



Salinity and fish effects on Salton Sea microecosystems: benthos

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Abstract

The Salton Sea, the largest lake in California, has a surface elevation 69 m below sea level which is maintained predominantly by the balance of agricultural runoff and evaporation. The lack of outflowing streams is resulting in a gradual buildup of salts in the lake, increasing the salinity. A 15 month microcosm experiment was conducted to determine the effects of salinity and tilapia (*Oreochromis mossambicus*) on an assemblage of benthic and planktonic Salton Sea algae and invertebrates. This article reports the responses of the benthic invertebrates.

Microcosms (312 l fiberglass tanks) were set up without tilapia at 30, 39, 48, 57, and 65 g·l⁻¹. Additional microcosms were set up with tilapia at 39 and 57 g·l⁻¹. In the absence of fish *Gammarus mucronatus* dominated the benthos at the lower salinities, and *Trichocorixa reticulata* and the larvae of *Ephydra riparia* were most abundant above 48 g·l⁻¹. The most abundant meiofaunal species included the harpacticoid copepod, *Cletocampus deitersi*, three nematodes, the rotifer *Brachionus plicatilis*, ciliates, including *Condylosoma* sp. and *Fabrea salina*, two foraminiferans including *Quinqueloculina* sp., and a large flagellate. Most meiofaunal species responding to salinity were most abundant at 65 g·l⁻¹, especially after 6 months when *Gammarus* dominated the lower salinities. The tilapia reduced the abundance of macrofaunal species, especially at 39 g·l⁻¹, and generally increased the abundance of meiofaunal species and ciliates.

The microcosm benthic macro- and meiofaunal communities were most likely structured by *Gammarus*, salinity and tilapia. *Gammarus* reduced the other species by predation and changing the detritus from an algal base to a fecal pellet base. *Gammarus* was itself reduced by tilapia and by reduced reproductive success above 39 g·l⁻¹. More species were therefore able to compete at higher salinities and in the presence of tilapia. Tilapia also affected the benthos by depositing loosely packaged fecal material which may support more meiofaunal species than either the robust *Gammarus* fecal pellets that were abundant at 39 g·l⁻¹ or the algae-fecal pellet mix at 57 g·l⁻¹.

Introduction

Increased salinity can modify benthic community biomass through reduction of primary production, substrate modification, deoxygenation, and other mechanisms (Rawson & Moore, 1944; Timms, 1983). Hammer (1986) summarized information showing that benthic macrofaunal diversity generally decreases with increasing salinity. Much experimental work has described the effects of salinity on individual species, including species found in the Salton Sea in Southern

California (e.g. Knowles & Williams, 1973; Kuhl & Oglesby, 1979; Fong, 1991; Dexter, 1993, 1995), but the effects of salinity on benthic communities have been studied experimentally only twice. The responses of an ephyrid fly and benthic algae to increasing salinity of Mono Lake, California, have been studied in a microcosm experiment (D. Herbst, unpubl. data), as have the effects of increased salinity on the benthic community of Pyramid Lake (Galat et al., 1988).

Salinity induced extinctions of system-structuring taxa such as fish may result in dramatic community

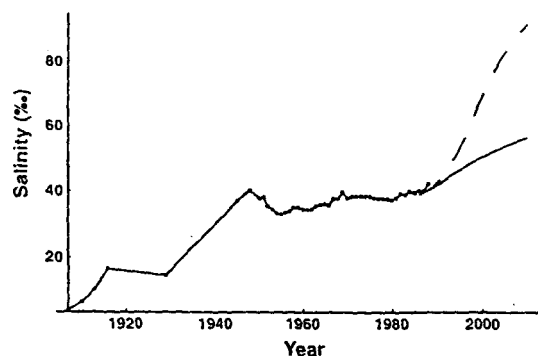


Figure 1. Projected salinity increases with (dashed line) and without (solid line) agricultural water conservation (Imperial Irrigation District 1986). Salinity values in ‰ can be converted to g/L by multiplying by approximately 1.01 at 10‰ and 1.07 at 100‰.

wide changes. No study has described the response of an entire community, including both the plankton and the benthos, to both salinity and fish. Fish can affect benthic community structure through disturbance and predation. Fish predation reduces macrofaunal abundance and limits the distribution of macrofaunal organisms to refugia (Healey, 1984). Fish and macrofaunal invertebrates reduce meiofaunal abundance through predation (Smith & Coull, 1987) and disturbance (Smith, 1986), and can increase benthic community diversity by increasing benthic community evenness (Diehl, 1992) and infaunal diversity (Smith, 1986). The influence of megafaunal organisms such as fish and crabs upon meiofaunal communities has been examined over a gradient of water flow regimes (Palmer, 1988), but changes in megafaunal influences upon benthic communities over chemical gradients such as salinity have never been described.

This microcosm experiment was designed to determine how salinity and fish affect a seminatural assemblage of Salton Sea organisms. Our specific objectives were to determine how salinity influenced the assemblage in microcosms maintained at 30, 39, 48, 57 and 65 g·l⁻¹, and to determine the effect of the presence of a single juvenile tilapia (*Oreochromis mossambicus* Peters) on the assemblages at 39 and 57 g·l⁻¹. This article reports the effects of these variables on the zoobenthos. Effects of salinity and fish on the water chemistry, phytoplankton, periphyton, zooplankton and barnacles in the same microcosms are reported elsewhere (González et al., 1998a, b; Hart et al., 1998; Simpson & Hurlbert, 1998).

The Salton Sea is a saline lake with a surface elevation of 69 m below sea level. It is the largest lake in California, and provides a unique opportunity for

experimental study of the effects of salinity and fish on benthic communities. Since the Salton Sea salinity is increasing, it will provide a test of the predictive ability of microcosm experiments. Fish comprise the entire submersed Salton Sea megafauna, and, although they are known to feed on the plankton and all adult macroinvertebrates, their impact on the Salton Sea benthic community is unknown. The Salton Sea fish can be represented in microcosms of a manageable size by a small individuals of an omnivorous species such as the tilapia *Oreochromis mossambicus*.

Increasing salinity has had a major effect on the Salton Sea benthic community. Since its accidental creation by the Colorado River in 1905 (Sykes, 1914; Hely et al., 1966), the Salton Sea salinity had increased to 44 g·l⁻¹ in 1991, and its increase is predicted to continue to between 56 g·l⁻¹ and > 91 g·l⁻¹ by 2010, depending on the extent of agricultural water conservation (Figure 1). Most of the fauna introduced to the Salton Sea with the Colorado River died out by 1907 (Ross, 1914; Hely et al., 1966). The present benthic fauna is predominately of marine origin and was introduced during the 1950s (Walker, 1961; Whitney, 1966). Apparently only 2 of the 29 macroinvertebrate species and 4 of the 35 fish species introduced at that time by California Department of Fish and Game survived and reproduced. The failure of most introductions was attributed to the differences in ionic composition of the Salton Sea compared to the ocean, the 20 °C annual water temperature fluctuations, and the occasional summertime hypoxia within the Salton Sea (Carpelan, 1961a; Linsley & Carpelan, 1961). The tilapia, an introduced species from Africa, became established in the lake in the early 1970s and quickly became one of the most abundant fish species present.

Today, the benthic macrofauna consists mainly of the amphipod *Gammarus mucronatus* Say, the polychaete *Neanthes succinea* Frey & Leuckart, the barnacle *Balanus amphitrite* Darwin, the corixid *Trichocorixa reticulata* Guérin-Ménéville, and larvae of the brine fly *Ephydra riparia* Fallén. Among the common meiofaunal elements are the harpacticoid copepod *Cletocamptus deitersi* Richard, the rotifer *Brachionus plicatilis* Muller, nematodes, and several protists including foraminiferans and the large ciliates *Condylostoma* sp. and *Fabrea salina* Henneguy.

As the salinity increases, the Salton Sea benthic community will undoubtedly change substantially. *Trichocorixa reticulata* has been found in ponds with salinities ranging from 0 to 190‰ (Balling & Resh, 1984) and *Brachionus plicatilis* has been re-

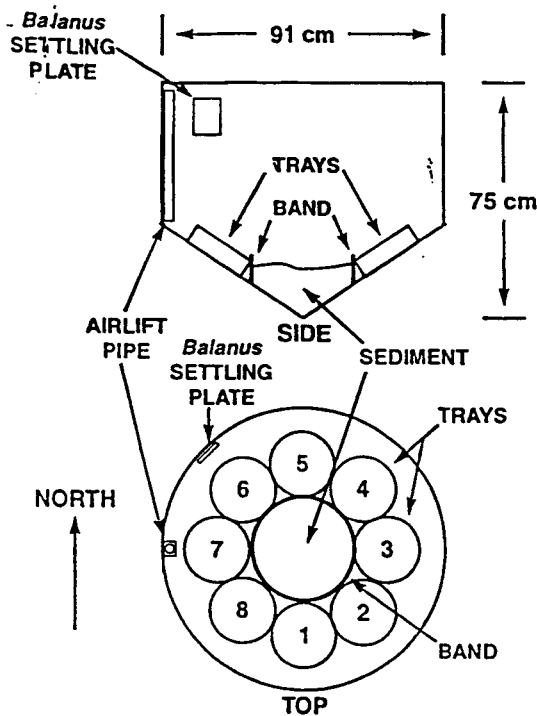


Figure 2. Microcosm experimental unit.

ported in lakes as high as 250‰ (Hammer, 1986), though this does not necessarily mean they can reproduce and maintain populations under these conditions. *Gammarus mucronatus* has successfully reproduced at 57‰ in the lab, but it is rarely found in salinities over 50‰ in the field (D. Dexter, pers. comm.). *Neanthes succinea* will probably not survive salinities much higher than 70‰, or at most 80‰ (Kuhl & Oglesby, 1979). Despite our knowledge of specific salinity tolerances, how increasing salinity will affect interactions among benthic species is unknown.

Methods

Experimental design

The experiment used a complete randomized block 5×2 incomplete factorial design to test the effects of 5 salinity levels (30, 39, 48, 57, and 65 g·l⁻¹) and 2 fish density levels (0 and 1 fish per tank) on an assemblage of Salton Sea organisms. The effects of fish were tested at 39 and 57 g·l⁻¹ only, resulting in 7 treatment combinations (30, 39, 39F, 48, 57, 57F, 65) each replicated 4 times. Blocks were designated A, B, C, and D. The experimental units were 380 l tanks with conical

bottoms maintained on the roof of the Life Sciences building at San Diego State University.

Microcosm establishment and maintenance

On November 20, 1990, 302 l of 47 g·l⁻¹ Salton Sea water from Salton City were pumped into each tank. The salinity in each tank was adjusted to 30 g·l⁻¹ by adding tap water to produce a final volume of 312 l. The experimental salinity levels were established over a period of days by adding pure salts (NaCl, MgSO₄, KCl, Na₂SO₄) in proportions calculated to yield ionic compositions expected to result from evaporative concentration of Salton Sea water. Details of these procedures, together with information on ionic compositions and nutrient levels are given in González et al. (1998a), and the spatial arrangement of tanks and temporal variations in salt are presented in Hart et al. (1994). By January 17, 1991, all tanks had been brought to the desired salinity levels.

Three liters of compressed, organically rich sediments collected from the Salton Sea shore near Barth Road were placed on the bottom of each tank as a nutrient source and substrate. In addition, 8 sediment trays (300 ml, 286 cm² petri dishes) were placed in a ring on the bottom of each microcosm (Figure 2). Each tray contained 200 ml of sand sifted through a 16 mm sieve. The sand was also collected near Barth Road but from a site with a lower organic content. The sand grain size distribution was determined using an Emery settling tube after it was sifted through a 2 mm sieve. A metal band was placed around the sediments in the center of the tank to prevent the sediment trays from sinking into them.

The tanks were inoculated on 5 occasions with algae and invertebrates from 10 locations around the Salton Sea where salinities ranged from 1 to 270 g·l⁻¹. In addition to the general inocula, *Neanthes succinea*, *Artemia franciscana* Kellogg, *Gammarus mucronatus*, and *Cletocampus deitersi* were added to each tank at various times. The tanks were not directly inoculated with *Ephydra riparia*, but 5 buckets containing pupae collected from the Salton Sea were interspersed among the tanks to allow adult colonization of the tanks. Details of these procedures are given in Hart (1994) and Hart et al. (1998).

A single juvenile tilapia was introduced to each of the 8 appropriate microcosms on July 7, 1991. Half of these initial fish died within 5 d, however, so all fish were removed until September 28, when juvenile tilapia (4–12 g wet weight, 5.1–7.4 cm long)

were successfully reintroduced into the microcosms. Before the end of the experiment, however, three of these died, as discussed later. Juveniles were used in order to keep low the ratio of fish biomass to tank volume. Details on the fish additions are provided in Hart (1994).

The water volume and salinity were maintained by adding dechlorinated tap water. The vertical microcosm walls were scrubbed every two weeks with plastic pot scrubbers to prevent excessive build-up of attached organisms, and *B. amphitrite* were periodically removed from the interior of the airlift pipes to ensure water circulation. The microcosms were covered with translucent fiberglass sheets when it rained to prevent excessive dilution or tank overflows.

Benthic sampling

Two sediment trays were collected from each microcosm within 5 d of the beginning of May, August, and November 1991 and February 1992. The sediment trays were collected prior to adding dechlorinated tap water or scrubbing the microcosm walls and at least three days after zooplankton sampling to minimize any effects on the distribution of benthic organisms caused by those procedures. The trays numbered 3 and 7 (Figure 2) were collected first, and on each subsequent sampling date the 2 trays counterclockwise to those previously removed were collected.

The sediment tray to be collected was covered with a lid the central portion of which consisted of 100 μm mesh mylon netting. The tray was then removed from the tank, and its entire contents were placed into a 1 l container. The process was repeated for the second sediment tray, and the contents of both trays were pooled in the same container. The 100 μm mesh lid reduced the bow shock effect which reduced the loss of material as it was pressed onto the tray. This mesh size was small enough to retain most organisms of interest. Into each sample was mixed 0.66 ml of 30% rose bengal (0.033% by volume) and 75 ml of formalin (15% by volume).

The organisms and essentially all other organic material were removed from the sand by washing with tap water. The volume of the material removed from the sediments was determined by measuring the height of the material after it had settled in vials. This was used as an indicator of sediment organic matter content since it was comprised mainly of algae and organic detritus. The sand was dried at 80 $^{\circ}\text{C}$ and its volume measured with a graduated cylinder.

The quantities of sand and organic material were converted to equivalent depth by dividing their volumes by the area of the 2 sediment trays. Details on these procedures are given in Simpson (1994).

The macrofauna were separated from the meiofauna and protists with a 500 μm filter. From the filtrate, 1 part in 1000 was subsampled using a pipet. Meiofaunal metazoans, eggs, and protists larger than 10 μm were counted in a 5 \times 4 cm counting chamber using a Nikon YS-2 binocular compound microscope with an eyepiece micrometer. The length and width of each organism was measured to the nearest eyepiece micrometer unit. The macrofaunal organisms were sorted at 6 \times using a Wild binocular dissecting microscope with an eyepiece micrometer. The organisms were identified, counted and the length measured. Specimens of *Gammarus*, *Artemia*, *Neanthes*, most nematodes and protists were placed into size classes. The ciliates were placed into 4 categories: *Condylostoma*, *Fabrea*, medium ciliates (51 to 80 μm), and small ciliates (10 to 50 μm). *Trichocorixa*, *Ephydra* and *Cletocamptus* were classified based on their life stages. Details on organism enumeration are in Simpson (1994).

For each species, biovolume estimates were calculated based on an empirical relationship between body volume and length. This relationship was determined by measuring the length, width and depth of individuals representing the size range of each species. Volume calculations were based on an ellipsoid model, so volume was calculated as $\pi * \text{width} * \text{depth} / 6$. Odd shaped animals such as copepods were broken down into elliptical sections which were calculated separately and summed for a total biovolume estimate. Results were expressed as number of individuals or biovolume per 100 cm^2 .

Experiment termination

The microcosms were dismantled after 15 months, in May 1992. The water and bottom sediments were sampled during the dismantling. The water was removed with buckets. When the water level was about 15 cm, two 4.5 cm diameter cores were taken from undisturbed sediments in the center of each microcosm and the thickness of the surface algal mat was measured through the transparent corer using a ruler.

Data analysis

For each taxon or size class on each date, a 1-way ANOVA was used to test for differences in numer-

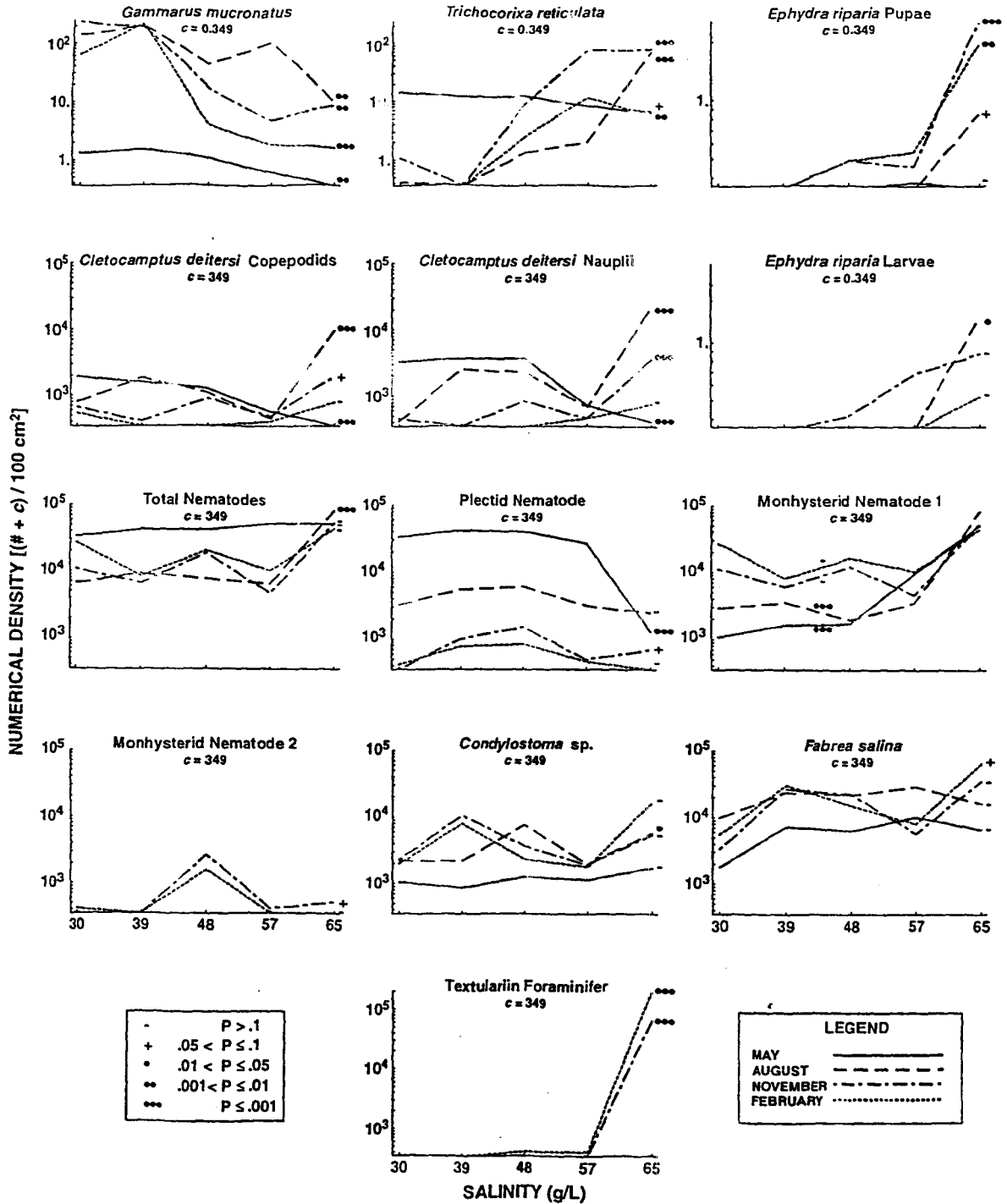


Figure 3. Effect of salinity on numerical densities of principal taxa, P values shown are for 1-way ANOVAs for each date.

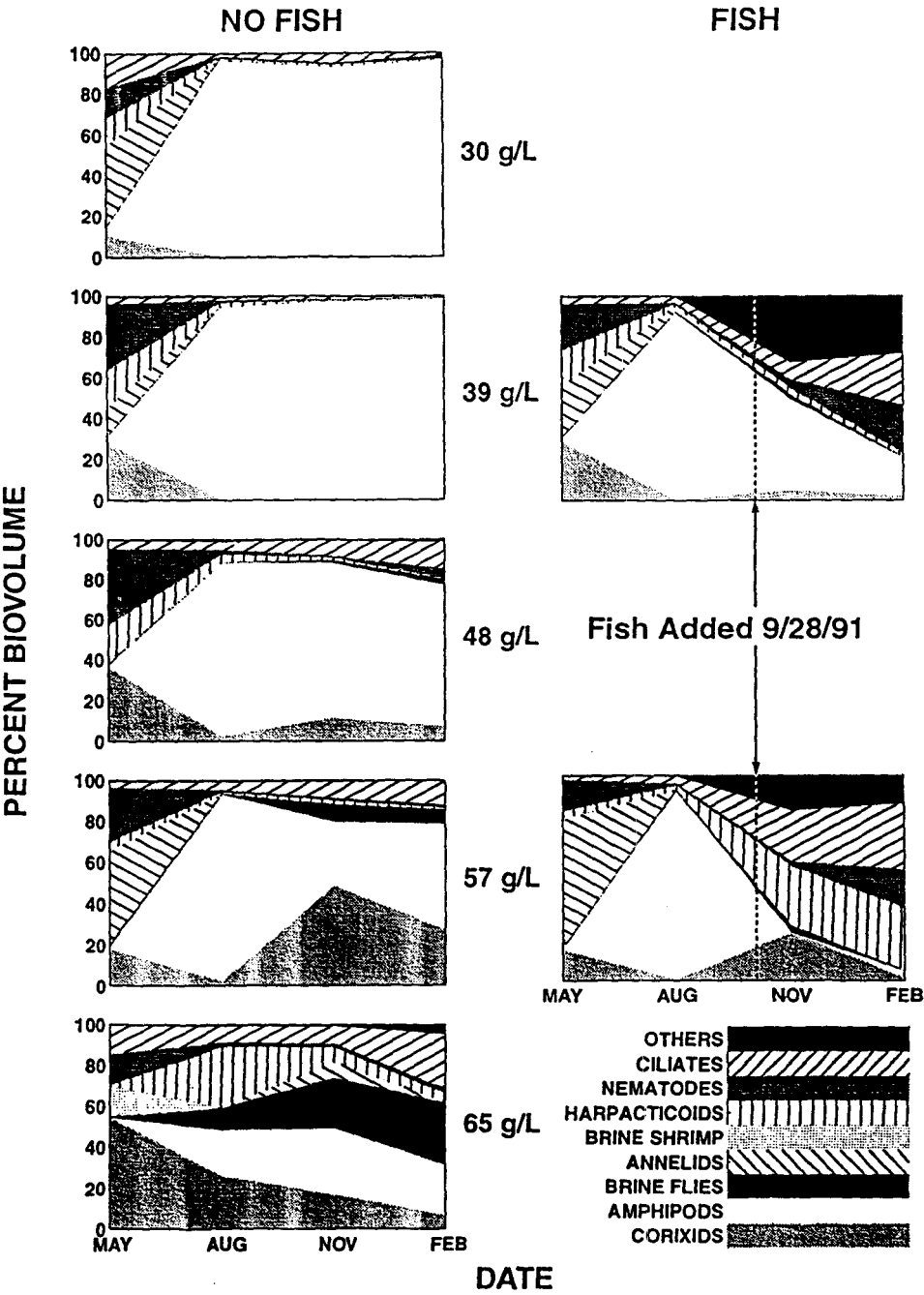


Figure 4. Relative abundances of zoobenthic taxa for each treatment.

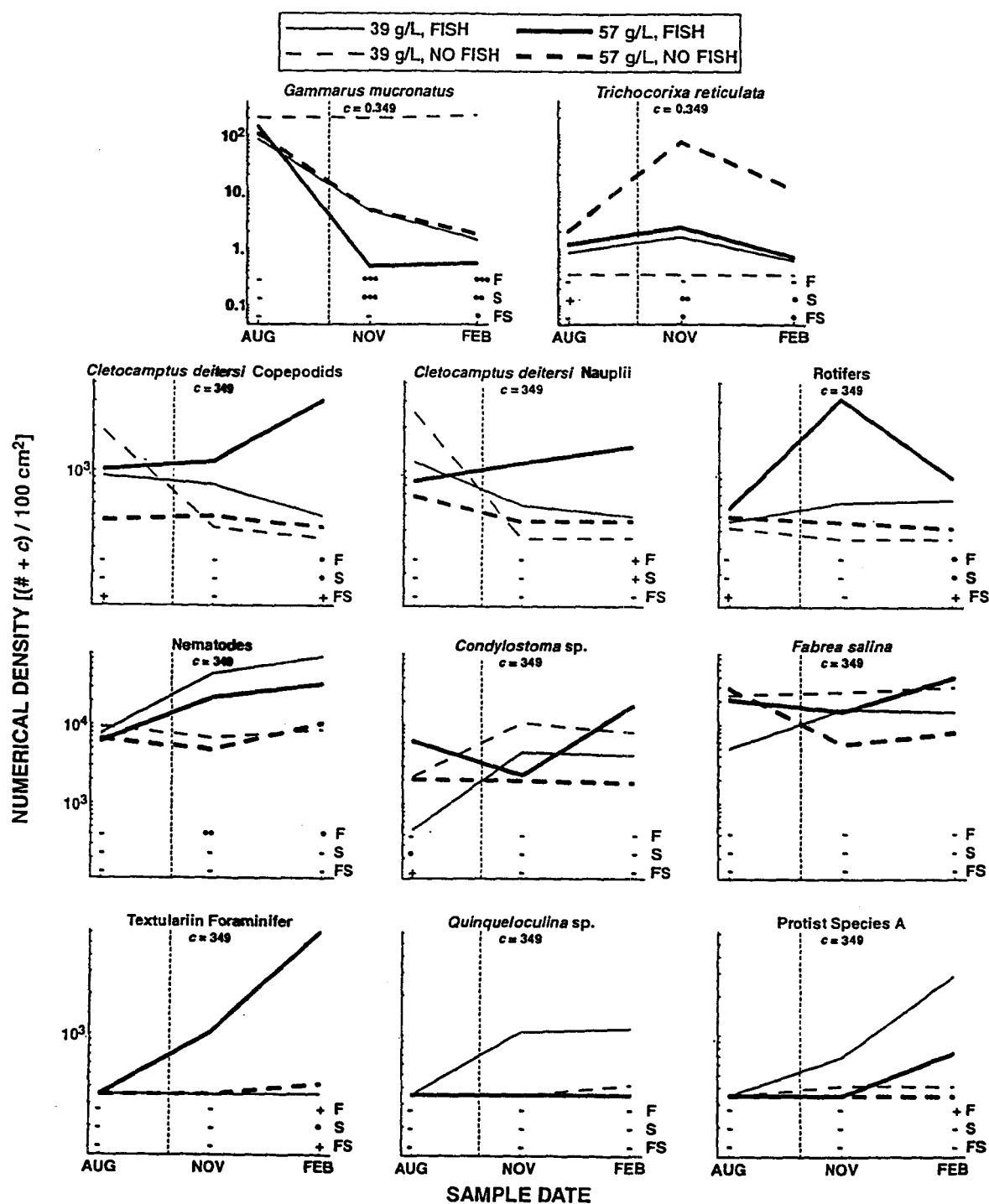


Figure 5. Effects of fish and salinity on numerical densities of principal taxa. P values are for 2-way ANOVAs for each date, testing for fish (F), salinity (S) and interaction (FS) effects, and are denoted as in Figure 3. Vertical dashed line indicates the date fish were established in microcosms.

ical or biovolume densities among salinities. The effects of fish and salinity were tested using 2-way ANOVAs for the November 1991 and February 1992 samples. All data were log transformed prior to statistical analysis, with a constant added to each raw datum equal to the smallest non-zero value possible given the sampling method. The values reported are geometric means. Effects of salinity and fish on multispecific faunal groups (e.g. total macrofauna, total ciliates), were tested for only with data on biovolume densities ($\text{mm}^3/100 \text{ cm}^2$). All graphical and statistical operations were performed using Mathematica (Wolfram Research, Inc., 1993) on a NeXT computer.

The ratio of total meiofaunal biovolume to total macrofaunal biovolume was calculated for each microcosm on each date for analysis of the benthic community size structure. Since no macrofauna were collected from some microcosms containing fish, the same constant was added to the macrofaunal and meiofaunal biovolume estimates for each tank as was added to biovolume data prior to log transformations. The ratios were then log transformed and tested for differences among salinity and fish combinations using 1-way and 2-way ANOVAs.

To examine the size structure of the *Gammarus mucronatus* population, the proportion of individuals in the smallest two size classes relative to the total number of amphipods was determined for each salinity. The proportion was arcsine transformed and differences among salinities were tested using a 1-way ANOVA.

Statistical analyses of fish effects used the data from all four microcosms in each of the fish treatments even though three fish died, two at undetermined times. Thus the results of those analyses likely are conservative, with P values biased upwards.

Results

Macrofauna

Gammarus mucronatus and *Trichocorixa reticulata* were the dominant macrofaunal species in the microcosm benthos. *Ephydra riparia*, *Neanthes succinea*, *Artemia franciscana* and an unidentified oligochaete were also present.

The abundance of *Gammarus* decreased with increasing salinity on all sample dates (Figures 3). *Gammarus* abundance at all salinities increased by 2 orders of magnitude from May to August. Total *Gammarus*

abundance was very high at $57 \text{ g} \cdot \text{l}^{-1}$ in August, but the size distribution included relatively few individuals (2–10%) in the smallest two size categories, in contrast to the abundance (10–60%) of small individuals at 30 and $39 \text{ g} \cdot \text{l}^{-1}$ ($F_{4,15} = 3.5$, $P < 0.05$). The abundance of *Gammarus* decreased after August at salinities above $39 \text{ g} \cdot \text{l}^{-1}$. Over the last three sampling dates, *Gammarus* composed 78–99% of the average total benthic biovolume at 30 and $39 \text{ g} \cdot \text{l}^{-1}$ (Figure 4).

Gammarus was reduced in the presence of juvenile tilapia, the effect being greater where *Gammarus* was dominant ($39 \text{ g} \cdot \text{l}^{-1}$) than where it was less abundant ($57 \text{ g} \cdot \text{l}^{-1}$) (Figure 5).

The abundance of *Trichocorixa* was similar at all salinities of the first sampling data, but subsequently became much more abundant at salinities above $48 \text{ g} \cdot \text{l}^{-1}$ than at salinities below $48 \text{ g} \cdot \text{l}^{-1}$. *Trichocorixa* were completely absent at $39 \text{ g} \cdot \text{l}^{-1}$ by August (Figure 3). *Trichocorixa* frequently comprised 50–90% of the macrofaunal individuals at salinities above $48 \text{ g} \cdot \text{l}^{-1}$. There were often 4 times as many *Trichocorixa* as *Gammarus* (Figure 3), but *Trichocorixa* biovolume was rarely greater than that of *Gammarus* after May (Figure 4).

The interaction between the effects of salinity and tilapia suggests that *Trichocorixa* abundance increased after fish were added at $39 \text{ g} \cdot \text{l}^{-1}$ and declined after fish were added at $57 \text{ g} \cdot \text{l}^{-1}$ (Figure 5). However, at $39 \text{ g} \cdot \text{l}^{-1}$ *Trichocorixa* was abundant only in microcosms within which fish either died (39-A and 39-C) prior to the end of the experiment or were never added, so the higher *Trichocorixa* abundance in the $39 \text{ g} \cdot \text{l}^{-1}$ tilapia added treatments may not reflect a true response to fish (Figure 6). The only $59 \text{ g} \cdot \text{l}^{-1}$ fish microcosm that contained a substantial number of *Trichocorixa* was the one, 57-D, in which the fish died (Figure 6).

The densities of *Ephydra* larvae and pupae increased with increasing salinity (Figure 3). This species comprised one-fourth to one-third of the zoobenthos biovolume at $65 \text{ g} \cdot \text{l}^{-1}$ (Figure 4). No response to fish was observed, as even in the absence of fish it was never found at $39 \text{ g} \cdot \text{l}^{-1}$ and was not abundant at $57 \text{ g} \cdot \text{l}^{-1}$.

Neanthes was the largest benthic organism in the microcosms. The 4 individuals collected in May from the eight $57 \text{ g} \cdot \text{l}^{-1}$ microcosms comprised 45% of the total biovolume for that treatment on that date (Figure 4). *Neanthes* were found at all salinities but were too rare for a response to salinity or fish to be evident. *Neanthes* did not appear to successfully reproduce in the microcosms.

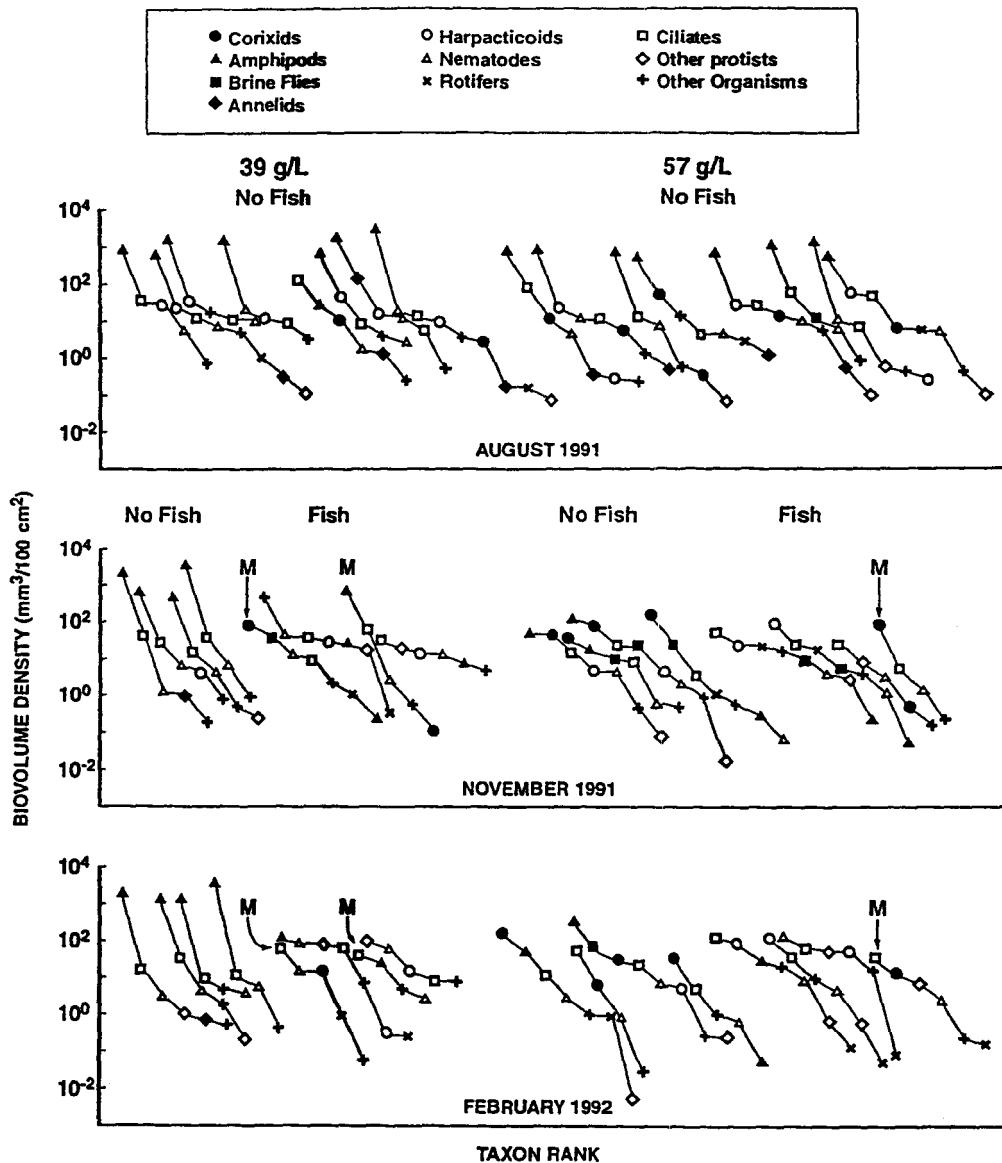


Figure 6. Whittaker or rank-abundance curves for 39 and 57 g/L treatments with and without tilapia. Microcosms within each treatment are presented in block order (A, B, C, D). Fish were successfully established on September 28, 1991. Curves representing microcosms to which fish were added but did not survive to the end of the experiment (microcosms 39F-A, 39F-C, 57F-D) are indicated with an 'M'.

An unidentified oligochaete was found sporadically at all salinities, occasionally in very high numbers and usually associated with thick benthic algal mats. The irregularity of its occurrence, however, obscured any effect that salinity may have on it.

Artemia was incidentally collected in the benthos samples in May, but only at the highest 2 salinities. It composed 14% of the average total benthic biovolume at 65 g·l⁻¹ (Figure 4).

Total macrofauna biovolume (Figure 7) showed trends paralleling those for biovolume of *Gammarus* (Figure 3), decreasing with increasing salinity by the third sample date as *Gammarus* declined at salinities above 39 g·l⁻¹. The greater biovolume densities of *Trichocorixa* at high salinities (Figure 3) dampened this trend. Total macrofauna biovolume declined by about three orders of magnitude at both 39 and 57 g·l⁻¹, in the presence of fish (Figure 8).

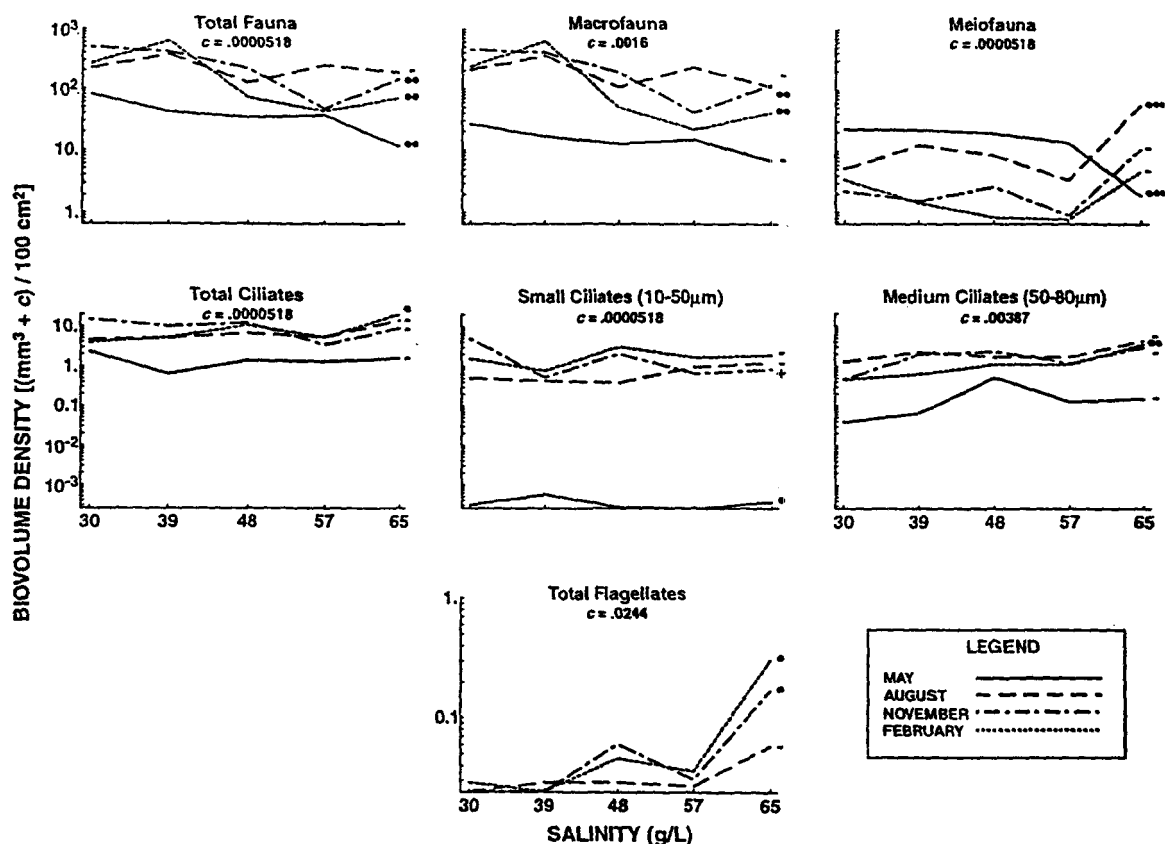


Figure 7. Effect of salinity on biovolume densities of principal taxa. P values are for 1-way ANOVAs on each date and are denoted as in Figure 3.

Meiofauna

The principal meiofaunal metazoans were *Cletocamptus deitersi* and 3 nematode species. Rotifers also became abundant in the presence of fish. Six other meiofaunal organisms were occasionally found in the sediments, including mites, tardigrades, and a flat-worm.

In May, *Cletocamptus* abundance was negatively correlated with salinity (Figure 3). By August, however, *Cletocamptus* was most abundant at 65 g·l⁻¹. Through the remainder of the experiment, *Cletocamptus* populations declined at all salinities, although it remained most abundant at 65 g·l⁻¹. Occasionally *Cletocamptus* comprised over one-third of the total benthic fauna biovolume. *Cletocamptus* was the most abundant benthic animal, by volume, at 65 g·l⁻¹ in August and at 57 g·l⁻¹ after fish were added (Figure 4). *Cletocamptus* nauplii and copepodids became more abundant in the presence of fish, especially in February (Figure 5).

Four nematode species were distinguished in the samples. The family Plectidae was represented by one species and Monhysteridae by two species. Individuals of these three species all ranged in length from 0.1–0.4 mm. The diameter of the plectid nematode is twice that of the monhysterids, however, and it possesses a large esophageal bulb and an obvious triangular spinneret. The monhysterid nematodes lack an esophageal bulb and have a smaller spinneret. Monhysterid species 1 was distinguished from monhysterid species 2 by primarily the relatively longer tail of the former. The fourth nematode species could not be identified to family and was represented by a single small individual.

The plectid nematode was initially very abundant at all salinities below 65 g·l⁻¹. Its population then declined over the next 6 months (Figure 3). This nematode composed 15–38% of the zoobenthos biovolume at salinities below 65 g·l⁻¹ in May, but afterwards

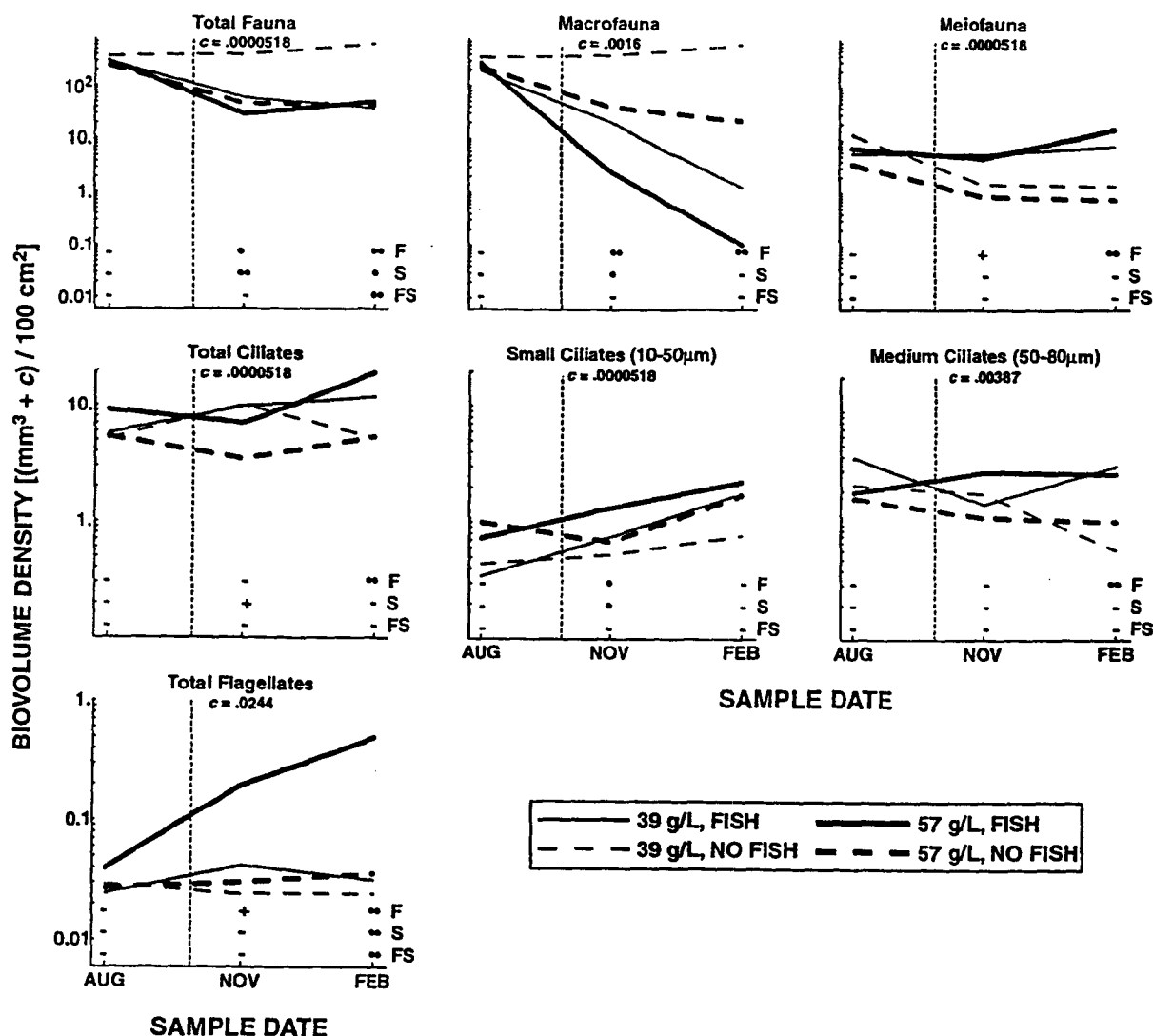


Figure 8. Effects of fish and salinity on biovolume densities of principal taxa. P values are for 2-way ANOVAs for each date, testing for fish (F), salinity (S) and interaction (FS) effects, and are denoted as in Figure 3. Vertical dashed line indicates date that fish were established in microcosms.

never constituted more than 2.2% of this biovolume in the absence of fish (Figure 4).

Monhysterid species 1 was most abundant at $65 \text{ g} \cdot \text{l}^{-1}$ through August. At salinities below $57 \text{ g} \cdot \text{l}^{-1}$ the population increased steadily after May, at the same time the plectid nematode was declining. By November there was no significant difference among salinities in abundance of monhysterid species 1, though it was still most abundant at $65 \text{ g} \cdot \text{l}^{-1}$ (Figure 3). Monhysterid species 1 was eventually as abundant as the plectid was, but it never comprised more than 13% of the total zoobenthos biovolume. Mon-

hysterid species 2 was occasionally present in large numbers, and was most often collected at $48 \text{ g} \cdot \text{l}^{-1}$ (Figure 3).

Total nematode abundance was unaffected by salinity in May, since the plectid was a abundant at $65 \text{ g} \cdot \text{l}^{-1}$ as monhysterid species 1 was at salinities below $65 \text{ g} \cdot \text{l}^{-1}$. Total nematode abundance after May became highest at $65 \text{ g} \cdot \text{l}^{-1}$ as monhysterid species 1 replaced the plectid, but the trend became less pronounced as the monhysterid numbers increased (Figure 3).

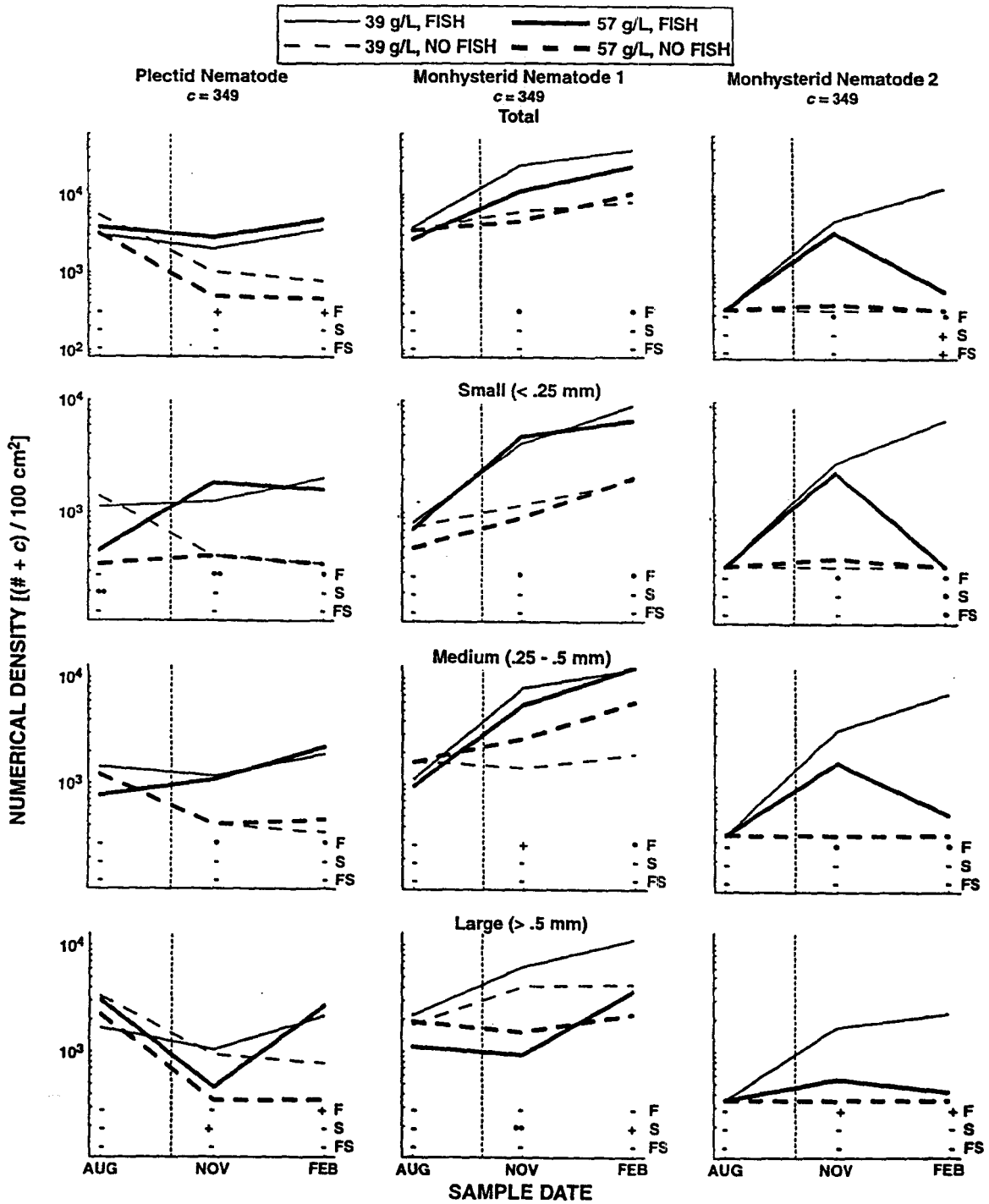


Figure 9. Effects of fish and salinity on numerical density of major nematode size classes. P values are for 2-way ANOVAs for each date, testing for fish (F), salinity (S) and interaction (FS) effects, and are denoted as in Figure 3. Vertical dashed line indicates date fish were established in microcosms.

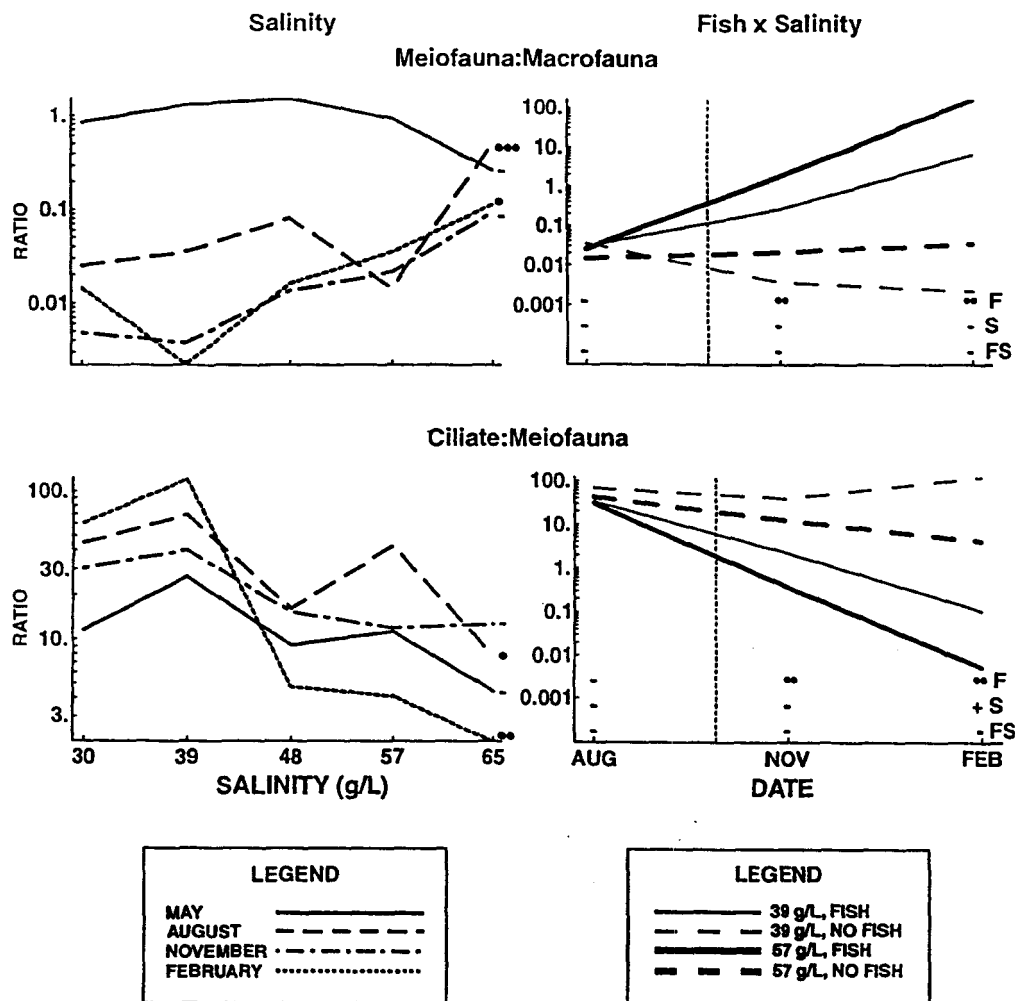


Figure 10. Effects of salinity and fish on biovolume ratios of meiofauna to macrofauna and ciliates to meiofaunal metazoans in sediment trays. 'Salinity' results are for 1-way ANOVAs for each date. 'Fish x Salinity' results are for 2-way ANOVAs for each date testing for fish (F), salinity (S) and interaction (FS) effects. P values are denoted as in Figure 3. Vertical dashed line indicates date that fish were established in microcosms.

Fish caused an increase in total nematode abundance (Figure 5). The total abundances of the plectid and both monhysterid species were increased by the fish, as were the abundances of the smaller two size classes of all three nematodes (Figure 9). However, the effect on the largest size class was smaller and did not appear in the plectid and monhysterid 1 until February. By February, monhysterid 2 in the presence of the fish was much more abundant at 39 g·l⁻¹ than at 57 g·l⁻¹ (Figure 9).

Three rotifers were found in the sediment; *Brachionus plicatilis* was the most common, followed by *Synchaeta* sp. and a unidentified species. *Brachionus* demonstrated no certain trends with salinity, owing

at least in part to the high within treatment variability, though it appeared to be more common at higher salinities. *Synchaeta* was uncommon but found at all salinities. The unidentified rotifer was found only in August and November at the highest two salinities. As a group, the rotifers increased after the fish were added, and were more abundant at 57 g·l⁻¹ than at 39 g·l⁻¹ (Figure 5).

In May the total meiofauna biovolume was lowest at 65 g·l⁻¹ (Figure 7) and composed 30–70% of the zoobenthos biovolume at all salinities. The meiofauna: macrofauna biovolume ratio was about 1.0, except at 65 g·l⁻¹ where it was less than 0.3 (Figure 10). After May meiofauna biovolume was highest at 65 g·l⁻¹ and

composed more than 20% of the zoobenthos biovolume only at 65 g·l⁻¹ or in the presence of the fish (Figure 4). The meiofauna: macrofauna ratio was also highest at 65 g·l⁻¹, although by November the ratio had declined to 0.1. Meiofauna abundance and the meiofauna: macrofauna ratio increased in the presence of juvenile tilapia (Figures 8 and 10).

Protists

The benthic protists in the microcosms were dominated by ciliates. The ciliates larger than 80 μ m consisted almost entirely of *Fabrea salina* and *Condylostoma* sp. Ciliate abundance increased nearly 10-fold between May and August, with the small ciliates increasing by three orders of magnitude (Figures 3 and 7). By February, the medium ciliate and total ciliate biovolumes increased with salinity (Figure 7). On average the proportion of the total zoobenthos represented by ciliates also tended to increase with salinity (Figure 4). In contrast, the ratio of ciliates to meiofaunal metazoans generally tended to decline as salinity increased (Figure 10).

By February, the total ciliate biovolume (Figure 8) and the ratio of ciliates to the rest of the benthos (Figure 4) was greater in the presence of fish. This trend was apparent by November at 57 g·l⁻¹, but not until February at 39 g·l⁻¹. However, the ratio of ciliates to meiofaunal metazoans declined dramatically in the presence of fish (Figure 10). Abundances of the small and medium sized ciliates tended to be higher in the presence of fish at both 39 and 57 g·l⁻¹ (Figure 8). Neither of the two large ciliates, *Fabrea* and *Condylostoma*, demonstrated conclusive responses to fish, but at the end of the experiment both species seemed to be positively affected by fish at 57 g·l⁻¹ and negatively affected at 39 g·l⁻¹ (Figure 5).

A large unidentified flagellate, 50–80 μ m in length, was collected beginning in August and became more abundant over time. During the latter half of the experiment it was several-fold more abundant at 65 g·l⁻¹ than at lower salinities (Figure 7). The flagellate population increased greatly in response to the addition of fish (Figure 8). In no treatment did it comprise a large proportion of the total zoobenthos biovolume (Figure 4).

Five other protists were found in the microcosm sediment. Two were foraminiferans, one belonged to the suborder Textulariina, and the other was *Quinqueloculina* sp. The third was a multiflagellated protist (protist species A), the fourth was *Vorticella* sp. and

the last was an amoeba. *Quinqueloculina*, the textulariin foraminifer, and protist species A were first collected in November. *Quinqueloculina* and protist species A were mostly found at salinities below 57 g·l⁻¹, and there was weak evidence that they were positively affected by fish at 39 g·l⁻¹ (Figure 5). The textulariin foraminifer occurred almost exclusively at 65 g·l⁻¹ (Figure 3) and at 59 g·l⁻¹ when fish were present (Figure 5). *Vorticella* occurred sporadically at all salinities beginning in August, but never attained densities exceeding 2000 individuals per cm².

Taxonomic composition

How the taxonomic composition of the microcosm benthos changed dramatically over time and with salinity. In May the benthic fauna was diverse at all salinities, with no taxon composing over 55% of the total biovolume (Figure 4). By August, *Gammarus* dominated the biovolume at salinities below 65 g·l⁻¹, and remained dominant thereafter at 30 and 39 g·l⁻¹. Although *Gammarus* generally dominated the biovolume at 48 and 57 g·l⁻¹ also, other species became increasingly important, including *Trichocorixa*, *Ephydra* (especially at salinities above 48 g·l⁻¹), and ciliates. With the exception of increased *Cletocampus* abundance, the assemblage at 65 g·l⁻¹ during and after August was dominated by the same species found at 48 and 56 g·l⁻¹ during and after November: *Gammarus*, *Trichocorixa*, *Ephydra*, and ciliates.

Total zoobenthos biovolume tended to decline with salinity (Figure 7) and was primarily determined by *Gammarus*. In terms of numbers of individuals, ciliates (54–99%) dominated at all salinities. Occasionally, a few other organisms which comprised a small proportion of the total biovolume were very abundant numerically, most notably the plectid nematode in May, monhysterid species 1 at 65 g·l⁻¹, and the textulariin foraminifer at 65 g·l⁻¹. Nematode eggs were also extremely abundant at lower salinities.

Zoobenthos biovolume declined in the presence of fish at 39 g·l⁻¹ but not at 57 g·l⁻¹ (Figure 8). *Gammarus* comprised 99% of the total biovolume at 39 g·l⁻¹ in the absence of fish (Figure 4) but only 19% of the total biovolume after fish were introduced when ciliates, nematodes, and protist species A became dominant. At 57 g·l⁻¹ fish caused *Gammarus* to decline from 20–50% to ca. 1% of the total biovolume. The relative abundance of *Trichocorixa* at 57 g·l⁻¹ also declined in the presence of fish. At this salinity, rotifers, ciliates and brine flies made up most

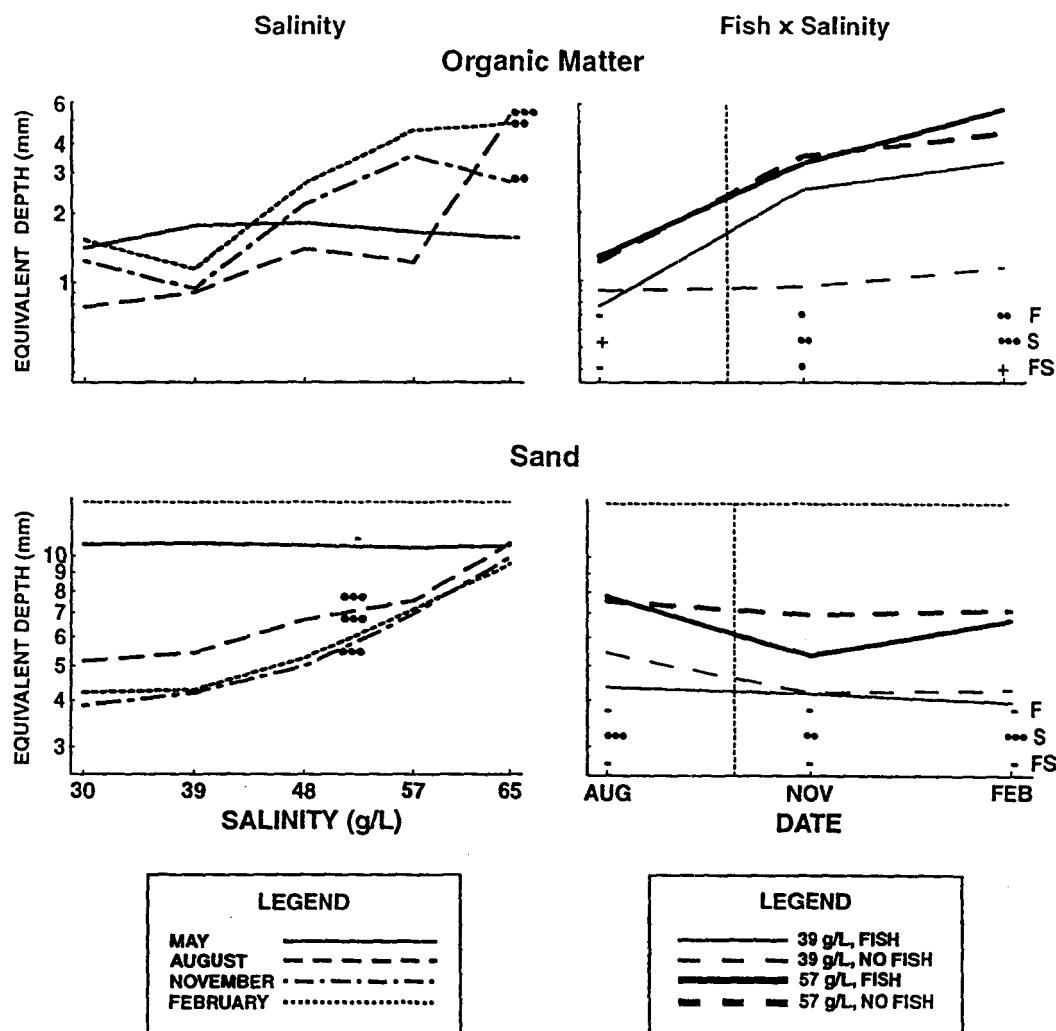


Figure 11. Effect of salinity and fish on equivalent depth of total organic matter (algae and detritus) and on sand remaining in sediment trays. 'Salinity' results are for 1-way ANOVAs for each date. 'Fish x Salinity' results are for 2-way ANOVAs for each date testing for fish (F), salinity (S) and interaction (FS) effects. P values are denoted as in Figure 3. Vertical dashed line indicates date that fish were established in microcosms. Horizontal dashed line indicates the original depth (14 mm) of sand at the time it was placed in sediment trays.

of the biovolume in the absence of fish, while in the presence of fish they were supplemented by harpacticoids, nematodes, and protist species A. Nematode eggs also contributed a large portion (4–44%) of the total biovolume after the fish were added.

Zoobenthic diversity, however defined, seemed to increase with salinity and with the addition of fish. At 30 g·l⁻¹ there was, during most of the experiment, one dominant taxon (*Gammarus*) and at 65 g·l⁻¹ there were four or five, and similar switches to shared dominance occurred with the addition of fish (Figure 4). The data are not adequate for a rigorous analysis of species richness, but several taxa found at 65 g·l⁻¹

were absent (or very rare) at 30 g·l⁻¹. They included *Ephydra*, *Artemia*, the textularin foraminifer, an unidentified rotifer, and the large unidentified flagellate.

By the end of the experiment, 3 of the 8 fish added to the microcosms had died, two at 39 g·l⁻¹ and one at 57 g·l⁻¹. The fish in microcosm 39F-A (Figure 6) was found dead on October 2, four days after being placed in its tank, and was replaced on October 8. The replacement fish was also dead at the end of the experiment. The fish in microcosms 39F-C and 57F-D were also not recovered and presumed dead at the end of the experiment.

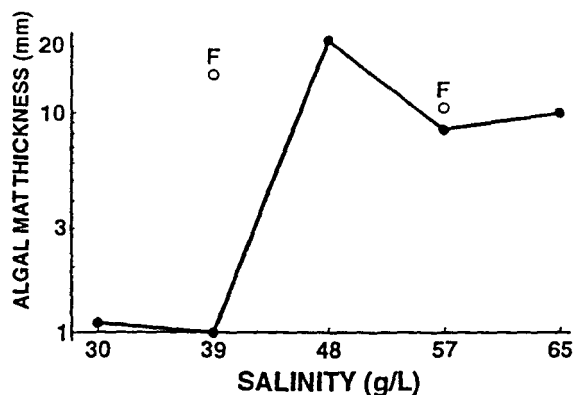


Figure 12. Effects of salinity and fish on benthic algal mat thickness at the end of the experiment. Open circles marked 'F' indicate thickness of algal mat in treatments containing fish (39F, 57F). $P < 0.001$ for salinity (1-way ANOVA). $P < 0.05$ for both fish and fish \times salinity effects (2-way ANOVA).

Sediments

The sand placed in the sediment trays ranged in size from 0 to 4Φ (0.0625–1 mm diameter) with an average of 1.6Φ (0.33 mm diameter). Essentially no silt or clay particles were present. The amount of sand that was lost from the sediment trays during the experiment increased as salinity declined, reaching a loss of 70 percent at the lower salinities (Figure 11). Fish introduction had no effect on loss of sand from trays.

By August the amount of benthic organic material (detritus and microalgae) was about 5 times greater at the higher salinities than at the lower salinities (Figure 11). Also, the algal mat itself, as measured at the end of the experiment, was an order of magnitude thicker at salinities above 39 g·l⁻¹ (Figure 12). The presence of fish at 39 g·l⁻¹ increased both the total organic matter (Figure 11) and the thickness of the algal mat (Figure 12).

Discussion

The dominance of *Gammarus*

Gammarus mucronatus was the most conspicuous invertebrate in the microcosms because of its high abundance and relatively large size. *Gammarus* was the only benthic organism to consistently be less abundant at the higher salinities, and a negative correlation existed between the abundance of *Gammarus* and the amount of sand, algal mat, and sediment organic matter in the trays. The activities of *Gammarus* may

therefore be the proximate cause of the changes observed in the sediments, and of the responses of many other species to salinity.

Gammarus appeared to control the quantity and quality of the benthic substrate at the lower salinities by consuming the algae and depositing small but very robust fecal pellets. *Gammarus* reduced the algal mat (Figure 12) and the total organic content of the sediments (Figure 11) and kept the microcosm walls and *B. amphitrite* settling plates essentially devoid of periphyton at salinities below 48 g·l⁻¹. Periphyton on vertically positioned clay tiles was, at the end of the experiment, 3–6 times more abundant at 48, 57, and 65 g·l⁻¹ than at 30 and 39 g·l⁻¹ (González et al., 1998b). In contrast, D. Herbst (in preparation) found in microcosms containing Mono Lake water adjusted to salinities between 50 and 160 g·l⁻¹ that benthic algae declined with increasing salinity. In that experiment, even at the lowest salinity no herbivores were abundant enough to appreciably graze down the algae. Whereas the benthic algae of the Salton Sea microcosms appeared to be controlled more by herbivory than by salinity stress, the opposite appears to have been true for the higher range of salinities studied in the Mono Lake microcosms.

Gammarus may also be responsible for the loss of sand from the experimental sediment trays in the lower salinities (Figure 11). The algal mat covering the sediment trays would tend to stabilize the sand (Black, 1933; Ginsberg & Lowenstam, 1958). The feeding activities of *Gammarus* reduced the algal mat at the lower salinities thus exposing the sediment to greater disturbance during water additions, zooplankton sampling, and other routine maintenance and monitoring activities. *Gammarus* probably also contributed directly to the loss of sand from the trays when they moved along the bottom. The tracks produced by *Gammarus* would tend to induce the entrainment of the sediment whenever the water was disturbed and any sediment grains dislodged would tend to saltate down the sloping tray (Figure 2) toward the center of the tank (Rhoads & Young, 1970; Cullen, 1973; Nowell et al., 1981).

The change in sediment quality undoubtedly affected the rest of the benthic community, especially since the Salton Sea benthic community is comprised predominantly of deposit feeders. A shift in the nature of the benthic organic matter from an algal base to a *Gammarus* fecal pellet base would reduce the availability of nutrients to other deposit feeders. Although *Gammarus* grazing would be expected to increase

microbial biomass and activity, fecal pellets usually contain much less readily assimilable nutrient than do algae and algal detritus (Tenore et al., 1982). The robustness of the fecal pellets produced by *Gammarus* would also tend to slow the rate of their microbial decomposition and essentially eliminate that material as a possible food source for those species unable to feed upon particles that large (Tenore et al., 1982). The result could be competitive reduction of other, less generalized deposit feeding species, and may partially explain the large number of benthic species demonstrating increased abundance with increased salinity in the microcosms, such as *Trichocorixa*, *Ephydra*, *Cletocamptus*, and the ciliates (Figure 3).

In addition to its effects on benthic algae and the sediments, *Gammarus* was probably the top benthic predator of the other macrofaunal species, such as *Trichocorixa* and *Ephydra*. Fries & Tesch (1965) and Savage (1981, 1982) found that other macrofaunal species, with very few exceptions, were reduced where *Gammarus tigrinus* was abundant. They also found *Gammarus tigrinus* to be a voracious predator of other species, including corixids. *Gammarus mucronatus* has been observed eating *Artemia* larvae in the lab (Hart et al., 1998), and the *Gammarus* associated reduction of macrofaunal species in the microcosms is similar to that described for the Weser River by Fries & Tesch (1965). It is therefore likely that predation by *Gammarus* contributed to the reduction in the abundances of other benthic macrofaunal species observed in the microcosms.

The efficiency of *Gammarus* as a predator of harpacticoid copepods, nematodes, or other meiofaunal organisms has not been determined, but predation by *Gammarus* may be less likely than competition to have caused the reduction of meiofaunal organisms at the lower salinities (Figure 4 and 9). Most macrofaunal organisms do not appear to prey significantly upon meiofauna. In studies of macrofaunal and fish communities, usually only one or two species are found to actually eat meiofaunal organisms (McIntyre & Muri-son, 1973; Kneib, 1985; Oliver & Slattery, 1985). Much other evidence of macrofaunal or fish predation upon meiofauna is circumstantial and may represent population reductions caused by disturbance (Palmer, 1988).

The relation between *Gammarus* and other invertebrates in the microcosms was similar to one observed between the amphipod *Hyaella azteca* and the brinefly *Ephydra hians* in Lake Abert, Oregon. Herbst (1988) observed that when the salinity of this

lake decreased from $\sim 33 \text{ g}\cdot\text{l}^{-1}$ to $\sim 23 \text{ g}\cdot\text{l}^{-1}$, *H. azteca* densities increased by > 400 percent (September data) and *E. hians* larval densities decreased by 50–80 percent. He suggested that *E. hians* was suppressed by competition from the less salinity tolerant *H. azteca* and possibly by predation by certain other invertebrates that also increased as the lake's salinity declined. Predation by *H. azteca* on small *E. hians* larvae may also have been a possibility.

Specific responses to increased salinity

The distribution of *Gammarus* among salinities was most likely limited by osmotic stress. Most other organisms, however, were probably limited by competition with *Gammarus* for algae and detritus, or by predation by *Gammarus*.

Gammarus mucronatus

The eventual failure of *Gammarus* to maintain its population at salinities above $39 \text{ g}\cdot\text{l}^{-1}$ appears to have been caused by either high juvenile mortality or low fecundity. The reduced proportion of individuals in the smallest two size categories ($< 2 \text{ mm}$ long) at salinities above $39 \text{ g}\cdot\text{l}^{-1}$ suggests reduced reproductive success. Gravid females were present at all salinities, so the young either did not hatch or died soon after hatching. The size distribution modes also tended to increase with salinity, which is consistent with increased mortality of smaller individuals. Detailed information on size distributions is given in Simpson (1994).

Potential causes of increased juvenile *Gammarus* mortality at salinities above $39 \text{ g}\cdot\text{l}^{-1}$ include osmotic stress and predation by *Trichocorixa*. *Trichocorixa verticalis* has been found to control *Artemia* populations in the Great Salt Lake through predation (Wurtsbaugh, 1992). *Trichocorixa reticulata* also eats *Artemia* larvae at least as large as 2.3 mm (Hammer & Hurlbert, 1992), but the larvae had to approach the mouth of the corixid before predatory behavior was elicited and no active hunting behavior was observed. *T. reticulata* starves when provided only cladocerans, copepods, *Paramecium multinucleatum*, or even intact filaments of *Rhizoclonium* for food, and has been described as incapable of piercing or cutting such prey (Cox, 1969). It is possible that *Trichocorixa* preyed on intact *Gammarus* as small as 2 mm , but it is more likely that *Gammarus* would escape predation by swimming away. Its thicker cuticle

would also provide more protection than does the cuticle of *Artemia*. Other salinity induced environmental changes such as reduced food quality are also possible reasons for the decline of *Gammarus*. However, since *Gammarus mucronatus* is a very generalized omnivore with digestion enhanced by digestive enzymes acquired from ingested microbes (Bärlocher & Howatt, 1986) and since the benthic community in the microcosms tended to become more diverse as salinity increased (Figure 4), it is doubtful that the decline in *Gammarus* is caused by reduced food availability. It seems most likely that osmotic stress was the main cause of the decline of *Gammarus* at salinities above $39 \text{ g}\cdot\text{l}^{-1}$.

Trichocorixa reticulata

The ability of *Trichocorixa reticulata* to thrive at salinities below $48 \text{ g}\cdot\text{l}^{-1}$ range is demonstrated by the May 1991 sample (Figure 3) and its success in fresh and brackish water ponds (Balling & Resh, 1984). Therefore, food limitation and predation, rather than osmotic stress, are more likely causes of the low *Trichocorixa* abundance at $30\text{--}39 \text{ g}\cdot\text{l}^{-1}$. *Trichocorixa reticulata* feeds primarily upon small cells ($< 140 \mu\text{m}$) and detritus and generally appears to ingest meiofaunal organisms incidental to the detritus upon which it is feeding (Carpelan, 1957; Davis, 1966; Cox, 1969; Balling & Resh, 1984), although it does take *Artemia* larvae that are within reach (Hammer & Hurlbert, 1992). Reduction of algae and algal detritus by *Gammarus* would therefore eliminate the primary food source of *Trichocorixa*. However, *Trichocorixa* has demonstrated an ability to filter feed on dense concentrations of small cell ($10 \mu\text{m}$) phytoplankters (Cox, 1969), which may alleviate the competitive advantage of *Gammarus* in the benthos.

Trichocorixa is also likely to have been directly affected by *Gammarus* through predation, on eggs as well as on instars. The negative relationship between *Gammarus* and *Trichocorixa* abundances in the microcosms (Figure 3) is similar to the negative correlation between corixids (*Sigara* spp.) and *Gammarus tigrinus* described by Savage (1981, 1982) which he attributed mainly to predation by *Gammarus*.

Ephydra riparia

Ephydra riparia larvae feed on algae and detritus, as do the adult flies (Stehr, 1987). Their absence at $30\text{--}39 \text{ g}\cdot\text{l}^{-1}$ may therefore be the result of competition

with or predation by *Gammarus* or of habitat availability. The *Ephydra* distribution could also be a result of the availability of desirable oviposition sites in floating or submerged algal mats. Adult flies were most often observed in tanks containing floating algal mats, which were more abundant at the higher salinities than at the lower salinities presumably because of grazing by *Gammarus*. Finally, the distribution of *Ephydra* may simply be an adult preference for salinities greater than $39 \text{ g}\cdot\text{l}^{-1}$. *Ephydra* is present at $43 \text{ g}\cdot\text{l}^{-1}$ in the Salton Sea (personal observation), and has been reported in lakes with salinities ranging from 47 to 300‰ (Hammer, 1986). However, *Ephydra riparia* larvae can survive at least 14 d and pupate in Salton Sea water diluted to $17 \text{ g}\cdot\text{l}^{-1}$ (personal observation), so physiological restriction to salinities higher than $39 \text{ g}\cdot\text{l}^{-1}$ seems unlikely.

Cletocamptus deitersi

Cletocamptus deitersi has been maintained in dense cultures at salinities ranging from 1 to $80 \text{ g}\cdot\text{l}^{-1}$ (Dexter, 1995), so its decline at salinities below $57 \text{ g}\cdot\text{l}^{-1}$ was not caused by osmotic stress. Since *C. deitersi* is essentially an infaunal species that grazes on microalgae, preferably benthic (Decho, 1986), and detritus, preferably aged (Cumplings & Ruber, 1987), competition with or predation by *Gammarus* would seem more likely.

It is not clear, however, why *Cletocamptus* was so abundant at $65 \text{ g}\cdot\text{l}^{-1}$ yet remained depressed at $57 \text{ g}\cdot\text{l}^{-1}$ after *Gammarus* declined (Figure 3). It is possible that, like most of the Salton Sea invertebrates (Carpelan, 1961b; Linsley & Carpelan, 1961), *Cletocamptus* has a seasonal life history with maximum potential reproduction occurring in the summer months. If *Gammarus* controlled the harpacticoid population, it would have continued to do so at $57 \text{ g}\cdot\text{l}^{-1}$ until the *Gammarus* population finally declined between August and November. The abundance of *Cletocamptus* declined at all salinities after August, so by the time *Gammarus* declined, the peak reproductive season for *Cletocamptus* may have already passed. The abundance of *Cletocamptus* at $57 \text{ g}\cdot\text{l}^{-1}$ therefore remained at relatively low levels. If the microcosms had been maintained through a second summer, we might therefore have expected *Cletocamptus* to become abundant at all salinities over $39 \text{ g}\cdot\text{l}^{-1}$.

Protists

The tendency of large ciliates to increase with salinity was observed not only in the benthos but also in the plankton (Hart et al., 1998). *Condylostoma* sp., an important predator on other ciliates and also an herbivore (Fenchel, 1968), and *Fabrea salina*, generally considered an herbivore (Fenchel, 1968), are found in sediments with a high organic content and thin oxidized layer, such as sediments covered with a thick layer of detritus (Fenchel, 1969). Both species remain entirely within the oxidized zone, however, and leave the sediment entirely if the reduced zone rises above the sediment-water interface. The removal of algae and detritus from the sediment by *Gammarus* might have resulted in reduced abundance of such ciliates at the lower salinities (Figure 3).

The dramatic response to salinity demonstrated by the textulariine foraminifer (Figure 3) may have been caused by a physiological limitation to high salinity waters, but the lack of detritus and the thinness of sediments at the lower salinities are also possible causes. *Quinqueloculina* remains on or near the sediment surface (Severin et al., 1982), so it may have been less strongly affected by the amount of detritus or sand.

Nematodes

Whereas monhysterid species 1 was capable of thriving over the entire range of salinities tested (Figure 3) the plectid nematode became abundant only at salinities less than $65 \text{ g} \cdot \text{l}^{-1}$. The abundance of the plectid at salinities below $65 \text{ g} \cdot \text{l}^{-1}$ on the first sample date, its subsequent decrease in the absence of fish, and its recovery after juvenile tilapia were introduced (Figures 4 and 7) suggests that the plectid was an opportunistic species capable of dominating the meiofauna in new or enriched substrates. Opportunistic nematodes, often undetectably rare in the sediments, can be easily cultured from those sediments in much the same way as the plectid responded to the tilapia-induced enrichment of the sediment (Warwick, 1981).

Possible causes of the replacement of the plectid nematode by monhysterid species 1 after May (Figure 3) include changes in their food supply, competition and predation. The narrow, toothless buccal cavities of the nematodes in the microcosms indicate that all had a non-selective, microphagous lifestyle consistent with most nematodes of the families Plectidae and Monhysteridae (Weiser, 1959; Bird & Bird, 1991). The monhysterids, however, lacked the muscular pharyngeal bulb which the plectid nematode used

to pump material into the gut (Bird & Bird, 1991). It is unclear under what circumstances pharyngeal pumping may be advantageous (Duncan et al., 1974), but the different nematode morphologies may indicate differences in their optimal feeding conditions. Microphagous nematodes have demonstrated strong preferences for particular bacterial species and levels of organic nutrients (Tietjen et al., 1970; Tietjen & Lee, 1977), and competitive interactions between microphagous nematodes have been demonstrated under laboratory conditions (Anderson & Coleman, 1981). Differential feeding abilities based on morphology combined with bacterial community succession may have contributed to the early dominance of the plectid over monhysterid species 1 at salinities less than $65 \text{ g} \cdot \text{l}^{-1}$, and the eventual replacement of the plectid by monhysterid species 1 at all salinities.

Selective predators may have also taken the plectid over monhysterid species 1 because it was larger (Anderson & Coleman, 1981), but selective predators of nematodes were rare in the microcosms, if present at all. There is little evidence that fish or macrofauna selectively eat benthic nematodes (McIntyre & Murison, 1973; Gerlach, 1978; Warwick et al., 1979; Nicholas 1984; Palmer, 1988; Escaravage & Castel, 1990; but see McIntyre, 1969; Bell & Coull, 1978; Kneib, 1985; Smith & Coull, 1987). *Apocyclops dengizicus* Lepeschkin, the only known meiofaunal predator in the microcosms, was planktonic and almost never found in the benthos. Harpacticoid copepods have been suggested as possible controllers of nematodes (Griffith, 1989), but evidence of this is circumstantial. Rare meiofaunal species may have selectively preyed upon the large plectids. Some mites and tardigrades prey upon nematodes (Nicholas, 1984), and both were found in the microcosms.

The delay of the response to fish by the largest size class of the plectid and monhysterid species 1 (Figure 9) was probably a result of the time required to grow to that size. Since it is most likely that the nematode response began more than a few days before the November samples were collected, the plectid and monhysterid species 1 probably grew to the largest size class in a matter of weeks or months as opposed to days. Nematodes are usually assumed to have a life span of days or weeks, but Tietjen & Lee (1972) extended the life span of *Monhystera denticulata* from 34 to 330 d by varying temperature and salinity.

The influence of tilapia

One effect of tilapia was to severely reduce the impact of *Gammarus* on the microcosm benthos. Juvenile *O. mossambicus* are opportunistic omnivores capable of feeding on phytoplankton, zooplankton, detritus, periphyton, and benthic invertebrates (Pullin & Lowe-McConnell, 1982). What is actually eaten depends on the availability of each food type, the size of the fish, and selective feeding behavior (Trewavas, 1983). *Gammarus* and *Trichocorixa* were undoubtedly high quality food for the fish, and were probably eaten whenever they were encountered. The reduction of *Gammarus* at salinities above $48 \text{ g} \cdot \text{l}^{-1}$ might be expected to impact juvenile fish growth, but in the microcosms the juvenile tilapia gained more weight at $57 \text{ g} \cdot \text{l}^{-1}$ than at $39 \text{ g} \cdot \text{l}^{-1}$ (Hart, 1994), so other food items must have been present in the microcosms which were at least equally suitable for tilapia growth.

The removal of *Gammarus* and other macrofaunal organisms by the juvenile tilapia (Figures 7 and 10) greatly reduced the grazing pressure upon the benthic algae and detritus, allowing recovery of the algal mat, especially at $39 \text{ g} \cdot \text{l}^{-1}$ (Figure 12). It also reduced the pelletization of the benthic algae and detritus by *Gammarus*, so the material was more accessible to both bacteria and the meiofauna. The reduction of the macrofauna probably also reduced predation on and disturbance of the meiofauna.

Whereas the meiofauna increased dramatically in response to the addition of fish at both 39 and $57 \text{ g} \cdot \text{l}^{-1}$, the macrofaunal decrease was greater at $39 \text{ g} \cdot \text{l}^{-1}$ than at $57 \text{ g} \cdot \text{l}^{-1}$ (Figure 8), probably because *Gammarus* densities were higher at the lower salinity (Figure 3). The removal of *Gammarus* therefore may not explain the entire meiofaunal increase after the fish were introduced.

In addition to removing *Gammarus*, the tilapia produced loosely packaged fecal material which eventually covered much of the bottoms of the microcosms. The fecal package was easily broken when disturbed and contained material macroscopically indistinguishable from the detritus. This material would be much easier for bacteria and meiofaunal detritivores to attack than the material in the fecal pellets of *Gammarus*. Also, whereas the fecal pellets of *Gammarus* were mostly repackaged benthic material, the tilapia feces were a source of added material to the benthos. This is because the tilapia were almost certainly feeding on the plankton, as well as on the benthos. The increased abundance of meiofaunal organisms such as

Cletocamptus and the nematodes in the presence of fish (Figures 7, 10 and 11) was therefore the result of reduced competition with and predation by macrofaunal organisms, and increased detritus in the form of fish fecal material.

Consequences of fish mortality

Although all microcosms assigned fish treatments were used in the analysis of the effect of fish on the microcosm benthos, the benthic assemblage in the three microcosms within which the fish died appeared to be different from that of those within which the fish survived (Figure 6). Macrofaunal organisms that the tilapia would normally be expected to eat were present in the tanks within which fish died, and the relative abundance of other species appeared more similar to those found in the treatments without fish than in those with fish.

Tank 39F-A was the only tank with a salinity less than $48 \text{ g} \cdot \text{l}^{-1}$ in which *Trichocorixa* were abundant after May, and in which *Gammarus* failed to dominate in August. *Gammarus* also disappeared completely from this tank by February despite the death of the fish. The differences between tank 39F-A and all other $39 \text{ g} \cdot \text{l}^{-1}$ tanks both before and after the fish were added suggests the activity of some uncontrolled factor in 39F-A not present in the other tanks.

On the third sample date (November) tanks 39F-C and 57F-C did not have community compositions consistent with those observed in the other tanks containing fish. Tank 39F-C was dominated by *Gammarus* and its community was similar to the $39 \text{ g} \cdot \text{l}^{-1}$ tanks without fish. By February, this tank had reduced numbers of *Gammarus* relative to the non-fish tanks, but the rest of the community was more similar to the tanks without fish than the two with fish. Especially conspicuous were the lack of harpacticoid copepods and miscellaneous protists. Tank 57F-D had more miscellaneous protists than did the $57 \text{ g} \cdot \text{l}^{-1}$ non-fish tanks, but it had no harpacticoid copepods and many more *Trichocorixa* than the three tanks in which fish survived (Figure 6).

The death of three fish generally increased the variation within the fish treatments. The presence of *Trichocorixa* in both $39 \text{ g} \cdot \text{l}^{-1}$ tanks within which fish died resulted, however, in the apparent fish-salinity interaction which probably does not reflect a true response to fish.

The microcosms as models of the benthic environment

The microcosms containing tilapia may be good models of the near shore Salton Sea community, although direct comparisons of the microcosms with the Salton Sea are complicated by clear differences between the two. Many of the differences were probably a result of the relatively small size of the microcosms. Despite the differences, however, most components of the microcosm benthos are consistent with field observations elsewhere, which suggests that microcosms at this scale may be useful models of moderate depth, soft bottom benthic communities.

Gammarus appears to be much less abundant on the open soft bottom of the lake, most likely because of the sizeable fish population, and *Neanthes succinea*, *Ephydra* and *Trichocorixa* densities are also probably higher in the Salton Sea proper, especially near shore, than they were in the microcosms (*personal observation*). *Neanthes succinea* has been a major component of the Salton Sea benthos, with an average of 6,500 individuals m^{-2} over the entire Salton Sea (Carpelan & Linsley, 1961). At such densities, *Neanthes* must have a dramatic effect on the Salton Sea benthos. The burrowing activities of *Neanthes* would increase the oxidized depth considerably, and its feeding behavior could assist in the breakdown of *Gammarus* fecal pellets. Reise (1981) showed that *Nereis* densities less than those found in the Salton Sea can have more meiofaunal organisms associated with the burrows than are found on the surface. In the microcosms, however, their impact was limited to the local area around each individual, where a mound surrounded the burrow openings.

Many species found in the Salton Sea, including additional foraminiferans, corophiid amphipods, and assorted insects were not observed in the microcosms. The foraminiferans have been described as the most abundant Salton Sea benthic protists (Arnal, 1961), so their reduced presence in the microcosms was unfortunate. The Salton Sea fish also comprise more trophic levels than that represented by juvenile tilapia. Adult tilapia feed more upon algae and detritus than do juveniles, and the impact of the adults upon the benthos could be significant and different from that of the juveniles.

The shallow microcosm sediment trays also provided a conservative model of the benthic community. Ciliate abundance depends on the size and sorting of the sediment as well as the availability of detritus and the depth of the redox discontinuity layer (Fenchel,

1967, 1969). Well sorted sand similar to that in the sediment trays is good ciliate habitat (Fenchel, 1967, 1969; Gerlach, 1978), and the abundance of ciliates found confirms that. Fenchel (1969) found the highest abundance of ciliates around the redox discontinuity layer where the surface oxidized layer connects with the underlying reduced layer. The ciliate subcommunity was therefore probably underestimated in the microcosms since the shallow sediment trays and well mixed water column did not allow a reduced zone to develop.

Despite the differences between the microcosms and the Salton Sea, the microcosms containing tilapia are reasonable models of the shallow Salton Sea benthic community, especially near rocky outcroppings. Although *Gammarus* may not be abundant on the soft bottom, the Salton Sea has sections of barnacle-covered rocky shoreline which provide refuge for *Gammarus*. Refugia were also present in the microcosms around the airlift tubes and in *B. amphitrite* clumps on the bottoms of the tanks. *Neanthes* densities near shore are also much lower than in 5–8 m of water (Carpelan & Linsley, 1961).

The abundance of nematodes and the relative abundance of ciliates, meiofauna and macrofauna within the microcosm benthic community were consistent with benthic assemblages observed elsewhere. Nematode densities in the microcosms ranged from 4,000 to 80,000 per 100 cm^2 , compared to an average of 125,000 per 100 cm^2 found by Warwick & Price (1979) in the Lynher estuarine mudflat. The nematode densities found by Warwick & Price were equal to 15% of the macrofauna biovolume, however, and nematodes usually comprise only 1–4% of the macrofauna (McIntyre, 1969; Stripp, 1969; Gerlach, 1971, 1978). Had Warwick & Price recovered nematode densities similar of those found in the microcosms, nematodes would have comprised 0.5 to 10% of the macrofauna biovolume, which is near the range found in the microcosms.

The meiofauna:macrofauna ratios (Figure 10) were, by August, similar to those of other studies, where ratios of 0.01 to 0.04 are common (McIntyre, 1969; Stripp, 1969; Gerlach, 1971), and a ratio of 0.1 was found in silty sand similar to that in the microcosms (Gerlach, 1978). The extremely high ratio in May might reflect the generally shorter generation times of meiofaunal organisms (McIntyre, 1964; Swedmark, 1964; Gerlach, 1971) which enabled them to more quickly exploit the nutrient rich, relatively predator and competitor free environment within the

newly established microcosms. The very high meiofauna:macrofauna ratios found early in the microcosms may have altered the detritus in such a way as to affect the benthic community succession, and future experiments could test this. However, the enhancement of bacterial production by meiofaunal grazing probably more than replaced the bacteria consumed (Gerlach, 1978; Tenore et al., 1982).

The ciliates constituted often over 90% of the number of benthic animals but a relatively small proportion of the biomass, a pattern also observed by Fenchel (1967). The ratio of ciliate to meiofaunal metazoan biovolume was lowest in the presence of fish and at salinities above $48 \text{ g} \cdot \text{l}^{-1}$ even though ciliate abundance was usually higher in these treatment. However, the sediment organic content was highest in these treatments (Figure 11), and Fenchel (1967) also found that ciliates were an abundant but proportionally less important part of the fauna in detritus covered sediments. The relationship between sediment organic content and ciliate abundance may have been dampened by the absence of a reduced zone in the sediment trays, because with fewer giant ciliates at the lower salinities, a larger proportion of the ciliate biovolume would be expected to occur around the redox discontinuity layer.

Implications for saline lake benthic community structure

In the microcosms, direct responses to salinity and interactions among species were both very important influences on the benthic community structure. The conversion of the algae and algal detritus to fecal pellets by *Gammarus*, and the removal of *Gammarus* and deposition of feces by tilapia seem to have had a major impact on the benthic community structure. The presence of *Gammarus* may have even caused extinction of *Trichocorixa* in particular microcosms. Colburn (1988) concluded that saline lake benthic faunas are usually controlled by salinity and often widely fluctuating physical factors such as temperature and oxygen, with biological interactions merely modifying the relative abundance of species. In a mesocosm study of the Pyramid Lake benthic community (Galat et al., 1988), the only biological interactions discussed were the eventual extinctions of some species as a result of excessive fish densities, so biological interactions may have played a minor role there. Salinity undoubtedly controls the species that can live in saline lakes, but this microcosm experiment demonstrates the im-

portance of interactions among species as proximate mechanisms structuring saline lake benthic communities. In particular, increased abundances of several species following the demise of *Gammarus* provides further indirect support for the idea that predators and competitors, not physiological limitations, determine the lowest salinities at which some salt lake invertebrates can prosper in nature (e.g. Hurlbert et al., 1986; Herbst, 1988; Hammer & Hurlbert, 1992). As the salinity of a lake increases, the loss of a dominant competitor or predator is likely to favor increased abundance of many of the remaining species at the same or lower trophic levels.

Hammer (1986) concluded that 'typically the number of macroscopic benthic faunal species declines with increasing salinity.' This seems true so long as it is taken to refer only to saline ($> 3 \text{ g} \cdot \text{l}^{-1}$) lakes and a wide salinity range, e.g. 3–50 or 5–100 $\text{g} \cdot \text{l}^{-1}$. Over narrower salinity ranges like the ~ 2 -fold range of this microcosm experiment, the biota-restricting physiological stress of increased salinity can easily be more than offset, in particular circumstances, by the liberating demise of a functionally dominant species like *Gammarus* that has reached the upper limit of its salinity tolerance.

Implications for the Salton Sea

Several predictions can be made as the salinity of the Salton Sea continues to increase. *Gammarus* will disappear from the Salton Sea as the salinity increases to 50–70 $\text{g} \cdot \text{l}^{-1}$. The microcosm experiment suggests that the population of *Gammarus* might decline sharply between 40 and 50 $\text{g} \cdot \text{l}^{-1}$, with extinction closer to 70 $\text{g} \cdot \text{l}^{-1}$. The effect of the reduction of *Gammarus* on the Salton Sea benthos will probably not be as profound as it was on the microcosm benthos, since *Gammarus* is much less abundant in the still fish-rich Salton Sea. Near shore algal cover could increase substantially, however, if other herbivores such as *Trichocorixa* and *Ephydra* are unable to control it.

The fish will probably disappear from the Salton Sea when the salinity reaches 60–70 $\text{g} \cdot \text{l}^{-1}$. The loss of the fish could result in increased abundance of macrofaunal invertebrates such as *Trichocorixa*, *Ephydra*, and other insect larvae, and may reduce the abundance of meiofaunal organisms. A *Gammarus* dominated benthic community such as that in the microcosms could develop if the fish disappear before *Gammarus*. Unless *Gammarus* adapts genetically to the higher salinities, however, the increased salinity

will probably prevent the overwhelming dominance of *Gammarus*.

Neanthes succinea will go extinct in the Salton Sea when the salinity is between 70 and 80 g·l⁻¹ (Kuhl & Oglesby, 1979). The loss of *Neanthes* could reduce the thickness of the oxidized layer in the sediments, slow the rate of detrital remineralization, and reduce the meiofaunal and ciliate populations. By the time the Salton Sea reaches 80 g·l⁻¹, the benthic community will probably consist mainly of ciliates, meiofaunal metazoans such as nematodes and possibly *Cletocamptus*, and insects such as *Trichocorixa* and *Ephydra*.

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