

# Ciliate plankton dynamics and survey of ciliate diversity in the Salton Sea, California, 1997-1999

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## Abstract

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Planktonic ciliates and other protozoa were monitored at mid-lake stations in the saline, polymictic Salton Sea during the period 1997-1999, at approximately two-week intervals. Additionally, in 1999, a survey of ciliate diversity in a variety of microhabitats was undertaken. Ciliates generally comprised < 20 percent of the total zooplankton biovolume, with copepods, rotifers and larvae of a barnacle and polychaete worm making up the rest. However, in early 1999 tintinnids constituted ~40 percent of total zooplankton biovolume, and in September 1998 when metazooplankters were very scarce, ciliates represented nearly 100 percent. An anaerobic ciliate, *Sonderia* sp., invaded the mid-water column during periods of anoxia and high sulfide levels in 1998 and 1999. Large ciliates, such as *Condylostoma* spp. and *Favella* sp. increased in abundance over the three-year period while the smaller forms, mostly scuticociliates, did not. This pattern may be due to a decrease during our study in abundance of the filter-feeding hybrid tilapia (*Oreochromis mossambicus* x *O. urolepis honorum*), which may have selectively grazed upon the larger forms. An inverse relationship between copepod abundance and large ciliate abundance suggests copepods also prey on the larger forms. A total of 143 ciliate taxa were found as well as protozoans in other groups such as heliozoans and choanoflagellates.

Key words: phytoplankton, saline lakes, polymixis, tilapia, sulfide, anoxia, *Condylostoma*, *Sonderia*, *Favella*, *Apo-cyclops dimorphus*

## Introduction

In the past protozoans were rarely studied or reported in lakes despite being important members of nearly all aquatic ecosystems (Fenchel 1987; Finlay *et al.* 1988; Hausmann and Hülsmann 1996). Difficulty of preservation and identification provides some explanation. With advent of the concept of the microbial loop (Azam *et al.* 1983), these organisms have received more attention. Reports of ciliates in saline lake environments, however, are still limited (*e.g.*, Al-Rashid 1996, 1997; Esteban *et al.* 2000). That they are important in hypersaline lakes was documented by Wilbert (1995) who found 96 species in thalassian and athalassian salt or saline lakes from sites in Saskatchewan, Canada, southwestern Australia, and Egypt.

The Salton Sea is a eutrophic, polymictic waterbody located in the agricultural region of southeastern California. The lake formed just over 100 years ago when a diversion structure was breached by the Colorado River. It began as a freshwater lake that gradually became more saline with time. It is 980 km<sup>2</sup> in area with a mean depth of about 8 m and plagued with a number of environmental problems including: rising salinity (salinity during our study of *ca.* 45 g l<sup>-1</sup>), high phytoplankton density, periods of water column anoxia, and sporadic overturn events that result in high sulfide levels in surface waters and “green tides” due to precipitating gypsum crystals (Watts *et al.* 2001; Holdren and Montañó 2002; Tiffany *et al.* 2007a, b).

Protozoans have been little studied at the Salton Sea. Arnal (1961) found that foraminifera were the most abundant benthic protists at that time. However, only two foraminiferan species were observed in a microcosm experiment performed on Salton Sea microecosystems in the early 1990s (Simpson *et al.* 1998). This group may have less importance in the present, more saline Sea, and, in any case, has likely never constituted a large portion of the zooplankton. Naked amoebae contribute to the plankton of the lake (Hauer and Rogerson 2001; Rogerson and Hauer 2002; E.B. Small, unpublished observations). A total of 45 morphotypes of naked amoebae, ranging in size from 3 to 100 µm in diameter, were found in shoreline and mid-lake samples taken in 1999 with abundance ranging from 14-237 cells ml<sup>-1</sup> (Rogerson and Hauer 2002).

In an experimental study of salinity effects on Salton Sea microecosystems, ciliates dominated total zooplankton biovolume in microcosms at all salinities (30 to 65 g l<sup>-1</sup>; Hart *et al.* 1998; Simpson *et al.* 1998). Two taxa, *Fabrea salina* Henneguy and *Condylostoma* spp., were favored at higher salinities with densities generally in the range of 1 ind. l<sup>-1</sup>. *Euplotes*, *Halteria*, *Pelatractus*, *Askenasia*, *Cyclidium* and an unidentified amoeba were also abundant (González 1997). These smaller taxa often exceeded 100-1000 ind. ml<sup>-1</sup> with a collective biovolume density ~1 mm<sup>3</sup> l<sup>-1</sup>. Hart *et al.* (1998)

suggested that the tilapia of the Salton Sea (*Oreochromis mossambicus* Peters x *O. urolepis honorum* Trewavas) might feed on some planktonic ciliates whose size lies within its range for filter feeding.

The “microbial loop” has been described by Azam *et al.* (1983), Sherr and Sherr (1986), Stoecker and Capuzzo (1990), and recently reviewed by Harvey (2006) wherein algal exudates (or other organic matter) are utilized by heterotrophic bacteria that in turn are cycled back into the food web via uptake by ciliates. Due to its frequent algal blooms and their subsequent die-off and rapid decomposition during overturn events, the microbial loop should be a substantial part of the food web of the Salton Sea, linking bacterial and ciliate production directly to the fish.

Wood *et al.* (2002) found that densities of heterotrophic bacteria in the Salton Sea, prey for many filter-feeding bacterivorous ciliates, were more than an order of magnitude higher than in typical neritic marine waters. Highly eutrophic environments are typically species rich in bacterivorous ciliates (Small 1973). Some large ciliates, such as *Euplotes* sp., *Condylostoma* spp. and *Frontonia* sp. feed on large algae such as dinoflagellates and diatoms (Fenchel 1987), which are abundant in the Salton Sea (Lange and Tiffany 2002; Tiffany *et al.* 2007a). Benthic algal mats, which occasionally break loose from the bottom, are commonplace in shallow areas at the Salton Sea; these teem with ciliates, benthic diatoms, filamentous cyanobacteria, and *Beggiatoa* spp., filamentous sulfur-oxidizing bacteria (Carpelan 1961; Wood *et al.* 2002).

The main objective of this study was to document seasonal and year-to-year variations in the abundance of planktonic ciliates in the Salton Sea over a three-year period (1997-1999) and to interpret those variations in relation to predation or grazing by fish, crustacean zooplankters, and periodic irruptions into surface waters of sulfide-rich bottom waters. A second objective was a preliminary inventory of ciliate diversity in the lake, carried out primarily by sampling a wide variety of microhabitats in nearshore shallow water areas. This investigation was carried out in parallel with three-year investigations of the phytoplankton (Tiffany *et al.* 2007a), metazooplankton (Tiffany *et al.* 2002) and temperature, oxygen and mixing regimes (Watts *et al.* 2001), and in the same general time frame (1998-2005) as numerous other shorter term studies at the Salton Sea of its birds, fish, macroinvertebrates, water chemistry, mixing regime, sediments, and pollutants.

## Methods

### *Sampling regime for planktonic dynamics*

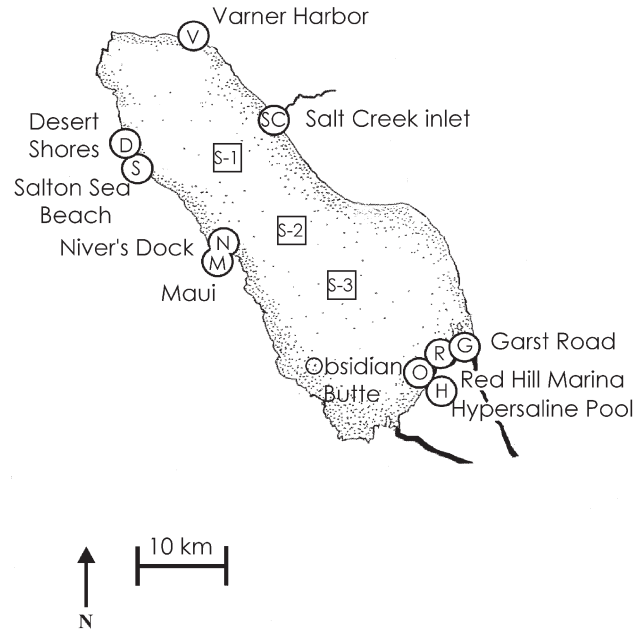
We sampled plankton at three mid-lake stations sited along the main axis of the lake at intervals of two to five weeks (S-1, S-2 and S-3, Fig. 1) in 1997-1999. Exact sampling dates and coordinates are given in Watts *et al.* (2001). Due to the wide range in length of individual protozooplankters (*ca.* 10  $\mu\text{m}$  to 200  $\mu\text{m}$ ), samples for enumeration were taken in two ways. Firstly, a 32-L Schindler trap with a mesh of 55  $\mu\text{m}$  was used to quantitatively collect individuals > 55  $\mu\text{m}$  in length at 2 m depth intervals. This trap also collected metazoan zooplankters such as rotifers, copepods and invertebrate larvae, as reported in Tiffany *et al.* (2002). Secondly, for small ciliates and phytoplankton, integrated water samples were collected for the 0-3 m, 3-6 m and 6-9 m depth strata with a PVC tube collector. Subsamples of 60 ml aliquots were immediately fixed in 1 percent Lugol's iodine (Tiffany *et al.* 2007a).

### *Sample analysis*

Procedures for enumerations of large protozoan species were as described in Tiffany *et al.* (2002). Briefly, the entire fixed sample from 32 liters was concentrated down to *ca.* 3 ml by settling and placed in a 40 mm  $\times$  50 mm Sedgwick-Rafter cell and enumerated at 40 $\times$  using brightfield illumination and a Reichart-Diastar microscope, which was also used to photograph selected specimens. When scarce, ciliates in the entire chamber were counted. When abundant, individuals in 4-10 transects of the chamber were enumerated. Some larger ciliates were contracted and difficult to identify, but based on appearance and inspection of live samples, most appeared to be in the genus *Condylostoma* and are reported here as "*Condylostoma*-like". Loricated tintinnids, euplotids and a large *Sonderia* sp. were always recognizable as such.

For smaller species, the Utermöhl method was used; a well mixed 25 ml subsample was settled for at least 24 hours and counted at 400 $\times$  using a Leitz Diavert inverted microscope (Tiffany *et al.* 2007a). Small ciliates were counted on two perpendicular transects across the center of the chamber. Small ciliates were not identified to species; many appeared to be scuticociliates and some resembled *Halteria* sp. or small *Euplotes* spp. Rarely, a miniature tintinnid *Eutintinnus* sp. or a choanoflagellate, *Desmarella moniliformis* Kent was encountered.

For large ciliates, arithmetic means densities over the six depths were determined for each station. The geometric mean for the three arithmetic means was then calculated along with the associated standard error factor (SEF = backtransformed value of SE yielded by log-transformed data) for each date in 1997-1999. Biovolumes of ciliate taxa were estimated using measurements of a minimum of 40 individuals per taxon and calculated with suitable geometric shapes (Table 1).



**Figure 1.**-Map of Salton Sea sample collection sites. Circles are nearshore locations; squares are mid-lake sites used for plankton collections.

**Table 1.**-Estimated biovolumes for ciliates and metazooplankters.

Taxon	Volume ( $10^3 \mu\text{m}^3$ )
small ciliates	1.6
<i>Sonderia</i> sp.	714
<i>Favella</i> sp.	166
<i>Euplotes</i> sp.	75.2
<i>Condylostoma</i> -like	1530
<i>Brachionus rotundiformis</i>	1130
<i>Synchaeta</i> aff. <i>vorax</i>	219
<i>Synchaeta</i> sp.	835
<i>Balanus amphitrite</i> nauplii	13100
<i>Balanus amphitrite</i> cyprids	19600*
<i>Apocyclops dengizicus</i> copepodids	8630
<i>Apocyclops dengizicus</i> nauplii	902
<i>Neanthes succinea</i> larvae	47600

\* corrected from Table 1 in Tiffany *et al.* (2002).

**Table 2.**—Sites of ciliate collections in the Salton Sea, January and June, 1999 and the primary plankton stations for 1997-1999.

Location		Latitude	Longitude	Collection method (s)
Varner Harbor	V	33° 30' 10" N	115° 54' 50" W	Tissue trap
Salt Creek inlet	SC	33° 26' 43" N	115° 50' 51" W	Plankton tow
Garst Road near Alamo River	G	33° 11' 58" N	115° 34' 48" W	Tissue trap
Red Hill Marina	R	33° 11' 44" N	115° 36' 51" W	Plankton tow
Salton Sea at Obsidian Butte	O	33° 10' 24" N	115° 38' 14" W	Tissue trap
Hypersaline pool at Obsidian Butte	H	33° 10' 23" N	115° 38' 15" W	Tissue trap
Maui and Crystal Streets	M	33° 17' 43" N	115° 55' 33" W	Uhlig and tissue trap
Norm Nivers dock	N	33° 18' 03" N	115° 55' 05" W	Plankton tow and tissue trap
Salton Sea Beach	S	33° 20' 41" N	116° 00' 34" W	Uhlig and plankton tow
Desert Shores	D	33° 24' 28" N	116° 02' 13" W	Tissue trap and scrapings from <i>Chaetomorpha</i>
S-1		33° 25' 00" N	115° 55' 00" W	Integrated sample and Schindler trap
S-2		33° 21' 00" N	115° 51' 00" W	Integrated sample and Schindler trap
S-3		33° 18' 00" N	115° 48' 00" W	Integrated sample and Schindler trap

As in most quantitative studies of protozoans, our ciliate biovolume estimates probably underestimate the true ciliate biovolume (Stoecker *et al.* 1994). Ciliates preserved in formalin contract and become distorted compared to live cells, losing up to 54 percent in volume (Choi and Stoecker 1989). Destruction of cells by formaldehyde also may occur. Additionally, during collection many soft-bodied ciliates > 55  $\mu\text{m}$  in length may be incompletely retained by the 55  $\mu\text{m}$  mesh of the Schindler trap due to their vermiform shape. Lugol's solution is probably less destructive and our counts of small ciliates may be more accurate.

### *Ciliate systematic survey*

Organisms were collected from ten different sites around the periphery of the lake on January 6-17, and June 8-22, 1999 (Fig. 1, Table 2). Sampling sites were chosen to provide a number of different microhabitats including both open water and lake bottom. All samples were taken nearshore in water < 1 m deep. Live samples were collected with three methods. Firstly, we employed a modified tissue trap technique using small containers and bits of canned tuna fish as bait (Small 1992). Secondly, we used a modified Uhlig technique extracting ciliates into a small Petri dish from sandy sediments using Nyltex nylon mesh between two plastic cups (Small 1992). And lastly, we used a 50  $\mu\text{m}$  mesh plankton net to concentrate individuals from the water column. Also, at Desert Shores, mats of an attached macroalga, *Chaetomorpha linum* (Muller) Kützing were sampled for ciliates in January; this alga was not present in June. Ciliates were examined live at 100 $\times$  or 400 $\times$  magnification. The samples were then fixed in modi-

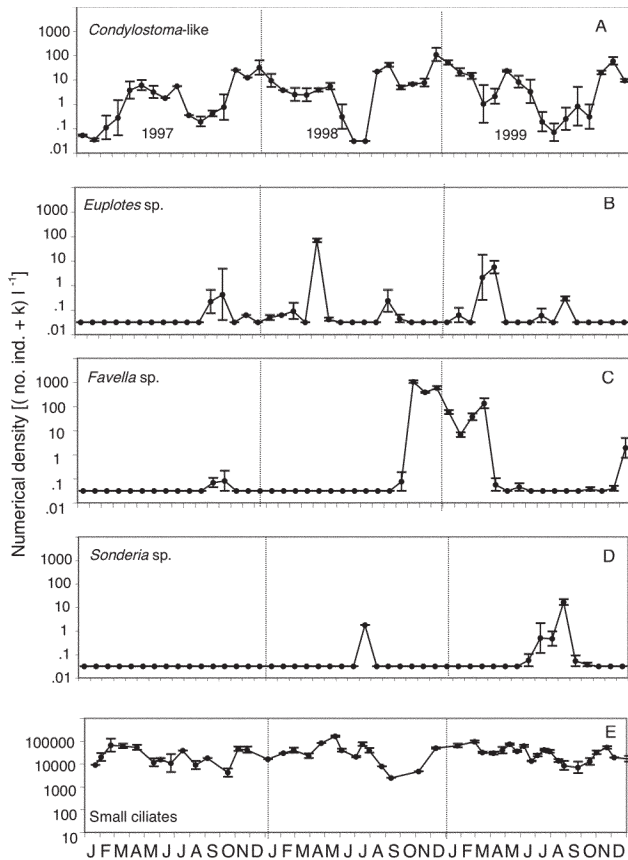
fied Bouin's fixative (Lynn 1992). Fixed samples were silver stained using the Protargol protocol of Montagnes and Lynn (1987). Ciliates were identified to either genus or species (where possible) and permanent slides catalogued.

## Results

### *Dynamics of individual taxa*

#### **Large soft-bodied ciliates**

Large vermiform ciliates were often present in the plankton, becoming especially abundant in spring of 1999, with densities up to ~100 individuals  $\text{l}^{-1}$  (Fig. 2A). These were often in contracted form due to fixation and were probably composed largely of *Condylostoma* spp. 100  $\mu\text{m}$  or longer (Fig. 3E). However, *Frontonia* sp., and possibly also other large ciliates such as *Tracheloraphis* sp., or *Trachelonema* sp. were also likely present at times and we include these in the category "*Condylostoma*-like." Due to its unique teardrop-shaped morphology, *Fabrea salina* was recognizable apart from these taxa but was only detected on rare occasions and so has not been charted separately. Very few *Condylostoma*-like ciliates were present on dates when the water column was anoxic or nearly so each year (August-September) suggesting that high hydrogen sulfide concentrations found then (Watts *et al.* 2001) may be lethal to them.



**Figure 2.**—Numerical density of taxa, 1997–1999, geomeans for three mid-lake stations. Error bars are standard errors. A. *Condylostoma*-like ciliates. B. *Euplotes* sp. C. *Favella* sp. D. *Sonderia* sp. E. Small ciliates.

### *Euplotes* sp.

A *Euplotes* sp. (mean length 92  $\mu\text{m}$ ) was smaller than other ciliates captured with the Schindler trap and had an average width of 55  $\mu\text{m}$  and thickness of 30  $\mu\text{m}$ . *Euplotes* sp. occasionally appeared in the plankton in high abundance in summer or fall (Figs 2B and 3F). Much of the time, however, it was not detected, especially in most of 1997. Paffenhöfer (1998) suggested the width of an organism is the most important factor determining whether it will pass through a given size mesh. Thus, some individual *Euplotes* likely passed through and were not collected and our densities likely are an underestimate.

### *Favella* sp.

This species was detected in low numbers during late 1997 and in a sustained bloom in the first half of 1999 where it attained densities as high as 1,000 individuals  $\text{l}^{-1}$ , but otherwise was usually not detected, other than briefly and in low

numbers, during late 1997 (Fig. 3C). It was just starting to reappear in December 1999 at the end of our study.

Tintinnids are usually identified by the morphology of their loricae. Loricae of tintinnids, abundant in spring 1999 (Fig. 2C), had two very different morphs. In the past one of these would have been described as a *Favella* with a pointed end (Fig. 3C), and the other as a *Coxliella*, with a more rounded end and spiral turns (Fig. 3D). These have been shown, at least in the case of *Favella ehrenbergii* (Claparède and Lachmann), to be the same species (Lavel-Peuto 1981) so they have been combined in our study. When, for some reason, e.g., attempted attack by a copepod, the ciliate escapes from its lorica, a new one is fashioned in the *Coxliella* form. Upon cellular division, only the *Favella* form is produced (Laval-Peuto 1977, 1983). In our samples many empty loricae of both forms were seen. These were noted but were not included in the enumerations, as they did not represent living individuals. The Salton Sea species resembles *Favella ehrenbergii* but its mean length of  $\sim 126 \mu\text{m}$  and oral diameter of  $\sim 71 \mu\text{m}$  are somewhat smaller than the measurements given for *F. ehrenbergii* by Hedin (1974).

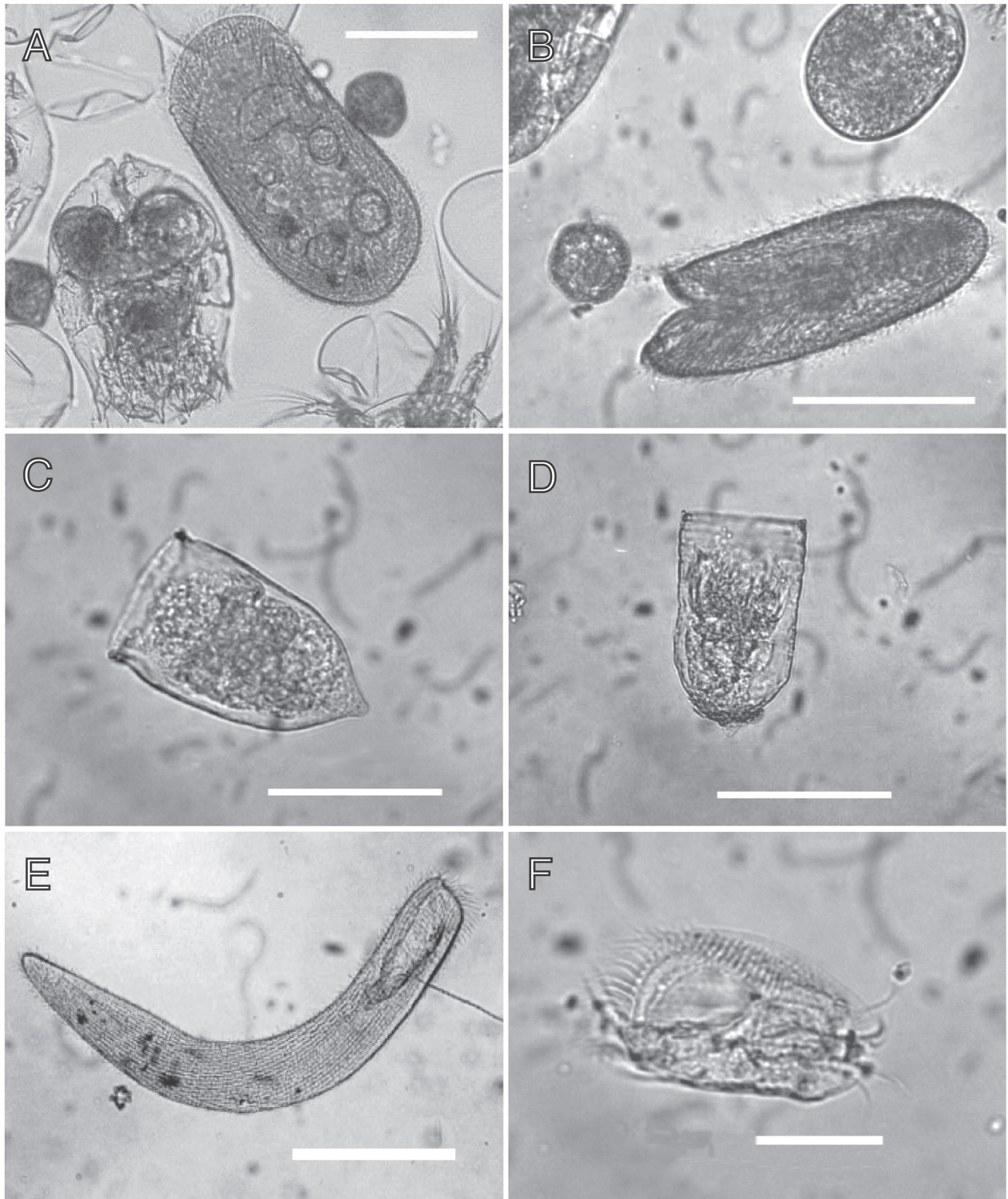
Tintinnids in the genus *Favella* are known to feed on small dinoflagellates such as *Heterocapsa* spp. (Yoo and Lee 1987; Stoecker *et al.* 1995; Kamiyama and Matsuyama 2005). *Heterocapsa niei* (Loeblich) Morrill et Loeblich is often abundant in the Salton Sea, especially in winter (Tiffany *et al.* 2007a), and likely provided prey for tintinnids in 1999. During the early part of that year the abundance of *H. niei* might have been suppressed by the dramatically increasing numbers of *Favella* sp. (Tiffany *et al.* 2007a).

### *Sonderia* sp.

Several large *Sonderia* species are found in the Salton Sea (Table 3). One of these (Figs 3A, B) suddenly appeared in mid-lake plankton in September 1998 and again in late July through mid-October 1999, during times when the entire water column was anoxic, sulfide levels were high, and other ciliates, metazoos and phytoplankters were absent or scarce (Fig. 2D; Tiffany *et al.* 2002, 2007a). During both these periods, large patches of bright green water, indicating the presence of gypsum crystals that form during these events, were observed by satellite at our stations (Tiffany *et al.* 2007b).

### Small ciliates.

Ciliates smaller than 55  $\mu\text{m}$  were numerically much more numerous than the larger ciliates reported above, usually with densities of 10–100 individuals  $\text{ml}^{-1}$  (10,000–100,000  $\text{l}^{-1}$ , Fig. 2E). These, however, are much lower than phytoplankton densities on any date (Tiffany *et al.* 2007a). Small ciliate density generally dipped in late summer–early fall.



**Figure 3.**-Light microscope images of large ciliates from zooplankton samples preserved in formalin. Scale bars = 50  $\mu$ m. A. and B. *Sonderia* sp. A. Ventral view, note overall size is similar to that of *Brachionus rotundiformis*, a common rotifer in the Salton Sea (to the right) and a nauplius larva of the copepod, *Apocyclops dimorphus* below. B. Lateral view. C. and D. *Favella* sp. C. *Favella* form of lorica. D. *Coxiella* form of lorica. E. *Condylostoma* sp. F. *Euplotes* sp.

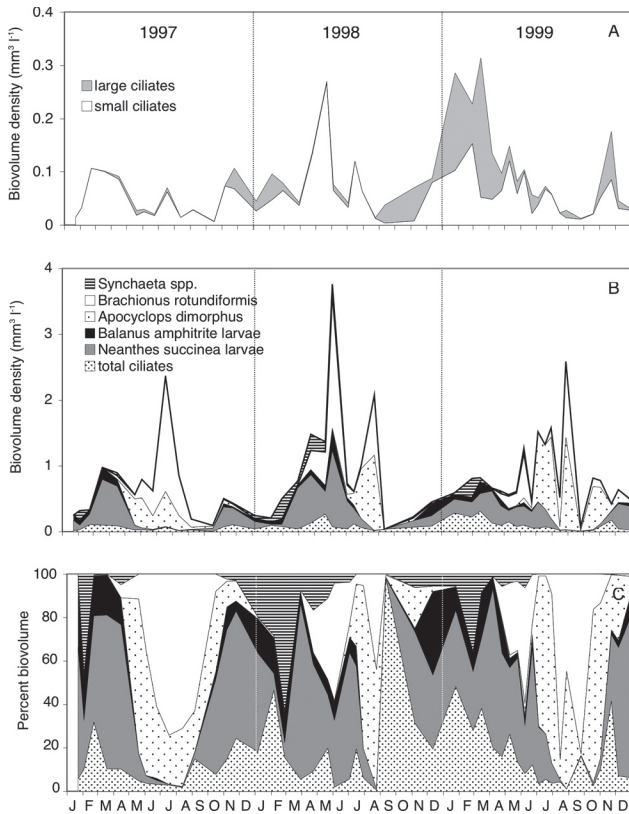
**Table 3.**—Ciliates identified from live and Protargol (Montagnes and Lynn) stained samples from the Salton Sea, 1999.

Taxon	Sample Site	Method	Taxon	Sample Site	Method
<b>Class Karyorelictea</b>			<b>Class Litostomatea</b>		
<i>Tracheloraphis</i> sp. 1	M	SS	<i>Chaenea</i> sp. 1	D:w	CM
<i>Tracheloraphis</i> sp. 2	M	SS	<i>Chaenea</i> sp. 2	D:w	CM
<i>Tracheloraphis</i> sp. 3	M	SS	<i>Chaenea</i> sp. 3	S	SS
<i>Trachelonema</i> sp. 1	M	SS	<i>Trachelophyllum</i> sp.	H	
<i>Trachelonema</i> sp. 2	S	TT	<i>Lacrymaria coronata</i>	M	CM
<i>Avelia</i> sp.	M,G:w	SS	Claparède & Lachmann		
<i>Geleia</i> sp.	D:w	CM	<i>Lacrymaria</i> sp. 1	D	CM
<i>Parduczia</i> sp.	D:w	CM	<i>Lacrymaria</i> sp. 2	M	CM
<i>Nouzaredia</i> sp.	D:w	CM	<i>Lacrymaria</i> sp. 3	D	
<b>Class Heterotrichea</b>			<i>Bryophyllum</i> sp.	M	SS
<i>Condylostoma</i> sp. 1	all:w	SS	<i>Monodinium</i> sp.	O,V:s	TT
<i>Condylostoma</i> sp. 2	all but M:w	SS	<i>Litonotus</i> sp. 1	M	SS
<i>Condylostoma</i> sp. 3	all but H,V	SS	<i>Litonotus</i> sp. 2	V	SS
<i>Parablepharisma</i> sp.	D:w	CM	<i>Amphileptus</i> sp.	N	SS
<i>Pseudoblepharisma</i> sp.	M:w	SS	<i>Enchelydon</i> sp.	M	SS
<i>Anigsteinia clarissima</i> Isquith	S,s	SS	<b>Class Phyllopharyngea</b>		
<i>Gruberia</i> spp.	M:s	SS,PS	<i>Clamydodon</i> sp. 1	G,V	TT
<i>Fabrea salina</i> Henneguy	O,H,R,D,G,M:w	TT,PS	<i>Clamydodon</i> sp. 2	M	TT
<i>Copmetopus</i> sp.	G:s	TT,SS	<i>Dysteria</i> sp. 1	G	TT
<i>Peritromus</i> sp.	G:s	PS	<i>Dysteria</i> sp. 2	D,M	TT
<b>Class Spirotrichea</b>			<i>Dysteria</i> sp. 3	D	TT
<b>Subclass Spirotrichia</b>			<i>Dysteria</i> sp. 4	S	SS
<i>Metopus</i> sp. 1	M:w	SS	<i>Dysteria</i> sp. 5	S:s	SS
<i>Metopus</i> sp. 2	D:w	SS	<i>Trochilia</i> sp. 1	G,M	TT
<i>Metopus</i> sp. 3	D:w	CM	<i>Trochilia</i> sp. 2	D:s	TT
<i>Metopus</i> sp. 4	G	SS	<i>Cyrtophoron</i> sp. 1	D:w	CM
<i>Metopus</i> sp. 5	G,w	SS	<i>Cyrtophoron</i> sp. 2	D:w	CM
<i>Metopus</i> sp. 6	G,w	TT	<i>Chilodonella</i> sp. 1	S,D:w	CM
<i>Eometopus</i> sp.	G,w	TT	<i>Chilodonella</i> sp. 2	M	SS
<b>Subclass Choreotrichia</b>			<i>Lynchella</i> sp.	M,G	TT
<i>Strombidium</i> sp. 1	M:w	SS	<i>Trigheimostoma</i> sp.	G,M	SS
<i>Strombidium</i> sp. 2	D:w	SS	<i>Pseudochilodonopsis</i> sp.	M	SS
<i>Strombidium</i> sp. 3	D:w	SS	<i>Ignotocoma</i> sp.	D:w	CM
<i>Strombidium</i> sp. 4	M:s		<i>Coeloperix</i> sp.	D:w	CM
<i>Strombidium</i> sp. 5	M:s		<i>Hypocoma</i> sp. 1	D:w	CM
<i>Strombidium</i> sp.	D:w	CM	<i>Hypocoma</i> sp. 2	D:w	CM
<i>Strombidinopsis</i> sp.	G,s	PS	<i>Chlamydonellopsis</i> sp.	D:w	CM
<i>Favella</i> sp.	G,SC:s	PS	<i>Acineta</i> sp.	S,V,O	SS
<i>Eutintinnus</i> sp.	M,S	SS	<b>Class Prostomatea</b>		
Oligotrich (new genus)	M	SS	<i>Holophrya</i> sp.	S:s	SS
<b>Subclass Stichtotrichia</b>			<i>Metacystis</i> sp. 1	S:s	
<i>Urostyla</i> sp. 1	N,D	PS	<i>Metacystis</i> sp. 2	S:s	SS
<i>Urostyla</i> sp. 2	D:s	PS	<i>Coleps</i> sp. 1	V	SS
<i>Tracheolostyla</i> sp.	M	SS	<i>Coleps</i> sp. 2	D:w	CM
<i>Pseudokeronopsis</i> sp.	D	SS	<i>Coleps</i> sp. 3	M:s	
<i>Tachysoma</i> sp.	M,D	CM	<i>Prorodon</i> sp. 1	D:w	CM
<i>Hypotrichidium</i> (like) sp.	S, O	SS	<i>Prorodon</i> sp. 2	M	SS
			<i>Prorodon</i> sp. 3	V,M	TT
			<i>Prorodon</i> sp. 4	M	SS
			<i>Urotricha</i> sp.	D, S:w,s	SS

Table 3.-Cont.

Taxon	Sample Site	Method	Taxon	Sample Site	Method
<b>Class Nassophorea</b>			<b>Class Plagiopylea</b>		
<b>Subclass Nassophoria</b>			<b>Subclass Plagiopylia</b>		
<i>Zosterodazys</i> sp.	D,R:w	CM	<i>Sonderia</i> sp. 1	D	SS
<i>Fontonia</i> sp.	M,V	SS	<i>Sonderia</i> sp. 2	V	SS
<b>Subclass Hypotrichia</b>			<i>Sonderia</i> sp. 3	D	CM
<i>Aspidisca</i> sp. 1	V:w	SS	<i>Plagiopyla</i> sp. 1	M,V	SS,TT
<i>Aspidisca</i> sp. 2	M:w	SS	<i>Plagiopyla</i> sp. 2	V	SS
<i>Aspidisca</i> sp. 3	M,D:w	SS	<i>Plagiopyla</i> sp. 3	H,M	SS
<i>Euplotes woodruffi</i> Gaw	G:s	TT	<i>Plagiopyla</i> sp. 4	S	SS
<i>Euplotes</i> sp. 1	D:w	SS	<i>Trimyema</i> sp.	S	TT
<i>Euplotes</i> sp. 2	M:w	SS	<i>Parasonderia kahli</i> Fauré-Fremiet		G SS
<i>Euplotes</i> sp. 3	M:w	SS	<i>Sonderiella</i> sp.	G	SS
Large <i>Euplotes</i> sp. 1	H:w	SS	<b>Sampling methods</b>		
Large <i>Euplotes</i> sp. 2	V:w	SS	SS = Sandy sediment, Uhlig technique		
Large <i>Euplotes</i> sp. 3	V:w	TT	CM = Chaetomorpha sample		
Large <i>Euplotes</i> sp. 4	M:w	SS	TT = Tissue trap		
<i>Uronychia transfuga</i> sp. 1	D:w	CM	PS = Plankton sample		
<i>Uronychia transfuga</i> sp. 2	S:w	SS	<b>Sample Sites</b>		
<i>Diophrys</i> sp. 1	D:w	CM	V = Varner harbor		
<i>Diophrys</i> sp. 2	S:w	SS	SC = Salt Creek inlet		
<b>Class Oligohymenophorea</b>			G = End of Garst Rd		
<b>Subclass Hymenostomatia</b>			R = Red Hill Marina		
Order Scuticociliatida			O = Obsidian Butte		
<i>Pleuronema</i> sp.	D:w	CM	H = Hypersaline Pool, Obsidian Butte		
<i>Cyclidium</i> sp. 1	O	CM	N = Dock at Mr. Norm Nivers residence		
<i>Cyclidium</i> sp. 2	M	CM	M = Maui and Crystal Rd		
<i>Cyclidium</i> sp. 3	M	TT	S = Salton Sea Beach		
<i>Cyclidium</i> sp. 4	V	TT	D = Desert Shores		
<i>Cristigera</i> sp.	H	SS	w=winter (January)		
<i>Ovilembus</i> sp.	M	SS	s=summer (June)		
<i>Paralembus</i> sp.	V	TT			
<i>Paraphilaster</i> sp.	M	TT			
<i>Porpostoma notatum</i> Möbius	M,R,G	PS			
<i>Ovilembus</i> sp.	M	SS			
<i>Pseudocohnilembus</i> sp.	V:w	SS			
<i>Cardiostomatella</i> sp.	V	SS			
<i>Uronema</i> sp.	M	SS			
<i>Cohnilembus reesi</i>	H:w	TT			
<i>Urocyclon</i> sp. 1	D:w	CM			
<i>Urocyclon</i> sp. 2	M	SS			
<b>Subclass Peritrichia</b>					
<i>Epistilis</i> sp.	S	PS			
<i>Zoothamnium</i> sp. 1	G	TT			
<i>Zoothamnium</i> sp. 2	D	PS			
<i>Vorticella</i> sp. 1	D:w	CM			
<i>Vorticella</i> sp. 2	D:w	CM			
<i>Vorticella</i> sp. 3	D:w	CM			
<i>Vorticella</i> sp. 4	D:w	CM			
<i>Vorticella</i> sp. 5	D:w	CM			
<i>Rhabdostyla</i> sp.	G	CM			
<i>Cothemia</i> sp.	D:w	CM			





**Figure 4.**—A. Mean biovolume density for three mid-lake stations of large ciliates (collected with a Schindler trap) and small ciliates (using the Utermöhl method), 1997–1999. B. Estimated biovolume density of metazooplankton (from Tiffany *et al.* 2002) with addition of total ciliate biovolume. C. Percent biovolume density of metazooplankton and ciliates.

### Ciliates relative to metazooplankton

Total ciliate abundance varied from < 10 percent to ~30 percent of total zooplankton during most of the study (Figs. 4B and 4C). It ranged from 0.007 to 0.31 mm<sup>3</sup> l<sup>-1</sup> (Fig. 4A) whereas the total metazooplankton biovolume density was generally on the order of 0.3 to 3 mm<sup>3</sup> l<sup>-1</sup> except during sulfide events. If we use the conversion factors to dry weight for ciliates in formalin and Lugol's solution respectively given by Putt and Stoecker (1989) of 0.14 pg C μm<sup>-3</sup> for the larger ciliates and 0.19 pg C μm<sup>-3</sup> for the small ciliates this translates to a range of about 0.1 to 5.1 μg C l<sup>-1</sup> for large and small ciliates combined.

Small ciliates often made up a large proportion of total ciliate biovolume, as they did during much of 1997 and April–August 1998 (Fig. 4A). At times, however, small ciliates accounted for only 50 percent or less of total ciliate biovolume, especially from September 1998–April 1999 and again in November 1999 (Fig. 4A).

Large ciliates made up a greater portion of total ciliate biovolume in each succeeding year. Although ciliate biovolume was not great in September 1998 it made up over 95 percent of total zooplankton biovolume. This occurred during a sulfide event in 1998 (Watts *et al.* 2001), when phytoplankton abundance plummeted and *Condylostoma*-like ciliates made up most of the scant zooplankton. From January–April 1999 the large numbers of tintinnids and *Condylostoma*-like ciliates together comprised 20–40 percent of total zooplankton biovolume. During plankton crashes later in 1999, when sulfide likely caused mass mortality of the copepod, *Apocyclops dimorphus* Kiefer (previously identified as *Apocyclops dengizicus* Lepeshkin, Reid *et al.* 2002), most of the surviving zooplankters were *Sonderia* spp. and the rotifer, *Brachionus rotundiformis* Tschugunoff. When copepod densities were high, usually in summer, densities of large ciliates plunged (Fig. 6). Large ciliates, however, often co-occurred with the larvae of the polychaete worm, *Neanthes succinea* Frey and Leuckart, and the barnacle *Balanus amphitrite* Darwin, perhaps because they were too large to be preyed upon by these metazooplankters.

### Survey of ciliate diversity

We found 143 species within 9 classes of Ciliophora during the 1999 survey, so ciliates can thus be considered one of the most diverse groups in the Salton Sea (Table 3). Most were identified only to generic level. It is likely many are species new to science, making further systematic studies of this fauna highly desirable. Ciliates were collected from a number of microhabitats in the Sea including: barnacle shell sands, cyanobacterial mats, epilithic *Chaetomorpha* mats, and open waters. Elongate ciliates such as *Tracheloraphis* (three species) and *Trachelonema* (two species) in the class Karyorelictea were observed in algal mats. A commonly observed genus was *Condylostoma* (in the class Heterotrichia). Genera usually considered favored by anaerobic conditions, such as *Metopus* (6 species) and *Eometopus* (1 species), in the class Spirotrichea, and *Sonderia* (3 species) and *Plagiopyla* (4 species) in the class Plagiopyleia were collected from nearshore sediments. Choreotrichia, a subclass within Spirotrichea which is generally planktonic, was represented by *Favella* sp. (a tintinnid), *Strombidium* spp., *Strobilidium* sp., and *Strombidonopsis* sp.

Heliozoans and choanoflagellates such as *Desmarella moniliformis* and *Sphaeroeca* cf. *volvox* Lauterborn were seen in live water samples by one of us (MAT) on occasions other than those described above (Fig. 5).

## Discussion

### *Protozoa and eutrophy*

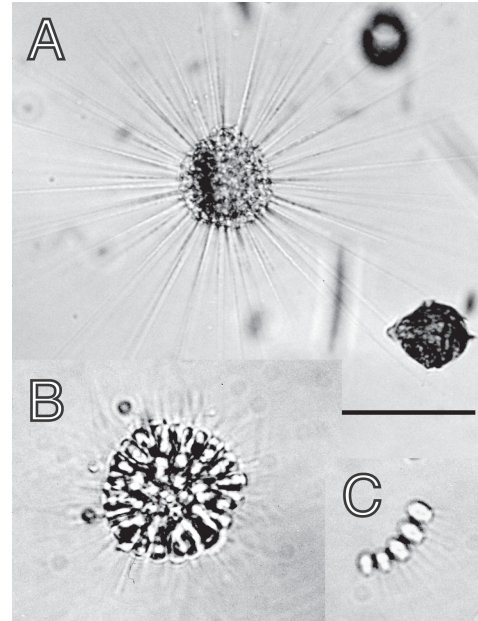
In many coastal marine and saline lake systems the protozooplankton rival the metazooplankton in biomass (García *et al.* 1995; López-González *et al.* 1998; Paffenhöfer 1998; Nielsen and Anderson 2002) whereas most of the time this does not seem to hold true for the Salton Sea. Smetacek (1981) studied meta- and protozooplankton in the Kiel Bight (depth 20 m) and found they had comparable biomass in summer. In a study of hypereutrophic freshwater lakes Auer *et al.* (2004) found that protozoans, consisting mainly of ciliates, averaged 42 percent of total zooplankton biomass as opposed to only 24 percent in mesotrophic lakes. Based on its algal biomass the Salton Sea can be considered extremely eutrophic with chlorophyll *a* concentrations often in the range of 30-40  $\mu\text{g l}^{-1}$  or higher (Tiffany *et al.* 2007a). Thus, the Salton Sea can support large metazooplankton populations, *e.g.*, the density of rotifers was often  $> 1000 \text{ ind. l}^{-1}$ , and that of copepods  $> 100 \text{ ind. l}^{-1}$  (Tiffany *et al.* 2002). These large populations can approach or exceed those of the relatively dense protozooplankton.

In nearshore habitats of the Salton Sea, *e.g.*, algal mats and sediments, ciliate fauna was highly diverse (Table 3). Except in anoxic bottom waters, benthic habitats often sport high ciliate diversity (*e.g.*, Fenchel 1969; Smetacek 1981; Azovsky and Mazei 2005). Also the eutrophic nature of the lake leads to high bacterial abundance (food for filter-feeding ciliates) (Wood *et al.* 2002) and benthic diatoms for forms such as *Frontonia* sp. (Lange and Tiffany 2002).

One might ask why, other than when the amphipod *Artemia franciscana* Kellogg was abundant, ciliates made up a larger fraction of total zooplankton in the microcosm experiments at all salinities, both in the presence and absence of fish (Hart *et al.* 1998), than they did in the Salton Sea proper. Chlorophyll *a* concentrations in both systems were high at  $\sim 10\text{-}100 \mu\text{g l}^{-1}$  (González 1997; Tiffany *et al.* 2007a). Biovolume density of ciliates in the microcosms, which was estimated in the same manner as in our study, was generally in the range of  $0.1\text{-}3 \text{ mm}^3 \text{ l}^{-1}$  whereas the total biovolume of ciliates during 1997-1999 was rarely  $> 0.1 \text{ mm}^3 \text{ l}^{-1}$ . The relatively high surface area of the container walls in the microcosms could have contributed to an abundance of ciliates, perhaps due to attached epibiota that provided refuge, food and habitat. Ciliates may have made excursions into the water column from both tank walls and from sediments, perhaps aided by an air-injection system that maintained a gentle vertical mixing during the experiment.

### *Species composition of planktonic protozoa*

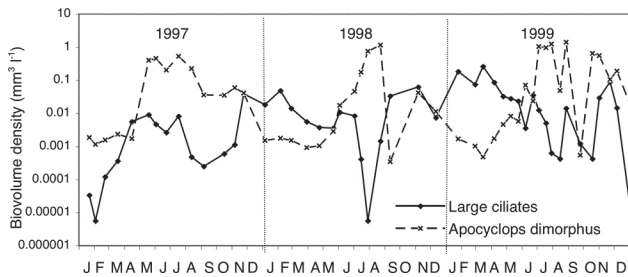
In the Salton Sea many of the unicellular taxa are of marine origin. This was indicated by the ciliate species composi-



**Figure 5.**—Light microscope images of live protozoa other than ciliates. Scale bar is 50  $\mu\text{m}$ . A. Heliozoan with a dinoflagellate, *Gonyaulax spinifera*. B. and C. Choanoflagellates. B. *Sphaeroeca* cf. *volvox*. C. *Desmarella moniliformis*.

tion and also the presence of marine choanoflagellates and foraminifera. Marine fish were introduced multiple times, mostly in the 1940s and 1950s and about the time the lake reached seawater salinity (Walker *et al.* 1961). Water from these introductions could easily have included marine ciliates of many species and may be the primary source of most of the Salton Sea ciliate diversity. The ciliates most often encountered in marine plankton belong to the subclass Choreotrichia (Pierce and Turner 1992). Many of these are aloricate species such as *Strombidium* spp.; others are loricate tintinnids. In eutrophic conditions other groups may become important, for example scuticociliates and hypotrichs such as *Euplotes* spp. Groups other than these are considered uncommon in marine plankton by Pierce and Turner (1992). Choreotrichs were certainly encountered in the Salton Sea, especially *Favella* sp. in 1999, but more often other groups dominated. Since they are often encountered in eutrophic conditions, finding *Euplotes* sp. in high abundance in the Salton Sea at times is not surprising. It probably feeds on microalgae or flagellates (Fenchel 1987). Diatoms, dinoflagellates, cryptomonads and other microalgae are highly abundant in the Salton Sea (Tiffany *et al.* 2007a).

Aloricate ciliates, other than the choreotrichs, scuticociliates and hypotrichs, are not often encountered in marine systems (Pierce and Turner 1992). One reason for finding other ciliates, such as *Condylostoma* spp., in such high abundance



**Figure 6.**—Comparison of biovolume density of large ciliates and the cyclopoid copepod, *Apocyclops dimorphus*, geomeans for three mid-lake stations.

in the Salton Sea may in part be due to mixing patterns in this dynamic lake, fueled by wind. Benthic organisms such as some large diatoms are found in the plankton, especially during the winter mixing period (Tiffany *et al.* 2007a). Thus the appearance of large protozoans in the plankton, usually considered benthic, *e.g.*, *Condylostoma* spp., is not unexpected.

### Grazing by copepods and tilapia

Two grazers may have had major influences on the abundance of larger ciliates. These are the cyclopoid copepod, *Apocyclops dimorphus*, and the filter-feeding hybrid fish, the omnivorous tilapia.

*A. dimorphus* was most common in summer months (Tiffany *et al.* 2002). Cyclopoid copepods are primarily raptorial (Williamson 1980) and, depending on the morphology of their mouthparts, some have capacity to feed on larger algae (Fryer 1957; Hopp and Meier 2005) and are known to be omnivorous (Adrian and Frost 1993). In the Salton Sea *A. dimorphus* likely partially subsists on metazooplankters, primarily a rotifer, *Brachionus rotundiformis*, and possibly also cannibalistically on its own nauplii. Wickham (1995a) suggested that cyclopoid copepods preferentially feed on soft-bodied defenseless organisms such as slow moving ciliates. There was a strong inverse relationship between *Apocyclops dimorphus* densities and that of large ciliates (Fig. 6). Thus, it appears that, when present, *A. dimorphus* is able to control the populations of large ciliates. This was especially noticeable in summer of 1998 and several times in mid 1999. Other studies have also shown that cyclopoid copepods feed on ciliates (Stoecker and Capuzzo 1990; Wickham 1995a, 1995b; Verity and Paffenhöfer 1996; Hansen 2000; Johannsen *et al.* 2004).

During the three-year period 1997-1999, tilapia abundance decreased steadily (Costa-Pierce and Riedel 2000; Riedel *et al.* 2002; Caskey *et al.* 2007). This decline was partially due to major fish kills during periods of anoxia and high sulfide and partially to lack of recruitment of the fish during these

years. Concomitantly, the density of large ciliates surged, most noticeably in 1999. Large phytoplankters also increased from 1997 to 1999 (Tiffany *et al.* 2007a). Size selectivity of the Salton Sea tilapia has not been studied, but related species can feed on particles even smaller than the large ciliates observed in this study. The Nile tilapia, *Oreochromis niloticus* Linnaeus, can feed on particles from 38  $\mu\text{m}$  to  $\sim 1000 \mu\text{m}$  using mucus entrainment (Sanderson *et al.* 1996); these are in the size range of the larger ciliates encountered in this study. *Tilapia galilaea* (= *Saratherodon galilaeus galilaeus* Linnaeus) feeds selectively on larger algal cells such as dinoflagellates and much less on nanoplankton (Drenner *et al.* 1987). The numerous smaller ciliates likely escape predation by tilapia due to their size but the larger ones cannot.

### Anaerobic ciliates

In most marine environments anoxia-tolerant ciliates are probably limited to dwelling near or within sediments where sulfide levels are high and oxygen concentrations are low (Fenchel and Riedl 1970; Dyer 1989; Fenchel and Finlay 1995; Wickham *et al.* 2000), and this probably holds true for the Salton Sea most of the time. Typically anaerobic ciliates such as *Metopus*, *Plagiopyla* and *Sonderia* were found in shore sediment samples and algal mats of the Salton Sea (Table 3). A startling find was the sporadic invasion of a large anaerobic ciliate, *Sonderia* sp., into the mid-lake water column. Conditions of high sulfide and anoxia apparently favored this species for short periods of time in late summer or early fall when mixing events brought up sulfide-laden waters from the hypolimnion, stripping the water of oxygen, and killing most other plankters (Watts *et al.* 2001; Tiffany *et al.* 2007a, 2007b). Sulfidic conditions may have lasted for days, allowing the ciliate to persist. When oxic conditions returned *Sonderia* sp. vanished rapidly. It is likely that it cannot withstand the presence of oxygen for long (Fenchel *et al.* 1977; Dyer 1989). Though it did not invade the entire water column, Laybourn-Parry *et al.* (1990) found an anaerobic *Plagiopyla* species in the plankton below the oxycline in a small eutrophic lake and concluded that it was a migrant from the benthos. Dolan and Coats (1991) studied ciliates during a severe hypoxia event in Chesapeake Bay and found large trachlocercid ciliates, more typically seen in anoxic sediments, to be dominant zooplankters in bottom waters below 8-10 m. They speculated that these benthic ciliates colonized the waters overlying the sediments when low oxygen concentrations favored them. It appears that anaerobic sulfide-tolerant ciliates occupy the entire water column of the Salton Sea when even surface waters become anoxic. The pervasive high sulfide levels seen after overturn events in the Sea (Tiffany *et al.* 2007b) precludes the survival of most aerobic organisms (Theede *et al.* 1969; Bagarinao 1992).

Fenchel (1968) demonstrated that *Sonderia schizostoma* feeds on the white sulfur filamentous bacterium *Beggiatoa*

and he suggested that most *Sonderia* species are specialized to feed on it. Dyer (1989) also reported *Sonderia tubigula* feeds on filamentous bacteria and speculated that its large buccal cavity allows it to ingest and package the long strands. At least two morphotypes of *Beggiatoa* are known to be common members of shoreline algal mats of the Salton Sea (Wood *et al.* 2002). However, it seems that during the brief excursions of *Sonderia* sp. into the mid-lake plankton of the Salton Sea, insufficient masses of this bacterium were present to sustain it since filamentous bacteria were not seen in routine phytoplankton samples at any time from 1997-1999 (Tiffany *et al.* 2007a). Even had anaerobic conditions persisted, it is likely that *Sonderia* in the water column would have eventually starved.

## Conclusions

Ciliates are abundant and diverse in the Salton Sea. Due to their rapid turnover rate and ability to reproduce quickly, ciliates have a large impact on its ecosystem by providing sustenance for higher trophic levels such as metazooplankton and fish and by feeding on bacteria and algae. The presence, at times, of species adapted to low oxygen and high sulfide levels is a consequence of the eutrophic and dynamic nature of the lake and these can be used as an indicator of poor water quality. These conditions also provide potential for valuable contributions to the study of ciliate systematics.

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