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Salinity and fish effects on Salton Sea microecosystems: zooplankton and nekton

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Abstract

The Salton Sea is the largest inland lake in California. Currently (1997) the salinity of the lake is about 44 g l^{-1} and is increasing gradually as a result of continued agricultural wastewater inflows, high evaporation rates, and lack of an outlet. A microcosm experiment was carried out to determine the effects of salinity (30, 39, 48, 57, and 65 g l^{-1}) on Salton Sea algae and invertebrates in outdoor aquatic microcosms. The experiment was also designed to assess the effects of tilapia (*Oreochromis mossambicus*) on this community at two of these salinities (39 and 57 g l^{-1}). Fiberglass tanks containing Salton Sea water were adjusted to the appropriate salinity by the addition of salts, identically inoculated with organisms from the Salton Sea and other saline water bodies in the region, and monitored for 15 months. Planktonic and nektonic invertebrates were sampled monthly at night from the upper part of the water column. The dominant invertebrates present were *Gammarus mucronatus*, *Artemia franciscana*, *Trichocorixa reticulata*, and an assemblage of ciliate protozoans. *Gammarus* decreased and *Trichocorixa* increased with increasing salinity. *Artemia* was present only at the two highest salinities. Rotifers, harpacticoid and cyclopoid copepods, barnacle larvae, and protozoans all showed marked and varied responses. During the latter half of the experiment, the invertebrate assemblage was dominated by *Gammarus* at 30 and 39 g l^{-1}, by protozoans at 48 g l^{-1}, and by protozoans and *Trichocorixa* at 57 and 65 g l^{-1}. The presence of tilapia caused a 99 percent reduction in *Gammarus* at 39 g l^{-1} and a 70–90 percent decrease in *Trichocorixa* at 57 g l^{-1}. These were accompanied by substantial increases in rotifers, copepods, and certain protozoans, and decreases in other protozoans. As the salinity of the Salton Sea continues to increase, large changes in the invertebrate populations are expected. This study suggests that the principal change would be an increase in *Trichocorixa* densities, the loss of *Gammarus*, and the appearance of *Artemia* at about 60–70 g l^{-1}, when both fish and invertebrate predators are likely to be scarce or absent. Protozooplankton abundance is likely to increase when tilapia declines and later decrease when and if large *Artemia* populations develop.

Introduction

Salinity has long been considered an important influence on the composition and dynamics of aquatic ecosystems. It is surprising, therefore, that most conclusions on this subject are based either on laboratory determinations of salinity tolerances of individual organisms or on descriptive studies of lakes (Greenwald & Hurlbert, 1993). Studies of the tolerances of individual species provide information on physiology but limited power to predict what will happen in nature. Understanding of ecological effects of increasing salinity requires study of the problem at the community level.

Descriptive comparative studies of saline lakes are one means to investigate the biotic community and

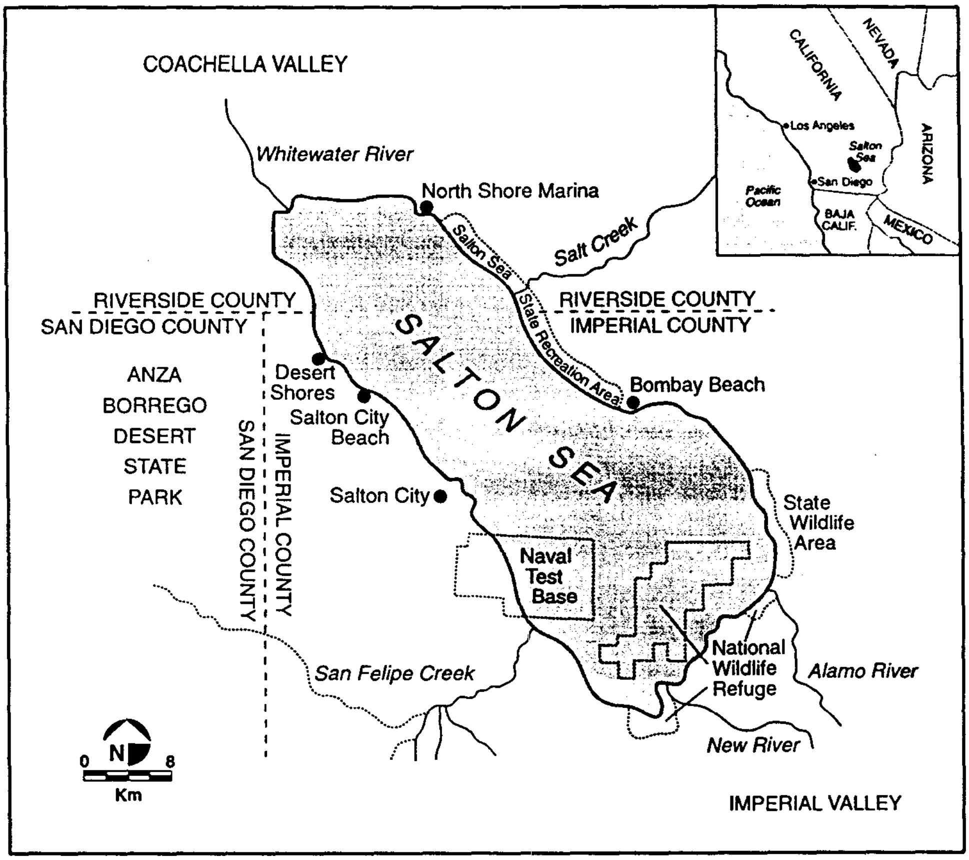

Figure 1. Location of the Salton Sea.

how it interacts with the environment. These studies allow for a comparison of biota at different salinities or ionic compositions, as these vary from lake to lake or over time. However, they are uncontrolled and cannot directly demonstrate cause and effect. Generally they describe the present community and suggest that the variations in salinity account for the variations in species richness and composition (e.g. Drabkova et al., 1978; Vareschi, & Jacobs, 1984; Vareschi & Vareschi, 1984; Hammer, 1986; Jakhor et al., 1990; Williams et al., 1990; Aladin et al., 1992; Frey, 1993; Green, 1993; Timms, 1993). Wurtsbaugh (1990, 1991) combined a descriptive study of Great Salt Lake in Utah with a microcosm experiment that investigated interactions among its phytoplankton, microzooplankton, *Artemia*, and *Trichocorixa* populations. Observed changes in the plankton community of Great Salt Lake were shown to be the result of direct effects of temporal salinity changes on the *Artemia* predator, *Trichocorixa verticalis*.

Microcosm experiments provide the control lacking in comparative limnological studies and provide realism to an experiment not possible in the laboratory (Beyers & Odum, 1993). Despite such advantages there has been a paucity of experiments using microcosms to study salinity effects at the community level (Greenwald & Hurlbert, 1993). The few studies that have been carried out have assessed salinity effects over very different ranges, but generally zooplankton diversity and density decreased with increasing salinity (Galat & Robinson, 1983; Greenwald & Hurlbert, 1993).

At present, one of the world's most dynamic salt lakes is the Salton Sea (Figure 1). This is the largest lake in California. It is approximately 58 km long and 14 to 22 km wide with a surface area of 980 km^2. It is important both biologically and economically, has a popular sport fishery, provides habitat for over 2 million migratory birds, and has several endangered species that nest on its perimeter. It is also the largest repository for agricultural wastewaters in California.

During recent decades wastewater inflows have constituted more than 95 percent of total annual inflows (Hely et al. 1966; Ogden, 1996).

The Salton Sea was formed over a period of 16 months between 1905 and 1907. Heavy river flows and the breaking of a diversion structure caused the entire flow of the Colorado River water to empty into the Salton Sink, at that time a dry salt bed with its lowest point 85 m below sea level. Since then the lake's salinity has increased from 3.5 g l^{-1} in 1907 to 47 g l^{-1} in 1992. Although salinity has fluctuated some in recent years, it is expected to continue increasing unless projects to stabilize salinity are implemented.

It is probable that during the breakthrough of the Colorado River all species in the lower river were introduced into the new Salton Sea. With the increase in salinity there have since been major changes in the biotic community. Currently, five major groups of invertebrates are represented in the lake: protozoans, Rotifera, Nematoda, Annelida, and Arthropoda. The dominant species include: ciliates, foraminiferans, *Brachionus plicatilis* Müller (rotifer), *Apocyclops dengizicus* (Lepeschkin) (copepod), *Balanus amphitrite* Darwin (barnacle), *Neanthes succinea* Frey and Leuckart (polychaete), *Gammarus mucronatus* Say (amphipod), and *Trichocorixa reticulata* Guérin-Menéville (corixid or water boatman). Aside from a recent unpublished study on the ichthyoplankton (Matsui et al., 1991), the only investigation of Salton Sea zooplankton was that conducted by Carpelan (1961b) in 1954–56. Sampling with a Kemmerer bottle and a 76 μ mesh net at two stations in the northwestern corner of the Sea, he found the plankton dominated by four species. *B. plicatilis* and *A. dengizicus* (or *Cyclops dimorphus* as it was then called) were most abundant in the summer, and the larvae of *B. amphitrite* and *N. succinea* were most abundant in the spring and fall.

The major fish present in the Sea are three marine species introduced in the 1950s (Walker 1961) – *Anisotremus davidsoni* Steindachner (sargo), *Bairdiella icistius* Jordan and Gilbert (bairdiella), *Cynoscion xanthulus* Jordan and Gilbert (corvina) – and *Oreochromis mossambicus* Peters (tilapia), an African cichlid that found its way into the Sea in the 1960s (Costa-Pierce & Doyle, 1997). Tilapia is a robust fish reaching up to 1.6 kg in weight and 40 cm in length and is probably the most abundant fish in the lake (Black 1981, 1988). It is a warm water fish sensitive to low winter water temperatures (< 15 °C) in the Salton Sea, which are thought to be the cause of some winter fishkills.

O. mossambicus is omnivorous and feeds opportunistically on phyto- and zooplankton, benthos, periphyton, and detritus, with smaller fish using predominantly animal matter and larger fish, algae (Neil, 1966; Whitfield & Blaber, 1978; Pullin et al., 1982; Trewavas, 1983; Maitipe & De Silva, 1983; de Moor et al., 1986). They are the dominant planktivore in the Salton Sea, and their disappearance would likely have dramatic effects on the plankton community. They are also one of the major items in the diet of corvina, sargo and bairdiella, and are an important sportfish (Black, 1981, 1988). The salinity range of this tilapia is thought not to exceed 70 g l^{-1} and its reproductive capabilities may be lost at 60 g l^{-1} (Pullin et al., 1982). Popper & Lichatowich (1975) reported reproduction at salinities as high as 49 ppt.

Biologically, the Salton Sea is a rather simple system (Walker, 1961). As the salinity of the Salton Sea increases further, physiological and ecological principles, as well as existing information on the species present in the lake, make it clear that large changes in the structure and functioning of the ecosystem, including the waterbird assemblage, are to be expected. The nature of these changes is impossible to predict, however, because (1) our information on the salinity tolerances and population interactions among Salton Sea organisms is scant; and (2) there have been few experimental studies on the effects of salinity on aquatic communities of any sort.

The objectives of this study were twofold. The first was to investigate the effects of increasing salinity on the Salton Sea algal and invertebrate assemblages in fish-free microcosms containing Salton Sea water experimentally adjusted to different salinity levels (30, 39, 48, 57, and 65 g l^{-1}). The second was to determine the effects of the presence of tilapia (*O. mossambicus*) on this community at two of these salinities (39 and 57 g l^{-1}). The higher salinity was that at which we believed reproduction of this fish would be affected and its abundance reduced in the Salton Sea. This paper reports only results for invertebrates (zooplankton and nekton) found in the upper part of the water column at night. Effects of salinity and tilapia on the water chemistry, algae and benthic invertebrates are reported in González et al. (1998a, 1998b), Simpson et al. (1998), and Simpson & Hurlbert (1998).

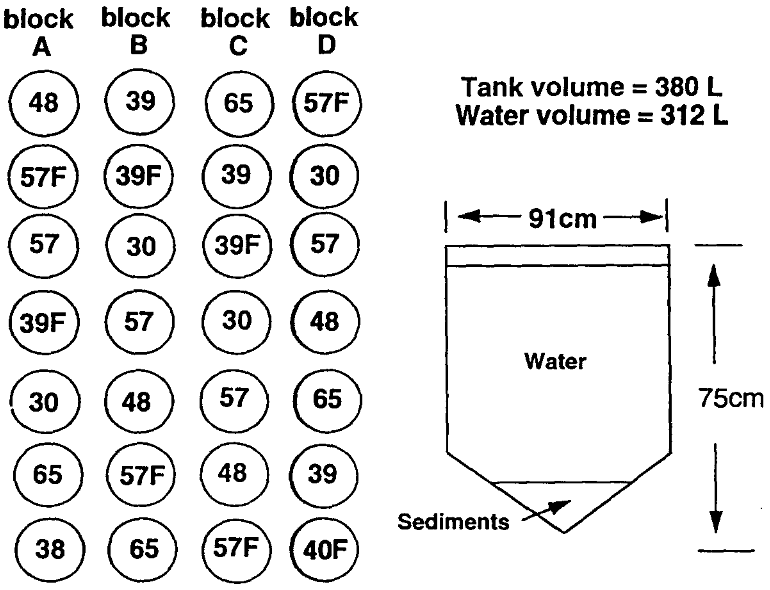

Figure 2. Layout and dimensions of tanks. Numbers represent the salinity within each tank in g l^{-1}. F designates the placement of one tilapia within that tank.

Methods

Experimental design

The experiment was carried out using a randomized block 2 × 5 incomplete factorial design with 4 replicate microcosms per treatment combination (Figure 2). The 7 treatments per block consisted of the five salinity levels (30, 39, 48, 57, and 65 g l^{-1}) without fish and two (39 and 57 g l^{-1}) with fish present.

Establishment of microcosms and salinity levels

Salton Sea water with a salinity of 47 g l^{-1} was transported by a tanker truck from the lake to San Diego State University and pumped into 28 380 l fiberglass tanks on the roof the San Diego State University Life Sciences building on November 19, 1990. Each tank was diluted to a salinity of 30 g l^{-1} and brought to a volume of 312 l.

We then created experimental salinity levels in such a way that (1) the major ion composition at each salinity was approximately the same as that which would be obtained by evaporating Salton Sea water to the given salinity; and (2) the treatments initially did not differ with respect to nutrient levels, organism densities, or any variables other than salinity defined as the sum of major ions. All earlier microcosm experiments on salinity effects have manipulated salinity through dilution and evaporative concentration. These procedures indeed change the salinity but also change the concentrations of nutrients and all other substances present making it difficult to separate the effects of these variables from those due to salinity itself. Experimental salinity levels thus were established by adding four salts (NaCl, Na_2SO_4, $MgSO_4$, and KCl) to the tanks during the period of January 4–12, 1991. These were added in proportions designed to keep ionic proportions similar to those of Salton Sea water and in amounts calculated to produce experimental salinities of 30.0, 38.8, 47.7, 56.5, and 65.4 g l^{-1}, or, for convenience, 30, 39, 48, 57, and 65 g l^{-1}. Prior to addition of salts, 3 l of Salton Sea sediments were placed over the bottom of each tank on January 3, 1991. This provided a substrate for the benthos and a nutrient source corresponding to that represented by sediments in the Salton Sea. Details on creation of salinity levels and on nutrient levels and sediment characteristics are given in González et al. (1998b) and Simpson et al. (1998).

Water level was kept at approximately 10 cm below the lip of each tank by the addition of tapwater from a holding tank that had been allowed to dechlorinate by sitting 2–4 d. Clear fiberglass covers were placed on each tank at the beginning of rainfall events and removed immediately thereafter. A PVC pipe (1.9 cm diameter, 44 cm long) with a styrofoam flotation collar and an airstone just inside its lower end was installed vertically in each tank and served to gently mix the water column and inhibit stratification. The microcosms possessed a much greater ratio of hard surface area (tank walls) to water volume than does the Salton Sea. The vertical portion of the walls therefore were scrubbed twice a month with plastic pot scrubbers to prevent buildup of attached organism assemblages on the tanks' vertical walls which could tie up nutrients and negatively affect plankton development. The material removed from the walls was left in the tanks.

Inoculation of tanks

Though all tanks started off with abundant plankton that came with the initial Salton Sea water, all tanks were also inoculated with algae and invertebrates on 5 occasions between January 1991 and August 1991. These were collected both from the Salton Sea and from several other waterbodies in the region with salinities ranging from 1 to 270 g l^{-1}. The wide range of inocula was intended to permit rapid colonization of the tanks at each salinity level by many organisms in the region that might be capable of establishing populations at that salinity level. Details concerning inoculation dates and the locations and salinities of sources of the inocula are given in Hart (1994).

Additionally, separate introductions of certain individual invertebrate species were made identically to each tank. These included: a polychaete (*Neanthes succinea*), a brine shrimp (*Artemia franciscana*), an amphipod (*Gammarus mucronatus*), a harpacticoid copepod (*Cletocamptus dietersi* Richard), and brine flies (*Ephydra riparia* (Fallén)). All occur either in the lake or in ponds along its margin. *A. franciscana* from a hypersaline pond (120 g l^{-1}) near the Salton Sea, were introduced on February 7, but did not survive, perhaps because the change in salinity was too abrupt. Thus, *A. franciscana* was introduced at various times as eggs (approximately 3,800/tank on March 12, and approximately 1,000/tank on May 7) and as laboratory-hatched nauplii (approximately 1,500/tank on March 22 and approximately 750/tank on May 24). These larger numbers reflected our expectation that egg viability and acclimation of nauplii would be low. To assist acclimation prior to addition to the tanks, the nauplii were placed in vials for 8 h containing a 50:50 mixture of the water in which they were hatched (70 g l^{-1}) and the water of tank to which they were to be introduced. *G. mucronatus* was added to each tank on April 8 in a similar manner. For acclimation, ten amphipods were placed for 8 h in a vial containing a 50:50 mixture of Salton Sea water and the water from the intended tank. Though abundant at certain times in the Salton Sea, *Gammarus* apparently was not present in the lakewater originally introduced into the tanks. Further details on introductions of *C. dietersi*, *N.succinea*, and *E. riparia* are given in Hart (1994) and Simpson et al. (1998).

Fish introductions

A single individual of *O. mossambicus*, 4–8 cm long was introduced on July 3, 1991 into each of the 39 and 57 g l^{-1} tanks designated to receive one. We desired that fish be introduced after some time had been allowed for development of invertebrate populations. Fish were collected from the southern end of the Salton Sea, transported to the university, divided into two groups of 10 fish each and slowly acclimated in the laboratory to salinities of 39 or 57 g l^{-1}. On July 7, 1991, four fish of similar size were chosen from each group. The fish were weighed and measured, and then randomly assigned to tanks. The remaining fish were kept in reserve at the two salinities in case an experimental fish died and needed to be replaced.

After being measured, each fish was put in a polyethylene bag with the water in which it was acclimated and suspended in the tank to which it was assigned, in order to acclimate to the temperature. Three hours later it was released from the bag. On the morning of July 8 the fish in tanks 39F–A, 39F–B, and 39F–C were found dead, floating at the surface (the letters A, B, C, and D are used to designate the four replicate tanks under each treatment condition; see Figure 2). High turbidity owing to phytoplankton prevented us from determining whether the fish in the other tanks were dead or alive. We decided to remove all fish in order to restock and be certain that each tank would have a fish. On July 16, a net was passed through the water column of each tank in order to retrieve the fish. The net was also passed through the tanks where the dead fish had already been retrieved in order that they receive the same mild stirring. All fish in the 39F tanks had died, while all of those in the 57F tanks were recovered alive.

On August 9, one of the remaining fish in the laboratory was randomly assigned to each tank in treatments 39F and 57F. They measured 5–7 cm in total length and 5–12 g in wet weight. For each tank a 3 l bucket was filled with its water, was covered with 1.0 cm mesh netting, and with the fish inside, was suspended in the tank. This allowed us to assess the success of initial acclimation to the tank's water. Within two days the fish had died in tanks 39F–A and 57F–D. Both were replaced with another fish acclimated to that salinity. On September 28 all fish appeared healthy and active. The buckets were removed and the fish were released into the tanks. On October 2, the fish in 39F–A was found dead. It was removed and another fish was placed in a mesh-covered bucket and released on October 10. This fish was found dead on December 12, but was not replaced. Hart (1994) gives additional detail on establishment and maintenance of these fish treatments.

Sampling methods and regimes

Selected physical and chemical variables were monitored on a regular basis. Salinity, temperature, dissolved oxygen, and pH were measured twice monthly between 12:00 and 12:30 pm. Nutrient (N, P, Si) concentrations were measured every 2 months for each tank, and major ion concentrations were measured on four dates. Only salinity and maximum-minimum temperature data are reported in this paper. Results for other chemical variables are reported in González et al. (1998b).

Salinity was measured using a Reichert-Jung hand refractometer (0–160 g kg^{-1}) and converted to g l^{-1} by multiplying readings by 1.13 (González et al., 1998b). Maximum and minimum temperatures were determined with a maximum-minimum thermometer read weekly.

Invertebrates were sampled monthly with a 76 cm long, 15 cm diameter tube sampler, that collected zooplankton as well as any nektonic and benthic organisms present in the upper part of the water column. Sampling was carried out at night, starting 2 h after sunset. The tube sampler was quickly lowered to a depth of 45 cm and collected a 3.5 l sample. Simultaneously another person used a 9 l bucket to scoop an 8.5 l sample from the upper 20–25 cm of the water column. The 12 l composite water sample was filtered through a 55 μm mesh plankton net and preserved in 8% formaldehyde. Important additional data on planktonic protozoans were obtained from the monthly collection and analysis of phytoplankton samples which were collected 8–10 h prior to zooplankton sampling. Details of those procedures are given in González et al. (1998a). The general procedure involved collecting a sample at midday from the upper 30 cm of the water column with a glass tube, preservation with Lugol's solution, and counting and measuring of protozoans (and phytoplankters) with an inverted compound microscope with phase contrast.

Sample analysis and data analysis

Zooplankton samples were analyzed using a 40 × 50 mm Sedgwick-Rafter chamber and compound microscope. A sample was concentrated to 3 ml and then placed in the chamber. For a given sample, taxa that appeared to be present in numbers greater than about 25 individuals per counting transect (4 × 40 mm strip) were counted over 40 percent of the chamber. All other taxa were enumerated over the entire chamber. Counts were made separately for different life stages or size classes for the crustaceans and corixids. This allowed for better estimates of the biovolume and provided insight concerning effects on reproduction. Details are given in Hart (1994).

For each taxon or group, a 1-way ANOVA was used to test for differences among the geometric mean densities for the 5 salinity levels on each sampling date. The count data were converted to number per l or per ml and log transformed. Prior to taking the logarithm, we added the lowest possible non-zero value (0.08 l^{-1} or 1.25 ml^{-1}) for numerical density to each datum for all data sets containing at least one zero value. Biovolume densities were also converted to a per l basis and log transformed. Prior to taking the logarithms we added the lowest possible non-zero value for that taxon (equal to 0.08 or 1.25 times the biovolume of the smallest individual) to each biovolume datum, for all data sets containing at least one zero value.

Fish treatments were first initiated in July. Therefore, from January 1991 to July 1991 the effect of salinity was tested for with 1-way ANOVAs for unequal replication, utilizing data for 8 tanks at 39 and 57 g l^{-1} and for 4 tanks at the other salinities ($F_{4,23}$). After July, 1-way ANOVAs for equal replication were used ($F_{4,15}$). Starting in October 1991, after the tilapia were finally established, two-way ANOVAs were carried out to assess the effects of fish and the fish-salinity interaction at 39 and 57 g l^{-1} ($F_{1,12}$).

Results

Salinity and temperature

The measured salinities were generally about 2 g l^{-1} above the nominal salinities (Figure 3). This may have resulted from salinity measurements usually being

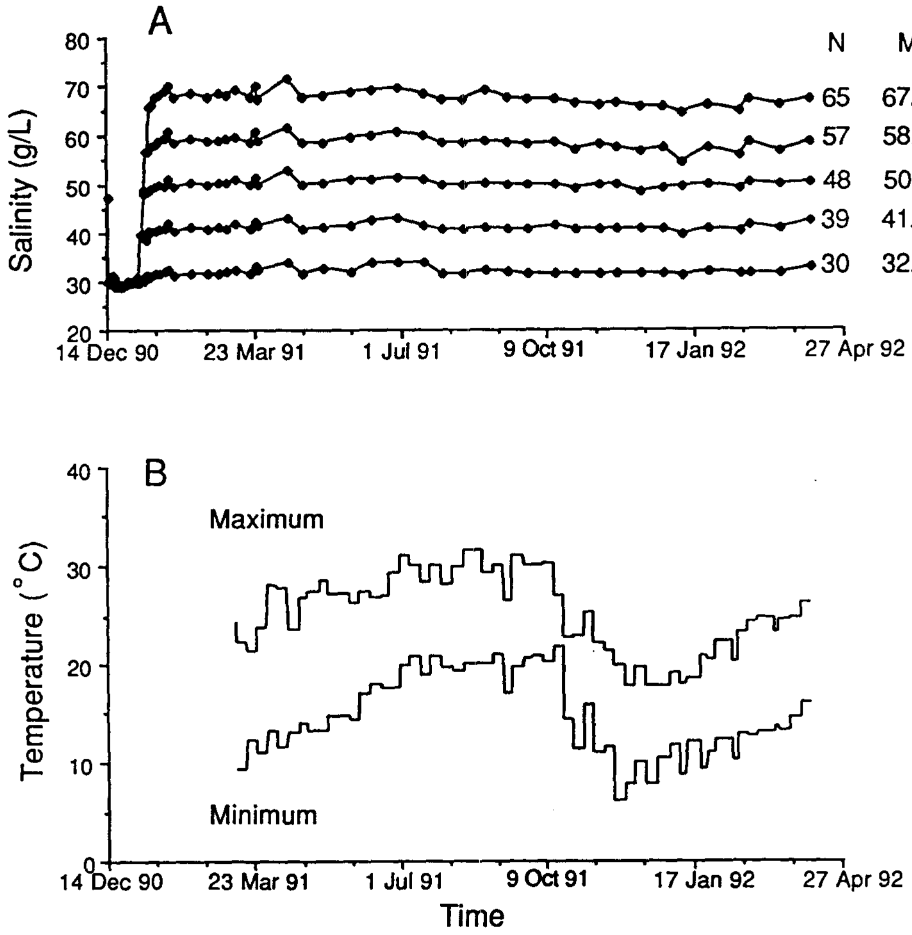

Figure 3. Salinity (A) and maximum and minimum water temperatures (B) during the course of the experiment. Each salinity value plotted represents mean of 4 tanks. Temperature values are averages for three thermometers maintained in tanks 48A, 48C, 48D. N = nominal salinity, M = mean observed salinity.

made just before tap water was added to compensate for evaporation, though there were other possible sources of error (González et al., 1998b).

The lowest recorded water temperature was 6 °C (November 25–December 2), and the highest was 31.5 °C (August 13–26) (Figure 3). The sharp drop in temperature recorded between October 21 and 28 corresponded to a sharp drop in air temperature (SDSU Department of Geography Weather Station). Seasonal minimum and maximum water temperatures at the Salton Sea are 12–14 °C and 31–35 °C, respectively (Carpelan, 1961a; M.A. Tiffany, unpubl. data).

Effects of salinity

The dominant invertebrates present in the water column of the microecosystems were crustaceans, insects, rotifers, protozoans, and nematodes. Strong effects of salinity were observed on numerical densities of individual taxa (Figures 4 and 5), on biovolume densities of major taxa (Figure 6), and on percent taxonomic composition (Figure 7). In these small systems, the distinctions between plankton, nekton and benthos are not sharp. Some of the taxa collected from the upper part of the water column were also collected in our sampling of the sediments. Results for densities of these species in or on the sediments are presented in Simpson et al. (1998).

Crustaceans. On a biovolume basis, crustaceans often were the most abundant group in the water column, especially at the lower salinities (Figures 6 and 7). Five species were present; an amphipod (*Gammarus mu-*

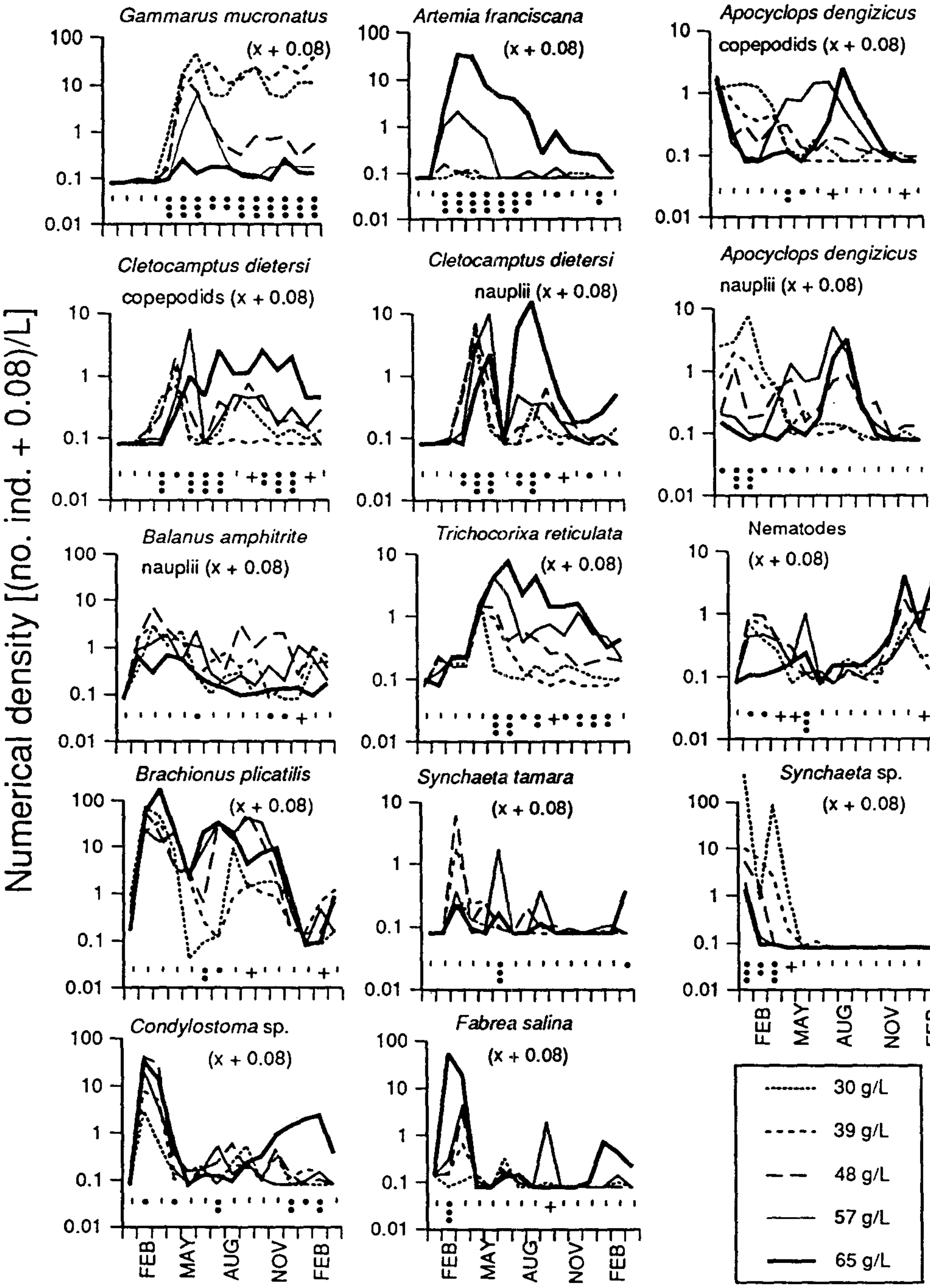

Figure 4. Effects of salinity on numerical densities of principal invertebrate taxa. P values for date-by-date ANOVAs are indicated by symbols as follows: –, $P > 0.1$; +, $0.05 < P \leq 0.1$; •, $0.01 < P \leq 0.05$; ••, $0.001 < P \leq 0.01$; • • •, $P \leq 0.001$. See text for explanation of constant, 0.08.

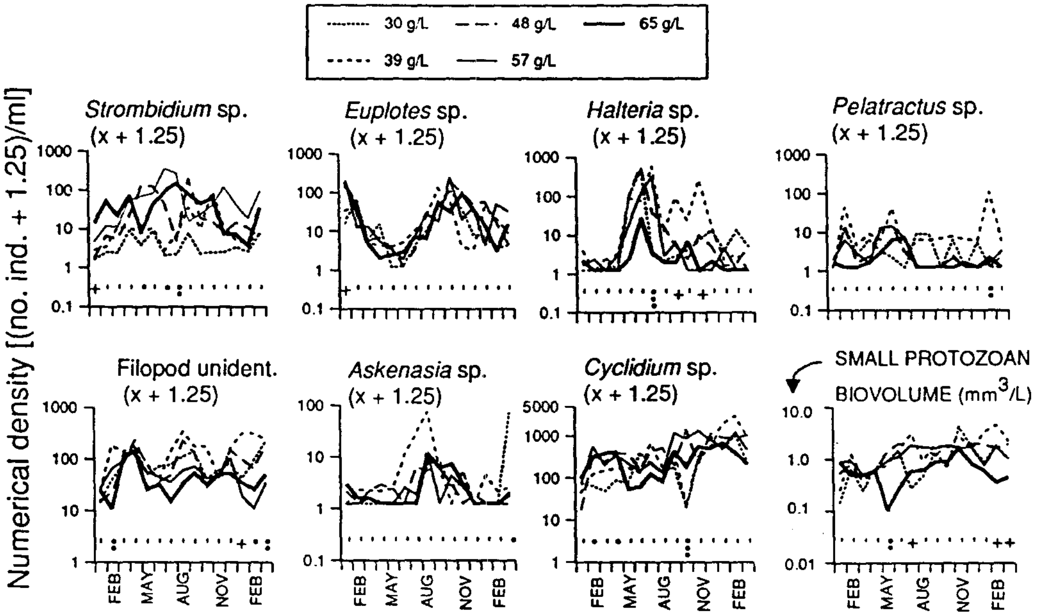

Figure 5. Effects of salinity on abundances of small protozoans, enumerated in samples collected for phytoplankton analysis. *P* values for date-by-date ANOVAs are indicated as in Figure 4.

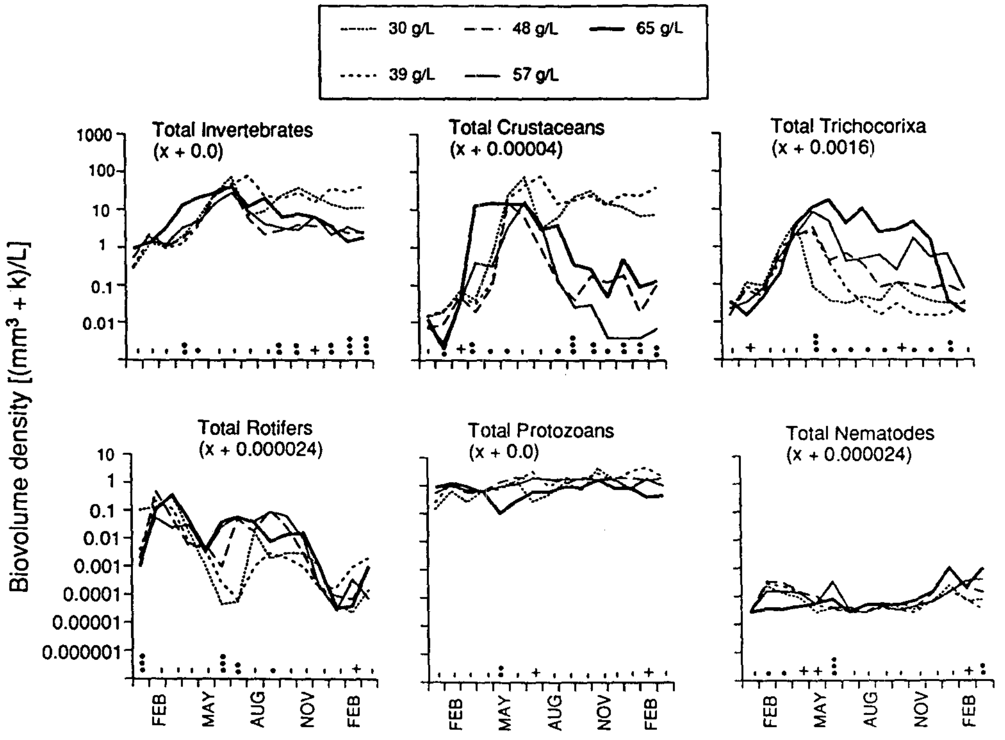

Figure 6. Effects of salinity on biovolume densitites for major groups of invertebrates. *P* values for date-by-date 1-way ANOVAs are denoted as in Figure 4.

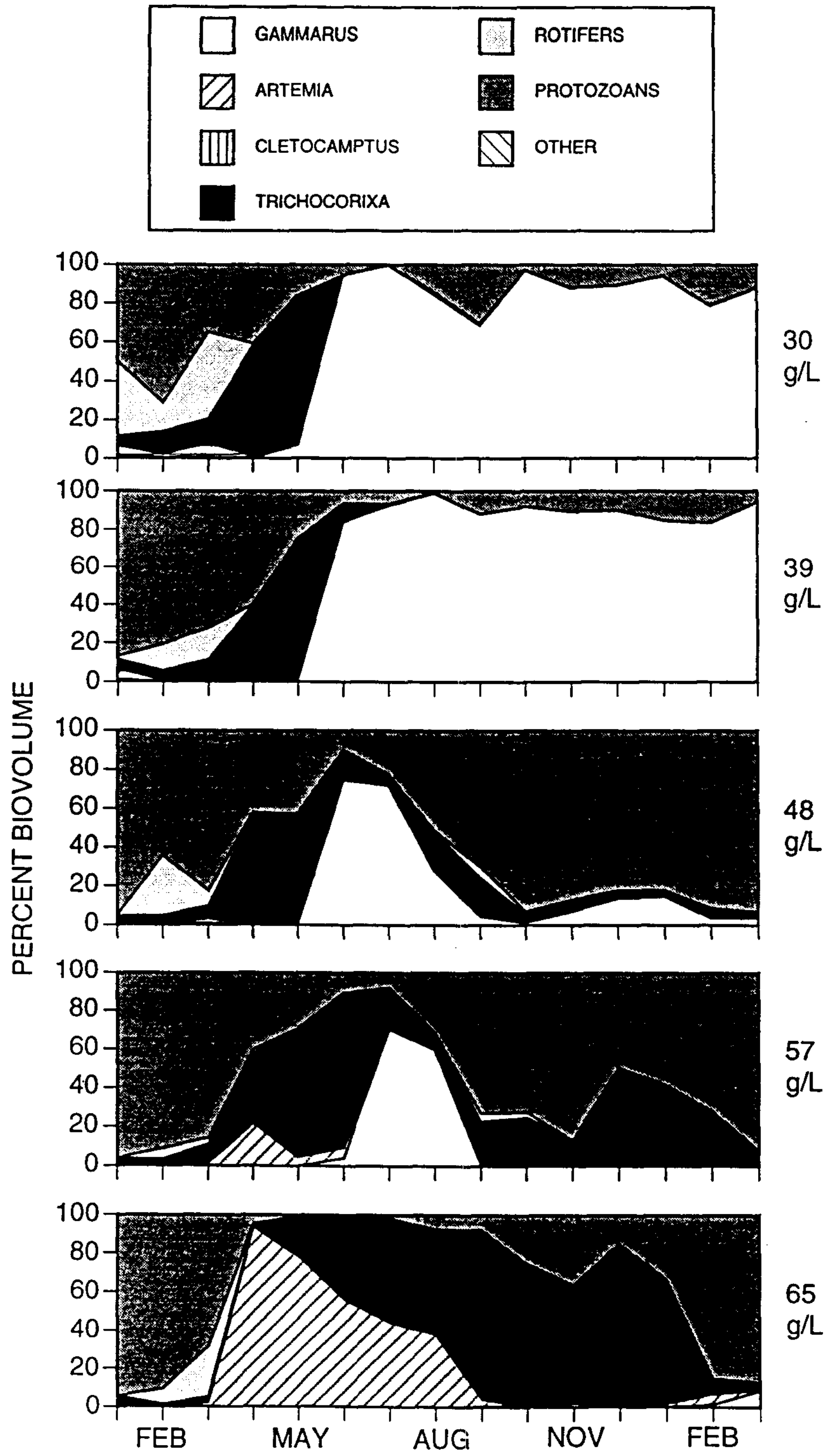

Figure 7. Effects of salinity on the taxonomic composition of the invertebrate assemblages at five salinities.

cronatus), a brine shrimp (*Artemia franciscana*), a cyclopoid copepod (*Apocyclops dengizicus*), a harpacticoid copepod (*Cletocamptus dietersi*), and a barnacle (*Balanus amphitrite*).

Gammarus usually was the most abundant crustacean (Figure 4). It was introduced into the tanks on April 8, and increased rapidly in May and June at all salinities except 65 g l^{-1}. It then decreased rapidly at 48 and 57 g l^{-1} but remained abundant at 30 and 39 g l^{-1} until the end of the experiment. *Gammarus* was continuously present, but in very low numbers, at 65 g l^{-1}.

Artemia was always absent or rare at 30, 39, and 48 g l^{-1} (Figure 4). Densities were moderate at 57 g l^{-1} and high at 65 g l^{-1}, but declined to low levels in the summer and did not recover. The general trends for the *Artemia* adults/post-nauplii and nauplii were the same. The presence of nauplii throughout the experiment at 65 g l^{-1} indicated that some reproduction was taking place at that salinity.

Apocyclops copepodids initially had similar densities at all 5 salinity treatments, perhaps a reflection of initial stocking rates (Figure 4). However, after January 1991, densities decreased in all salinities, most dramatically in the higher salinities. Initially, nauplii decreased very sharply with increasing salinity (Figure 4). In the summer the salinity effect reversed itself, and by September both copepodids and nauplii were more abundant at 57 and 65 g l^{-1} than at the lower salinities.

Cletocamptus was essentially absent the first few months of the experiment (Figure 4). Densities began to increase in all salinities in the spring, but by April and May densities were highest at the lower salinities, 30 and 39 g l^{-1}, for both the copepodids and nauplii. This tendency was reversed in the summer (June, July, and August), and in the winter (November, December, and January) for the copepodids, and in June, August, September, October, and January for the nauplii, when highest densities were recorded at 65 g l^{-1}.

Salinity effects on *Balanus* nauplii densities were especially marked on 4 dates (Figure 4). In general the highest densities occurred at 48 g l^{-1} and the lowest at 65 and 30 g l^{-1}.

The results for total crustacean abundance reflected the foregoing patterns (Figure 6). In February 1991, total crustacean abundance was greatest at the three lowest salinities reflecting the pattern shown by the then dominant *Apocyclops* (Figure 4). During the spring when *Artemia* populations peaked, total crustacean abundance was greatest at 65 g l^{-1}. From late summer onwards, total crustacean abundance was greatest at 30 and 39 g l^{-1}, reflecting the pattern for *Gammarus*, and lowest at 57 g l^{-1} where neither *Gammarus* nor *Artemia* prospered.

Trichocorixa. *T. reticulata* was the only insect collected in our samples. Initially its populations increased rapidly and to about the same extent in all treatments (Figures 4 and 6). Then, populations declined, especially at 30 and 39 g l^{-1}, and *Trichocorixa* were markedly more abundant at 57 and 65 g l^{-1} than at the lower salinities, until the very end of the experiment when treatment means converged.

Rotifers. Initially there were 6 rotifer taxa present in high densities. These were *Brachionus plicatilis*, *Synchaeta tamara*, *Synchaeta* sp., *Colurella* sp. and two unidentified species. However, after March only three species (*Brachionus* and the two *Synchaeta* spp.) were abundant, and we present data only for these (Figure 4). *B. plicatilis* was the most abundant rotifer and present throughout the experiment at all salinities. During the summer (June–September) densities were notably lower at 30 and 39 g l^{-1} than at higher salinities, but no other clear differences among treatments were apparent. The two *Synchaeta* species were found mostly during the first four months of the experiment. During that time *Synchaeta* sp. densities decreased with increasing salinity. Salinity effects on *S. tamara* were less evident but in June 1991 and March 1992 it showed maximal densities at 57 and 65 g l^{-1}, respectively. Patterns in total rotifer abundance initially reflected the higher densities of *Synchaeta* sp. at the lower salinities and later in June, July, and September, *Brachionus* densities at the higher salinities (Figure 6).

Protozoans. Protozoans were a dominant component of the assemblage at all salinities early in the experiment and at the three highest salinities during the latter part of the experiment (Figures 6 and 7). Nine genera were observed. Two were ciliates large enough to be at least moderately efficiently retained by our 55 μm mesh zooplankton net. These were *Fabrea salina* Kirby (mean length, 125 μm) and *Condylostoma*, which was represented by at least three forms (mean lengths of 100, 144, and 214 μm) (Figure 4). The other seven protozoan taxa were too small to be well retained by the zooplankton net. They were occasionally observed and enumerated in zooplankton samples, but the data on them we present here are those obtained from the phytoplankton samples via the Utermohl method (Figure 5) (González et al., 1998a). These seven taxa included one filopod ameba (mean length, 11 μm), and six ciliates: *Askenasia* sp. (14 μm), *Cyclidium* sp. (16 μm), *Euplotes* sp. (23 μm), *Halteria* sp. (16 μm), *Pelatractus* sp. (24 μm), and *Strombidium* sp. (20 μm).

Condylostoma increased rapidly at the beginning of the experiment (Figure 4). By February they became briefly more abundant at the three higher salinities than at the lower ones. In April the populations declined sharply. However, the highest densities still occurred at the higher salinities in April and at 57 g l^{-1} in July. During winter (December–February) densities were notably higher at 65 g l^{-1}.

Like *Condylostoma*, *Fabrea* was abundant early in the experiment and was favored by high salinities (Figure 4). Densities declined rapidly in March and April and remained low for the remainder of the experiment, with the possible exception of a slight increase in September at 57 g l^{-1} and in January at 65 g l^{-1}.

The smaller protozoans as a group tended to increase in abundance over the course of the experiment, a trend due in large measure to *Cyclidium*, the most abundant of these (Figure 5). *Euplotes* populations at the different salinities changed over time in much the same way, having high initial densities in January 1991 followed by sharp declines and then a large increase in the summer. *Halteria* populations changed in a manner complementary to that of the *Euplotes* populations. Temporal patterns were more irregular for other forms. Clear salinity effects usually involved lower densities at 57 and/or 65 g l^{-1} in the case of the unidentified filopod, *Halteria*, and total small protozoan biovolume, and lower densities at 30 and/or 39 g l^{-1} in the case of *Strombidium* and *Cyclidium*.

Total protozoan biovolume showed remarkably little variation over time or among salinities (Figure 6). In May 1991, however, it was much lower at 65 g l^{-1} than at other salinities. That was due to declines of several of the smaller protozoans, as well as of *Fabrea* and *Condylostoma*, and coincided with the peak densities of *Artemia* at 65 g l^{-1} (Figure 4).

Nematodes. Of the five major invertebrate groups present, nematodes composed the smallest portion of the total biovolume (Figure 7). During February and March 1991 they were much less abundant at 65 g l^{-1} than at lower salinities (Figures 4 and 6). In June 1991 and April 1992, however, highest nematode densities occurred at 57 and 65 g l^{-1}.

Total invertebrates. Reflecting all the trends of the individual taxa, total invertebrate abundance increased 20- to 300-fold during the first part of the experiment peaking at 20 to 80 mm^3/l in summer 1991, when differences among treatments were minimal, and then declining slightly (30 and 39 g l^{-1}) or moderately (48, 57, and 65 g l^{-1}). Primary determinants of the marked salinity effects demonstrated on total invertebrate biovolume were the responses of protozoans, *Gammarus*, *Artemia*, and *Trichocorixa*.

Taxonomic composition. The relative abundances of the different major taxa differed markedly among the different salinities (Figure 7). Initially, all treatments were dominated by protozoans. Rotifers briefly attained moderate relative abundance, especially at 30 g l^{-1}. By April, *Trichocorixa* and protozoans codominated at the four lower salinities, and *Artemia* dominated at 65 g l^{-1}. *Gammarus* was strongly dominant at 30 and 39 g l^{-1} for the latter two thirds of the experiment and at 48 and 57 g l^{-1} for a couple of months in the summer. For the latter half of the experiment protozoans strongly dominated at 48 g l^{-1} and protozoans and *Trichocorixa* at 57 and 65 g l^{-1}.

Effects of tilapia. Effects of tilapia on the abundances of individual taxa were very strong at both 39 and 57 g l^{-1} (Figures 8 and 9). Strong interactive effects of salinity and fish existed for many taxa on many dates. In most cases these reflected simply a marked fish effect at one salinity and an undetectable fish effect at the other salinity because of the absence or rarity of the taxon in both fish and no-fish tanks.

At 39 g l^{-1} the most notable effects of tilapia were a ~99 percent reduction of *Gammarus* densities, with a consequent large reduction in total crustacean and total invertebrates, a ~90 percent increase in *Brachionus* in January, and, on the final sampling date, a ~90 percent increase in nematodes and total protozoans. By the end of the experiment, tilapia at 39 g l^{-1} had also caused apparent reductions in some of the smaller protozoans, especially the filopod, and in total protozoan biomass.

At 57 g l^{-1} the presence of tilapia reduced *Trichocorixa* by 90 and 70 percent in December and January, respectively, and caused a 90–99 percent increase in *Cletocamptus* in November, January, February and April. Fish increased *Brachionus* densities by ~90 percent in January, *Condylostoma* densities by ~67 percent in April, and *Synchaeta* densities by ~90 percent in February and April.

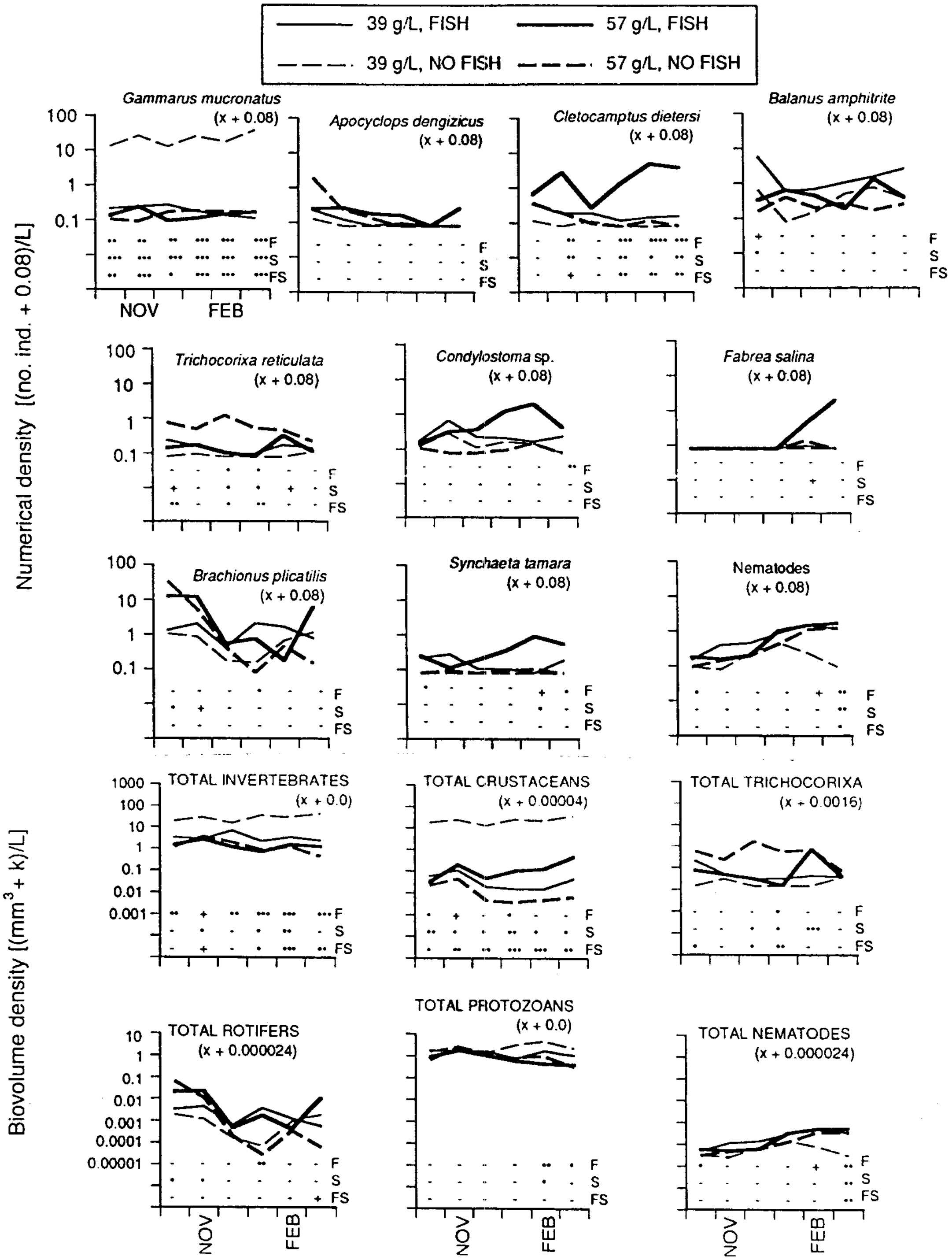

Figure 8. Effects of tilapia (F) on abundances of invertebrate taxa at two salinities (S). *P* values for date-by-date 2-way ANOVAs testing for main (F, S) and interaction (FS) effects are shown at bottom of each graph and denoted as in Figure 4.

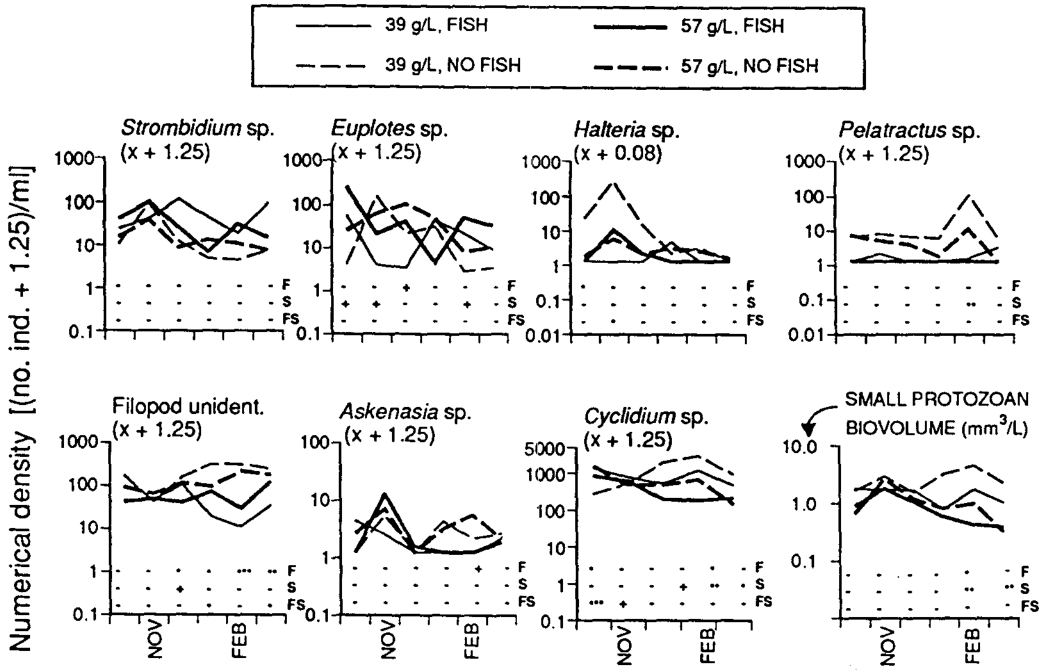

Figure 9. Effects of tilapia (F) on abundances of small protozoans collected in phytoplankton samples, at two salinities (S). *P* values for date-by-date 2-way ANOVAs denoted as in Figure 8.

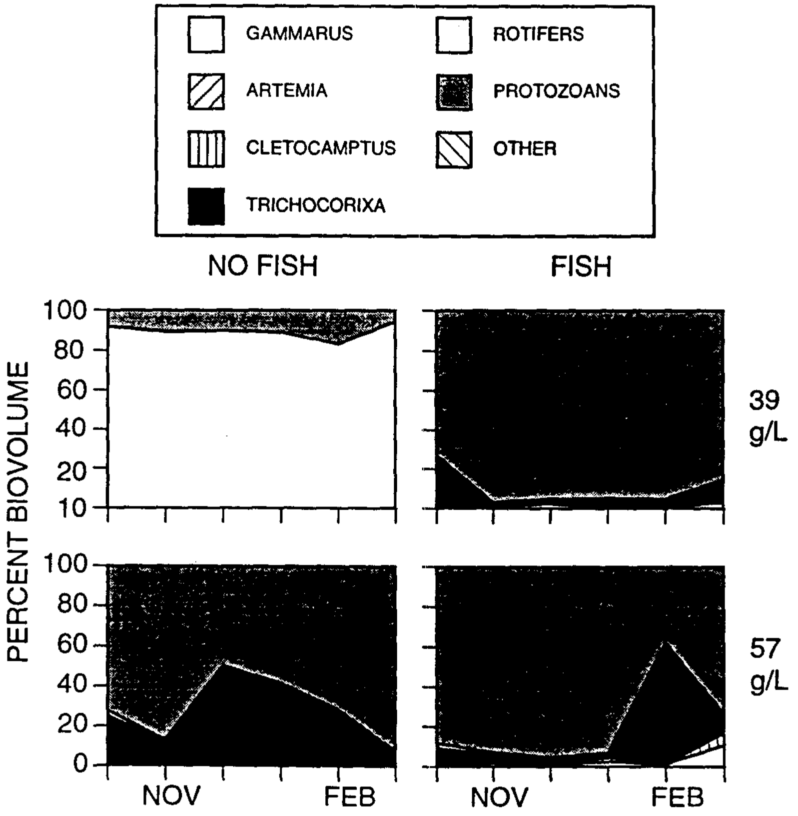

Figure 10. Effects of tilapia on the taxonomic composition of the invertebrate assemblages at two salinities (39 and 57 g l^{-1}).

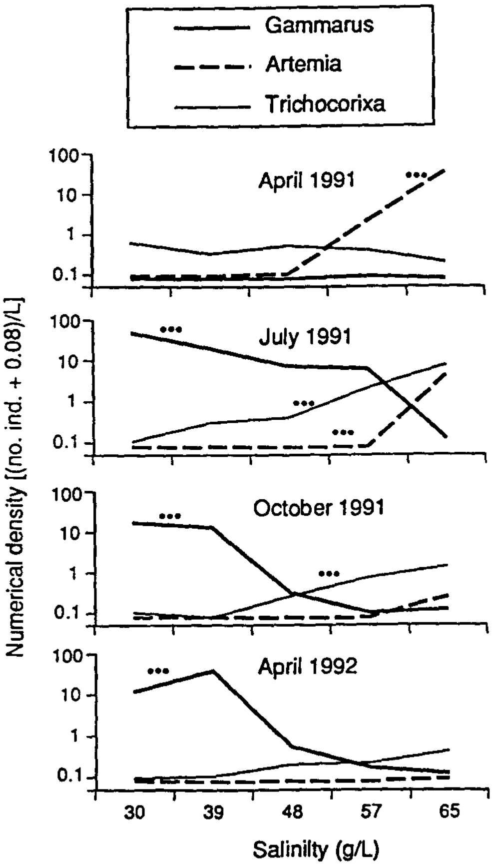

Figure 11. Effect of salinity on three of the dominant invertebrates on four sampling dates. *P* values for date-by-date 1-way ANOVAs denoted as in Figure 4.

The relative abundances of the different major taxa were markedly affected by the tilapia (Figure 10). At 39 g l^{-1} there was a shift from strong dominance by *Gammarus* to strong dominance by protozoans. Fish decreased the absolute abundances of both groups but affected *Gammarus* to a much greater degree than total protozoans. At 57 g l^{-1} the effect of fish on percent composition was less dramatic. Protozoans and *Trichocorixa* dominated in the absence of fish, and protozoans in the presence of fish.

Correlations among taxa

Variations in the densities of *Gammarus*, *Artemia*, and *Trichocorixa* in relation to salinity on four sampling dates are compared in Figure 11 to more clearly display correlations among the response of these species. There were negative correlations between *Gammarus* and *Artemia*, and *Gammarus* and *Trichocorixa*. *Gammarus* densities were highest at the lower salinities and *Artemia* and *Trichocorixa* densities were greatest at the higher salinities. There was frequently an inverse relationship between *Artemia* and *Trichocorixa* (Figures 4 and 11). Both species had low densities at low salinities. But at the two highest salinities *Artemia* densities increased until April 1991 and then decreased until the end of the experiment, while *Trichocorixa* numbers began to increase in April 1991, peaked in July, and then decreased.

An inverse relationship sometimes was apparent between other taxa. At 30 g l^{-1} *Apocyclops* decreased and remained low in April as *Gammarus* densities increased and remained high for the duration of the experiment (Figure 4). At 57 and 65 g l^{-1}, *Apocyclops* and *Artemia* exhibited an inverse relationship. By March, *Apocyclops* had greatly decreased and *Artemia* greatly increased. Then *Artemia* decreased throughout the spring and summer (April-September) as *Apocyclops* increased during the summer and fall (August-October). *Artemia* densities increased slightly during October–January at 65 g l^{-1}, while *Apocyclops* densities decreased.

Fabrea and *Artemia* densities were also negatively correlated (Figure 4). *Fabrea* densities increased in February and March and fell quickly in April, as *Artemia* densities increased. *Fabrea* densities remained low until December when there was a slight increase following a decline in *Artemia* densities.

The fish-caused reduction in the densities of *Gammarus* at 39 g l^{-1} and of *Trichocorixa* at 57 g l^{-1} (Figure 7) were associated with increases in the other invertebrates (Figures 8 and 9). At 39 g l^{-1} the decrease in *Gammarus* is correlated with increases in rotifers, *Balanus*, *Cletocamptus*, *Trichocorixa*, *Strombidium*, and nematodes. At 57 g l^{-1} the fish-caused decrease in *Trichocorixa* was associated with probable increases in *Cletocamptus*, rotifers, *Apocyclops*, and large protozoans (*Fabrea*, *Condylostoma*).

Discussion

These results merit analysis and discussion in three broad contexts: their statistical conclusiveness; the mechanisms whereby fish and salinity treatments exerted their effects; and the relevance of the findings to the Salton Sea itself.

The statistical evidence

Evaluation of the results of our statistical analyses should be straightforward. We offer the following comments partly to forestall objections on the part of those who favor the elaborate statistical formalism now fashionable in some quarters. These comments apply as well to the other papers reporting results from this experiment (González et al., 1998a, b; Simpson et al., 1998; Simpson & Hurlbert, 1998). In all papers we have forgone much conventional statistical apparatus. We refrain from specifying alpha, from dichotomizing our results into 'significant' and 'non-significant' ones, from using repeated measures ANOVA even though the experiment has a repeated measures design, from worrying about the theoretical potential for high set-wise Type I error rates, and from *post hoc* power analyses. None of these often blindly implemented rituals are necessary or useful here.

For analyses that we did carry out, we focus discussion on those taxa and sampling dates where effects of fish or salinity were clearly demonstrated, as evidenced by low *P* values. In these cases we can be reasonably confident not only that an effect existed but also that the sample or estimated treatment means provide at least a rough idea of the *nature* of the effect. For example, they tells us with some certainty at which salinities a taxon was most abundant and at which, least.

The majority of our analyses, however, yielded high *P* values. This is typical for such data sets and does not diminish the value of the information on treatment effects that were conclusively demonstrated by the other analyses. But it is important to restate that no high *P* value constitutes evidence in favor of the null hypothesis. A high *P* value is as consistent with the alternative hypothesis (effect > 0) as with the null hypothesis (effect=0). And, indeed, we usually can be confident that each experimental variable affected each taxon on every date. This confidence is provided by general principles and existing information in the literature. It is difficult to imagine how the abundance of any species could be completely refractory to the altered physical, chemical, and biological conditions resulting from the salinity and tilapia treatments.

Despite our confidence that treatment effects occurred in these cases, we generally have made no reference to analyses yielding high *P* values and the estimated treatment effects associated with them. The reason for this is simple: a high *P* value signifies that the sample or estimated treatment means are not precise enough for us to be confident that the rank order of the true means is at least approximately that of the sample means. On general principles we can be fairly certain that there is an effect but cannot be sure even of its qualitative nature, let alone of its true magnitude. The sample means notwithstanding, we cannot be sure, for example, whether the species was more abundant at 30 g l^{-1} or at 65 g l^{-1}. With apologies to those for whom the above considerations are self-evident, we return to biology.

The microcosm foodweb

A schematic of the microcosm foodweb is shown in Figure 12. This incorporates information from the literature and our own observations. Note the omnivory indicated for all the larger taxa. Representation of bacteria, protozoan, nematodes and algae is oversimplified. There is great diversity within each of these groups with respect to diet or palatability to potential consumers. The probably important 'microbial loop' structure in the foodweb is not indicated. *Balanus* probably consumes protozoans as well as algae. Though introduced, *Neanthes* failed to establish populations in the tanks but is nevertheless included as it is an important component of the Salton Sea food web. *Artemia*, on the other hand, is not yet part of the Salton Sea foodweb but is present in highly saline waterbodies near the Sea and established large populations at certain salinities when inoculated into the tanks.

Gammarus, salinity, and indirect effects

Gammarus appeared to be physiologically sensitive to the higher salinities and steadily declined in numbers as salinity increased. There are no published studies of salinity tolerance in *G. mucronatus*, but the species has been reported in estuaries and coastal areas with salinities as low as 4 g l^{-1} (Barnard & Gray, 1968), as well as in hypersaline lagoons of up to 50 g l^{-1} (Hedgepeth, 1967). This information says little about the salinity range over which the species can reproduce and sustain a population, but we infer from our data that the effective upper salinity limit would be < 57 g l^{-1}. Its absence from the two highest salinities seems not explicable in terms of its suppression by other organisms present at those salinities.

Changes in the abundance of *Gammarus* seem likely to have been a major proximate cause of changes in other invertebrate populations, as well as changes in algal populations (González et al., 1998a; Simpson et al., 1998) and in nutrient cycling in the microecosystems (González et al., 1998b). The best explanation for the scarcity of the other invertebrates at the lower salinities is that in addition to being a voracious herbivore, *Gammarus* is also a voracious predator. It may have been either competing with or preying on most of the other invertebrates present (Figure 12). This is consistent with the sketchy information in the literature on its diet. Amphipods are thought to play an important role as herbivores and as food for predators in saline lakes at lower salinities (Hammer, 1986), and *Gammarus* species are generally regarded as grazers of bacterial and microalgal films and mats and of macroalgae (Zimmerman et al., 1979; Smith et al., 1982; La France & Ruber, 1985). In the present experiment, where high salinities or the presence of fish depressed *Gammarus* populations, thick algal mats developed on the sediments and thick algal films on hard substrates (González et al., 1998a; Simpson et al., 1998). The increased abundance of *Trichocorixa* at high salinities. which was also evident in the benthic samples (Simpson et al., 1998), thus may reflect the greater algal food supply there, i.e. the release of *Trichocorixa* from competitive suppression by *Gammarus*.

In the past a strongly carnivorous diet for amphipods was thought uncommon, though many were known to supplement their diet by catching small invertebrates (Barnes, 1987). Now there is increasing evidence of predatory capabilities and habits. When we placed unstarved *G. mucronatus* in vials with *Artemia*, both juvenile and adult *Gammarus* immediately attacked and ingested large and small *Artemia*. Hunte & Myers (1984) reported that *G. mucronatus*, *G. tigrinus* and *G. lawrencianus* adults preyed on juvenile gammarideans in plastic containers in the laboratory. *G. pulex* is known to prey on the isopod *Asellus aquaticus* (Bengtsson, 1982). *G. tigrinus* has been observed to feed upon both *Sigara lateralis* (Corixidae; up to 3rd instar nymphs) and *G. dubeni* (up to 2.5 mm) (Savage, 1980); and both of these disappeared when *G. tigrinus* increased in a lake following die-off of its subaquatic vegetation.

Such circumstantial evidence suggests that the negative correlations observed in this experiment, between *Gammarus* on the one hand and *Trichocorixa*, *Artemia*, *Apocyclops*, *Balanus*, and nematodes on the other, thus may reflect 'salinity effects' mediated in part by the predatory activities of *Gammarus*. We made no direct observations of predation by *Gammarus* on these forms. The protein-rich egg capsules of *Trichocorixa* might be especially susceptible to *Gammarus* predation. Detailed analysis of the diet of *G. mucronatus* in the wide variety of habitats in which this species is found would assist our understanding of the functional importance of this species.

Effects of *Gammarus* on algal mats covering the sediment surface suggest another mechanism that may account for the increased abundance of nematodes in the plankton at the highest salinities at the end of the experiment (Figure 4) and in the presence of fish (Figure 8). Nematodes were uncommon members of the plankton, but in these situations the scarcity of *Gammarus* permitted strong development of algal mats and high densities of benthic nematodes (Simpson et al., 1998). Small fragments of these mats sometimes broke off, floated to the water surface, and were incidentally included in the water collected during zooplankton sampling. The 'planktonic' nematodes thus exhibited salinity and fish effects qualitatively very similar to those shown by the benthic nematodes because the former in fact *were* benthic nematodes. The algal mats and their microflora served both as a habitat and food source for the nematodes as well as a vehicle for their delivery into the upper part of the water column.

Development of these algal mats also can account for the great increase in *Cletocamptus* abundance during the latter part of the experiment at 65 g l^{-1} (Figure 4) and in the absence of fish (Figure 8). This benthic harpacticoid presumably feeds on bacteria, algae and protozoans attached to sediment, algae, or sea grasses, as do others (Hammer, 1986; Barnes, 1987). It may not only compete with *Gammarus* but be susceptible to predation by it. Our plankton sampling only collected from that 'marginal' segment of the population that had moved at night, for whatever reason, into the upper part of the water column. Only once did a treatment mean exceed 10 individuals per l. Benthic samples collected during the day showed the same types of treatment effects as demonstrated by the plankton data but with *Cletocamptus* mean densities frequently in the range of 10 to 100 individuals per cm^2 (Simpson et al., 1998).

Trichocorixa, Apocyclops and Artemia as predators

Predation by these omnivores on each other and other invertebrates likely accounted for several observed 'salinity' effects (Figure 12). All three have salinity tolerances wider than the range of salinities used in this experiment. *Trichocorixa reticulata* can acclimate to water ranging from fresh to 300 ppt in a laboratory setting (Jang & Tullis, 1980), was found abundant in evaporation basins in the southern San Joaquin Valley, California, at salinities from 7–70 g l^{-1} (Parker & Knight, 1992), and observed reproducing over a salinity range of 5–148 ppt in San Diego coastal habitats (Cox, 1969). *Artemia franciscana* is not commonly found at salinities < 80 g l^{-1} (Hammer, 1986), but is routinely cultured in sea water and in the laboratory does well at salinities ranging from 10 percent seawater up to 'saturated crystallizing sea-water brine' (Croghan, 1958). It grows well (0.4 mm to 3.6–4.0 mm in 27 d) in Salton Sea water adjusted to salinities over the range 38–125 g l^{-1} (Hammer & Hurlbert, 1992). Predaceous vertebrates and invertebrates are thought to prevent *Artemia* species from successfully colonizing natural waters of lower salinity (Kristensen, 1963; Edmondson, 1966; Kristensen & Hulscher-Emeis, 1972; Persoone & Sorgeloos, 1980; Wurtsbaugh, 1991; Hammer & Hurlbert, 1992). *Apocyclops dengizicus* is peculiar to arid regions and has been found in salinities from 4–69 g l^{-1} (Hammer, 1986; Timms, 1993). In laboratory cultures it persisted, reproductively active, for 120 d at salinities over the range 0.5–68 g l^{-1}, and some individuals were able to survive more than 90 d at 79 g l^{-1} (Dexter, 1993).

Predation by *Trichocorixa* and *Apocyclops* on *Artemia* seems the most likely explanation for the observed negative correlations in time between these first two species and the latter (Figure 11). *T. reticulata* is capable of preying on *Artemia* nauplii and adults (Hammer & Hurlbert, 1992) and probably caused the *Artemia* declines at 57 and 65 g l^{-1} during the latter part of the experiment. In Great Salt Lake a congener, *T. verticalis*, has been shown to prey strongly on *Artemia* nauplii which leads to an inverse relationship between *Artemia* and *Trichocorixa* abundances over time (Wurtsbaugh, 1989, 1991). On another scale, *Artemia* and *Trichocorixa* both did best at the higher salinities. This may have reflected the value of *Artemia* as food for *Trichocorixa*. It is unclear which factor was more important to *Trichocorixa's* success at high salinities – the availability of high quality animal prey (*Artemia*) or of more abundant periphyton.

Like many other cyclopoid copepods (e.g. Fryer, 1957; McQueen, 1969; Brandl & Fernando, 1978), *A. dengizicus* presumably is an omnivore capable of preying on protozoans, rotifers, other small crustaceans, and perhaps even tiny insect larvae. Adult *A. dengizicus* about 1070 μm long have been shown in the laboratory to readily attack and consume *Artemia* nauplii 400–1500 μm in length (Hammer & Hurlbert, 1992). The failure of *Artemia* to develop populations at lower salinities in the early part of the experiment, before *Trichocorixa* or *Gammarus* became abundant, may have been due to predation by the high *Apocyclops* populations present at those lower salinities. Or it may have reflected competitive suppression via *Apocyclops*'s depression of particular algal or protozoan populations also used for food by *Artemia*. Kristensen (1963) found that *Artemia* occurred over salinities from 10 to 200 g l^{-1} when predaceous and competing invertebrates were absent. *Apocycylops* predation perhaps was also a cause of the greatly reduced abundance of the rotifer *B. plicatilis* at the two lowest salinities during the spring and summer (Figure 4). This rotifer tolerates a very wide salinity range, having been recorded from lakes and coastal lagoons with salinities ranging from 3 to 250 ppt (Hammer, 1986).

Artemia are efficient filter-feeders on bacteria, algae and protozoans (Persoone & Sorgeloos, 1980; Hammer, 1986). Their great abundance at 65 g l^{-1} apparently was the cause of a > 90 percent reduction in phytoplankton abundance at that salinity relative to the others (González et al., 1998a). It seems likely that *Artemia* predation would have affected some protozoan densities as well. Wurtsbaugh (1991) noted that the densities of protozoans increased when *Trichocorixa* predation brought about decreases in *Artemia* abundance. Most of the protozoans present in our tanks were smaller than 50 μm which is about the upper size limit for food particles useful for culturing *Artemia* (Dobbeleir et al., 1980). Reduced small protozoan biomass at 65 g l^{-1} in spring 1991 (Figure 5) perhaps reflected *Artemia* predation on forms such as *Cyclidium*, *Halteria*, and the unidentified filopod ameba.

Competition from *Artemia* may have been one factor in the abundance patterns of *Balanus* nauplii. At least during autumn these were most abundant at 48 g l^{-1}, the same salinity at which adult *Balanus* showed the highest growth rates (Simpson & Hurlbert, 1998). Low numbers of nauplii, as well as poorer growth of *Balanus* adults, at 65 g l^{-1} perhaps was a consequence of *Artemia* having grazed down the phytoplankton (González et al., 1998b) and small protozoan populations (Figure 5) on which all stages of *Balanus* also feed. Physiological stress of 65 g l^{-1} salinities on *Balanus* is an alternative or supplementary explanation. Poor performance of the barnacle at the lowest salinities might relate to mechanical interference by the abundant *Gammarus*.

Reduced abundance of *Cletocamptus* at 57 and 65 g l^{-1} early in the experiment also might have been due to predation by *Artemia* on *Cletocamptus* nauplii, though such has never been reported. Stress caused by high salinity is unlikely to have been a factor. In the latter part of the experiment, this harpacticoid had its greatest abundance at 65 g l^{-1}, and Dexter (1995) has shown that it can thrive in laboratory cultures for at least 120 d at salinities ranging from 0.5 to 80 g l^{-1}.

Protozooplankton dominance and responses

Salinity effects on protozoan taxa usually were unclear and difficult to interpret, but the protozoan results nevertheless are of special interest. In part this is because so little is known about the protozoans of saline lakes; together, Hammer's (1986), Fenchel's (1987), and Laybourn-Parry's (1992) monographs dedicate only four pages to them. And in part it is because protozoans were such a dominant component of the microecosystems. To the extent that our results reflect protozoan ecology in the Salton Sea and other saline lakes, they may represent a significant increment in knowledge.

The most striking finding was that, with numerical densities of usually 100–1000 per ml and biovolume densities in the range 0.1–3 mm^3/ml, the protozoans completely dominated the zooplankton at all times, at all salinities, and in both the presence and absence of fish – except when *Artemia* was abundant (Figures 7 and 10). Rotifers, copepods, and barnacle larvae always collectively represented a minor fraction of total biovolume, and *Gammarus* and *Trichocorixa* are more accurately regarded as nekto-benthic in habit rather than planktonic. Given the high metabolic and production rates associated with their small size, protozoans presumably dominated the metabolism of these microecoystems to an even greater degree than they did the zooplankton biovolume. To what extent was that a function of the highly eutrophic state of these microcosms (chl *a* concentrations mostly 10–100 μg l^{-1}; González et al., 1998a) and to what extent was it a result of high salinity restricting the number of metazoan taxa that might consume or compete with the protozoans? Should we expect to find protozoans similarly dominant in the zooplankton of saline lakes with salinities of 30-65 g l^{-1} if we take the trouble to sample them? These are questions that cannot yet be answered.

Protozoan abundance suggests that unanalyzed 'microbial loop' foodwebs were well developed in the microcosms (Porter et al., 1979; Azam et al., 1983; Stockner & Porter, 1987; Laybourn-Parry, 1992). Dissolved organic matter secreted by the abundant phytoplankton could have served as a nutrient supply for bacteria. These would be consumed by bacterivorous heterotrophic nanoflagellates and ciliates such as *Cyclidium*, which was usually the most abundant protozooplankter (Figure 5). These, along with microalgae, would be consumed by the other protozoan and rotifer taxa, and these in turn perhaps by *Artemia*, *Apocyclops*, *Balanus* and other metazoans as well as by tilapia. Microbial loop foodwebs have been studied almost solely in freshwater and marine environments where there are numerous metazoan taxa capable of feeding on protozoa and channeling this energy to higher trophic levels. The relative paucity of metazoan taxa in most highly saline lakes may inhibit this upward transfer, as is likely true for the transfer of phytoplankton productivity to higher trophic levels. In the Salton Sea, however, utilization of planktonic ciliates by tilapia could be a significant conduit for transfer of microbial loop production to tilapia and its predators such as corvina and fish-eating birds.

The relative constancy of total protozoan biomass over time and from one salinity to another (Figure 6) may have reflected the broad euryhalinity of many taxa (Fenchel, 1987) as well as a tendency for some to negatively covary or substitute for each other over time. The oligotrich genera *Halteria* and *Strombidium* exemplify both phenomena (Figure 5). They are found worldwide across the oligo- to eutrophic spectrum and in marine, estuarine and lacustrine environments, with *Strombidium* being a dominant zooplankter even in permanently ice-covered lakes of Antarctica (Laybourn-Parry, 1992).

Our poor knowledge base on protozooplankton is in large part due to the difficulties in collecting and analyzing them. In this study, smaller protozoans usually made up > 90 percent of the protozoan biomass but passed easily through our 55 μm mesh net, and were rarely seen in the zooplankton samples. Even smaller mesh (e.g. 35 μm) nets would inadequately retain most forms. Fortunately the dominant protozoans were usually abundant enough that they could be enumerated in the phytoplankton samples, even though our protocol involved enumerating phytoplankton in only 0.8 ml of water as phytoplankton densities were high (González et al., 1998a). The large-bodied taxa, *Fabrea* and *Condylostoma*, however, were rarely seen in those samples, as their densities usually were < 1 per l. They were frequently detected in the zooplankton samples because each of these was obtained by filtering 12 l of water. Given the large ranges of sizes and densities of protozoans, full analysis of the protozooplankton would seem to require at a minimum the two sampling/counting protocols we used plus at least one other one to deal with tiny forms, such as heterotrophic nanoflagellates.

Condylostoma and *Fabrea* might have been found in larger numbers in the phytoplankton samples had these been collected at night, as were the zooplankton samples. These two forms may have retreated to deeper water or the sediment surface by midday when the phytoplankton samples were taken. For most of the experiment *Fabrea* and *Condylostoma* daytime densities were 10–100 individuals/cm^2 at the sediment surface (Simpson et al., 1998). It is also likely that, given its slender form, *Condylostoma* was retained with less than 100 percent efficiency by the zooplankton net and was a more important component of the protozoan assemblage than our data suggest.

A comparable experiment

Offering useful contrasts with the present study is a microcosm experiment that examined effects of five salinities (0.5, 8.5, 17, 34, and 51 g kg^{-1}) on a plankton assemblage derived from a California coastal lagoon and nearby freshwaters (Greenwald & Hurlbert, 1993). The salinity ranges of the two experiments overlapped and some taxa were common to both. The comparison illustrates how context-dependent the results for a particular taxon can be.

In the coastal lagoon experiment, *Brachionus plicatilis* was most abundant at 8.5 g kg^{-1}. Other zooplankters abundant at 0.5 g kg^{-1} (*Keratella, Ceriodaphnia, Diaptomus*) and 17 g kg^{-1} (*Oithona, Acartia*) may have kept *Brachionus* densities low at those salinities through competition or predation. The scarcity of *Brachionus* at 51 g kg^{-1} is more puzzling as other zooplankters were also scarce there. It also contrasts with the present study where *Brachionus* did better at salinities of 48–65 g l^{-1} than at lower ones.

A *Cletocamptus* species in the coastal lagoon study did best initially at 17 g kg^{-1} and, later on, at 34 g kg^{-1}. This parallels the finding of the present study that *Cletocamptus* was most abundant initially at 30 and 39 g l^{-1} but later on at 65 g l^{-1}. As with *Brachionus* we do not see any way to explain in terms of interspecific interactions the scarcity of *Cletocamptus* at 51 g kg^{-1} in the earlier study.

Trichocorixa sp. (probably *T. reticulata*) was also present in the coastal lagoon experiment. On all four sampling dates it was most abundant at 8.5 or 17 g kg^{-1}, and on three of those dates it was not observed at 51 g kg^{-1}. This contrasts with our results but also supports our interpretation of them in terms of *Artemia* as a *Trichocorixa* food supply at high salinities, and *Gammarus* as a *Trichocorixa* predator and/or competitor at low salinities. *Artemia* and *Gammarus* were absent from the coastal lagoon microcosms. The ecologically optimal salinity for *Trichocorixa* thus was lower in them than in the Salton Sea microcosms.

Finally, in the coastal lagoon study neither total ciliate nor total protozoan biomass (as sampled with a 35 μm mesh net) showed any clear effect of salinity. This paralleled the usual absence of salinity effects on total protozoan biomass in our study.

Tilapia impacts: major but underestimated

Tilapia caused clear, order of magnitude decreases or increases in abundance for most taxa on one or more dates. Two factors suggest, however, that its influence was underestimated by our data. First, tilapia were finally established in the tanks in October 1991 and the expermient was terminated in April 1992. Thus tilapia's effects were assessed during the coldest part of the year (Figure 3). Our tanks had mean water temperatures of ~ 15°C during November–March, and temperatures dropped to < 10 °C in five different weeks during that time. In ponds in Alabama this tilapia species ceased feeding at ~ 15° (Kelly, 1956). In many situations tilapia mortality has occurred when water temperature dropped into the 10– 14°C range (Trewavas, 1983). The observed effects of tilapia thus may have been generated primarily by its feeding activities during the warmer periods at the very beginning and very end of its period of residence in the tanks.

Fish mortality was the second factor. After the definitive fish introductions on October 10, 1991, two died and disappeared sometime during the experiment (tanks 39F–C and 39F–D) and a third (tank 39F–A) was found dead in December. Use of data from these tanks in our statistical analyses resulted in underestimation of fish effects. Variances were increased, differences between treatment means were diminished, and *P* values were biased upwards. For example, the abundances of *Fabrea*, *Cletocamptus*, *Brachionus*, and *Trichocorixa* in tanks 57F–D were similar to those in the 57 g l^{-1} tanks without fish and quite different from those of the three 57 g l^{-1} tanks where fish survived (Hart, 1994). The fish in 57F–D may have died soon after introduction.

At both 39 and 57 g l^{-1} fish converted invertebrate assemblages dominated by large forms (*Trichocorixa, Gammarus*) into ones dominated by smaller forms, just as fish have been shown to do in many freshwater systems. Selective visual feeding on larger taxa was one mechanism involved, but rapid production rates of small forms subject to filter-feeding by tilapia or to predation by *Gammarus* and *Trichocorixa* was another. Like a closely related tilapia, *Oreochromis aureus* (Drenner & Taylor, 1984), our tilapia probably filtered efficiently particles as small as 20 μm in diameter. Thus it reduced abundances of protozoans (Figure 8) and phytoplankton (González et al., 1998a). Since these reductions were lesser in degree than those of metazoan invertebrates, protozoans came to dominate the invertebrate assemblages (Figure 10).

Several taxa that increased in the presence of tilapia were organisms primarily associated with the sediments. These included *Cletocamptus*, *Condylostoma*, nematodes, and possibly *Fabrea* (Figure 8). Their increases in both the water column and the sediments (Simpson et al., 1998) may have been due in part to the reduction of *Gammarus* and *Trichocorixa* populations but they also likely were stimulated by increased organic matter deposition in the form of fish feces (Simpson et al., 1998). By such deposition the fish shifted the microecosystems from being plankton- and nekton-dominated systems to being bethos-dominated ones, as evidenced by large reductions in total P and total N levels in the water column (González et al., 1998b). As a phytoplanktivore (Figure 12) that reduced the abundance and altered the compositon of the phytoplankton (González et al., 1998a), tilapia undoubtedly had effects on phytoplanktivorous invertebrates that we have not identified.

Scaling upward by 10^9

Does this ecosystem experiment carried out in 0.65 m^2 microcosms tell us anything of importance about the functioning of zooplankton and nekto-benthos populations in the 980 km^2 Salton Sea? Most physical, chemical and biological processes are likely to be modified greatly when spatial scale changes by a factor of 10^9. On these grounds it is easy to disparage the value of microcosm studies (e.g. Carpenter, 1996). But the proof is in the pudding. Drenner and Mazumder (1998) show that such criticism misses the mark. Our understanding of plankton ecology in freshwater lakes has benefitted greatly from experimental microcosm studies. The same is now proving true for saline lakes as well.

Our microcosms were similar to the Salton Sea in temperature and faunal composition. Had they been set up in the desert near the Salton Sea, their small size would have led to water temperature fluctuations greater than those of the Sea. But set up in the milder San Diego coastal region, they exhibited seasonal temperature variations similar to those likely for the littoral zone of the Sea (Carpelan, 1961a, M.A. Tiffany, unpubl. data). The dominant metazoans in the microcosms included most of those that dominate in the Sea – *Gammarus, Trichocorixa, Balanus, Apocyclops, Cletocamptus, Brachionus. Neanthes* larvae and planktonic eggs and larvae of sciaenid fish were the only Salton Sea metazooplankters missing from the microcosms. Carpelan (1961b) found *Neanthes* combined larval and egg densities as high as 30–40/l in the Sea. He did not report *Synchaeta* species from the Sea, but this genus is now periodically abundant there (M.A. Tiffany, unpubl. data), and it was in our microcosms. Protozooplankton of the Sea has never been studied and so cannot be compared with that of the microcosms.

Microcosms without fish obviously were unrepresentative of the Sea in that regard. Those with tilapia were also unrepresentative in that the other fish species in the Sea were omitted. Fish biomass per tank, however was equivalent to 130 kg/ha and 430 kg/ha in October 1991 and April 1992, respectively. Such fish standing crops are typical of eutrophic lakes (Carlander, 1955) and could well obtain in the Salton Sea. And, importantly, we estimated the effects of tilapia only during the colder part of the year. Understanding of these similarities and disparities aids judicious interpretation and extrapolation, but these ultimately are subjective. If salinity of the Salton Sea continues to increase for some years, however, the predictions below will be testable.

As salinity increases, large changes in the structure of the Salton Sea biocenosis can be expected. It is unlikely that fish will be present in the Sea when salinity reaches 60 g l^{-1}. The decline of fish will lead to disappearance of fish-eating birds from the system. Release from fish predation will result in large increases in invertebrate biomass, though some invertebrates intolerant of high salinities will decline and disappear. The consequences for invertebrate-eating waterbirds would be positive. As salinity increases to

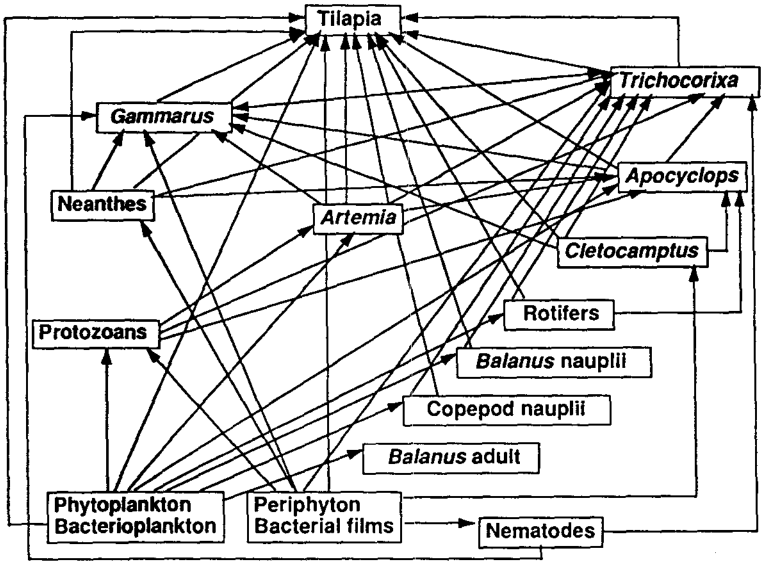

Figure 12. A schematic foodweb for the microecosystems.

50 g l^{-1}, *Gammarus* density should decrease substantially and *Trichocorixa* densities should increase due to the reductions in both *Gammarus* and fish populations. *Trichocorixa* and *Apocyclops* are likely to be the dominant metazoans of the water column once tilapia is gone. When salinity approaches 60–70 g l^{-1} *Apocyclops* may be sufficiently stressed physiologically (Dexter, 1993) that it will decline, and perhaps *Trichocorixa* will also though to a lesser degree. Any changes in *Apocyclops* abundance may generate changes in the opposite direction on the part of particular rotifer and protozoan species this copepod preys on. Elimination of *Apocyclops* from the Sea would likely soon be followed by appearance of *Artemia* as the dominant metazooplankter. The protozooplankton is likely to undergo three major changes in abundance as salinity increases. When tilapia, presumably a heavy grazer of protozoans (and most everything else), disappears, a large increase in protozoan biomass density is anticipated. When *Artemia* appears and attains high densities, a decrease in protozoans would be predicted. Finally, at very high salinities ($\gg >$ 100 g l^{-1}) physiological stress would more than cancel out the benefits of reduced predation, and protozoans would decline to low levels.

Engineering projects have been designed that could halt the current rise in salinity at the Salton Sea and eventually bring it back down to 35–40 g l^{-1} (Ogden, 1995; USBR, 1997). If one of these is implemented we will be able to monitor the changes that take place, starting several years from now, as salinity drops from, say, 55 g l^{-1} to 40 g l^{-1}. From a physiological point of view, that decrease would be favorable for all the fish species and most of the metazoan invertebrates of the plankton, nekton, and benthos. Actual population responses of invertebrates are likely, however, to be influenced by population changes in tilapia, corvina and other fish species. Corvina in the Sea attains weights of up to 12 kg and preys on other fish (Black, 1988). Improved reproduction and survival of corvina could result in increased predation by it on tilapia, a reduced tilapia population, and a multitude of adjustments among all the algal and invertebrate populations grazed by tilapia or influenced by tilipia's augmentation of sediment organic matter via fecal deposition.

Conclusions

This experiment has given insight into how the zooplankton and and nekton of the Salton Sea are likely to be affected by change in salinity, and into some of the mechanisms likely to be involved. It raises specific and easily answered questions concerning diets, feeding behavior, and salinity tolerances of tilapia and several dominant invertebrates. With respect to the Sea itself, the study emphasizes a need for analysis of its protozoan populations, microbial loop food web, and present fish assemblage. The U.S. federal government has recently made a commitment to fund research and monitoring programs in support of an effort to restore the health of the Salton Sea ecosystem. The prospect for early answers to many questions raised here are thus excellent.

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