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Salinity and fish effects on Salton Sea microecosystems: water chemistry and nutrient cycling

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Abstract

A 15 month long experiment was undertaken to document responses of the Salton Sea biota to experimentally manipulated salinity levels (30, 39, 48, 57, and 65 g l^{-1}) in 312-liter fiberglass tanks maintained outdoors. At two salinities (39 and 57 g l^{-1}) microcosms were set up each having one small tilapia (*Oreochromis mossambicus*) in order to assess its influence on the system. To 28 tanks filled with Salton Sea water diluted to 30 g l^{-1}, different salts (NaCl, Na_2SO_4, $MgSO_4 \cdot 7H_2O$, KCl) were added in constant proportions to produce the desired salinity levels. Salton Sea shoreline sediment was added to the bottom of each tank, and inocula of algae and invertebrates were added on several occasions. Invertebrate populations, phytoplankton, periphyton, and water chemistry were monitored at regular intervals. This article present the results concerning water chemistry and nutrient cycling.

There was no apparent increase in salinity over time, though ~ 1190 l of tapwater with a salinity of ~ 0.65 g l^{-1} were added to each tank during the experiment. Ionic composition varied both among treatments and over time to some degree. Ca^2 concentrations were the same at all salinities, while K^1 concentrations were > 3 times greater at the highest salinity than at the lowest. pH showed little consistent variation among salinities until the last few months when it was higher by ~ 0.4 units at the two higher salinities than at the lower ones; it was unaffected by fish. Absolute oxygen concentrations were negatively correlated with salinity, and occasionally depressed by the presence of fish. PO_4^{3-}, dissolved organic phosphorus, and particulate phosphorus concentrations were often reduced by 30–80% at 65 g l^{-1} relative to lower salinities and by the presence of fish. Early in the experiment NO_3^{2-} concentrations were > 2 times higher at 57 and 65 g l^{-1} than at lower salinities, but otherwise effects of salinity on dissolved forms of nitrogen were not marked; particulate nitrogen was much lower at 65 g l^{-1} than at other salinities and also was reduced by up to 90% by the presence of fish. Silica concentrations increased over time at all salinities, but, relative to those at lower salinities, were reduced by 60–90% at 65 g l^{-1} by abundant periphytic diatoms. The TN:TP ratio (molar basis) was 24–30 initially and 35–110 at the end of the experiment; it was positively correlated with salinity and the presence of fish. Mechanisms accounting for the above patterns involve principally the biological activities of phytoplankton and periphyton, as modified by grazing by *Artemia franciscana* and *Gammarus mucronatus*, and the feeding and metabolic activities of the tilapia. The large reduction in water column TN and TP levels brought about by the fast-growing, phyto- and zooplanktivorous tilapia suggest that amelioration of the Salton Sea's hypereutrophic state might be assisted by a large scale, sustained yield fish harvesting operation.

Introduction

Salinity is an important factor determining the nature of saline ecosystems. The chemistry of major ions in saline lakes is well known, but less is known about the behavior of nutrients. Despite the increasing importance given to saline lakes, comprehensive studies of the effects of salinity on nutrient levels and nutrient cycling are lacking. Nutrients concentrations in saline lakes vary widely. Inorganic phosphorus concentrations have been reported to be high at high salinities; in less saline lakes, phosphorus and nitrogen concentrations are variable, but phosphorus tends to be low

(Hutchinson, 1957; Stephens & Gillespie, 1976; Por, 1980; Hammer, 1981; Melack et al., 1982; Hammer, 1986). Salinity can influence the equilibrium phosphate concentration (Tominaga et al., 1987; Atkinson, 1987), nitrate and ammonium fluxes, nitrification and denitrification rates (Seitsinger et al., 1991; Gardner et al., 1991) in aquatic systems. For 10 saline lakes of Australia, Tominaga et al. (1987) found that the ratio of inorganic nitrogen to inorganic phosphorus was negatively correlated with salinity over the range 27–250 g l^{-1} and suggested that P was limiting in the least saline lakes and N limiting in the more saline. For 20 lakes in Alberta, Canada, with TDS values of 1–90 g l^{-1}, there was a negative correlation between the TN:TP ratio and salinity (Bierhuizen & Prepas, 1985). Clavero et al. (1990; 1993) found experimentally that over the salinity range 10–70 g l^{-1} phosphate was released more rapidly from sediments at higher salinities. The mechanisms by which salts affect ammonium and phosphate release from sediments probably include ion pairing, cation exchange interactions on sediment particles, and other processes (Seitsinger et al., 1991; Gardner et al., 1991; Caraco et al., 1989).

Microcosm studies of the effects of salinity on the benthos and plankton communities in Mono Lake, California (D. Herbst, in prep.) and Pyramid Lake, Nevada (Galat & Robinson, 1983; Galat et al., 1988) provided no direct information on nutrients. However, a study of salinity effects on a coastal lagoon plankton assemblage documented large increases in NH_3 concentration and large decreases in SiO_2 concentration as salinity went from 0.5 to 51 g l^{-1}, though at least the latter effect was an artifact of the procedure used to create the experimental salinity levels (Greenwald & Hurlbert, 1993).

The influence of fish on the plankton, the benthos, and nutrient cycling in moderately saline systems has not been studied; we do not know whether the relationships established for freshwaters apply to saline lakes. In highly saline systems fish are usually absent. Where salinity is greater than 50 g l^{-1} usually not more than a single species is found (Hammer, 1986). Salinity may determine the presence or absence of predaceous fish and invertebrates which in turn may affect other invertebrates, algae, and nutrient dynamics (Weiderholm, 1980; Wurtsbaugh & Berry, 1990; Wurtsbaugh, 1992; Hart et al., 1998; Simpson et al., 1998). Wurtsbaugh (1992) demonstrated that in Great Salt Lake (Utah) where fish are absent, an invertebrate predator (*Trichocorixa verticalis*) was important in structuring the food web. In freshwater lakes, planktivorous fish causes significant changes in the zooplankton which affects lower trophic levels and nutrient cycling (e.g., Hrbácek et al., 1961; Brooks, 1969; Hurlbert et al., 1972; Shapiro & Wright, 1984; McQueen et al., 1986; Lazzaro, 1987; Post & McQueen, 1987; Northcote, 1988; Carpenter & Kitchell, 1993)). Likewise fish may increase internal nutrient loading via their excretions, feces, and mortality (Kraft, 1992; Threlkeld, 1988) or fish may reduce P by serving as a sink for P as they grow (Kitchell et al., 1975; Nakashima & Leggett, 1980; Mazumdar et al., 1989; Kraft, 1992; Kitchell et al., 1993).

The Salton Sea

The Salton Sea is the largest inland body of water in California, having a total surface area of 980 km^2. It is sustained mostly by inflow of agricultural wastewaters from the Coachella and Imperial valleys. It has a maximum depth of ~ 15 m (Black, 1983). The tendency of the lake is toward increasing salinity, having gone from 3.55 g l^{-1} in 1907 to 47 g l^{-1} in 1992. Its salinity varied from 42 to 44 g l^{-1} in 1990, depending on location, depth and metereological conditions. Its salinity is increasing and has been predicted to exceed 90 g l^{-1} by the year 2010 (Black, 1983). Large changes in the structure and functioning of the community are to be expected as a result of this increase. The ionic composition of the Salton Sea is dominated by sodium, chloride, and sulfate ions (Table 1).

Having received agricultural wastewaters for nearly a century, the lake is very eutrophic with high nitrogen and phosphorus concentrations (Table 2). In 1968–69, total N and total P concentrations for the water column averaged 236 μM and 3.2 μM, respectively (USDI, 1970). External loading rates were 0.93 moles N m^{-2} yr^{-1} (= 13 g N m^{-2} yr^{-1}) and 0.022 moles P m^{-2} yr^{-1} (= 0.68 g P m^{-2} yr^{-1}). Similar loading rates have probably existed since that time.

The sediments also have high levels of phosphorus and nitrogen. Bottom sediment samples taken between July 1968 and May 1969 were 5% organic carbon, 0.3% organic nitrogen and 0.1% phosphorus (dry weight basis; USDI, 1970). Samples taken in 1986 were 0.089% P and 0.15% N on a dry weight basis (Setmire et al., 1990).

The fish assemblage of the Salton Sea includes 4–5 marine species which were introduced in the 1950s and the African tilapia (*Oreochromis mossambicus*) which colonized the lake in the 1970s (Walker, 1961;

Table 1. Ionic composition of Salton Sea, compared with ocean water; and amounts of ions and salts added to achieve an increase of 8.84 g l^{-1}

	Concentration g l^{-1}						
		Salton Sea		Predicted concentrations after dilution of 47 to 30 g l^{-1} [d]	Amount (g) of each ion added per L to achieve increase of 8.84 g l^{-1}	Salt added per liter to achieve a total increase of 8.84 g l^{-1}	
Ion	Ocean water[a]	1986[b]	1994[c]			Salt	Amount (g)
Na^1	10.980	9.22	12.4	7.15	2.95	NaCl	6.09
K^1	0.407	0.42	0.20	0.32	0.11	KCl	0.20
Mg^2	1.319	1.31	1.40	1.02	0.17	Na_2SO_4	1.72
Ca^2	0.420	1.33	1.18	0.88	–	$MgSO_4 \cdot 7H_2O$	1.67
Cl^{1-}	19.715	16.60	18.4	12.86	3.79		
SO_4^{2-}	2.764	9.66	9.85	7.49	1.82	Total salts	9.69
HCO_3^{1-}	0.145	0.18	0.24	0.17	–		
Total	35.75	38.72	43.5	29.89	8.84	Total ions	8.84

[a] Culkin & Cox (1966).
[b] Average values for three depths at two stations in center of lake in 1986 (Parsons, 1986).
[c] Average values for three stations in center of lake in April 1994 (O.E.E.S., 1995).
[d] Predicted concentrations of ions based on 1986 data for Salton Sea and estimated tapwater concentrations (in g l^{-1}) of: 0.0745 Na^1, 0.0042 Na^1, 0.0262 Mg^2, 0.0520 Ca^2, 0.0940 Cl^{1-}, 0.1470 SO_4^{2-}, 0.1476 HCO_3^{1-} (mean values for November 1991 effluent from Alvarado Filtration Plant, City of San Diego).

Table 2. Nutrient concentrations in the Salton Sea

	Concentration (μM)					
Source	NO_2^{1-}	NO_3^{1-}	NH_3	PO_4^{3-}	TN	TP
Carpelan (1961)[a]		0.85	5.35	0.47		
		0.91	5.5	0.47		
		0.93	4.8	0.71		
		7.63	12.3	1.1		
USDI (1970)[b]	2.12	2.39	15.3	0.40	236	3.20

[a] Samples were taken at four stations (1–4) as the sequence in the table. Samples for the first two stations were taken weekly from September 1954 to July 1956. The first station represented the deepest part of the lake (12 m), about 4.8 km off Fish Springs, while the second was a near shore station, 100 m off Fish Springs. The third and fourth stations were sampled monthly May 1955 to May 1956. The third was on the south shore (depth 1.5 m) with little influence of stream discharge into the Sea and the fourth station was off Mullet Island (depth 1.5 m), in zone influenced by inflow of Alamo River.
[b] Water samples collected monthly between July 1968 and 1969 from ten stations at several depths (not well specified). Report notes that 'the method used (persulfate) does not measure all of the phosphorus in organic matter'.

Black, 1988). Tilapia is now probably the most abundant fish in the lake. As a fast-growing omnivore feeding on phytoplankton, periphyton, zooplankton, zoobenthos, and detritus (Maitipe & De Silva, 1985; de Moore et al., 1986), it likely is a major influence on many components and processes of the Salton Sea ecosystem, including nutrient cycling.

To evaluate the potential effects of future salinity increases and fish die-offs at the Salton Sea, a microcosm experiment was carried out in outdoor tanks containing Salton Sea water adjusted to five different salinities levels (30, 39, 48, 57, 65 g l^{-1}). A second set of tanks with one small tilapia (*Oreochromis mosssambicus*) each were established at two of these

salinities (39 and 57 g l^{-1}). This article reports only results for the water chemistry. The responses of algae, zooplankton, nekton and zoobenthos are reported in González et al. (1998), Hart et al. (1998), Simpson et al. (1998) and Simpson & Hurlbert (1998).

Methods

Experimental design

This experiment was performed using a randomized block 2 × 5 incomplete factorial design with 4 microcosms per treatment combination and monitoring for response variables over a 15 month period. Each block consisted of 7 tanks, one without fish at each of 5 salinity levels (30, 39, 48, 57 and 65 g l^{-1}) and one with fish at each of two salinity levels (39 and 57 g l^{-1}). Details on layout and tank design are given in Hart et al. (1998) and Simpson et al. (1998).

Establishment of tanks, salinity levels and fish

On November 19, 1990, Salton Sea water was transported from the lake to the Life Sciences building at San Diego State University. The water, with a salinity of 47 g l^{-1}, was pumped into the experimental tanks which were located on the building's roof. Each tank was diluted with tapwater to 30 g l^{-1} and a final volume of 312 l was established.

Target salinity levels were reached by adding four salts (NaCl, Na_2SO_4, $MgSO_4 \cdot 7H_2O$, and KCl). The amount of each salt needed to increase the salinity of a tank by 8.84 g l^{-1} while maintaining essentially the same ionic proportions as found in the Salton Sea was calculated (Table 1). This information was then used to create experimental salinity levels of 30.0,38.8, 47.7, 56.4 and 65.3 g l^{-1}, which henceforth are labeled 30, 39, 48, 57 and 65 g l^{-1}.

In these calculations we assumed that Ca^2 and HCO_3^{1-} concentrations would remain approximately the same as those at 30 g l^{-1}. These ions were not added as salts because $CaCO_3$ was presumably at saturation levels in the lake, and was, in any case, available in various forms (e.g. barnacle shells, fish bones) in the sediments placed in each tank.

The salts needed to produce an 8.84 g l^{-1} salinity increase in a tank were individually weighed and then combined in a plastic bag. We prepared 56 such bags. One bag of salts was transferred into a nylon stocking, which was then hung over the side of the tank and the salts allowed to dissolve. Only the 39 to 65 g l^{-1} treatments received bags on January 4. This process was repeated on January 6 for the 48 to 65 g l^{-1} treatments, and so on at two-day intervals until each tank was at its target salinity. This procedure was intended to guarantee: a) that each experimental salinity level would have approximately the same major ion composition that Salton Sea water would have if concentrated by evaporation; and b) that treatments would not differ in variables such as initial nutrient levels, organism densities or any variable other than salinity defined as the sum of major ions.

One juvenile tilapia was introduced into each of four tanks at both 39 and 57 g l^{-1} (treatments designated at 39F and 57F) in July 1991, but some of these died, and were removed, and these fish treatments were not fully established until September 28. Details of fish additions are given in Hart (1994), Hart et al. (1998), and Simpson et al. (1998).

Nutrient conditions

The tanks were very nutrient-rich ecosystems, as is the Salton Sea. There were four sources of nutrients for the tanks: 1) Salton Sea water itself, 2) inocula, 3) sediments, and 4) tap water (Table 3). On January 3, to each tank were added 3 l of sifted (6 mm mesh sieve) and homogenized sediments. These contained organic material, sand, silt, salts, and fragments of barnacle shells and fish bones from the southwestern shoreline of the lake and were placed on the bottom of each tank prior to the addition of salts. These sediments served as a source of nutrients and as substrate for the benthos. Three aliquots each of sediments, water and inocula were stored for later analysis, to estimate the amounts of N and P present initially in each tank. The amount of nutrients contributed to the tanks by each of the four sources was quite different (Table 3).

Inoculation

In addition to the planktonic organisms introduced with the Salton Sea water, additional inoculations were made into each tank between January 16 and August 21, 1991 of algae and invertebrates from the Salton Sea and other saline water bodies in the region ranging from 1–270 g l^{-1} in salinity. Details of these inoculations are given in Hart (1994) and Hart et al. (1998). All tanks received the same inocula. After each inoculation, three replicate samples of the inocula were saved and immediately frozen. At the end of the experiment these were analyzed for total nitrogen and

Table 3. Nutrient content of each microcosm as derived from Salton Sea water, inocula and sediment at the beginning of the experiment, and tapwater during the experiment

	Concentration (μM) in tank attributable to source				
Nutrient	Initial Water	Inocula	Sediments	Water Addition[e]	Total[f]
Silicon	200[a]	–	–	607	–
Nitrogen	534[b]	18.0[b]	443.0[d]	45.6	1040
Phosphorus	55.9[c]	4.04[c]	849[d]	5.12	914
TN:TP ratio	9.5:1	4.5:1	0.5:1	8.9:1	1.1:1

[a] Surrogate estimate, based on samples from center of south basin, October 11, 1989 (Schroeder et al., 1993, p. 101).
[b] Total N (TN), the sum of dissolved and particulate N.
[c] Total P (TP), the sum of dissolved and particulate phosphorus.
[d] Total N (TN) and Total P (TP) on each case measured in a raw sediment sample.
[e] Based on average concentrations of SiO_2, NH_4^1, NO_2^{1-} and NO_3^{1-}, PO_4^{3-} in the effluent from the Alvarado Filtration plant (City of San Diego, from November 1990 to April 1992.
[f] Assumes all nutrients are ofr potentially are in water column (312 l).

total phosphorus to determine the amounts contributed to the tanks by the inocula.

Tank maintenance

The water level and salinity of each tank were maintained by periodically adding dechlorinated tapwater that had been allowed to sit in another large tank. During rainy days, all tanks were covered with clear fiberglass covers. To avoid stratification in the water column, a 44 cm long PVC airlift pipe was installed vertically on one side of each tank and connected to a central air pump. The vertical walls of each tank were scrubbed twice a month with a plastic pot scrubber to prevent the accumulation of attached organisms and their potential dominance of the community metabolism of these microecosystems, which have a high ratio of hard surface area to water volume relative to the corresponding ratio for the Salton Sea. The material scrubbed from the walls was left in each tank.

Sampling methods and data analysis

Temperature, salinity, pH and dissolved oxygen were monitored at 12:00 to 12:30 pm every two weeks from January 24, 1991 to April 6, 1992. Temperature was taken with a YSI Tele-Thermometer Model 44TD. Measurements of pH were made with a Beckman Chem-mate pH meter equipped with a combination electrode. Salinity was measured using a Reichert-Jung salinity refractometer with a range of 0 to 160 g kg^{-1} (ppt). The scale of the refractometer is based on the calibration with pure NaCl solutions. For our reporting, we converted the refractometer readings into g l^{-1} by multiplying them by a factor of 1.13. This factor was determined by filtering Salton Sea water with a salinity of 42 g kg^{-1} through a GF/C glass fiber filter an concentrating it by evaporation to a putative 80 g kg^{-1}, as indicated by the refractometer. The water was then diluted with deionized water to prepare putative salinities of 42, 40, 30, 20 and 10 g kg^{-1}. Triplicate 50 ml samples of each prepared salinity, including 80 g kg^{-1}, were placed in a pre-weighed containers and oven dried at 110 °C. All samples were cooled in a vacuum and total filtrable residue (TFR) was determined by weighing (APHA 1985). For all salinities tested, the refractometer reading was ~ 88% of the true value in g l^{-1}. At 110 °C some water of hydration may not have been driven off, and silica and dissolved organics could have affected both TFR and refractometer values; our estimated conversion factor of 1.13 (= 1/0.88) thus may contain some error.

Samples for major ion (Na^1, K^1, Mg^2, Ca^2, Cl^{1-}, SO_4^{2-} and HCO_3^{1-}) analysis were taken from each microcosm, 15 cm below water surface, on four occasions during the experiment (January 24, and July 29, 1991; January 27 and April 6, 1992). Each sample was filtered through a GF/C filter and acidified with nitric acid to pH 2.0. Acidified samples were stored in the dark until analysis. Samples at salinities at or above 39 g l^{-1} were diluted with deionized water so that all

samples were approximately 30 g l^{-1}. Ionic concentrations were measured by inductively coupled plasma emission spectroscopy (Perkin-Elmer ICP/6500).

Oxygen was measured with a YSI (model 57) dissolved oxygen meter, calibrated against the Winkler method. A series of filtered Salton Sea water samples were prepared with salinities of (10, 20, 30, 40, 60 and 90 g kg^{-1}) at 25 °C with two replicates for each salinity level. Each water sample was air-saturated. The oxygen concentration then was measured with both the Winkler method and oxygen meter. Values yielded by the meter, with the salinity knob set at 40 g kg^{-1} (maximum value on scale), were higher by about 0, 2, 4, 15, and 15 percent at salinities of 10, 20, 40, 60 and 90 g l^{-1}, respectively, than those given by the Winkler method. The knob was also kept at 40 g kg^{-1} when oxygen measurements in the tanks were also carried out, and meter readings were corrected by factors based on the percent errors given above. Percent saturation was calculated as 100× (measured concentration)/(predicted concentration at saturation). The predicted oxygen concentrations at saturation were approximated with a state equation given by Sherwood et al. (1992) for NaCl solutions. For these calculations we used the salinity and temperature values obtained from the biweekly monitorings.

Two 250 ml water samples for nutrient (N, P, Si) analysis were collected at midday every 60 days, starting in January 24 1991, from about 20 cm below the surface of each tank. One sample was immediately filtered through a Whatman GF/F filter and stored at –20 °C. Later the filtered water was thawed, and PO_4^{3-}, NO_3^{1-}, NH_4^1 and SiO_2 concentrations were determined with conventional techniques with a Technicon Auto-Analyzer II (PO_4^{3-} by measuring a phosphomolybdenum blue complex at 880 nm, Technicon #155–71W, 1973; NO_3^{1-} by reduction to NO_2^{1-} and measurement of the azo-compound formed by reaction with sulfanilamide and N-1-naphthylethylenediamine at 550 nm, Technicon #158–71W/A, 1977; NH_4^1 by measurement of the result of the Berthelot reaction at 630 nm, Technicon 154–71W, 1973; and SiO_2 by measurement of a silicomolybdenum blue complex at 660 nm, Technicon #186–72W/B). The second sample was frozen and stored at –20 °C without filtration. Later it was thawed and 25 ml was filtered through a Whatman GF/F filter. The filtered water was digested with 5 ml of H_2SO_4 and 3 g of K_2SO_4 with 60 mg of HgO to permit determination of total dissolved phosphorus (DP) and total dissolved Kjeldahl nitrogen (TDKN). The filters were folded, wrapped in aluminum foil, and frozen at –20 °C until analysis for particulate phosphorus (PP) and particulate nitrogen (PN). The filters were digested with the same procedure used for water samples. After digestion all samples were diluted to 75 ml and then analyzed with the autoanalyzer (using a ammonia-salicylate complex for N analysis and a molybdenum-phosphate complex for P, both measured at 660 nm, Technicon #329–74W/B, 1977). Dissolved organic phosphorus (DOP) was calculated as DP minus PO_4^{3-}, and dissolved organic nitrogen (DON) as TDKN minus NH_4^1. Total phosphorus was calculated as DP plus PP, and total nitrogen (TN) as the sum of NO_3^{1-}, TDKN, and PN.

Particulate Si (PSi) was defined as the Si present in the frustules of planktonic diatoms. PSi levels were determined indirectly from data on planktonic diatom biovolume (μm^3 ml^{-1}; González et al., 1998) and from an assumed Si content per unit diatom biovolume of 0.006 pmol Si μm^{-3} (Sommer, 1988, Conley et al., 1989). This value is an average for freshwater diatoms. We use it in preference to the mean value Conley et al. give for marine diatoms (0.0005 pmol Si μm^{-3}) since the Salton Sea is neither freshwater or marine and since the shallow ($z_{max} = 15$ m), well-mixed water column and high Si levels (Table 3) at the Salton Sea remove the severe disadvantages posed by heavily silicified frustules in the marine environment.

Beginning in January 24, 1991, all tanks were sampled at monthly intervals for phytoplankton and zooplankton; the zoobenthos, phytoplankton primary production and periphyton were monitored at less frequent intervals. Results for these biological variables are reported elsewhere (González et al., 1998; Hart et al., 1998; Simpson et al., 1998; Simpson & Hurlbert, 1998).

Responses to salinity were tested with date-by-date 1-way Anovas. Date-by-date two-way Anovas were applied to data for the two salinities where there were tanks with and without fish. Data for nutrients were log transformed when data sets contained zeros; prior to transformation a constant was added to each datum. The constant was the lowest possible non-zero value for the variable and is represented in each graph as the c in $\log(X + c)$. This constant corresponds to the detection limit (DL) for each analytical procedure. We note that there is much controversy as to the best way to analyze data sets with some values reported as 'not detected' or 'below detection limit' (Helsel & Hirsch, 1992).

Table 4. Ionic compositions of treatments as predicted and measured following dilution of Salton Sea water and addition of salts (January 1991) and as measured at end of experiment (April 1992)

Date and ion	Nominal salinity level (g l^{-1})					
	30	39[a]	48	57[a]	65	C_{65}/C_{30} [b]
	Concentration (g l^{-1})					
Predicted initial (January 1991)						
Na^1	7.15	10.1	13.0	16.0	19.0	2.66
K^1	0.32	0.43	0.54	0.65	0.76	2.4
Mg^2	1.02	1.19	1.36	1.53	1.70	1.67
Ca^2	0.88	0.88	0.88	0.88	0.88	1.0
Cl^{1-}	12.9	16.6	20.4	24.2	28.0	2.17
SO_4^{2-}	7.49	9.31	11.1	13.0	14.8	1.98
HCO_3^{1-}	0.17	0.17	0.17	0.17	0.17	1.0
Total ions	29.9	38.7	47.6	56.4	65.2	2.18
Observed initial (January 1991)						
Na^1	9.38	12.8	16.3	19.7	22.8	2.43
K^1	0.157	0.271	0.380	0.499	0.585	3.73
Mg^2	0.989	1.15	1.32	1.52	1.70	1.72
Ca^2	0.913	0.930	0.942	0.912	0.908	0.994
Cl^{1-}	12.4	17.0	21.7	25.2	28.1	2.27
SO_4^{2-}	7.48	9.34	11.2	13.0	15.1	2.02
HCO_3^{1-}	0.109	0.111	0.119	0.134	0.118	1.08
Total ions	31.4	41.6	52.0	61.0	69.3	2.21
Observed final (April 1992)						
Na^1	9.42	12.6	15.8	18.6	21.5	2.28
K^1	0.176	0.274	0.390	0.487	0.578	3.28
Mg^2	1.25	1.42	1.59	1.68	1.87	1.50
Ca^2	0.907	0.904	0.908	0.875	0.857	0.945
Cl^{1-}	12.6	16.5	19.9	24.3	28.4	2.25
SO_4^{2-}	7.77	10.3	11.9	14.0	15.2	1.96
HCO_3^{1-}	0.135	0.190	0.220	0.197	0.146	1.08
Total ions	32.3	42.2	50.7	60.2	68.5	2.12

[a] No effects of fish were observed on either salinity or ionic composition. Thus data for tanks with fish and for those without fish have been combined, and the means presented in this table are based on 8 tanks for the 39 and 57 g l^{-1} salinity levels and 4 tanks for the other levels.

[b] The ratio of the predicted or measured concentrations of the ion in the 65 and 30 g l^{-1} treatments respectively.

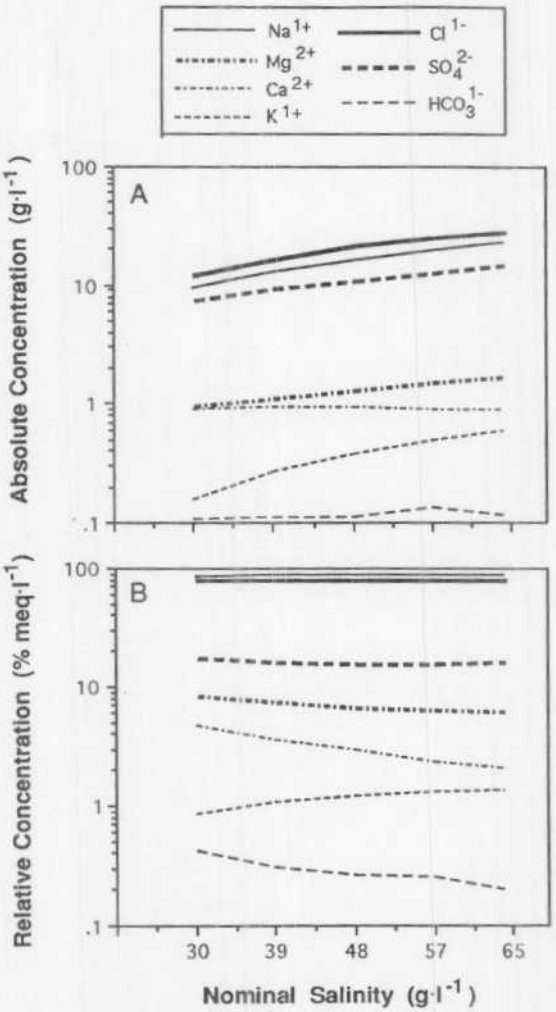

Figure 1. Mean absolute ($g\ l^{-1}$) and relative (percent meq l^{-1}) concentrations of the major ions at different salinity levels in January 1991.

Results

Salinity and ionic composition

The salinity levels measured during the experiment (Observed Jan 1991, Observed Apr 1992) were usually 2–4 $g\ l^{-1}$ higher than those (Predicted Jan 1991) we attempted to establish (Table 4). There was, however, no apparent increase in salinity over time despite the fact that approximately $\sim$ 1190 l of tapwater with a salinity of $\sim$ 0.65 $g\ l^{-1}$ was added to each tank during the experiment (Table 5; Figure 3 in Hart et al., 1998). If all ions in this added tapwater had remained in solution the salinity of each treatment would have increased by $\sim$ 2.5 $g\ l^{-1}$.

There were differences between the predicted and observed (January 1991) initial ionic compositions. For example, observed Na^1, Ca^2, Cl^{1-} concentrations were higher while K^1, Mg^2, and HCO_3^{1-} concentrations were slightly lower than predicted (Table 4).

Observed ionic composition varied among treatments. While Ca^2 and HCO_3^{1-} concentrations were roughly the same in all treatments, other major ions increased with salinity though to differing degrees (Table 4, Figure 1). In January 1991, for example, while salinity increased 2.2-fold from the highest to the lowest treatment, K^1 increased 3.7-fold and Mg^2 only 1.7-fold (Table 4).

Changes in ionic composition from January 1991 to April 1992 were small but seemingly real (Table 4). During this period and at each salinity level, Mg^2, HCO_3^{1-} and SO_4^{2-} concentrations increased while Ca^2 decreased.

pH and dissolved oxygen

pH varied over time and among salinity levels but was unaffected by the presence of fish (Figures 2A, E). During the first six months of the experiment mean pH values were mostly 8.3–8.5 and very similar among treatments. Between June and July 1991, pH values in all treatments increased abruptly and variation among salinity levels also increased. During the last half of the experiment the most common pattern was for pH to average 0.2–0.3 units higher at the higher salinities (65, 57) than at the lower (48, 39, 30).

Midday oxygen concentrations were affected by both salinity and fish (Figure 2B, F). They varied seasonally in a manner primarily reflecting the negative relationship between water temperature and oxygen solubility. During midsummer, treatment means were mostly 5.5–8.5 $g\ l^{-1}$, while during midwinter they were 7.5–10.8 $g\ l^{-1}$. As with pH, variation in oxygen among salinity levels was low during the first six months and much greater thereafter (Figure 2B, F). During the latter period the apparent effects of salinity varied from date to date and were not always accompanied by low P values. Generally concentrations were lower at 65 $g\ l^{-1}$ than at other salinities and 9–30% lower than at 30 $g\ l^{-1}$. Temporal fluctuations in oxygen seemed markedly greater at 57 $g\ l^{-1}$ than at other salinities (Figure 2B, F). The effect of fish on oxygen, when one was apparent, was to decrease it by ca. 0.5–1.5 mg l^{-1} ($P < 0.10$ on 4 dates: Figure 2F).

Table 5. Mean ionic composition of tap water, total mass of ions added to each microcosm, and the predicted increase in ionic concentrations resulting from water additions to microcosms to replace evaporative losses over 15 months

Ion	Mean concentration in tapwater used to replace evaporated water ($g\ l^{-1}$)[a]	Total amount added during the experiment (g)[b]	Predicted increase in concentration due to tapwater addition ($g\ l^{-1}$)[c]
Na^{1}	0.0827	98.6	0.316
K^{1}	0.00465	5.54	0.0178
Mg^{2}	0.0279	33.3	0.107
Ca^{2}	0.0697	83.1	0.266
Cl^{1-}	0.0924	110	0.353
SO_4^{2-}	0.216	258	0.826
HCO_3^{1-}	0.160	190	0.609
Total	0.653	779	2.50
SiO_2	0.0095	11.3	0.0364

[a] Mean concentration of ions calculated from monthly (January 1991 to April 1992) values for effluent water from Alvarado Filtration Plant, City of San Diego.
[b] Estimated amount in the ~ 1192 l of tapwater added to each microcosm, based on evaporation data from the SDSU Department of Geography Metereological Station, located ca. 200 m from the site of our experiment.
[c] These calculations presume that all ions added remained in solution (312 l).

When expressed as percent saturation, with both temperature and salinity taken into account, oxygen showed more interesting patterns than were anticipated, given that the tanks were continuously aerated (Figure 2C, G). During the first six months, the percent saturation was generally 85–95% and varied little among all salinities. During the latter two thirds of the experiment, percent saturation values fluctuated considerably and were in excess of 110% for most salinity levels on most dates. A clear and consistent effect of salinity was not apparent, though on most dates percent saturation values were lowest at 65 $g\ l^{-1}$. On the four occasions when the test for a fish effect yielded $P < 0.10$, percent saturation was higher by ~ 10–20 percent in the absence of fish (Figure 2G).

Midday water temperature patterns reflected normal seasonal changes with no differences among treatments (Figure 2D). The minimum temperature during winter was 6 °C (December 2, 1991) and the maximum during summer was 32.0 °C (August 26, 1991) (Figure 3 in Hart et al., 1998). The temperature difference among the four tanks in a given treatment monitored was never greater than 0.5 °C.

Phosphorus, nitrogen and silica

Most P was in the organic fractions (Figure 3A, D, G, Table 6). During first few months, for all forms of P, differences among salinity levels were minimal. Later, however, PO_4^{3-}, dissolved organic P (DOP), and particulate P (PP) concentrations tended to be negatively correlated with salinity and to be particularly low at 65 $g\ l^{-1}$, where PO_4^{3-} concentrations were 30–85% lower and DOP 30–70% lower than at 30 $g\ l^{-1}$.

The addition of tilapia to the tanks caused a reduction in PO_4^{3-}, DOP and PP concentrations (Figure 4A, D, G, Table 6). On the last sampling date, these reductions were maximal and in the range of 39–80% at both 39 and 57 $g\ l^{-1}$.

Dissolved inorganic nitrogen (DIN) was in form of ammonium and nitrate (Figure 3B, C, Table 6). Nitrate became positively correlated with salinity during the early part of the experiment with concentrations 30–68% lower at 30 and 39 $g\ l^{-1}$ than at higher salinities. In September its concentration was 40–90% higher at 48 and 57 $g\ l^{-1}$ than at other salinities. Ammonium concentration was initially high at all salinities, declined in March to that it was below the detec-

Table 6. Mean nutrient concentrations (μM) in different treatments on selected dates. P values for 1-way (P_1) and 2-way (P_2) ANOVAs are denoted as in Figure 2 and 4

		Treatments and P values										
										P_2		
Nutrient	Month	30	39	48	57	65	P_1	39F	57F	F	S	FS
PO_4	Jan	1.6	1.6	1.2	1.6	1.2	–					
	July	2.9	2.7	2.6	2.6	0.71	••	1.9	1.5	•	-	–
	Nov	1.9	1.6	0.96	1.4	1.0	•	0.83	0.82	•	–	–
	Apr	2.2	2.2	0.84	1.7	0.29	•••	0.51	0.31	•••	–	–
DOP	Jan	4.3	5.5	6.9	5.4	4.7	–					
	July	6.4	10.	10.	11	5.9	•	8.8	8.8	–	–	–
	Nov	6.6	6.6	4.8	5.6	4.4	•	4.4	4.2	•	–	–
	Apr	7.6	7.4	4.8	5	3.0	•••	2.4	2.7	•••	–	+
PP	Jan	3.9	5.2	5.9	4.4	4.4	–					
	July	10.	9.5	8.2	14	4.9	•	6.5	7.8	••	+	–
	Nov	14	12	5.2	8.6	5.3	•	4.6	2.3	•••	••	–
	Apr	7.2	9.6	1.9	2.8	0.78	••	2.8	1.1	•	•	–
TP	Jan	9.9	13	14	12	11	–					
	July	19	23	21	28	12	••	17	18	••	–	–
	Nov	23	20.	11	16	11	••	10.	7.4	•••	•	–
	Apr	17	20.	8.6	10.	4.2	•••	7.1	4.3	••	•	–
NO_3	Jan	0.09	0.13	0.12	0.14	0.12	–					
	July	0.11	0.084	0.21	0.16	0.11	–	0.089	0.11	–	–	–
	Nov	0.12	0.12	0.11	0.16	0.12	–	0.083	0.12	–	–	–
	Apr	0.24	0.20	0.15	0.16	0.23	–	0.16	0.15	–	–	–
NH_4	Jan	25	19	15	25	22	–					
	July	1.3	2.6	4.7	3.0	1.6	–	2.7	2.9	–	–	–
	Nov	25	23	12	11	3.8	–	12	2.3	••	••	–
	Apr	26	15	15	14	16	–	7.6	9.4	–	–	–
DON	Jan	237	258	330	264	250	–					
	July	338	354	434	509	335	••	441	386	–	–	•
	Nov	501	460	497	546	460	–	484	472	–	–	–
	Apr	456	442	467	565	384	+	410	453	–	+	–
PN	Jan	25	37	24	31	20	+					
	July	107	83	72	114	24	•	67	69	–	–	–
	Nov	215	204	116	183	96	•	103	70	•••	–	–
	Apr	259	262	120	150	47	••	64	63	•••	–	–
TN	Jan	290	320	385	322	293	+					
	July	451	441	543	628	373	•	511	467	–	–	+
	Nov	750	693	637	746	564	+	607	540	•	–	–
	Apr	755	736	611	750	457	•	486	533	••	–	–
DSi	Jan	6.1	4.3	6.3	5.4	2.0	–					
	July	200	163	130	130	19	•	43	93	•	–	–
	Nov	221	236	112	132	73	+	230	67	–	•	–
	Apr	436	324	293	168	56	•••	187	109	–	+	–

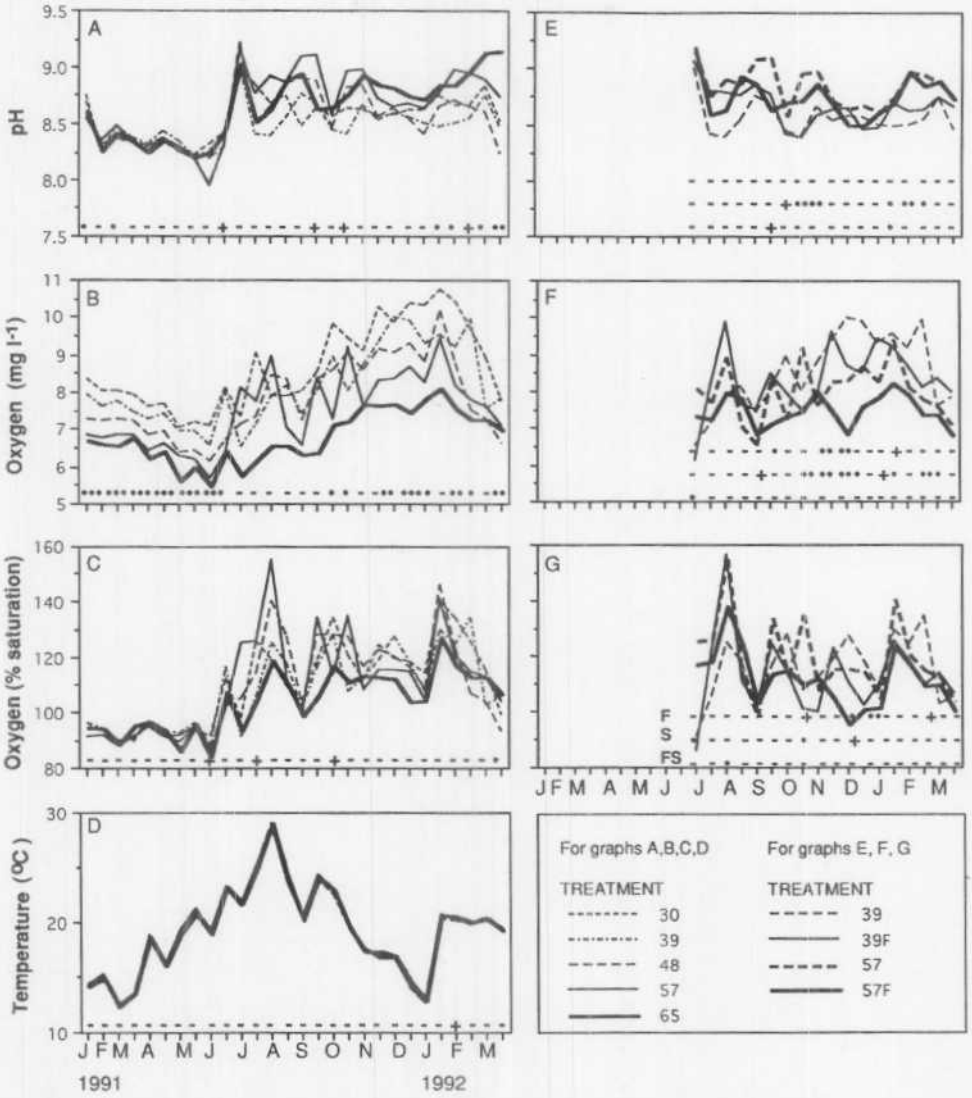

Figure 2. Effects of salinity and fish effects on mid-day values for pH, oxygen, and temperature. P values for one-way ANOVAs (A, B, C, D) and two-way ANOVAs (E, F, G) testing for main (F, S) and interaction (FS) effects are shown along bottom of each graph (as in G) and denoted as follows: –, $P > .1$; +, $.05 < P \leq .1$; •, $.01 < P \leq .05$; ••, $.001 < P \leq .01$; •••, $P < .001$.

tion limit, and then increased at least 10-fold over the remainder of the experiment. There was no clear evidence of a salinity effect.

DON concentrations at the various salinities were similar for the first few months, but in July were higher at 48 and 57 g l^{-1} than at other salinities (Figure 3E, Table 6). At the end of the experiment DON was about twice as high at 57 g l^{-1} as at 65 g l^{-1}, with intermediate values for the lower salinities (Figure 3E, Table 6). At the four lower salinities, PN increased gradually and by 5–10-fold over the course of the experiment (Figure 3H). At 65 g l^{-1}, PN values showed strong fluctuations but were generally much lower than at the other salinities.

The presence of fish tended to reduce total water column N (Figure 4B, C, E, H, Table 6). Where an effect was evident, the percent reduction was up to 80% for PN, up to 87% for NH_4^1, up to 45% for NO_3^{1-} and up to 25% for DON. Where interaction was apparent (DON and PN, Jan. 1992), the percent reduction due to fish was greater at 57 than at 39 g l^{-1}.

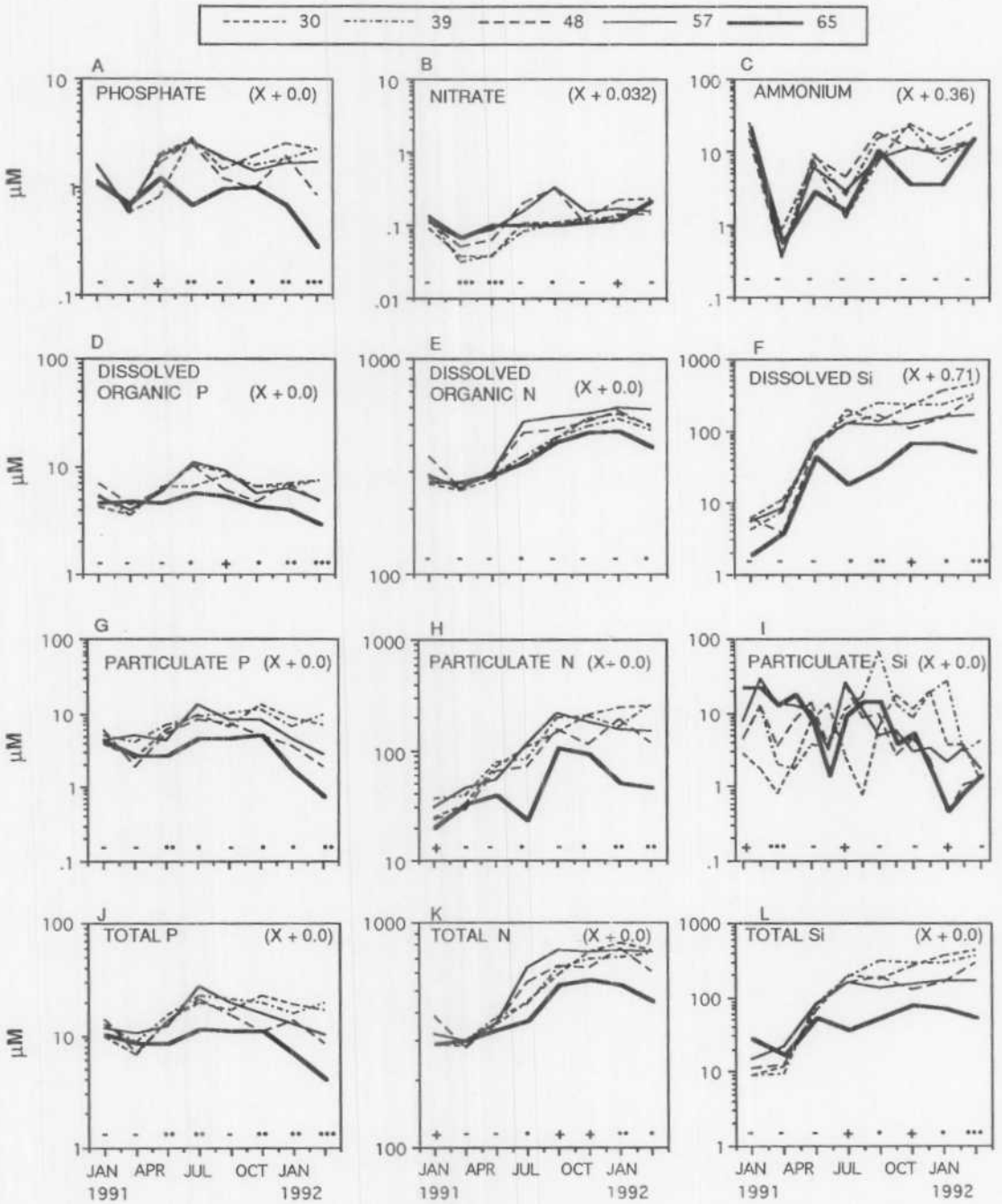

Figure 3. Salinity effects on nutrients concentrations. P values for date-by-date ANOVAs are shown at the bottom of each graph and denoted as in Figure 2. Constants in (X + c) are explained in the text.

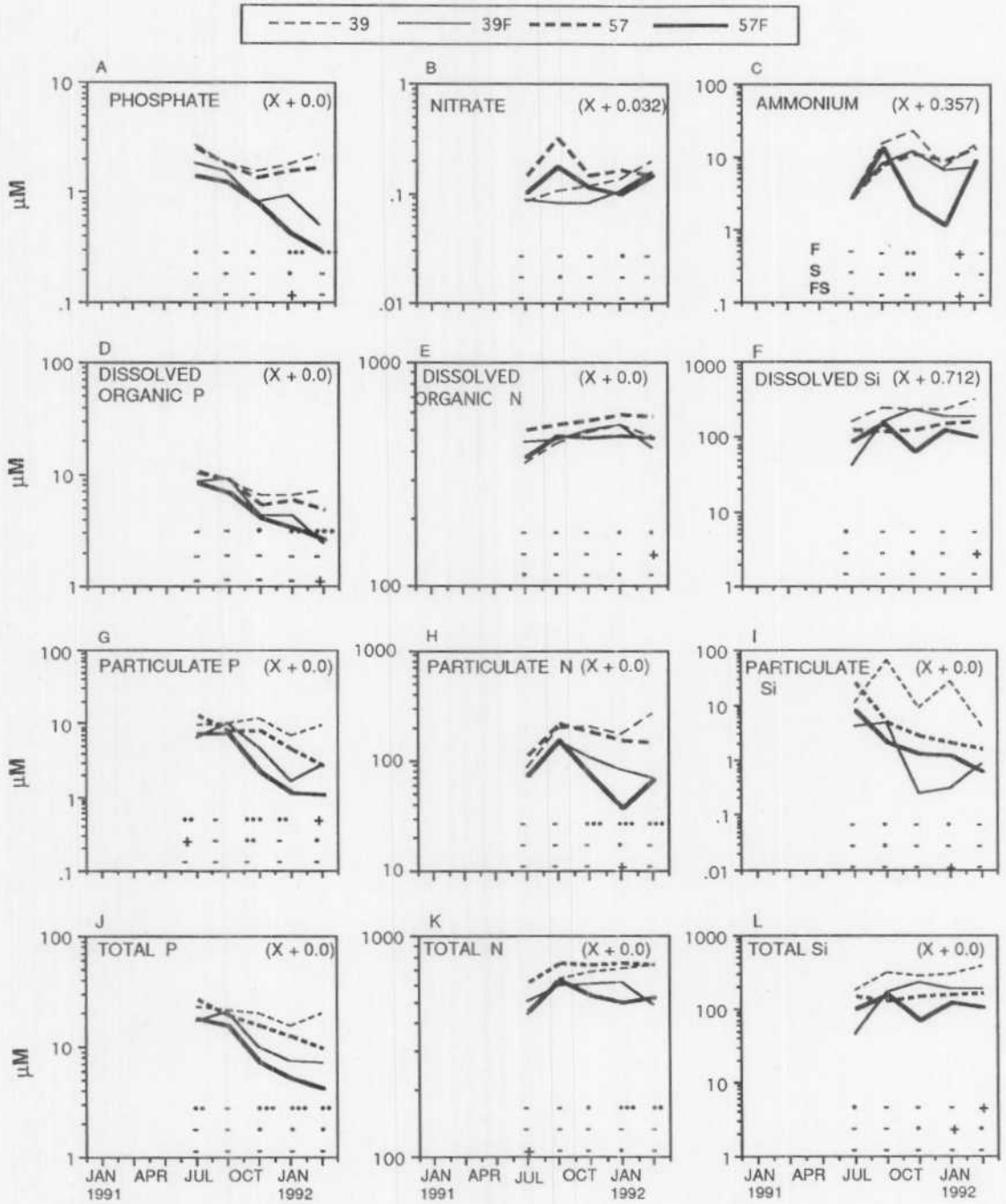

Figure 4. Salinity and fish effects on nutrient concentrations. P values for date-by-date 2-way ANOVAs are shown at bottom of each graph with tests for main (F,S) and interaction (FS) effects and denoted as in Figure 2. Constants in (X + c) are explained in the text.

The response of TN and TP levels to increased salinity and the presence of fish mirrored the responses of the dominant N and P fractions (Figures 3J, K, Figures 4J, K, Table 6).

The TN:TP ratio was always higher than the Redfield ratio of 16 (Figure 5D). It initially was ~ 25–40 at all salinities, increasing slightly at most salinities after July. During the latter part of experiment, there developed a positive correlation between the ratio and salinity, with a 2–4 fold difference between the TN:TP ratio for 30 and that for 65 g l^{-1}. After November, the TN:TP ratio was increased by 50–80% by the presence of fish at both 39 and 57 g l^{-1} (Figure 5I). The N:P ratios for the different fractions behaved differently (Figure 5). Reflecting the dominance of the organic fraction, the DON:DOP ratio changed over time and responded to salinity and fish much as did the TN:TP ratio (Figure 5B, G). The DIN:DIP ratio was markedly lower than the DON:DOP ratio. Initially DIN:DIP was in the range 4–20, dropped to < 1 by April, and increased to 5–40 by the end of the experiment (Figures 5A, F). No effects of fish or salinity were evident, except possibly for a decrease due to fish in November. The PN:PP ratio also tended increase over time from initial values of 4–7 to final ones of 25–60 and to show no clear effects of either salinity or fish (Figures 5C, H).

DSi levels increased rapidly in all treatments during the first five months then somewhat less rapidly thereafter. During latter part of experiment, Si concentrations were negatively correlated with salinity, being generally 60–90% lower at 65 g l^{-1} than at 30 and 39 g l^{-1} (Figure 3F, Table 6). There was weak evidence that fish may have reduced Dsi levels (Figure 4F, Table 6).

PSi levels, reflecting abundance of planktonic diatoms, fluctuated mostly in the range 1–30 μM and, despite increasing DSi levels, showed a slight tendency to decrease over time (Figures 3I, 4I). Early in the experiment PSi values were several-fold greater at high salinities than at low. Later in the experiment, mean PSi levels tended to be higher at the lower salinities, though statistical confirmation of the difference was weak. PSi levels were markedly reduced by the addition of fish, the reduction being on the order of 50% at 39 g l^{-1} and of 90–95% at 57 g l^{-1} (Figure 4I).

The TSi:TP ratio should both reflect the taxonomic composition and physiological state of the phytoplankton as well as be a determinant of it. It increased fairly steadily over time from initial mean values of 0.6–3 to final ones of 10–30 (Figure 5E). The ratio showed some evidence of being 30–60% lower at the higher salinites, especially 65 g l^{-1}, than at the lower ones, especially during the middle portion of the experiment. No certain evidence of an effect of fish on the ratio was apparent (Figure 5J).

Discussion

Interpretation of these results will focus on three aspects. First is the degree of success in establishing the desired salinities and ionic compositions. Second are the mechanisms accounting for both the observed effects of salinity and fish on the water chemistry and the temporal changes in it. And third is the relevance of our findings to natural systems.

As this research has involved no direct study of mechanisms, our inferences about them are somewhat speculative. The abundance of a chemical species is determined by many physical, chemical and biological processes and all of these are likely to have been modified by salinity. Volume fluctuations, inputs via tapwater, release from sediments, release to the atmosphere, sorption and desorption on surfaces, including those of clay, particulate organic matter, and tank walls, and uptake, secretion, and excretion by organisms are among the processes likely to have been operative. Our interpretations focus especially on the role of biological processes, as many patterns in the water chemistry data correlate strongly with observed changes in the algal and invertebrate populations as reported in González et al. (1998), Hart et al. (1998), and Simpson et al. (1998). Reference to the tables and figures in those companion reports will be helpful in following this discussion. Figure 6 provides a capsule summary of a few of the major biological effects of increased salinity at a point about halfway through the experiment.

Salinity

By the method of salt addition, this experiment successfully established and maintained five experimental salinity levels. This method we strongly recommend to other researchers who wish to investigate salinity effects at the community and ecosystem level. Certain differences were observed, however, between the observed and predicted and the initial and final salinities and ionic compositions.

That observed salinities were higher by 2–4 g l^{-1} than those (predicted) salinities we intended to establish (Table 3; Figure 3 in Hart et al., 1998) compromises the study in no way. An evaluation of effects

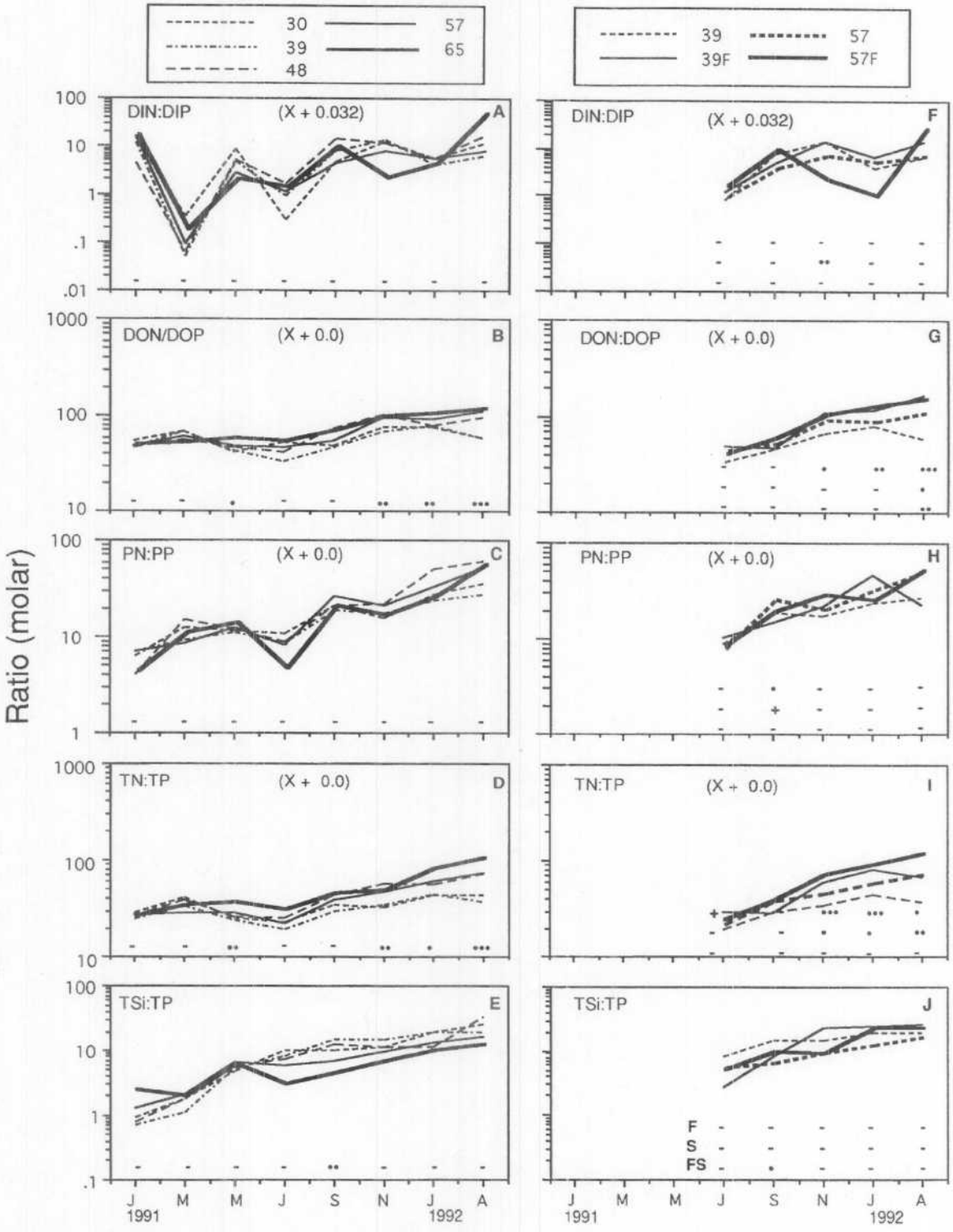

Figure 5. Salinity and fish effects on various N:P and Si:P ratios (mol/mol). P values for date-by-date for one-way ANOVAs (A–E) and two-way ANOVAs (F–J) testing for main (F,S) and interaction (FS) effects are denoted as in Figure 2.

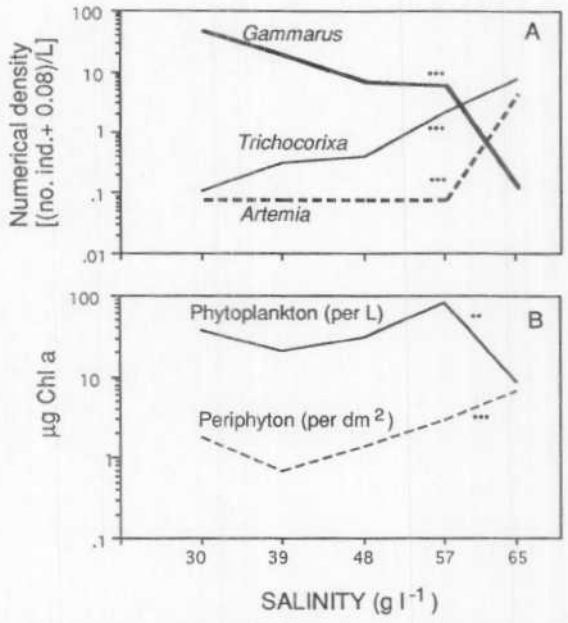

Figure 6. Salinity effects on three dominant invertebrates and on phytoplanktonic and periphytic chlorophyll concentrations, July 1991. P values for one-way ANOVAs denoted as in Figure 2. Chlorophyll values can be converted to μg per dm^2 of water surface by multiplying shown values by 4.8 (phytoplankton) or 2.2 (periphyton). Data from González et al. (1998) and Hart et al. (1998).

over the salinity range 32–69 g l^{-1} is as useful as one over the intended range of 30–65 g l^{-1}. The discrepancy requires explanation, however, and we see three possible sources of it. First, the 31 of dry sediments placed on the bottom of each tank contained salts. These were not identified or quantified. To assess prior to setting up the experiment the likely magnitude of this effect, 500 ml of sediments were added to 1000 ml of Salton Sea water, and salinity changes were monitored over 1 week. For three replicate set-ups, the average salinity increase was 68 g l^{-1}. A similar rate of release of salts from the 3 l of sediments in each tank would have caused a salinity increase of $\sim$ 1.3 g l^{-1}. Such an increase was not considered to pose a problem to the experiment, though obviously it could to one involving lower salinity levels. Release of salts from sediments could have been greater in the tanks than in the pilot study because of the experiment's long duration. In retrospect it would have been useful to have quantified the amount of each ion likely to be released from the sediments in the tanks; or alternatively, to have leached salts out of the sediments prior to their being placed in the tanks.

There also may have been an error in the conversion factor (1.13) used to convert refractometer readings to g l^{-1}: for example, if the true factor was 1.16, then our refractometer-based estimates of salinity in g l^{-1} would have been too low by about 2.6 percent. A third possibility is that the tanks may have had different water levels on the occasions when samples were collected for ion analyses. As a result of evaporation and the periodic additions of tapwater, water level fluctuated over a few cm. Evaporation of 6.5 l from a tank would produce a 1 cm drop in water level, a $\sim$ 2 percent decrease in water volume, and a $\sim$ 2 percent increase in salinity. The relative contribution of these error sources we cannot assess. A need for accurate factors for converting refractometer readings to true salinity (g kg^{-1} and g l^{-1}) values for waters of different ionic compositions is evident.

As anticipated, salinity changed negligibly or not at all over time (Table 3) despite the constant addition of tapwater. If we assume that all Ca^2 and HCO_3^{1-} ions in the added tapwater precipitated out and that all other ions remained in solution in the tanks, then a salinity increase of $\sim$ 1.6 g l^{-1} would have been expected over the 15 months (Table 5). Our measurement procedures, discussed above, were not precise enough to assess whether a change of that magnitude occurred. In any case, it is not a change likely to have biological importance at the salinities we used. Such changes may be more consequential for freshwater microcosm studies. During an 8-month long experiment on freshwater plankton using the same tanks at the same location, replacement of evaporative losses with tapwater caused an almost 3-fold increase in salinity (Soto & Hurlbert, 1991).

Ionic composition

Despite our intent to minimize variations in ionic composition, this varied both among salinities and over time. The biological consequences of variations such as those observed are unstudied and nothing can be said about them.

The among-treatment variation in ionic composition is evident in the C_{65}/C_{30} ratios (Table 4). If ionic composition was identical at 30 and 65 g l^{-1}, then this ratio should have been $\sim$ 2.17 (=65/30) for each ion. That this was not the case was due to three factors. The first was the impossibility of increasing Ca^2 and HCO_3^{1-} concentrations which we did not attempt to manipulate and which changed only slightly over time

despite these ions being repeatedly added via tapwater. Thus C_{65}/C_{30} was about 1.0 for both Ca^2 and HCO_3^{1-}.

The second factor was simple error. Our original objective had been to create five salinity levels ranging from 30 to 70 g l^{-1} by 10 g l^{-1} increments. However, in calculating the amounts of salts needed, we neglected the water of hydration in $MgSO_4 \cdot 7H_2O$. This caused the salinity interval between treatments to be 8.84 g l^{-1} rather than 10 g l^{-1}. This caused $MgSO_4 \cdot 7H_2O$ to make up a smaller percentage of the mixed salts added to the tanks than was intended. The low C_{65}/C_{30} values for Mg^2 and SO_4^{2-} are a measure of this underrepresentation. The values are lower for Mg^2 than for SO_4^{2-} because some of the SO_4^{2-} was introduced as Na_2SO_4. Another consequence of this error, was that Na^1 and K^1 salts were relatively overrepresented. This accounts, in part, for the predicted and observed C_{65}/C_{30} values for those two ions being higher than 2.17 (Table 4).

Third, the large discrepancy between observed and predicted K^1 values and the high C_{65}/C_{30} (and C_{39}/C_{30}) values for K^1 seem to be partly the result of an error in the data that we used in estimating the ionic composition of the Salton Sea water used in setting up the experiment. Parsons (1986) reported a value for K^1 of 0.42 g l^{-1} when the lake salinity was at 38.7 g l^{-1} (Table 1). However, analyses for samples from three stations in 1994 when salinity was 43.5 g l^{-1} yielded a mean K^1 concentration of 0.20 g l^{-1}. For other ions, the 1986 and 1994 values are more concordant (Table 1). We thus suspect that 1986 K^1 datum reflects analytical error. Using the 1994 value, we estimate that to achieve a salinity increment of 8.84 g l^{-1} we should have added, for each liter in a tank, not 0.11 g of K^1 (Table 1) but rather 0.04 g [=0.20(30/43.5)(8.84/30)] of that ion.

Slight changes in ionic composition over time were expected as a result of tapwater additions and particular physical, chemical and biological processes. On a percentage basis, the greatest change was an increase in HCO_3^{1-} concentrations (Table 4). This perhaps was caused by the increase in pH over time (Figure 2A) which in turn was correlated with increases in algal abundance and primary production over time (González et al., 1998). The slight decline in Ca^2 values may have resulted from $CaCO_3$ precipitation driven by the same pH increase. The increases in Mg^2 and SO_4^{2-} concentrations can be explained as resulting from tapwater inputs (Table 5), though further (post-January 1991) dissolution of salts in the sediments cannot be ruled out as a possibility.

Early dynamics of the microecosystems

During the first few months of the experiment, many chemical variables exhibited trajectories that differed little among the different salinity treatments. These trajectories identified the nature of the system in which marked salinity effects appeared only later. The trajectories were determined by the nature and timing of operations involved in setting up the microecosystems: Salton Sea water at 47 g l^{-1} was put into the tanks on November 19, this was diluted to 30 g l^{-1} on December 14, sediments were added on January 3, salts on January 4–10, and inocula of algae and invertebrates were added on 10 occasions between January 16 and April 10 (and on five later occasions).

During the first two months there likely was rapid bacterial decomposition of sediment organic matter and release of soluble forms of N and P into the water column, followed by bacterial and algal uptake of these nutrients and increased population densities of small invertebrates. These processes may explain the early and sustained depression of pH (Figure 2A), the undersaturation of dissolved oxygen even at midday (Figure 2C), and the marked initial declines in inorganic forms of N and P (FIgure 3A, B, C). We gathered no data on bacterial populations but from January to February 1991 there were marked increases in zooplankton, especially ciliates and rotifers (Hart et al., 1998).

Despite the likely release of soluble N and P from the sediments, there were initial decreases in TN and TP in the water column. This suggested an early net movement of these nutrients from the plankton and water itself into the sediment, nekton and benthos. In November 1990, water column TN was 534 μM (Table 3) and by January mean TN values had declined to 250–350 μM. Mean TP values showed a much greater decline, dropping during this period from 56 μM (Table 3) to 10–15 μM. Consequently the TN:TP ratio increased during this period from 9.5 to 23–30. To the extent that algal production was nutrient-limited in the tanks, this increase in the ratio may have signified a shift from N-limitation to P-limitation. The ratio continued to increase during January-March 1991, primarily reflecting a continued decline in TP during that period (Figures 3, 5).

During the period April-July 1991 two major factors driving the metabolism of the microecosystems, and the effects of salinity on them, were higher temperatures (Figure 2D) and the development of macroinvertebrate populations that came, at different

salinities, to dominate the consumer portion of the foodweb – the brineshrimp *Artemia franciscana* Kellogg, the amphipod *Gammarus mucronatus* Say, and the corixid *Trichocorixa reticulata* Guérin-Menéville. Between April and July, total invertebrate biomass increased by 10- to 50-fold at all salinities (Hart et al., 1998). The increases in concentrations of dissolved forms of N and P during March-June (Figure 3A–E) can be attributed to the grazing, excretory, and, possibly, sediment-disturbing activities of these and other invertebrates (Hart et al., 1998; Simpson et al., 1998). The springtime patterns for particulate N and P likewise reflect the changing abundances of plankton, especially phytoplankton (González et al., 1998), populations. The increasing variability among treatment means observed for oxygen and pH starting in July probably reflected, in part, true differences in these variables among treatments, though the statistical evidence for these was weak – at least until the end of the experiment. But this increasing among-treatment variability also was due simply to 'noise' – to increased among-tank variances in pH and oxygen resulting from the rapid but unequal development of macroinvertebrate populations in replicate tanks under the same treatment (appendices in Hart, 1994, and Simpson, 1994).

The effects of salinity and fish on water chemistry were mediated in part by their effects on algal populations which, in turn, were the sequelae of effects of salinity on invertebrate populations (Figure 6). In general, as salinity increased, *Gammarus* populations decreased and *Artemia* and *Trichocorixa* populations increased. For algal populations the strongest and most persistent pattern was for phytoplankton abundance to be lowest and attached algae or periphyton to be greatest at 65 g l^{-1}. The following discussion is thus organized around these mediator species and trophic relationships.

Artemia as a mediator

The earliest certain effect of salinity on nutrient levels was observed for NO_3^{1-} in March and May (Figure 3B). It was ~ 2-fold more abundant at the two highest than the two lowest salinities. This likely reflected NO_3^{1-} uptake by phytoplankton which was several-fold more abundant at low than at high salinities at this time (González et al., 1998). Heavy grazing of phytoplankton by *Artemia* at the two higher salinities generated this phytoplankton differential. Predation by the copepod *Apocyclops dengizicus* (Lepeschkin) and by *Gammarus* apparently prevented development of *Artemia* populations at the three lower salinities (Hart et al., 1998).

PO_4^{3-} and NH_4^1 presumably were also being taken up actively by phytoplankton during March-May, but their concentrations evinced no clear influence of salinity. Unlike NO_3^{1-} these two ions are continually being directly replenished by the excretion of invertebrates and by bacterial decomposition. The rates of those processes can exceed the rate of uptake by the algal populations. During April and May, total invertebrate biomass was several-fold greater at 65 g l^{-1} than at other salinities (Hart et al., 1998).

Artemia continued as a mediator of salinity effects for the duration of the experiment. At almost all times it was at least an order of magnitude more abundant at 65 g l^{-1} than at lower salinities (Hart et al., 1998). This correlated with generally lower concentrations of the various forms of N, P, and Si at this salinity throughout the last two thirds of the experiment (Figure 3). The lower PN and PP values at 65 g l^{-1} simply reflect the persistently low phytoplankton densities at that salinity (González et al., 1998). The lower concentrations of dissolved nutrients at 65 g l^{-1} probably reflected their incorporation into benthic and periphytic algae. The abundance of these algae was positively correlated with salinity (Figure 6; González et al., 1998; Simpson et al., 1998). This was due in part to the greater light penetration permitted in these tanks by the grazing down of phytoplankton populations by *Artemia*. It was due in even greater part to the activities of *Gammarus*, as discussed below.

As in the case of other response variables, nutrient levels often responded to salinity in non-linear fashion. While these levels were often lowest at the highest salinity (65 g l^{-1}), they were sometimes highest at the second highest salinity (57 g l^{-1}; Figure 3). This seemed in part a consequence of the behavior of *Artemia* populations. At 57 g l^{-1} these populations initially developed quite well but then crashed to zero by July (Hart et al., 1998). Released from grazing pressure, the phytoplankton at this salinity increased rapidly and during the period July-October was more abundant than at any other salinity (Figure 6; González et al., 1998). The high levels of DOP and DON at 57 g l^{-1} during this period presumably were secreted by this phytoplankton.

Gammarus as a mediator

Gammarus was scarce, though not absent, at 57 and 65 g l^{-1} for most of the experiment apparently for physiological reasons (Hart et al., 1998; Simpson et al., 1998). This, combined with its ability at lower salinities to prey on, compete with and generally dominate other invertebrates and to consume attached algae, was the proximate cause of many of the salinity effects observed on water chemistry as well as on the biota.

The abundance of *Artemia* may have been partially under the control of *Gammarus* which readily preys on it (Hart et al., 1998; Simpson et al., 1998). Since *Gammarus* was introduced into the tanks only after (April 8) a suppression of *Artemia* populations at low salinities was already evident (March), that early suppression was attributed to the large populations of the omnivorous *Apocyclops* present at low salinities. From June until the end of the experiment, however, *Gammarus* was very abundant at the two lower salinities and may have been the major cause of the near absence of *Artemia* from them and of the changes in algal and nutrient dynamics resulting therefrom.

Where present, *Gammarus* grazed attached algae on the tank walls, on the sediments, and on clay tiles placed in the tanks for assessment of periphyton. By July a marked positive correlation between salinity and periphyton abundance had developed (Figure 6); by the end of the experiment, periphyton was six times more abundant at the two highest salinities than at the lowest (González et al., 1998). Likewise, a thick algal mat covered the sediment surface at the three highest salinities and was essentially absent at the two lower ones (Simpson et al., 1998).

Where *Gammarus* was scarce these attached algae may have accounted for most primary production in the tanks. That would explain why at the end of the experiment, pH and percent oxygen saturation were highest at 65 g l^{-1} (Figure 2A, C) even though phytoplankton abundance was lowest there (González et al., 1998). That most forms of N and P were most of the time less abundant at 65 g l^{-1} than at other salinities also undoubtedly reflected their utilization by the abundant attached algae at 65 g l^{-1}. Diatoms were the dominant group of algae found on the clay tiles (González et al., 1998) and their flourishing under the *Gammarus*-free conditions at 65 g l^{-1} was likely part, but only part, of the explanation for the low dissolved Si levels at that salinity (Figure 3F, Table 6).

Silica

Though the statistical evidence is uncertain, the effect of salinity on dissolved Si appeared to develop at the very beginning of the experiment and to increase over time (Figure 3F, Table 6). Unravelling the causes of this effect is made difficult because, for the Salton Sea water used to initiate the experiment, we measured neither DSi nor diatom abundance. Nor did we measure the Si content of the added sediments. On the first sampling date, January 24, two months after the tanks were filled with water in November and two weeks after the addition of salts. DSi concentrations were only 2–6 μM. This was much lower than 200 μM, the only value for Salton Sea water available (Table 3). However, on January 24 planktonic diatoms were abundant at all salinities and already exhibited a strong salinity effects. The dominant species was *Nitzschia longissima* (Brébisson), with mean densities ranging from 1000 cells ml^{-1} at 30 g l^{-1} to 20 000 cells ml^{-1} at 65 g l^{-1} (González et al., 1998). As this species has been reported to be a dominant in the Salton Sea and to have reached densities there in November 1955 of 46 000 cells ml^{-1} (Carpelan, 1961), similar densities may have been introduced into our tanks when they were filled with Salton Sea water collected in November 1990. A salinity effect on DSi in January 1991 then was to be expected, given the observed salinity effect on PSi. On the assumption that the Si content per unit of diatom biovolume was 0.006 pmol Si μm^{-3} (Conley et al., 1989), the January 1991 difference between the 30 and 65 g l^{-1} tanks in diatom abundance (489 000 vs 4 027 000 μm^3 ml^{-1}) corresponds to a difference in Si concentration of 21 μM. This seems more than adequate to account for the possible initial differences among treatments in DSi (Figure 3, Table 6). The larger differences that developed later may have resulted in part from uptake by the diatom-rich periphyton which was most abundant at the higher salinities (Figure 6; González et al., 1998) and in part from lower regeneration rates, at high salinities, for the Si precipitated to the sediments as diatom frustules. The activities of *Gammarus* may have kept those regeneration rates high at the lower salinities.

Physical-chemical processes may have worked in the opposite direction. The rate of dissolution of biogenic silica doubles with a salinity increase from 1 to 5 g kg^{-1} (Hurd, 1983); the implications of this for our range of experimental salinities is unclear. The slightly higher pH values at the higher salinities (Figure 2) would also favor more rapid dissolution of

diatom frustules. Abiogenic precipitation of Si seems improbable; the solubility of Si in seawater at 25 °C is 2464 μM (Spencer, 1983), but 510 μM was the highest DSi value we ever recorded in one of our tanks. Uptake by planktonic diatoms cannot explain the lower levels of DSi at the high salinities during the latter half of the experiment, as those diatoms were not more abundant at higher than at lower salinities (Figure 4I; González et al., 1998).

The effect of fish on dissolved Si levels was relatively weak, if it existed at all (Figure 4F, Table 6). A strong effect of fish on Si dynamics was nevertheless apparent in the fact that they caused a decrease in abundance of planktonic diatoms and an increase in abundance of periphytic diatoms (González et al., 1998). The opposing effects of those changes in particulate Si apparently had a stabilizing effect on DSi levels.

At all salinities, DSi increased 10–50-fold over time. The Si provided by the weekly additions of tapwater (Table 5) was more than sufficient to account for this increase, though we cannot rule out the sediments put in each tank as another possible source of Si (Table 3).

High DSi levels may have resulted from low turbulence and the consequently weak development of populations of planktonic diatoms (González et al., 1998). It has been suggested that diatoms can dominate other groups when DSi levels remain above 2 μM (Egge & Aksnes, 1992). Yet despite DSi levels of 10–400 μM during most of the experiment and a molar DSi:PO_4^{3-} ratio that increased from 1–10 in January 1991 to 100–400 by April 1992, diatoms were a dominant component of the phytoplankton only at 65 g l^{-1} (González et al., 1998). Though these outdoor microcosms were moderately exposed to the wind and were weakly mixed by the airlift systems for inhibiting stratification, the turbulence in them surely was weaker than that in the Salton Sea. Had turbulence been greater, better development of planktonic diatoms and correspondingly lower DSi levels would have been expected.

In the only other experimental study to examine the relation between salinity and DSi levels, Greenwald and Hurlbert (1993) also observed that DSi levels, as well as planktonic diatoms, decreased with increasing salinity. These apparently were not true salinity effects, however, but rather consequences of experimental salinity levels having been established by mixing, in different proportions, Si-rich freshwater with Si-poor concentrated coastal lagoon water. Differences between these two source waters in levels of other nutrients (N, P) caused further confounding of nutrient and salinity effects. The salinity effects observed on Si and other nutrients in the present study, on the other hand, are clearly attributable to salinity, even if the mechanisms involved are not known with certainty. This presumes that the slight variations among salinity treatments in ionic proportions had no more than minor effects.

Influences of tilapia

Reductions of PO_4^{3-}, DOP, PP, NO_3^{1-}, DON, and NH_4^1 levels by tilapia likely resulted from incorporation of nutrients into new fish tissue and from changes in algal and invertebrate populations. During the six month following their introduction on September 28, the tilapia mean weight increased from 8.4 g (=0.027 g l^{-1} = 130 kg ha^{-1}) to 28 g. This growth represented a net uptake of nutrients from the tank ecosystems. Data for other tilapia species (*O. aureus* and *O. niloticus*) suggest that P and N constitute ca. 0.75 and 2.2 percent, respectively, of tilapia wet weight (Boyd & Green, 1998). A single tilapia in 312 l then would have represented 6.3 μM of P and 43 μM of N at the time of introduction and 20.4 μM of P and 140 μM of N at the end of the experiment. The implied net uptakes are similar to the final differences in TN and TP between treatments with and without tilapia (Figure 4J, K, Table 6). Fish growth alone apparently caused much of the reduction in the levels of those nutrients.

Restructuring of the whole food web by tilapia's feeding activities also affected the dynamics of those portions of the nutrient pools that were not sequestered in new fish tissue. In general, tilapia shifted plankton-dominated systems to benthos-dominated ones (González et al., 1998; Hart et al., 1998; Simpson et al., 1998). The tilapia-caused declines in water column TN and TP must then reflect a shifting of N and P flows not only into their own growth but also into the benthos and sediments, including fish fecal pellets, at the expense of the plankton. This parallels the similar shift of Si flows discussed earlier. Differential uptake of P relative to N by the fish and benthos would be expected, given the high water column TN:TP ratios in these systems. This may account for the large tilapia-induced increase in the TN:TP ratio (Figure 5I). The effectiveness of tilapia in 'vacuuming' the water column is undoubtedly determined by its ability to feed on both phytoplankton and zooplankton (Maitipe & De Silva, 1985; de Moor et al., 1986). It thereby re-

moves both PN and PP which of course are mostly in the form of planktonic organisms that secrete and excrete these nutrients in soluble form.

The standing crop of tilapia or other fish in the Salton Sea is unknown. The density used in our tanks (130–430 kg ha^{-1}) may be similar to that in the lake, given the eutrophic nature of the lake and given that for various types of lakes and reservoirs in the U.S. and Canada mean standing crops for fish assemblages (excepting those for trout lakes) fall in the range 140–450 kg ha^{-1} (Carlander, 1955). The effects of tilapia that we have observed on the water chemistry, as well as on other variables, thus are not ones that can be dismissed as artifacts of unrealistically high experimental tilapia densities.

Tilapia as a restoration tool?

Tilapia's ability to sequester nutrients suggests it might be used to help reverse the hypereutrophic state of the Salton Sea. For many decades there have been periodic massive fish kills, and in the 1990s large dieoffs of pelicans, grebes, cormorants, ducks and other birds have also occurred at the Salton Sea. The known or suggested proximate causes of these mortalities include botulism, toxic algal blooms, anoxia, and high ammonia concentrations. All of these, however, are merely specific symptoms of excessive nutrient enrichment.

In lakes with outflow streams, eutrophication reversal can be accomplished by reducing external nutrient loadings and then letting natural flushing lower nutrient levels in the lake. In closed basin lakes like the Salton Sea, however, eutrophication reversal calls not only for reducing nutrient inputs but also for an active or engineered removal or immobilization of nutrients already in the lake, since no natural flushing takes place. For any large closed basin lake, most engineering options would be prohibitively expensive. Massive, sustained yield harvesting of tilapia, however, might be not only a feasible way to remove nutrients in helpfully large quantities but also an economically profitable venture.

Full analysis of this possibility is not attempted here, but we note some relevant facts. Given the high TN:TP ratio for the Salton Sea (Table 2), P is more likely to be limiting than is N. By the end of the microcosm experiment, at 39 g l^{-1} tilapia had reduced TP levels by 64 percent (Table 6). Removal of the 28 g tilapia from the tanks at that time represented a sustained yield harvest equivalent to $\sim$ 300 kg ha^{-1} for only the cooler half of the year. With a seemingly unlimited food supply for tilapia and with mean water temperatures that exceed 30 °C by the end of summer, annual tilapia production in the Salton Sea could be several-fold greater than 300 kg ha^{-1}. There are a number of problematic factors that need to be considered here, such as the amount of P stored in the lake's sediments, the degree to which it might recycle back into the water column, and the degree to which external P loadings can be reduced. The biggest challenge, however, might be finding or creating a market for the many thousands of tons of fish or fish product per year that would have to be harvested from this 980 km^2 lake in order to restore it to a more mesotrophic condition.

Implications of N:P ratios

Reaching final mean values of 32–120, the TN:TP ratio increased with time, with salinity and with the addition of fish (Figure 5D, I). Enrichment bioassay studies generally find that N, rather than P, is limiting to phytoplankton populations in lakes where the TN:TP ratio < 31 and TP is high (Downing & McCauley, 1992). Thus in our experiment, time, salinity and fish may have tended to push the microecosystems into states where P was more likely to be limiting than N. The earlier TN:TP value of 74 for the Salton Sea (Table 2), though not the value of 9.5 for the Salton Sea water used to fill the tanks (Table 3), suggest possible P limitation in the lake itself. It is also possible that self-shading by phytoplankton or light availability may be limiting primary production in this hypereutrophic lake (USDI, 1970).

The relation demonstrated between salinity and TN:TP in this study is the opposite of that usually observed in comparative analyses of natural systems. As one moves from lakes or down an estuary to the sea, or from well-flushed to poorly-flushed coastal lagoons, salinity increases, the TN:TP ratio decreases, and N replaces P as the limiting nutrient (Caraco et al., 1987; Hecky & Kilham, 1988; Howarth et al., 1988). Likewise among lakes there often is a rough negative correlation between salinity and the TN:TP ratio (Bierhuizen & Prepas, 1985; Tominaga et al., 1987). Such studies are not designed for understanding the effects on nutrient dynamics of increasing salinity in a given lake, and it is worth emphasizing their unreliability for that purpose. There simply is no way of factoring out the strong influences of the hydrological, hydrographic, geological, and other differences among the systems that covary with salinity.

Laboratory studies have the opposite difficulty. They eliminate not only many extraneous variables but also key non-extraneous ones. Thus studies of nutrient flux at the sediment-water interface indicate that release into the water column of both PO_4^{3-} and NH_3, through quite different mechanisms, increases with salinity (Clavero et al., 1990; Seitzinger et al., 1991), though the direction of the effect on the TN:TP ratio has not been examined. But when sediment-water systems are brought into the laboratory for such studies, naturally the fish and macroinvertebrates are left behind. An experimental salinity increase of, say, 10 or 20 g l^{-1} may alter some aspect of nutrient cycling through strictly physico-chemical or microbe-mediated biochemical mechanisms in such simplified laboratory systems. But these alterations will often be small, even trivial, relative to those generated by direct salinity effects on key living members of the natural biogeochemical system – such as the *Artemia*, *Gammarus*, and tilapia in our tanks. The appearance, disappearance, or marked change in abundance of a single such functionally important species may shift the entire system into a radically new state.

The values for the PN:PP ratio pose an enigma. One might expect they would reflect the nutrient content of the zooplankton. On a biovolume basis this was 10–100 times more abundant than the phytoplankton on all dates (González et al., 1998; Hart et al., 1998). Yet the PN:PP ratio rose from low values of 4–7 at the beginning to 23–60 at the end, and on both occasions protozoans, mainly ciliates, were the dominant (> 85 percent of the biovolume) zooplankters. Moreover, though both salinity and fish markedly altered the relative proportions of protozoans, rotifers, crustaceans and other components of the zooplankton, as well as the composition of the phytoplankton, neither salinity or fish seemed to have any clear effect on the PN:PP ratio (Figure 5C, H). Without information on N:P ratios for each individual group of organisms, including detritus and bacteria, all we can suggest is that the nutrient content of the planktonic assemblage in general changed in concert with changes in the relative availabilities of N and P, as reflected in the DIN:DIP ratio (Figure 5A), and with the presumed shift from P-limited algal production to N-limited production.

Conclusions

Microcosm experiments like this one have advantages and disadvantages. The main advantage is the possibility of demonstrating unequivocally the effects of the selected experimental variables on other components of a semi-natural system. The main difficulty is that the small size and artificial nature of the microecosystems may so influence processes in them that they are very different from those in the larger scale systems of principal interest. That is to say, so different that even at a qualitative level, relations demonstrated in the microcosms give little insight into corresponding relations in the natural system.

We believe our findings on nutrient dynamics in the microcosms provide some understanding of nutrient dynamics in the Salton Sea and how future increases in the salinity of the lake might affect those dynamics. Given that the salinity of this lake continues to rise, testing of that understanding is a possibility for the near future, and we are now initiating a long term ecosystemic study of the lake. Biotic interactions such as grazing and predation by fish and invertebrates proved important mediators of salinity effects on nutrient dynamics in the microcosms. We expect similar interactions will mediate the effects of rising salinity on the whole Salton Sea ecosystem. There will be two critical points when the system will undergo major restructuring, and these are discussed in detail elsewhere (González et al., 1998; Hart et al., 1998; Simpson et al., 1998). One will be when salinity rises high enough that tilapia and other fish are mostly or completely eliminated from the lake. And the other will be at a much higher salinity when *Artemia* becomes abundant following the demise of less salinity tolerant invertebrates (*Trichocorixa, Apocyclops*) that prey on it. On the other hand, after many decades of study of the problems that lake salinity increases would cause to the sport fishery, other wildlife, and the regional economy, federal, state and local government authorities now seem committed to implement salinity stabilization measures, expensive as they will be.

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