. Christensen, 1969. Significance of chlorinated hydrocarbon residues to breeding pelicans and cormorants. Can. Field-Natur. 83: 91–112.

Atkinson, C. T. & C. Van Riper III, 1991. Pathogenicity and epizootiology of avian haematozoa: *Plasmodium*, *Leucocytozoon*, and *Haemoproteus*. In Loye, J. E. & M. Zuk (eds), Bird–Parasite Interactions, Ecology, Evolution, and Behaviour. Oxford University Press, New York: 19–48.

Arnal, R. E., 1961. Limnology, sedimentation, and micro-organisms of the Salton Sea, Cal. Geolog. Soc. am. Bull. 72: 427–478.

Black, G.F., 1988. Description of the Salton Sea sport fishery 1982–1983. Cal. Fish Game Admin. Rept: 88–89.

Blaxland, J. D., 1951. Newcastle disease in shags and cormorants its significance as a factor in the spread of this disease among domestic poultry. Vet. Rec. 63: 731–733.

Brand, C. J., 1981. Migratory bird mortality transects in California – 1980–81. National Wildlife Health Center, Madison, WI: 20 pp.

Brand, C. J., 1984. Avian cholera in the Central and Mississippi Flyways during 1979–80. J. Wildl. Manage. 48: 399–406.

Brand, C. J. & R. M. Duncan, 1983. Avian cholera in the American flamingo, Phoenicopterus ruber: a new host record. Calif. Fish and Game 69: 190–191.

Brandly, C. A. & R. P. Hanson, 1965. Newcastle disease. In Biester, H. E. & L. H. Schwarte (eds), Diseases of Poultry, 5th edn. Iowa State University Press, Ames: 633–674.

Carson, R., 1962. Silent spring. Houghton-Mifflin Co., Boston: 368 pp.

Dahl, T. E., 1990. Wetland losses in the United States 1780s to 1980s. U.S. Fish and Wildlife Services, Washington, DC.: 13 pp.

Da Silva, E. & M. Iaccarino, 1999. Emerging diseases: a global threat. Biotech. Adv. 17: 363–384.

de Buys, W. & J. Myers, 1999. Salt Dreams. University of New Mexico Press, Albuquerque: 307 pp.

Epstein, P. R., B. H. Sherman, E. Spanger-Siegfried, A. N. Langston, S. Prasad & B. McKay, 1998. Marine ecosystems: emerging disease as indicators of change. Center for Health and the Global Environment, Harvard Medical School, Boston: 85 pp.

Ewald, P. W., 1995. The evolution of virulence: a unifying link between parasitology and ecology. J. Parasitol. 81: 659–669.

Ficken, M. D., 1991. Necrotic enteritis. In Calnek, B. E., H. J. Barnes, C. W. Beard, W. M. Reid & H. W. Yoder, Jr. (eds), Diseases of Poultry, 9th edn. Iowa State University Press, Ames: 264–267.

Friend, M., 1992. Environmental influences on major waterfowl diseases. Trans. N. am. Wildl. and Natural Resour. Conf. 57: 517–525.

Friend, M., 1995a. Increase avian disease with habitat change. In LaRoe, E. T., G. S. Farris, C. E. Puckett, P. D. Doran & M. J. Mac (eds), Our Living Resources: A Report to the Nation on the Distribution, Abundance, and Health of U.S. Plants, Animals, and Ecosystems. U.S. Dept. Interior, Natl. Biol. Ser., Washington D.C.: 401–405.

Friend, M., 1995b. Conservation landmarks: Bureau of Biological Survey and National Biological Service. In LaRoe, E. T., G. S. Farris, C. E. Puckett, P. D. Doran & M. J. Mac (eds), Our Living Resources: A Report to the Nation on the Distribution, Abundance, and Health of U.S. Plants, Animals, and Ecosystems. U.S. Dept. Interior, Natl. Biol. Ser., Washington D.C.: 7–9.

Friend, M. & C. J. Franson (eds), 1999. Field Manual of Wildlife Disease. General Field Procedures and Diseases of Birds. U.S. Dept. Interior, U.S. Geological Survey, Information and Technology Report 1999–1001, Washington, D.C.: 426 pp.

Friend, M. & D. O. Trainer, 1970. Polychlorinated biphenyl: interaction with DHV. Science 170: 1314–1316.

Friend, M. & D. O. Trainer, 1974a. Experimental DDT–duck hepatitis virus interaction studies. J. Wildl. Manage. 38: 887–895.

Friend, M. & D. O. Trainer, 1974b. Experimental dieldrin–duck hepatitis virus interaction studies. J. Wildl. Manage. 38: 896–902.

Giltner, L. T. & J. F. Couch, 1930. Western duck sickness and botulism. Science 72: 660.

Gonzalez, M. R., C. M. Hart, J. R. Verfaillie & S. H. Hurlbert, 1998. Salinity and fish effects on Salton Sea microecosystems: water chemistry and nutrient cycling. Hydrobiologia 381: 105–128.

Gratz, N. G., 1999. Emerging and resurging vector-borne disease. Annu. Rev. Entomol. 44: 51–75.

Hanson, R. P. (ed.), 1964. Newcastle Disease Virus: an Evolving Pathogen. University of Wisconsin Press, Madison: 353 pp.

Haschek, W. M. & C. G. Rousseaux, 1998. Fundamentals of Toxicologic Pathology. Academic Press, San Diego: 563 pp.

Hillis, D. M., 2000. Origins of HIV. Science 288: 1757–1758.

Hobmaier, M., 1930a. Duck disease caused by the toxin of *Clostridium botulinum*, type C. Proc. Soc. Exp. Biol. Med. 28: 339–340.

Hobmaier, M., 1930b. Duck disease caused by the poison of *Bacillus botulinus*, California Fish & Game 16: 5–21.

Hobmaier, M., 1932. Conditions and control of botulism (duck disease) in waterfowl. California Fish and Game 18: 5–21.

Holmes, S. W., 1933a. November 16 letter to U.S. Department of Agriculture, Bureau of Biological Survey, Washington, D.C., National Archives, Washington, D.C.: 1 pp.

Holmes, S. W., 1933b. November 17 letter to H.P Sheldon, Bureau of Biological Survey, Washington, D.C., National Archives, Washington, D.C.: 2 pp.

Horvitz, S., 1999. Salton Sea 101 an introduction to the issues of the Salton Sea – California's greatest resource. California State Parks: 38 pp.

Hosier, D. J., 1975. The ecology of avian botulism at the Salton Sea, California. M.S. Thesis, Calf. State Polytechnic University, Pomona: 66 pp.

Jehl, J. R., Jr., 1996. Mass mortality events of eared grebes in North America. J. Field Ornithol. 67: 471–476.

Kalmbach, E. R., 1930. Western duck sickness produced experimentally. Science 72: 658–660.

Kalmbach, E. R., 1934. The Salton Sea refuge with respect to possible future outbreaks of duck sickness and their control. U.S. Bureau of Biological Survey, Denver, CO.

Kalmbach, E. R., 1935a. Botulism and the proposed enlargement of the Salton Sea refuge. U.S. Bureau of Biological Survey, Denver, CO., March 20, National Archives, Washington, D.C.: 2 pp.

Kalmbach, E. R., 1935b. Supplementary statement with respect to the development of the Salton Sea refuge and its relation to botulism. U.S. Bureau of Biological Survey, Denver, CO., March 28, National Archives, Washington, D.C.: 2 pp.

Kalmbach, E. R., 1938. Botulism, a recurring hazard to waterfowl with notes on recent outbreaks in the United States, Canada, and Australia. Wildlife Research and Management Leaflet BS–120, Bureau of Biological Survey, Washington, D.C.: 8 pp.

Kalmbach, E. R., 1968. Type C botulism among wild birds – a historical sketch. Bureau Sport Fisheries and Wildlife, Special Scientific Report, Wildlife No. 10, Washington, D.C.: 8 pp.

Kalmbach, E. R. & M. F. Gunderson., 1934. Western duck sickness, a form of botulism. U.S. Dept Agriculture, Tech. Bull. 411: 82 pp.

Kennan, G., 1971. The Salton Sea: an Account of Harriman's Fight with the Colorado River. Macmillan, New York: 106 pp.

Laflin, P., 1995. The Salton Sea California's Overlooked Treasure. The Periscope, Coachella Valley Historical Society, Indio: 56 pp.

Lockhart, A. B., P. H. Thrall & J. Antonovics, 1966. Sexually transmitted disease in animals: evolutionary implications. Biol. Rev. 71: 415–471.

Lloyd, S., 1995. Environmental influences on host immunity. In B. T. Grenfell & A. P. Dobson (eds), Ecology of Infectious Disease in Natural Populations. Cambridge University Press, Cambridge: 327–361.

May, R. M., 1933. Ecology and evolution of host-virus associations. In Morse, S. S. (ed.), Emerging Viruses. Oxford University Press, New York, Oxford: 58–68.

Metcalf, H. E. D. W. Luchsinger & W. C. Ray, 1994. Brucellosis. In Beran, G. W. & J. H. Steele (eds), Handbook of Zoonoses 2nd edn. Section A: Bacterial, Rickettsial, Chlamydial, and Mycotic. CRC Press, Boca Raton: 9–39.

O'Neill, E. J., 1999. From behind the blue goose sign • Graphic Press, Klamath Falls: 412 pp.

Price, J. I. & C. J. Brand, 1984. Persistence of *Pasteurella multocida* in Nebraska wetlands under epizootic conditions. J. Wildl. Dis. 20: 90–94.

Rapport, D. J. & W. G. Whitford, 1999. How ecosystems respond to stress. BioScience 49: 193–203.

Read, A. F., S. D. Albon, J. Antonovics, V. Apanius, G. Dwyer, R. D. Holt, O. Judson, C. M. Lively, A. Martin-Löf, A. R. McLean, J. A. J. Metz, P. Schmid-Hempel, P. H. Thrall, S. Via & K. Wilson, 1995. Group report: genetics and evolution of infectious disease in natural populations. In Grenfell, B. T. & A. P. Dobson (eds), Ecology of Infectious Disease in Natural Populations. Cambridge University Press, Cambridge: 450–477.

Rocke, T. E. & M. Friend, 1999. Avian Botulism. In Friend, M. & J. C. Franson (eds), Field Manual of Wildlife Disease. General Field Procedures and Diseases of Birds. U.S. Dept. Interior, U.S. Geological Survey, Information and Technology Report 1999–2001, Washington, D.C.: 271–281.

Rocke, T. E. & M. D. Samuel, 1999. Water and sediment characteristics associated with avian botulism outbreaks in wetlands. J. Wildl. Manage. 63: 1249–1260.

Rosen, M. N., 1971. Avian cholera. In Davis, J. W., R. C. Anderson, L. Karstad & D. O. Trainer (eds), Infectious and Parasitic Diseases of Wild Birds. Iowa State University Press, Ames: 59–74.

Salton Sea Science Office, 78–401 Highway 111, Suite R, La Quinta, CA 92253.

Samuel, M. D., D. R. Goldberg, D. J. Shadduck, J. I. Price & E. G. Cooch, 1997. *Pasteurella multocida* serotype 1 isolated from a lesser snow goose: evidence of a carrier state. J. Wildl. Dis. 33: 332–335.

Schrag, S. J. & P. Wiener, 1995. Emerging infectious disease: what are the relative roles of ecology and evolution? Tree 10: 319–234.

Steele, J. H. & M. M. Galton, 1971. Salmonellosis. In Davis, J. W., R. C. Anderson, L. Karstad & D. O. Trainer (eds), Infectious and Parasitic Disease of Wild Birds. Iowa State University Press, Ames: 51–58.

Stickel, W. H., L. F. Stickel & J. W. Spann. 1969. Tissue residues of dieldrin in relation to mortality in birds and mammals. In Miller, M. W. & C. C. Berg (eds), Chemical Fallout. Current Research on Persistent Pesticides, C.C. Thomas, Springfield: 174–204.

Tonkin, G., 1933. November 26 letter to Chief, Bureau of Biological Survey, Washington, D.C., National Archives, Washington, D.C.: 2 pp.

U.S. Fish and Wildlife Service, Sonny Bono National Wildlife Refuge Complex, 906 West Sinclair Road, Calipatria, CA 92233.

U.S. Geological Survey, National Wildlife Health Center, 6006 Schroeder Road, Madison, WI 537711.

Walker, B. W. (ed.), 1961. The Ecology of the Salton Sea, California, in Relation to the Sport Fishery. Calif. Fish and Game Bull. 113: 1–204.

Williams, J. E., 1965. Paratyphoid and Arizona infections. In Biester, H. E. & L. H. Schwarte (eds), Disease of Poultry, 5th edn. Iowa State University Press, Ames: 260–328.

Wilson, J. E., 1950. Newcastle disease in a gannet (*Sula bassana*). A preliminary note. Vet. Rec. 62: 33–34.

Wobeser, G. A., 1981. Disease of Wild Waterfowl. Plenum Press, New York and London: 78 p.

Wobeser, G. A., 1994. Investigation and Management of Disease in Wild Animals. Plenum Press, New York and London: 265 pp.

Wood, A. M., S. R. Miller, W. K. W. Li & R. W. Castenholz, 2002. Hydrobiologia 473/Dev. Hydrobiol. 161: 77–92.

Zapata, A. G. & E. L. Cooper, 1990. The Immune System: Comparative Histophysiology. John Wiley & Sons, New York: 335 pp.