

EXPERIMENTAL MESOCOSM STUDIES OF SALINITY EFFECTS ON THE BENTHIC ALGAL COMMUNITY OF A SALINE LAKE¹

David B. Herbst²

Sierra Nevada Aquatic Research Laboratory, University of California, Route 1, Box 198, Mammoth Lakes, California 93546

and

Dean W. Blinn

Department of Biological Sciences, Northern Arizona University, Flagstaff, Arizona 86001

ABSTRACT

As closed-basin systems, saline lakes are prone to fluctuate in level and salinity with climate change and hydrologic alterations. Loss of many Great Basin lakes has resulted from the diversion of tributary streams for agricultural or municipal uses. At Mono Lake, an alkaline salt lake in eastern California, salinities have risen from 50 to 100 g·L⁻¹ in just 50 years. Experimental mesocosms were established to simulate some of the potential ecological effects that could have accompanied this change. The influence of salinity on diatom diversity, taxonomic structure, and primary production was tested using mesocosms deployed at Mono Lake. Mesocosm tanks were 500 L in volume, 1 m square, and 0.5 m deep, with open tops covered by 1 mm mesh net. Five treatments (50, 75, 100, 125, and 150 g·L⁻¹) with four replicates per treatment were used over a 2-month period. The diatom-dominated benthic algae were reduced both in standing crop (from 6 to <0.1 g·m⁻²) and diversity (from 30 to 12 taxa) with increased salinity, with most loss occurring in salinities ≥ 75 g·L⁻¹. Photosynthetic oxygen production also was significantly lower at salinities ≥ 75 g·L⁻¹. Diatom indicator taxa for these shifts included *Denticula* sp., *Nitzschia frustulum*, *N. monoensis*, *N. communis*, and *Stephanodiscus oregonicus* increasing in relative abundance in higher salinity treatments, accompanied by decreases in *Achnanthes minutissima*, *Cymbella minuta*, *N. dissipata*, and *Rhoicosphenia abbreviata*. Exhibiting dominance at moderate salinity levels (75 to 125 g·L⁻¹) were *Nitzschia frustulum*, *N. communis*, *N. palea*, and *Navicula crucialis*. These latter species may be limited by both physiological stress at high salinity and grazing and competition at low salinity. The filamentous chlorophyte, *Ctenocladus circinnatus*, and cyanobacteria (*Oscillatoria* spp.) occurred only in salinity treatments from 50 to 100 g·L⁻¹. Diversion of tributary stream flow and resulting salinity increases in this lake threaten sustained benthic primary production and algal species diversity relative to conditions prior to stream diversion. The 1994 decision of the California State Water Resources Control Board to return stream flows to Mono Lake will raise the lake level and reduce salinity to around 75 g·L⁻¹ and is expected to increase the diversity and productivity of the benthic algae of this ecosystem.

Key index words: conservation; diatoms; mesocosms; Mono Lake; periphyton; salinity; salt lakes

Inland saline lakes within closed hydrologic basins are subject to natural and induced fluctuations in size and salt concentration over both short and long time intervals. Global and regional climate changes have altered Holocene lake chemistry in North America, as evidenced both in paleohydrological data (e.g. Benson and Thompson 1987, Stine 1990) and in paleobiological indicators such as the diatom stratigraphy of sediments (e.g. Bradbury 1987, Fritz 1990, Blinn et al. 1994). More recent changes and drying of Great Basin lakes have resulted from the diversion of tributary streams for agricultural or municipal uses. At Mono Lake, an alkaline salt lake in eastern California, approximately half the volume of the lake was lost in the 50 years following stream diversions that began in 1941. Lake levels have risen recently following wet years and an order by the California State Water Resources Control Board to return stream flow to the lake. Management and protection of these changing ecosystems depend upon an understanding of the influence of salinity on biological productivity and community structure. The goal of our research was to predict ecological changes along temporal salinity gradients associated with rising and falling lake levels. The present paper describes benthic algal dynamics with emphasis on the distribution of diatom diversity.

Previous studies of salt lake benthic algae have focused on distributions in surveys of lakes with both varied salinities and environmental settings (Hammer et al. 1983, Blinn 1993, 1995), or laboratory cultures of isolated species over a salinity range (Blinn 1984, Herbst and Castenholz 1994). Studies of mixed species cultures of algal mat from saline lakes showed growth yields were reduced by salinity but did not examine changes in species composition (Herbst and Bradley 1989). Though the traditional use of laboratory bioassays has yielded much information on physiological chemical toxicity, there are limited data integrating the response of aquatic communities to salinity stress. Experimental microecosystems or microcosms provide a valuable approach for more realistic simulations integrating the community level response to ecological variables

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² Author for reprint requests; e-mail herbst@lifesci.ucsb.edu.

(Kimball and Levin 1985, Cooper and Barmuta 1993). Though freshwater lake research has utilized microcosms, few studies of saline lake ecosystems have used this method to examine benthic communities, even though shallow-water habitats are an ideal application. Here, we use the term "mesocosm" to distinguish the size and duration of experimental salinity treatments employed in these Mono Lake studies (Cooper and Barmuta 1993). Experimental field mesocosms permit more authentic simulations of salinity effects on the benthic littoral ecosystem of Mono Lake because mesocosms allow environmental control, replication, and manipulation of salinity in understanding how this variable may regulate a mixed community of algae and invertebrates. These mesocosms are also appropriate comparisons to the shallow-water environment (<1 m deep) where most production occurs (Herbst and Bradley 1993). Results may be used to approximate historical and future ecological changes and to aid in the design of lake restoration plans to optimize ecological values (productivity and diversity). This research will find further application in the interpretation of paleoenvironmental climate change based on diatom stratigraphic records from lake sediment cores and in understanding the dynamics of saline lake food chains.

MATERIALS AND METHODS

The effects of salinity on the structure and productivity of the benthic algal community of Mono Lake were tested in large fiberglass mesocosm tanks (1- by 1-m sides, 0.5 m deep, open tops covered with 1 mm mesh net) located in a shallow concrete basin about 100 m from the shore of Mono Lake, California. Water was pumped from Mono Lake through a 200- μ m mesh screen into 20 tanks to a depth of 45 cm (near 500 L). Salinities were gradually adjusted in each mesocosm over a 5-week period by dilution with water from nearby Lee Vining Creek and/or by replacement of evaporated water with hypersaline Mono Lake water to the desired target salinity levels of 50, 75, 100, 125, and 150 $\text{g}\cdot\text{L}^{-1}$. (Mono Lake salinity was ca. 100 $\text{g}\cdot\text{L}^{-1}$ at the time of these experiments in 1991.) Each salinity level was replicated four times, and tank treatments were arrayed in a Latin square design (Fig. 1). During the 5-week acclimation period, 10 L of sand substrate from Mono Lake were added to each tank, followed by 2 L of mixed fine organic sediments. Upon reaching the target salinities, each mesocosm was further inoculated with 5 L of Mono Lake sediments containing algal mats and associated invertebrates. In addition, to serve as external colonization sources from a wide salinity range, 0.5 L of sediments from nearby Black Lake (salinity ca. 50 $\text{g}\cdot\text{L}^{-1}$) and 0.5 L of sediment from hypersaline Mono Lake onshore ponds (ca. 150 $\text{g}\cdot\text{L}^{-1}$) were added to each mesocosm tank. Evaporated water from each mesocosm was replaced every 3–5 days over the course of the experiment with water from Lee Vining Creek, holding salinities to within less than 10% deviation from target levels. Aeration was supplied from a single high volume air pump (43 $\text{L}\cdot\text{min}^{-1}$ capacity) with air lines to plexiglass air-lift tubes in each tank, and was powered by photovoltaic panels charging a deep-cycle battery system (Fig. 1). The air pump operated through a remote timer on daily cycles of 16 h on and 8 h off. This aeration, along with daily temperatures that typically ranged between 15° and 25° C in all tanks and treatments, provided water circulation and oxygenation. Water samples for nutrient ammonium analysis were taken after mesocosm filling and at the initiation and termination of the experiment (indophenol blue method; Strickland and Parsons 1972). Temperature of each

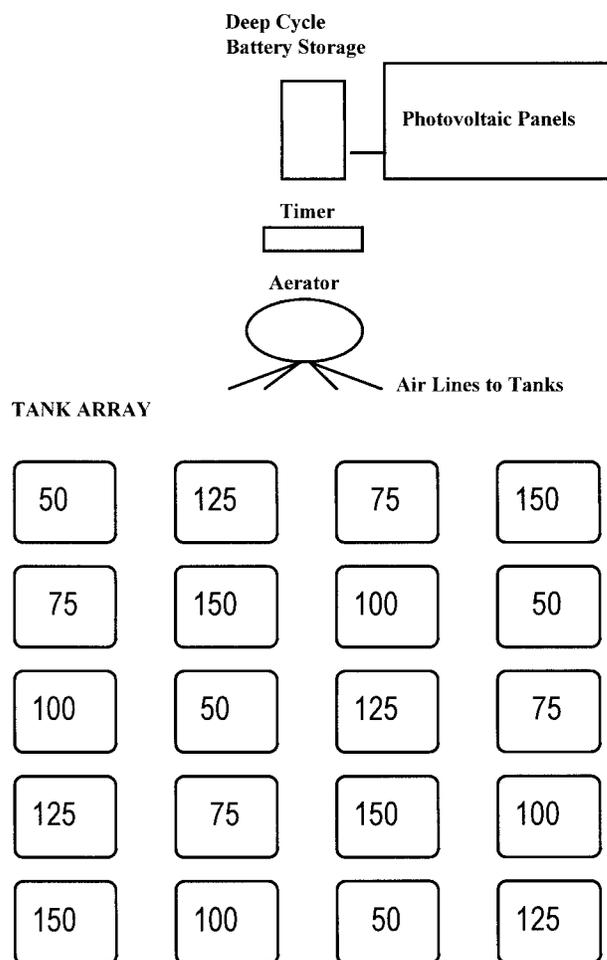


FIG. 1. Latin square array of mesocosm tanks at Mono Lake, California. No salinity treatments were repeated in rows or columns. Photovoltaic panels were used to charge deep cycle batteries, which powered the aeration system.

treatment level was monitored with submerged maximum-minimum recording thermometers.

Algal production was estimated by measuring dissolved oxygen concentrations in each mesocosm over a full day-night period, using the light:dark periods to estimate net photosynthesis and respiration, respectively. Dawn, dusk, noon, and midnight readings were taken with a YSI model 58 oxygen meter equipped with a model 5739 probe. Net daytime oxygen production was added to night respiration to determine gross photosynthetic oxygen production. Standing crop of periphyton at the end of the experiment was determined by measuring chlorophyll *a* according to Lind (1979) from scrubs of algae attached to the outside of submerged air-lift tubes of known area. These suspended tubes were isolated from grazing by benthic ephydrid larvae, but were colonized by the same type and amount of diatoms and filamentous algae found on benthic substrates in each treatment. This provided a standard measure for comparing periphyton density over all treatments that was independent of grazing.

Taxonomic composition of benthic diatoms was determined from benthic surface sediment cores (12.6 cm^2) at the end of the 2-month experiment. Samples were oxidized by the hydrogen peroxide-dichromate method (van der Werff 1955). Slides were prepared in Hyrax® mounting medium, and diatom taxa were counted at magnifications of 1400 \times . A minimum of 300 valves was counted for each experimental replicate (i.e. mesocosm), and the average relative abundance of each diatom taxon (based on cell

TABLE 1. Mean percent relative abundance (\pm SE), number of taxa, and Shannon diversity of diatom communities in sediments from Mono Lake mesocosm experiments for selected salinity treatments after 8 weeks of incubation.

	50 g/L	75 g/L	100 g/L	125 g/L	150 g/L
<i>Achnanthes minutissima</i> Kütz.	8.0 (1.6)	0.5 (0.3)			
<i>Amphora pediculus</i> (Kütz.) Grun.	2.4 (0.8)		0.6 (0.3)		
<i>Anomoeoneis sphaerophora</i> (Ehr.) Pfitz.	3.1 (1.0)	5.6 (1.1)	2.8 (1.5)	9.1 (1.8)	4.5 (3.4)
<i>Cocconeis placentula</i> Ehr.	3.0 (1.0)	1.4 (0.4)	1.3 (1.0)		
<i>Campylodiscus</i> sp.			0.6 (0.6)		
<i>Cymbella minuta</i> Hilse ex. Rabh.	18.2 (3.2)				
<i>Cymbella pusilla</i> Grun.					2.1 (2.1)
<i>Denticula</i> sp.	1.8 (0.4)	1.1 (0.5)	1.7 (1.1)	5.3 (2.2)	10.3 (4.0)
<i>Diatoma tenue</i> Ag.	0.3 (0.3)				
<i>Diatoma vulgare</i> Bory	1.6 (0.7)				
<i>Epithemia</i> sp.	1.6 (0.4)	1.6 (1.0)	2.9 (1.0)	4.8 (0.6)	
<i>Fragilaria acus</i> Kütz.	1.1 (0.2)		0.6 (0.6)	1.3 (1.3)	
<i>Fragilaria brevistriata</i> Grun.	0.2 (0.2)				
<i>Fragilaria construens</i> v. <i>venter</i> (Ehr.) Grun.	0.2 (0.2)				
<i>Fragilaria fasciculata</i> (Ag.) Kütz.	1.7 (0.5)				
<i>Fragilaria pinnata</i> Ehr.					2.1 (2.1)
<i>Fragilaria ulna</i> (Nitz.) Ehr.	1.5 (0.4)				2.1 (2.1)
<i>Fragilaria vaucheria</i> (Kütz.) Peters.	1.5 (0.4)				
<i>Gomphonema subclavatum</i> (Grun.) Grun.	0.2 (0.2)				
<i>Melosira varians</i> Ag.	1.4 (0.4)				
<i>Navicula crucialis</i> (O. Müll.) Frenguelli	4.0 (0.8)	14.0 (1.6)	7.0 (1.3)	3.2 (1.9)	8.1 (6.9)
<i>Navicula cryptocephala</i> Kütz.	0.4 (0.2)				
<i>Navicula cryptonella</i> Lange-Bertalot	3.9 (1.0)				
<i>Navicula radiosa</i> Kütz.	2.6 (0.6)				
<i>Nedium</i> sp.					5.7 (3.5)
<i>Nitzschia amphibia</i> Grun.	2.1 (0.7)	1.3 (1.0)			
<i>Nitzschia communis</i> Rabh.	2.4 (0.4)	10.5 (0.6)	11.5 (1.0)	18.3 (5.2)	4.2 (4.2)
<i>Nitzschia dissipata</i> (Kütz.) Grun.	15.6 (4.5)	0.5 (0.3)	0.5 (0.5)		
<i>Nitzschia frustulum</i> Kütz.	4.9 (0.7)	41.0 (1.6)	41.7 (16.8)	33.2 (3.6)	19.5 (1.6)
<i>Nitzschia monoensis</i> Kociolet et Herbst	1.2 (0.5)	1.1 (0.1)	9.3 (2.6)	16.0 (3.2)	33.4 (5.9)
<i>Nitzschia palea</i> (Kütz.) W. Sm.	1.5 (0.4)	16.7 (2.2)	13.8 (4.8)	1.3 (1.3)	
<i>Nitzschia reimerii</i> Kociolek et Herbst	0.9 (0.4)	2.8 (0.3)	1.9 (0.9)		
<i>Rhoicosphenia abbreviata</i> (Ag.) Lange-Bertalot	12.0 (3.3)	0.6 (0.3)		2.9 (2.9)	2.9 (2.9)
<i>Rhopalodia</i> sp.	0.5 (0.2)		1.2 (0.8)	0.9 (0.9)	
<i>Stephanodiscus oregonicus</i> (Ehr.) Hak.	0.2 (0.2)	1.3 (0.5)	2.6 (1.1)	4.0 (1.4)	5.1 (4.0)
Number of taxa	30	15	16	12	12
Shannon diversity	4.03	2.57	2.82	2.90	2.96

counts) was determined for each salinity treatment. Diatom cells were unlikely to have appeared in sample counts of cleaned frustules unless some survival and growth of cells occurred. Differential growth and survival under varied salinity conditions produced consistent patterns of diatom distribution in each treatment rather than the random sampling of rare cells across treatments that would be expected if dead cells or empty frustules were an important component of benthic samples.

Samples for algal periphyton other than diatoms were taken from the south-facing walls of each tank after 2 months using a razor blade to scrape 20-cm² areas. When feasible, a minimum of 40 cell dimensions were taken from each treatment replicate for the primary forms found, filaments of *Ctenocladus circinnatus* Borzi (Chlorophyceae) and cyanobacteria (mainly *Oscillatoria* spp.). Estimates of biovolume ($\mu\text{m}^3\cdot\text{cm}^{-2}$) for *C. circinnatus* and cyanobacteria were made for each salinity using a Palmer counting chamber at 400 \times . Calculations of biovolume were based on the volume of a cylinder.

Statistical comparisons of the effects of salinity treatments were made using one-way ANOVA. Chlorophyll *a* biomass data were log transformed prior to analysis, and multiple comparisons were made using Scheffe's test. A diversity index (H') was calculated for diatom assemblages for each treatment (Shannon and Weaver 1949).

RESULTS AND DISCUSSION

The greatest change in species richness and diversity of the diatom-dominated benthic algal com-

munity of Mono Lake mesocosms occurred for a salinity change from 50 to 75 g·L⁻¹, with only minor changes in biotic indices in treatments >75 g·L⁻¹ (Table 1). The Shannon diversity index dropped from 4.0 to 2.6 and the number of diatom taxa decreased from 30 to 15 between treatments of 50 and 75 g·L⁻¹. Blinn (1993) also reported a strong negative relationship between salinity and H' diversity and richness of diatom taxa in saline lakes of western North America, with the greatest decline in biotic indices at salinities >45 mS specific conductance (near 50 g·L⁻¹). Blinn (1995) found a similar relationship in diatom communities of the saline lakes of Western Victoria, Australia. Furthermore, Wilson et al. (1996) reported <20% of the 204 diatom taxa used in assessing salinity inference models had an upper tolerance limit of ≥ 50 g·L⁻¹ salinity.

Denticula sp., *Nitzschia frustulum*, *N. monoensis*, *N. communis*, and *Stephanodiscus oregonicus* increased in relative importance in higher salinity treatments, making up over 70% of the diatom assemblage at 125 to 150 g·L⁻¹ (Table 1). In contrast, *Achnanthes minutissima*, *Cymbella minuta*, *N. dissipata*, and *Rhoi-*

TABLE 2. Mean cell widths and lengths (μm ; \pm SE) and biovolumes ($\mu\text{m cm}^{-2}$; \pm SE) for *Ctenocladus circinnatus* and filamentous cyanobacteria from various mesocosm salinity treatments after 8 weeks of incubation.

Salinity (g/L)	<i>Ctenocladus circinnatus</i>			Cyanobacteria		
	Mean cell width (μm)	Mean cell length (μm)	Biovolume ($\mu\text{m cm}^{-2}$)	Mean cell width (μm)	Mean cell length (μm)	Biovolume ($\mu\text{m cm}^{-2}$)
50	5.6 (0.6)	118.1 (72.8)	149×10^6 (115×10^6)	1.05 (0.06)	1.12 (0.02)	3.7×10^4 (3.4×10^4)
75	8.8 (0.6)	55.4 (25.8)	46.6×10^6 (32.8×10^6)	1.03 (0.05)	1.11 (0.01)	16.7×10^4 (22.7×10^4)
100	9.7 (0.2)	53.7 (20.1)	3.5×10^6 (0.9×10^6)	1.1 (0.05)	1.14 (0.03)	16.2×10^4 (3.4×10^4)
125			No cells			
150			No cells			

cosphenia abbreviata decreased in relative importance in elevated salinities. Although Wilson et al. (1996) reported that *S. oregonicus* was tolerant only of moderately high salinities (upper limit of $19.4 \text{ g}\cdot\text{L}^{-1}$), our study showed this species tolerant of salinities up to $150 \text{ g}\cdot\text{L}^{-1}$. *Nitzschia frustulum*, *N. communis*, *N. palea*, and *Navicula crucialis* exhibited dominance at intermediate salinity levels (75 to $125 \text{ g}\cdot\text{L}^{-1}$). These taxa are among the most common species in salt lakes of western North America, and our results are consistent with the intermediate salinity hypothesis (Herbst 1988), which suggests the abundance of these halophiles may be controlled by ecological factors, such as grazing and competition, at low salinity, and by physiological intolerance at higher salinities. Ephydrid larvae were most productive in low salinity mesocosms; thus, it is possible that increased grazing activity may also have contributed in part to the higher diatom diversity observed at $50 \text{ g}\cdot\text{L}^{-1}$ salinity through cropping of competitive dominants (grazer-mediated coexistence).

Other studies have shown similar patterns in diatom community structure with elevated salinities. Blinn (1993) and Wilson et al. (1996) reported that certain species of *Denticula* as well as *Nitzschia frustulum* tolerate relatively high salinities and are often

the dominant diatom taxa in nonmarine saline environments, whereas *N. dissipata* and *R. abbreviata* have only a moderate tolerance to elevated salinities. The clearly salt-tolerant *N. monoensis* was recently described by Kociolek and Herbst (1992) from deep sediments in Mono Lake and has also been found in Owens Lake cores (Bradbury 1993). These and other taxa exhibiting clear trends in the studies reported here may be useful as indicator signals for calibrating paleolimnological studies. Reconstruction of ancient lake levels using diatom stratigraphy has been based on correlations with distributions along environmental salinity gradients (e.g. the transfer functions of Fritz et al. 1991). Mesocosm results may permit a more direct and accurate calibration of stratigraphic records against the actual growth response of mixed species assemblages of diatoms and other benthic algae exposed to changing salinity levels.

The dramatic decrease in species richness at salinities $>50 \text{ g}\cdot\text{L}^{-1}$ further suggests that evolutionary pathways for the radiation of lacustrine diatom species occurred along salinity gradients that ranged from sea to freshwater rather than from seawater to hypersaline conditions. Blinn (1993) further supports this hypothesis in a study of 63 North American saline lakes, where he shows a striking increase in the number of diatom taxa at specific conductance loadings $<45 \text{ mS}$, with the greatest species diversity in waters dominated by NaCl rather than in carbonate or sulfate waters. This may indicate that highly saline nonmarine habitats provided only limited opportunity for the radiation of marine diatoms during the Oligocene and that these habitats presented physiological barriers to colonization. The importance of saline lake environments in the adaptive radiation of diatoms into lacustrine ecosystems requires laboratory studies in molecular genetics to further develop this hypothesis.

The filamentous chlorophyte, *Ctenocladus circinnatus*, occurred in salinity treatments ranging from 50 to $100 \text{ g}\cdot\text{L}^{-1}$. Over this growth range, there was a significant ($F = 5.2$, $P = 0.01$) decrease in the biovolume density of this alga at higher salinities (Table 2). Average biovolumes were >40 -fold high-

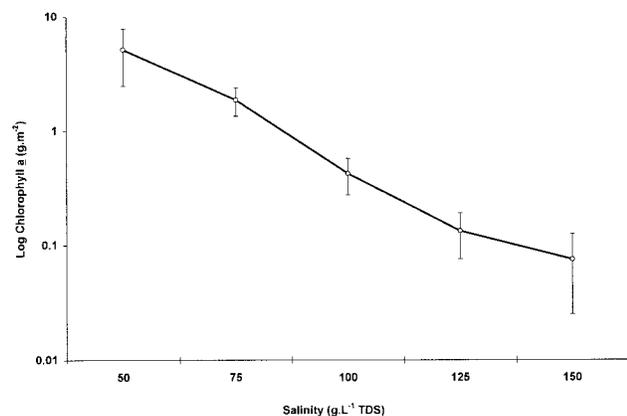


FIG. 2. Standing crop of periphyton in Mono Lake mesocosms, expressed as log-transformed chlorophyll *a* taken from samples of tank air-lift tubes. Error bars indicate standard deviations for four replicates per salinity treatment level.

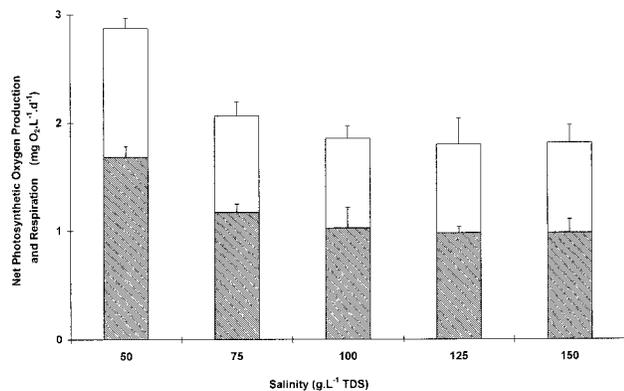


FIG. 3. Mesocosm metabolism expressed as net photosynthetic oxygen production during daylight hours (lower cross-hatched portion of bars) and oxygen consumption by respiration during the night (upper open portion of bars); total bar height estimates gross photosynthetic oxygen production. Diel measurements of dissolved oxygen changes taken 1 month into the 2-month experiment. Error bars indicate standard deviations for four replicates per salinity treatment level.

er at 50 than at 100 g·L⁻¹, and cells were not observed above 100 g·L⁻¹. These findings agree with those of Ruinen (1933), Blinn (1971), and Herbst and Castenholz (1994), where threshold salinity for akinete germination and vegetative growth was between 100 and 150 g·L⁻¹. This salt-tolerant alga has been reported from a number of saline lakes throughout North America (Blinn and Stein 1970, Blinn 1971, Hammer et al. 1983, Hammer 1986) and is a common constituent of the phytobenthos in Mono Lake and Abert Lake (Oregon) at salinities

below 100 g·L⁻¹ (Herbst 1988, Herbst and Castenholz 1994).

In addition to lower total biovolume, *Ctenocladus* cell width increased and length decreased with elevated salinity (Table 2). Width of cells averaged 5.6 and 9.7 μm, and length 118.1 and 53.7 μm, in treatments of 50 and 100 g·L⁻¹, respectively. Blinn and Stein (1970) and Blinn (1971) also found that cell dimensions of *C. circinnatus* became wider and shorter or formed akinetes under increased salinities. Herbst and Castenholz (1994) noted similar changes in cell size in *C. circinnatus* at salinities >50 g·L⁻¹ and suggested that a lower surface-to-volume ratio may reduce osmotic water loss from cells exposed to high external salt concentrations.

The average biovolumes of cyanobacteria in the various salinity treatments were several orders of magnitude lower than those for *C. circinnatus* (Table 2). Cyanobacteria also were absent from salinity treatments >100 g·L⁻¹ and were variable at lower salinities, but they showed no significant differences ($P > 0.1$) as noted in *C. circinnatus*. The absence of these *Oscillatoria* spp., capable of nonheterocystous nitrogen fixation, from high salinity treatments suggests that nitrogen fixation by cyanobacteria may be confined to lower salinity levels. Nitrogenase activity in Mono Lake sediments has also been found to be inhibited by salinity (Herbst, unpubl.).

There were significant reductions in chlorophyll *a* of benthic algae ($F = 9.4$, $P = 0.001$) and mesocosm net photosynthesis ($F = 10.7$, $P = 0.001$) between salinity treatments (Figs. 2, 3). A post hoc

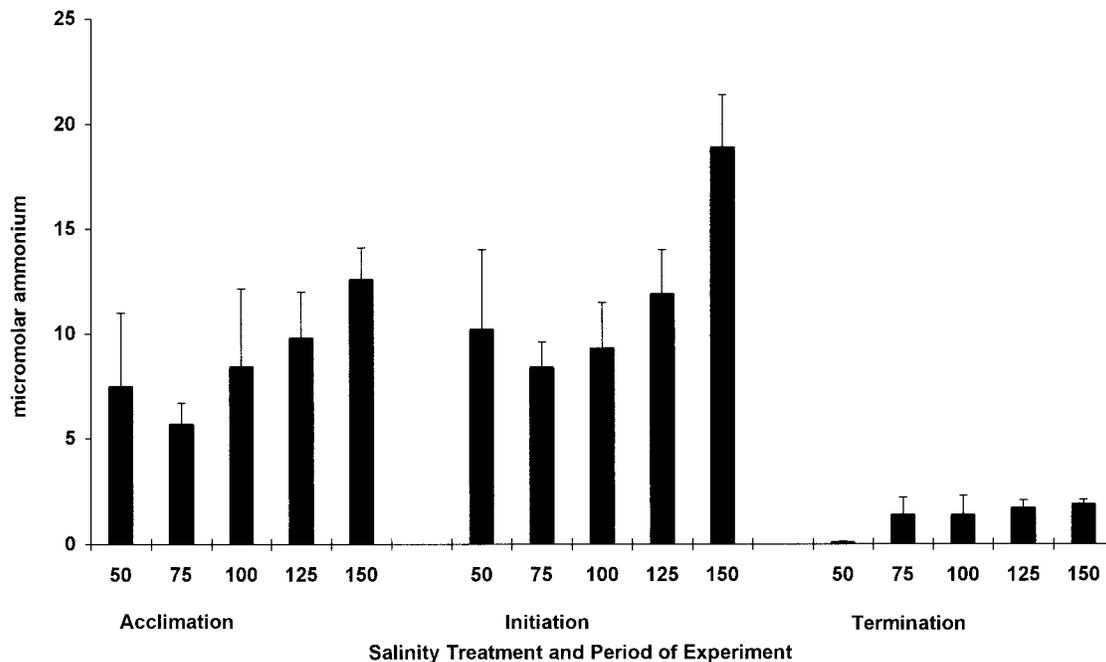


FIG. 4. Ammonium nutrient levels in experimental mesocosm salinity treatments. Samples taken during salinity acclimation phase, at experiment initiation (inoculation), and at termination (2 months after initiation). Error bars indicate standard deviations for four replicates per salinity treatment level.

Scheffe multiple comparison test on log-transformed data of chlorophyll *a* standing crops showed significant differences ($\alpha = 0.05$) as follows: $50 > 75 > 100 > 125 = 150 \text{ g}\cdot\text{L}^{-1}$. Mesocosm metabolism, however, showed differences only between $50 \text{ g}\cdot\text{L}^{-1}$ and all other treatments. The large decrease in periphyton chlorophyll *a* standing crop without a concomitant drop in net photosynthetic oxygen production may have resulted from chlorophyll *a* estimates having been made on attached algae, whereas net oxygen production of mesocosms was the product of both planktonic and benthic photosynthesis. It is possible that planktonic algae increased in the higher salinity treatments and maintained oxygen production even while benthic algae were reduced. This is supported by the observation that turbidity was sometimes higher in tanks at high salinity treatments, possibly due to the presence of halophilic phytoplankton such as *Dunaliella*, which has optimum growth above $100 \text{ g}\cdot\text{L}^{-1}$ (Javor 1989).

The nitrogen source in Mono Lake occurs mainly in the form of ammonium (Jellison et al. 1993). Ammonium in mesocosm tanks was found to increase with salinity before inoculation (ranging from about 5 to $20 \mu\text{M}$, Fig. 4) but was depleted in all treatments at termination of the experiment. This suggests that while all treatments supported biological uptake activity, benthic primary production was reduced at high salinity even though more nitrogen was available. Greater nutrient availability apparently cannot compensate for the inhibitory effects of salinity.

Although caution should be used in applying the results of mesocosm experiments to nature (Carpenter 1996), separate laboratory and field observations support the conclusions and generality of our studies. Independent data from field surveys (Blinn 1993) and lab cultures (Herbst and Castenholz 1994) are consistent with our interpretation of salinity constraints on periphyton production and diversity.

This work contributes to an understanding of saline lake food chains because diatoms and other benthic algae form the primary food source of the alkali fly *Ephydra* (*Hydrophyrus*) *hians* Say (Diptera: Ephydriidae), often the dominant benthic invertebrate of many alkaline salt lakes and ponds in the Great Basin (Herbst 1988, Bradley and Herbst 1994). This insect and other *Ephydra* species are integral to saline lakes as wildlife habitats because they support the food requirements of dozens of species of shorebirds and waterfowl, which may number in the hundreds of thousands (Boula 1985, Jehl 1994, Rubega and Inouye 1994, Elphick and Rubega 1995). Few of these productive lakes remain in the Great Basin, and our results argue that their conservation should be tied to management of salinity levels that sustain their diversity and productivity. Though we have not yet examined salinity effects below $50 \text{ g}\cdot\text{L}^{-1}$, from this level to $75 \text{ g}\cdot\text{L}^{-1}$ appears

to permit the best conditions for production and diversification of benthic algae in Mono Lake. Prolonged salinity exposures above $100 \text{ g}\cdot\text{L}^{-1}$ without local low salinity refugia on lake and playa margins, could limit the capacity of Mono and other saline lakes to support large populations of consumers.

CONCLUSIONS

Mono Lake is one of a few perennial deep alkaline salt lakes in the world (Melack 1983). Diversion of tributary stream flow and resulting salinity increases in this lake threaten sustained benthic primary production and algal species diversity relative to conditions prior to stream diversion. Evidence of such changes was shown in experimental mesocosms where the prediversion salinity of $50 \text{ g}\cdot\text{L}^{-1}$ supported significantly higher periphyton chlorophyll *a* biomass and twice the diatom diversity found at higher salinity treatment levels. Lower salinities supported greater biomass and diversity of algae despite the availability of more ammonium in the higher salinities. Maintenance of a benthic algal community is critical to aquatic foodwebs in saline ecosystems, because these primary producers are the principal food source of brine flies of the genus *Ephydra*, often the dominant benthic invertebrate of saline lakes in the Great Basin. These invertebrates in turn support diverse and abundant bird communities that frequent these habitats. The 1994 decision of the California State Water Resources Control Board ordering the return of stream flows to Mono Lake was based in part on the evidence of lost production and diversity presented in this paper. The Water Board order will raise the lake level and reduce salinity to around $75 \text{ g}\cdot\text{L}^{-1}$ and is expected to enhance the diversity and productivity of the benthic algae of this ecosystem.

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