

SALINITY AND NUTRIENT LIMITATIONS ON GROWTH OF BENTHIC ALGAE FROM TWO ALKALINE SALT LAKES OF THE WESTERN GREAT BASIN (USA)¹

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ABSTRACT

Enrichment cultures of littoral benthic algae from Mono Lake, California, and Abert Lake, Oregon, were grown under conditions of varied salinity and nutrient content. Field-collected inocula were composed mainly of diatoms and filamentous blue-green and green algae. The yield of long-term cultures (30 days) showed tolerance over a broad salinity range (50–150 g·L⁻¹) for Mono Lake-derived algae. Algae from Abert Lake had a lower range of tolerance (25–100 g·L⁻¹). Organic content and pigment concentrations of algae from both lakes were also reduced above the tolerated salinity level. Within the range of salinity tolerance for Mono Lake algae, initial growth rates and organic content were reduced by increased salinity. The effects of macro- and micronutrient enrichment on algal growth in Mono Lake water were also tested. Only nitrogen enrichment (either as ammonium or nitrate) stimulated algal growth. Although the benthic algae cultured here had wide optima for salinity tolerance, the rates of growth and storage were limited by increased salinity within the optimum range. Although the lakes compared had similar species composition, the range and limits of tolerance of the algae were related to the salinity of the lake of origin.

Key index words: Abert Lake; algal mat; benthic algae; blue-green algae; diatoms; green algae; halotolerance; Mono Lake; periphyton; saline lakes

Benthic algae in saline lake ecosystems inhabit a varied and often extreme chemical environment. Due to climatic variations, saline lakes are subject to increased salinity and even desiccation in ephemeral ponds or under drought conditions. Regional differences in geochemistry and geomorphology produce waters with a wide range of ionic composition, pH, suspended solids, and redox potential. Growth and persistence of algae under these conditions require physiological tolerance and/or resistant stages in the life cycle. The spectrum of variation present between habitats or through time in a changing habitat may alter the species and organic

composition, growth rates and form, and productivity of the algal flora.

Benthic algae in saline lakes often occur in cohesive microbial mats, composed mostly of filamentous blue-green algae and diatoms (Bauld 1981). These mats grow on sediment or rock surfaces and sometimes form calcareous deposits. Although some detailed studies of mat structure and metabolism have been conducted (Cohen et al. 1977, Jorgensen et al. 1979), very little information is available on the influence of salinity on the growth of algal mat assemblages.

Studies of phytoplankton production in lakes undergoing natural increases in salinity have shown dramatic declines in abundance (Vareschi 1982) and/or species composition (Comin et al. 1983), sometimes followed by increased productivity of benthic algae (Melack 1988) due to higher light levels. Osmoregulation in naked planktonic algal cells exposed to increased salinity is achieved by accumulation of organic solutes such as glycerol (Hellebust 1976). Although osmoregulation in *Dunaliella* and other halotolerant algae permits salinity tolerance, optimal growth usually occurs over the lower range of tolerance (Van Auken and McNulty 1973, Brock 1975, Ben-Amotz and Avron 1983, Hellebust and Le Gresley 1985).

Despite the attention given saline lake phytoplankton, comparable information on benthic algae is scant. Knowledge of the type of osmolyte used by blue-green algae in osmoregulation shows promise for predicting salinity tolerance (Reed et al. 1986) but only over broad ranges for certain species. Both the relationship of habitat salinity to the biogeography and productivity of benthic algal species and autoecological experiments on growth at varied salinities need to be studied.

Benthic algal assemblages used in this study were derived from Mono Lake, California, and Abert Lake, Oregon. Mono Lake is an alkaline salt lake, located at nearly 2000 m elevation on the western edge of the Great Basin, adjacent to the eastern escarpment of the Sierra Nevada Mountains. At the time of this study (spring 1986), the lake had a total dissolved salts (TDS) concentration of about 85 g·

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L^{-1} and a pH of 10 (Herbst, unpubl. data). Mono Lake has an anion chemical composition consisting of high proportions of carbonate, bicarbonate, sulphate, and borate, in addition to chloride (Herbst 1988). Sodium is the principal cation. Since the diversion of tributary streams in 1941, Mono Lake has dropped over 12 m in elevation and more than doubled in salinity. The effect of these changes on the aquatic organisms of the lake has become a significant conservation issue because of the importance of Mono Lake to wildlife. Mono Lake produces abundant populations of a benthic insect (the alkali fly, *Ephedra hians* Say) that serves as food to hundreds of thousands of breeding and migratory birds that depend upon Mono Lake as a habitat (Herbst 1988). Benthic algae are the primary food resource to the larvae and adults of the alkali fly.

Abert Lake is a shallow fault-scarp lake at 1300 m in south-central Oregon. It had a salinity of around $20\text{ g}\cdot\text{L}^{-1}$ in the spring of 1986 (Herbst, unpubl. data) and is also composed of chloride and carbonate salts of sodium, with a pH of 10. Abert thus has a similar chemical composition to Mono Lake, differing mainly in salinity, and also shares many of the same benthic algal species. Both lakes had as their primary benthic algal taxa the diatom *Nitzschia frustulum* Kützing, the filamentous blue-green *Oscillatoria* spp. (several forms), and the filamentous green alga *Ctenocladus circinnatus* Borzi. Other less abundant taxa that were probably present have been listed elsewhere (Herbst 1988).

The objective of this study was to examine the growth responses of the same taxa of benthic algae derived from the two different source lakes. Experiments were designed to test for (1) salinity effects on tolerance, measured as yield and biochemical composition after prolonged culture, (2) salinity effects on initial growth rates within the range of tolerance under conditions where nutrients were not limiting, and (3) nutrient limitation in cultures at constant salinity. These studies will contribute to an understanding of the tolerance and growth of natural assemblages of benthic algae in relation to changes in the salinity of alkaline lake water. A related goal of this study was to provide an understanding of the effects of salinity on the algal food resources of the benthic grazing alkali fly at Mono Lake.

MATERIAL AND METHODS

Benthic algal inocula for experimental cultures were collected in late spring 1986 from shallow water (<30 cm). Samples were collected from mats on surface detritus and mud and off rocks (limestone tufa at Mono Lake and basalt at Abert Lake). Microscopic examination of samples from both sediment and epilithic sources showed essentially the same species were present, so samples from both sites were pooled as the inoculum from each lake.

Collected algae were combined in a small volume of sterile-filtered lake water ($0.45\text{ }\mu\text{m}$ filter) and homogenized by repeatedly drawing the contents into and out of a 10 mL sterile syringe (1.5 mm opening). This procedure disrupted cohesiveness of the algae

but did not break the cells. The mixed inoculum was delivered in 0.5 mL aliquots into 50 mL of the various culture media.

Algal cultures were grown in replicate 250 mL Erlenmeyer flasks and 50 mL of sterile-filtered Mono Lake or Abert Lake water media. Varied salinities of natural lake water were prepared either by evaporating the water slowly in large shallow pans at 25°C (for elevated salinities), or by dilution with distilled water (for low salinities). In experiments in which salinity was a variable, all cultures were given the following standard nutrient enrichments: 1.8 mM NaNO_3 , 0.3 mM Na_2HPO_4 , 0.2 mM sodium metasilicate, trace elements (in μM), Fe 1.8, Mn 7.3, Zn 0.8, Cu 0.3, Mo 2.0, Co 0.2 (all chelated with $25\text{ }\mu\text{M}$ EDTA); vitamins (in $\mu\text{g}\cdot\text{L}^{-1}$), thiamine 250, biotin 5, and cyanocobalamin 2.5. Light irradiance was approximately $85\text{ }\mu\text{E}\cdot\text{m}^{-2}\cdot\text{sec}^{-1}$ at culture level, on a photoperiodic cycle of 14:10 h L:D.

Three separate experiments were conducted. In the first experiment, salt tolerance of benthic algae from both Mono and Abert Lakes were evaluated by measuring the organic growth yield of cultures at salinities of 25, 50, 75, 100, 150, and $200\text{ g}\cdot\text{L}^{-1}$ TDS and a temperature of 14°C (average late spring shallow water temperature). After exposure for 30 days, half of each replicate culture (3 or 4 replicates per salinity) was removed and centrifuged. The supernatant was decanted, and the pelleted algae were resuspended in distilled water, centrifuged, and transferred to pre-weighed aluminum pans. Samples were dried to constant weight, ashed at 550°C for 3 h, and reweighed.

The other half of each culture replicate was centrifuged and washed as above. The final pellet was frozen at -20°C for 1 day, thawed, and pulverized with a glass stirring rod in 5 mL alkaline 90% acetone. After 1 day of extraction at 4°C in darkness, the light absorbance spectrum of the supernatant pigment extract was read at 750, 663, 630, and 480 nm. The extract was then acidified and readings repeated at 750 and 663 nm. Chlorophyll *a* concentration was determined using the equation of Jeffrey and Humphrey (1975) for algae containing mainly Chl *a* and *c*. Carotenoid pigment content was determined from the equation in Wetzel and Likens (1979) for algae composed mostly of diatoms. Growth response to salinity was expressed as net organic weight gain (ash-free dry weight = AFDW), % organic content, and pigment content (chlorophyll *a* and carotenoid, in $\mu\text{g}\cdot\text{mg}^{-1}$ AFDW).

In the second experiment, specific growth rates of Mono Lake benthic algae were measured within the salinity tolerance range, at 50, 100, and $150\text{ g}\cdot\text{L}^{-1}$, and a temperature of 20°C . Cultures were harvested at 3, 6, and 10 days after inoculation, and net dry weight yield plotted against time. Organic content was also measured in these cultures.

In the third experiment, natural nutrient limitations on growth of algae from Mono Lake were assessed by comparing complete standard enrichment cultures with cultures selectively enriched with one of the following: (1) 2 mM NaNO_3 , (2) 2 mM NH_4Cl , (3) 2 mM Na_2HPO_4 , (4) 0.2 mM sodium metasilicate, (5) trace elements (as above), and (6) vitamins (as above). Selective enrichments were done in duplicate at salinities of 50 and $100\text{ g}\cdot\text{L}^{-1}$, and recorded as net dry weight yield after 10 days (at 20°C).

RESULTS

The optimum yield of Mono Lake benthic algae occurred over a salinity range of $50\text{--}150\text{ g}\cdot\text{L}^{-1}$ TDS (Fig. 1A). At the most dilute ($25\text{ g}\cdot\text{L}^{-1}$) and most concentrated ($200\text{ g}\cdot\text{L}^{-1}$) salinities, the net organic weight yield was significantly lower than for intermediate salinities (ANOVA and Fisher's least significant difference test at the 0.05 level). Percent organic content of algae was, however, greatest at $25\text{ g}\cdot\text{L}^{-1}$, where it reached about 45% of the total biomass (Fig. 1B). Organic content was lowest (17%)

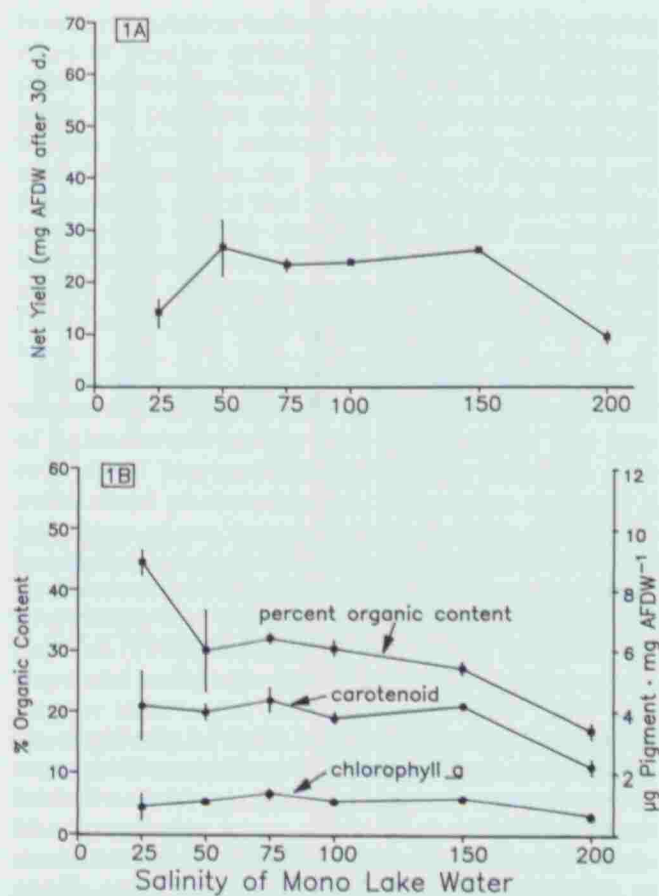


FIG. 1A, B. Response of Mono Lake benthic algae to salinity. Three replicates per salinity. Error bars show standard errors. (A) Net organic growth yield (ash-free dry weight = AFDW) of cultures from a range of salinities after 30 days. (B) Percent organic content and pigment content (carotenoid and chlorophyll *a*) of algae harvested from cultures shown in Fig. 1A.

at 200 g·L⁻¹. Algae cultured in the 50–150 g·L⁻¹ range contained intermediate levels of organic matter at around 30% of the total dry weight (Fig. 1B). In addition, chlorophyll *a* and carotenoid pigment content were reduced in algae grown at 200 g·L⁻¹ relative to algae grown at all other salinities examined (Fig. 1B). Qualitative inspection of these cultures indicated higher proportions of blue-green algae at lower salinities (50 g·L⁻¹ and especially 25 g·L⁻¹) and a predominance of diatoms at higher salinities.

Optimum yield of Abert Lake algae occurred over a lower and more narrow salinity range of 25–100 g·L⁻¹ (Fig. 2A) compared to Mono Lake algae. However, the percent organic content also declined with increased salinity over this range (Fig. 2B). At 150 and 200 g·L⁻¹, growth yield and organic content were reduced significantly compared to lower salinities (ANOVA and Fisher's LSD test at 0.05 level), and pigments were undetectable at 200 g·L⁻¹ (Fig. 2B). Again, qualitative inspection suggested that filamentous green and blue-green algae were the dom-

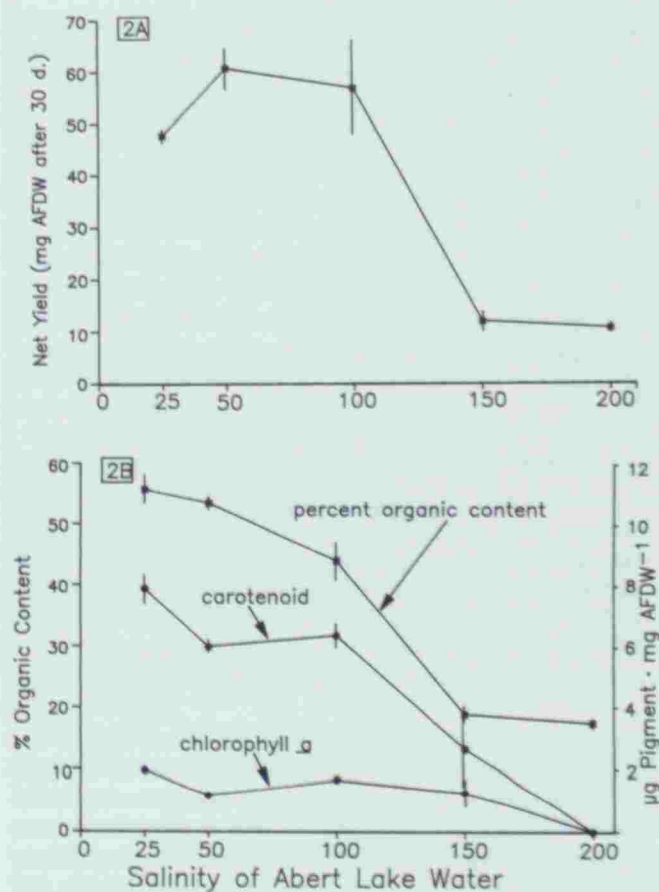


FIG. 2A, B. Response of Abert Lake benthic algae to salinity. Four replicates per salinity. Error bars show standard errors. (A) Net organic growth yield (ash-free dry weight = AFDW) of cultures from a range of salinities after 30 days. (B) Percent organic content and pigment content (carotenoid and chlorophyll *a*) of algae harvested from cultures shown in Fig. 2A.

inant forms at low salinity, and diatoms were more common at 100 g·L⁻¹.

Within the optimum range of tolerance for Mono Lake algae defined by the experiment above, initial growth rates were found to be reduced with increasing salinity due to delays in the maximum growth phase (Fig. 3). The period of most rapid growth occurred over days 0–3 at 50 g·L⁻¹, over days 3–6 at 100 g·L⁻¹, and over days 6–10 at 150 g·L⁻¹. At final harvest (10 days), combustion of the dried algae showed decreasing organic content with increased salinity (50 g·L⁻¹, 72% (SD = 7%); 100 g·L⁻¹, 66% (SD = 5%); 150 g·L⁻¹, 52% (SD = 4%)). After prolonged growth (stationary phase) the organic weight yields at these salinities converged to similar amounts (evident in Fig. 1A).

Selective nutrient enrichment experiments showed that only nitrogen was limiting in Mono Lake water (Fig. 4). Furthermore, nitrogen was used either as nitrate or ammonium. Enrichments at 50 vs. 100 g·L⁻¹ salinity produced no marked differences in growth, with the possible exception of a reduced

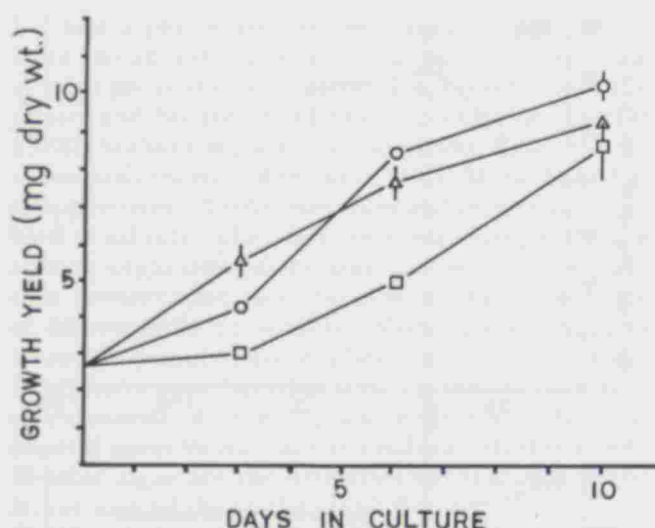


FIG. 3. Influence of salinity on initial growth rates of Mono Lake benthic algae. Δ = 50 $\text{g}\cdot\text{L}^{-1}$, \circ = 100 $\text{g}\cdot\text{L}^{-1}$, \square = 150 $\text{g}\cdot\text{L}^{-1}$, $n = 2$ for harvests at 3 and 6 days, and 3 at 10 days. Error bars show standard deviations.

growth response to ammonium at 50 $\text{g}\cdot\text{L}^{-1}$. Ambient concentrations of dissolved inorganic nitrogen in Mono Lake water are extremely low, typically below 3 μM , and mainly in the form of ammonium (Jellison and Melack 1986). Concentrating or diluting natural lake water would thus have made no significant changes in dissolved nitrogen concentrations relative to the enrichments added to these experimental cultures (2 mM).

DISCUSSION

The range of salinity tolerance found in this study suggests that the benthic algae examined are broadly halotolerant (euryhaline), but not halophilic (sensu Ben-Amotz and Avron 1983). Golubic (1980) criticized the use of this latter term in that salt requirements may exist but are not restricted to the extreme high salinities to which the term has usually been applied. Moreover, Golubic stressed the need to define halotolerance in terms of growth, recognizing that growth is affected by salinity within the range of tolerance. The mixed species assemblages of benthic algae studied here grew best over low to moderate salinity ranges (oligo- to meso-euryhaline, sensu Golubic) but appeared to have some limitations imposed on growth at the lowest salinity examined (25 $\text{g}\cdot\text{L}^{-1}$). High organic content of Mono Lake algae showing poor growth at 25 $\text{g}\cdot\text{L}^{-1}$ may be associated with lower rates of cell division and accumulation of storage compounds. Halotolerance above this low salinity level, however, is not equal over the entire range defined by stationary phase growth yields. Though Mono Lake algae showed optimum yield up to 150 $\text{g}\cdot\text{L}^{-1}$ and some growth even at 200 $\text{g}\cdot\text{L}^{-1}$, increased salinity reduced the initial rate of growth and the organic and pigment

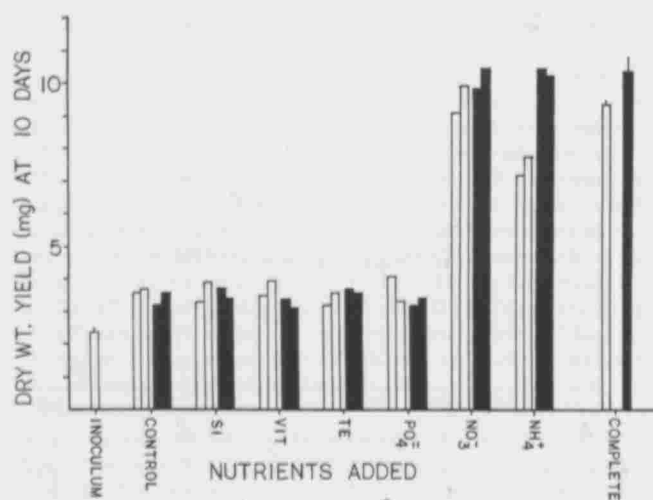


FIG. 4. Selective nutrient enrichments of Mono Lake water at 50 $\text{g}\cdot\text{L}^{-1}$ (white bars) and 100 $\text{g}\cdot\text{L}^{-1}$ (black bars) [duplicates for each nutrient/salinity]. Enrichment abbreviations: Si, silicate; Vit, vitamins; TE, trace elements. Error bars for complete enrichment and inoculum show standard deviations (for $n = 3$).

contents. Optimum yields of Abert Lake algae occurred only up to 100 $\text{g}\cdot\text{L}^{-1}$ and showed the same reduced organic and pigment content with increased salinity.

Abert Lake algae achieved high yields over a lower salinity range than did Mono Lake algae. Since the source waters of Abert Lake are less saline than Mono Lake, this suggests that algal growth was better at salinities closer to those of native waters. This may be due in part to differences in the proportions of the dominant algal species present in the inocula. *C. circinnatus* appeared to be the dominant form in the Abert inoculum, and growth of clones of this species from either lake were maximal at 25–75 $\text{g}\cdot\text{L}^{-1}$ with no growth occurring at 150 $\text{g}\cdot\text{L}^{-1}$ (Herbst 1986). *N. frustulum* appeared to be the most common algal form in Mono inoculum and was predominant in high salinity cultures. Other explanations of the differences observed in growth response to salinity between algae from each lake are that different genetic varieties of algal species may exist in each lake or that physiological acclimation may produce better growth at salinities near those of the native habitat. Morphological and ecological variation within *N. frustulum* and *Oscillatoria* is widely recognized (Reimer 1954) and probably has both genetic and physiological bases. Pre-acclimation of *C. circinnatus* clones to high salinity, however, did not enhance growth at high salinity (Herbst 1986). Finally, competition between the algal species present may further modify the extent to which salinity determines growth and species distributions. Distinguishing between these explanations awaits isolation of unialgal cultures and clones from different habitats and further descriptions of growth physiology.

Salinity-induced growth delays and reduced car-

bon accumulation indicate that decreases in relative rates of benthic primary production could accompany increased salinity in Mono Lake. Reduced organic and pigment content of algae at increased salinities probably reflects poor growth within taxa and differences in the proportions of diatoms and filamentous green and blue-green forms occurring in different salinity treatments. These results also indicate that increased salinity will limit the availability and nutritional value of the benthic algae food resource to benthic herbivores such as *Ephydra hians*.

Batterton and Van Baalen (1971) found inhibitory effects of increased NaCl concentration on growth of halotolerant marine blue-green algae. The heterocystous marine blue-green alga *Rivularia atra* maintained photosynthetic competence through a full range of sea water salinities from 0–100‰ SW, but N-fixation declined with increased salinity (Reed and Stewart 1983). Morphology of marine blue-green algae also was shown to be affected by salinity. Sanders (1979) described a 10–20 mm thick mat on intertidal sediments underlain by 33 ppt sea water. Higher tidal zones held a deeper water table at a lower salinity of 3–15 ppt and developed only thin mats (1–5 mm). Growth of these mats occurred in both 0 and 20 ppt salinity, but only one species of blue-green alga grew at the higher salinity. Non-marine blue-green algae such as *Aphanothece halophytica* and *Phormidium hypolimneticum* are known to be extremely halotolerant, growing at salinities in excess of 200 g·L⁻¹ (Borowitzka 1981, Dor and Ehrlich 1987).

Autecological studies of salinity effects on benthic marine intertidal diatoms have shown relatively wide tolerance to varied salinity (Admiraal 1977). Above 60 ppt, however, both unialgal cultures and mixed field collections showed reduced rates of net photosynthesis. Pre-acclimation of cultures permitted only slightly enhanced photosynthesis at elevated salinities.

Ehrlich (1978) found a more abundant and diversified diatom flora at low, winter salinities (75–100 ppt) in the sea water-evaporated brines of Solar Lake (Sinai) than at summer salinities (130–180 ppt). Similarly, Dor and Ehrlich (1987) reported diatoms in solar salt ponds near the Dead Sea to be the dominant benthic algae at salinities between 30–72 g·L⁻¹ but at lower densities at salinities up to 180 g·L⁻¹. Fischer (1979) found that Solar Lake diatoms had a high tolerance for increasing osmotic concentration. High osmotic potential of the cell sap, combined with a tolerance of plasmolysis, permitted survival in 160+ ppt Solar Lake water, though the effect of salinity on growth was not determined. Intertidal diatoms displayed a more rapid osmotic response to changing salinity compared to the more tolerant but slower adjusting diatom cells from Solar Lake. In an unpublished study (W. Thomas, pers. comm.), *Nitzschia* sp. isolated from Mono Lake

showed maximal growth response (measured as optical density of cultures) at a salinity of about 50 g·L⁻¹ but grew up to 150 g·L⁻¹.

Since growth of the benthic algae examined here was restricted above 150 g·L⁻¹ Mono Lake water, other algal/microbial species may replace these algae in more saline waters. Enrichment cultures of benthic algae from Great Salt Lake, Utah, were dominated by a mixture of diatoms and filamentous blue-green algae up to a salinity of 160 ppt (Brock 1975). Above this salinity, from 160–230 ppt, the unicellular blue-green, *Aphanothece halophytica* dominated, and above 230 ppt, *Dunaliella salina* outgrew *A. halophytica*.

Algal succession may occur in Mono Lake with increasing salinity. We have observed *Aphanothece* and *Dunaliella* in small numbers in the lake or in adjacent pools. Furthermore, bacteria may become a more important component of microbial mats under hypersaline conditions. The purple sulphur bacterium *Ectothiorhodospira* from alkaline lakes, for example, has a growth range from 100 to over 300 ppt NaCl, with an optimum at around 200 ppt (Borowitzka 1981).

Nitrogen concentration in Mono Lake water appeared to be limiting growth of the benthic algae. Either ammonium or nitrate can be utilized. The rate at which nitrogen is supplied, either by decomposition or excretion at the benthic interface, or by the upwelling of nitrogen-rich hypolimnetic water, probably limits benthic algal growth in Mono Lake. Nitrogen also limits productivity of the phytoplankton community in Mono Lake (Jellison and Melack 1986).

The growth of mixed species cultures of benthic algae from saline lakes provides a bioassay for the tolerance and response of natural assemblages to changing salinity. The causes of change in growth rate and biochemical composition, however, cannot be ascertained without monitoring changes in species composition or comparing responses of unialgal cultures. We plan to apply this approach in an attempt to better understand benthic productivity in saline lake ecosystems.

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VARIATION IN DIATOM COMMUNITY STRUCTURE AMONG HABITATS IN SANDY STREAMS¹

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ABSTRACT

Community structure of benthic diatoms in two sandy streams was studied for two summers to assess differences in abundances and species composition among habitats and between years and streams. The greatest differences in abundances (cells·cm⁻²) were lower abundances on rocks than on sand, whether the sand was clean or covered with flocculent organic material. Relatively little variation in abundances occurred between years and streams. Species composition of diatom communities varied more among habitats and between streams than from year to year. Species composition was most unique in floc-covered sand when communities in clean and floc-covered sand, rock, plant,

and plankton were compared. Diatom species composition in these sandy streams was most similar on sand and rocks.

Key index words: benthos; diatoms; epilithon; epiphyton; epipsammon; habitats; periphyton; plankton; substrata

In some environments, different benthic diatom communities can be found on different substrata (e.g. Douglas 1958), whereas in others epilithic, pelagic, and epiphytic communities are similar (e.g. Moore and McIntire 1977, Sullivan 1982). The physicochemical conditions of both water and substratum can affect benthic diatoms (Pringle 1987, Cox 1988). Variations in organic content of sediments and even the mineral content of individual sand grains have been correlated to community composition (Amspoker and McIntire 1978, Krecji and Lowe 1986), but effects of substratum charac-

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