

The Great Salt Lake Ecosystem (Utah, USA): long term data and a structural equation approach

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Abstract. Great Salt Lake (Utah, USA) is one of the world's largest hypersaline lakes, supporting many of the western U.S.'s migratory waterbirds. This unique ecosystem is threatened, but it and other large hypersaline lakes are not well understood. The ecosystem consists of two weakly linked food webs: one phytoplankton-based, the other organic particle/benthic algae-based.

Seventeen years of data on the phytoplankton-based food web are presented: abundances of nutrients (N and P), phytoplankton (Chlorophyta, Bacillariophyta, Cyanophyta), brine shrimp (*Artemia franciscana*), corixids (*Trichocorixa verticalis*), and Eared Grebes (*Podiceps nigricollis*). Abundances of less common species, as well as brine fly larvae (*Ephydria cinerea* and *hians*) from the organic particle/benthic algae-based food web are also presented. Abiotic parameters were monitored: lake elevation, temperature, salinity, PAR, light penetration, and DO. We use these data to test hypotheses about the phytoplankton-based food web and its weak linkage with the organic particle/benthic algae-based food web via structural equation modeling.

Counter to common perceptions, the phytoplankton-based food web is not limited by high salinity, but principally through phytoplankton production, which is limited by N and grazing by brine shrimp. Annual N abundance is highly variable and depends on lake volume, complex mixing given thermo- and chemo-clines, and recycling by brine shrimp. Brine shrimp are food-limited, and predation by corixids and Eared Grebes does not depress their numbers. Eared Grebe numbers appear to be limited by brine shrimp abundance. Finally, there is little interaction of brine fly larvae with brine shrimp through competition, or with corixids or grebes through predation, indicating that the lake's two food webs are weakly connected.

Results are used to examine some general concepts regarding food web structure and dynamics, as well as the lake's future given expected anthropogenic impacts.

Key words: *Artemia franciscana*; brine shrimp; food webs; Great Salt Lake, Utah; hypersaline; phytoplankton; *Podiceps nigricollis*; terminal lake; waterbirds.

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INTRODUCTION

We summarize results from 13 years (1994–2006) of our ongoing study on the ecosystem of the Great Salt Lake (Utah), a hypersaline terminal lake, along with four years found in the literature (1970–1994). Data collection focused on physical characteristics of the lake, nutrients (nitrogen and phosphorus), phytoplankton (Chlorophyta, Bacillariophyta, Cyanophyta), brine shrimp (*Artemia franciscana*) populations, and Eared Grebe (*Podiceps nigricollis*) populations. Incidental population data on other species, such as brine fly larvae (*Ephydria cinerea* and *hians*), corixids (*Trichocorixa verticalis*), protozoans, dinoflagellates, and copepods, are presented. These data were employed to address hypotheses regarding intra- and inter-annual variability in abiotic and biotic effects on the food web involving nutrients, phytoplankton, brine shrimp and Eared Grebes, as well as incidental interactions with other species. We hypothesize that this simple highly productive food web is driven by the bottom-up process of nutrient availability, not the stressful conditions posed by extreme salinity and seasonal temperatures. Each trophic level is examined using a structural equation approach (regression models constructed a priori based on hypothesized relationships).

Lack of long term and extensive data on the Great Salt Lake became a concern due to the Great Salt Lake's potential environmental degradation with urbanization along its shores, increased agricultural runoff, decreased freshwater inputs, mining of its waters for minerals, and commercial harvesting of brine shrimp. In addition, the commercial harvesting of brine shrimp became a conservation issue, because the lake's large waterbird populations (one-third of all western U.S. waterbirds nest or migrate through Great Salt Lake: Paul and Manning 2002) rely upon this abundant and relatively large zooplankton, as well as brine fly larvae (*Ephydria* spp.), to supply energy for spring and fall migrations. Therefore, our study was initiated in 1994 to monitor the brine shrimp and waterbird populations, as well as the lake's general limnological dynamics.

The Great Salt Lake is the fourth or fifth largest

terminal saline lake in the world (depending on metric): only the Caspian Sea (Russia and Iran), Aral Sea (Kazakhstan and Uzbekistan), Lake Balkash (Kazakhstan), which is partially freshwater, and Lake Urmia (Iran) are larger. Great Salt Lake is the largest terminal lake in the western hemisphere. Hypersaline lakes are interesting because their harsh environmental conditions, especially high salinity, lead to relatively simple food webs and ecosystems, which allow basic ecological concepts (e.g., top-down vs. bottom-up control) to be more easily investigated. Yet the food webs and ecosystems are not so simple (Boetius and Joye 2009) that they do not reflect the dynamics shared by more complex ecosystems. Therefore, hypersaline systems may provide a model that combines some of the simplicity of laboratory experiments and the complexity of natural systems.

Saline, especially hypersaline, lakes and inland seas have not received much attention from ecologists for a number of reasons (Collins 1977, Hammer 1986). First, these ecosystems are not considered common, which is true for North America and Europe, but this is not the case worldwide where saline lakes and inland seas encompass nearly as much water volume as freshwater lakes (1.04×10^5 versus 1.25×10^5 km³: Horne and Goldman 1994). Second, saline lakes are often considered uninteresting because of their simplicity due to the small number of species that are able to cope with the stresses of high salinity (Williams 1978, Williams et al. 1990). Finally, saline lakes are often considered unimportant to people because they provide few economic benefits, especially such as not having potable waters, which makes their environmental degradation of less concern to societies (e.g., destruction of Aral Sea: Pala 2006).

This is not to say that hypersaline environments have gone unstudied: recent microbial work in hypersaline ponds (Yannarell and Paerl 2007, Yannarell et al. 2007, Paerl and Yannarell 2010) and concern over the conservation of saline lakes (Williams 1993a, b, 1998, 2002) are notable. However, after an extensive bibliographic compilation of saline lake and inland sea literature (>1200 papers dated prior to 1994, Larson and Belovsky 1999), we found few studies available

on the Great Salt Lake ecosystem and its biota (e.g., Hayes 1971, Wirick 1972, Porcella and Holman 1972, Stephens 1974, Brock 1975, Stephens 1990, 1998, Post 1975, 1980, Stephens and Gillespie 1976, Cuellar 1990, Collins 1977, Felix and Rushforth 1977, 1979, 1980, Rushforth and Felix 1982, Stephens and Birdsey 2002, Wurtsbaugh 1988, Wurtsbaugh and Berry 1990), and these were short term and very limited in scope. In addition, most of the extensive and long term studies of other hypersaline lakes were for much smaller lakes with very different environmental patterns (e.g., Mono Lake, USA, a deep lake basin: Dana et al. 1990, 1993, 1995; Lake Grassmere, NZ, a seaside lagoon lake: Wear and Haslett 1986, 1987, Wear et al. 1986).

STUDY SYSTEM

Gwynn (1980, 2002) provides a detailed description of the Great Salt Lake's history, natural history and geology, as well as its economic values. Great Salt Lake (Fig. 1) is a hypersaline terminal lake that is the remnant of Pleistocene Lake Bonneville. In historical times the lake's watershed has encompassed $> 89,000 \text{ km}^2$. The lake's salinity has ranged between 50 and 280 ppt (~5–28%) as the lake's surface area varied between 5490 and 2470 km^2 . At its highest surface elevation (1284 m), the lake's maximum depth was 13.7 m; at its lowest surface elevation (1277 m) the lake's maximum depth was 7.6 m. At the historical mean lake elevation of 1280 m, the mean depth is only 5.5 m. Because it has a large watershed, is shallow, and is a terminal lake, Great Salt Lake is hypereutrophic.

The lake is composed of two major arms that are now separated by a railroad causeway through which some exchange occurs via culverts and a more recently constructed breach (Fig. 1). The South Arm has a lower salinity, because 95% of the lake's surface inflows are located here (Bear, Weber, Ogden and Jordan Rivers: Fig. 1), and contains a much more diverse biota. The North Arm, because of its current separation from most surface inflow by the railroad causeway constructed in 1959 (Fig. 1), has a salinity that is usually near halite saturation (~26–28%) so that most of the biota is bacteria and cyanophytes, and *Dunaliella salina* can be present when salinities decline below saturation

levels. The same railroad causeway crosses Bear River Bay and maintains a much lower salinity there due to the Bear River's inflow so that the biota in places contains fish. Another more recent causeway partially isolates Farmington Bay in the South Arm (Fig. 1) and maintains lower salinity (~1–9%) there due to the Jordan River's inflow and higher nutrient concentrations due to treated sewage inflows from Salt Lake, Davis and Tooele Counties. A series of dikes in the Stansbury Basin in Carrington Bay (Fig. 1) were constructed to enhance evaporation for salt extraction from the lake. Therefore, the South Arm today is more representative of the original lake prior to separation of three of its bays and the North Arm by causeways and dikes.

The South Arm of the lake's biota has been typically characterized as brine shrimp (*Artemia franciscana*), two species of phytoplankton (*Dunaliella viridis* and *salina*: Chlorophyta), two species of brine fly (*Ephydria cinerea* and *hians*), a corixid (*Trichocorixa verticalis*), and numerous water birds. However, as our investigations of the lake have progressed, the number of identified phytoplankton species (Chlorophyta, Bacillariophyta, Cyanophyta, Dinophyta) and benthic algae has increased to > 60 species and several species of rotifers, nematodes, ciliates, and crustacean zooplankton have been found resident (Belovsky et al. 2000, Belovsky and Larson 2001, 2002, Larson 2004).

More than a third of all western US water birds pass through the Great Salt Lake in their spring and fall migrations, many of which are species of conservation concern (e.g., Snowy Plover, *Charadrius alexandrinus*), and a number nest along the lakeshore (Aldrich and Paul 2002); this makes the lake of high conservation value. Most abundant are the Eared Grebe (*Podiceps nigricollis*), three common gulls (Franklin's: *Larus pipixcan*, California: *L. californicus* and Ring-billed: *L. delawarensis*), and two common phalaropes (Red-necked: *Phalaropus lobatus* and Wilson's: *P. tricolor*) (Post 1975, 1980). The Eared Grebe is particularly important not only given its abundance and reliance on the lake as a migratory staging location ($> 70\%$ of all individuals of the species), but because this species forages intensely on brine shrimp (~90% of diet) to continue its spring and fall migration (Caudell 2001, Conover and Caudell 2009, Conover et al. 2009). Studies

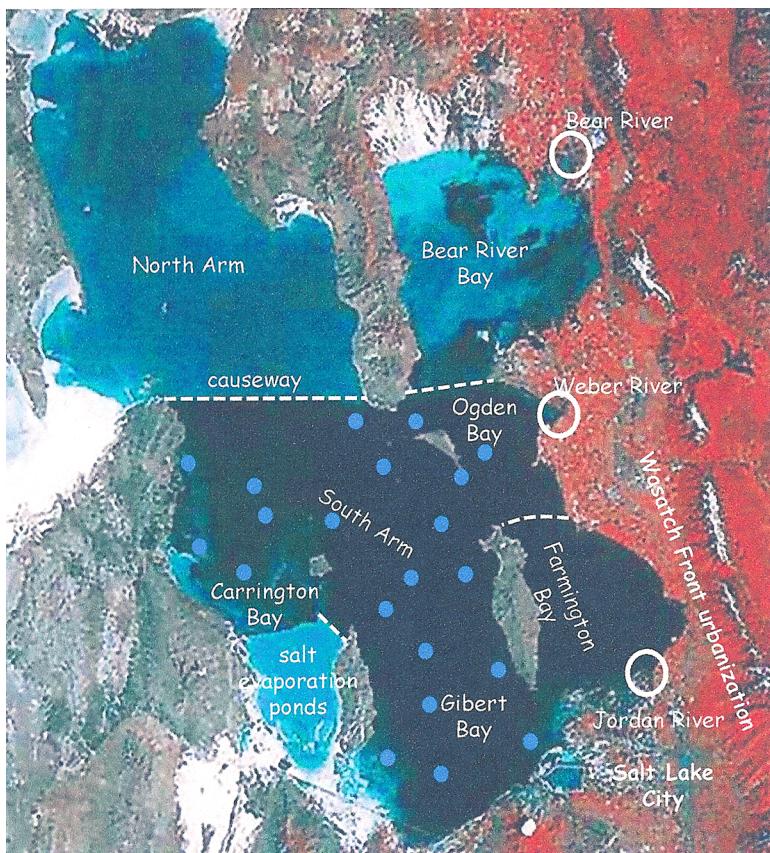


Fig. 1. Satellite image of Great Salt Lake, Utah (USGS Earth Shots) identifies major areas and aspects of the region. South Arm sampling sites in our study are indicated by blue dots.

reporting lower consumption of brine shrimp (Gafney 2008) were based on Eared Grebes collected from areas of very low salinity in Farmington Bay where brine shrimp were absent (collected by J. Luft, personal communication).

However, the single species that most typifies the ecosystem is the brine shrimp (*Artemia franciscana*), because of its abundance and uniqueness for saline lakes. The Great Salt Lake brine shrimp is an Anastrocan crustacean zooplankton that reaches up to 12 mm in length and reproduces sexually via two modes: ovoviparity which produces eggs that hatch in the ovisac and the nauplii are released to the lake, and oviparity which produces diapausing cysts. Ovoviparity is the primary way that the population grows during the summer. Cysts (oviparity) are the means by which brine shrimp overwinter when water temperatures are too cold for nauplii, juvenile or adult survival, and they hatch in

spring when water temperatures rise and a freshwater lens (less dense freshwater floating on dense hypersaline water) appears on the lake. The cysts of brine shrimp in the Great Salt Lake float and at times accumulate in wind rows called “streaks”. Cysts can remain in the lake over the winter or can be deposited on beaches, where they may or may not be washed or blown back into the lake. Cysts deposited on the beach can also serve as a “refuge” for brine shrimp populations in areas that may dry up.

Brine shrimp cysts are commercially harvested for the aquaculture industry, because they can be hatched to provide a highly nutritious food for larval fish and other crustaceans that are commercially cultured. Floating and beach-deposited cysts are easy to gather, and with minimal treatment the cysts can be packaged, transported and made ready for hatching. The commercial harvest of cysts in the Great Salt Lake began in

1952 by the Sanders Brine Shrimp Company; by 2000, the number of companies harvesting cysts increased to 32, and since then the number of companies has declined as a few large companies bought up smaller ones (Sturm et al. 1980, Kuehn 2002). The annual economic value of this industry has been estimated between US \$50–100 million (Isaacson et al. 2002).

Based on available natural history, a simplified food web diagram for the Great Salt Lake ecosystem can be constructed (Fig. 2). We hypothesize that the food web is actually comprised of two weakly linked food chains: one based on direct consumption of phytoplankton (autotrophs), and the other based on consumption of particulate detritus (detritivores) and benthic algae. The data reported here is restricted to the food web based on direct consumption of phytoplankton (right of dashed line in Fig. 2), because the commercial harvesting of brine shrimp cysts was the initial concern of Utah Division of Wildlife Resources (UDWR), which funded the study.

METHODS

We report here on our sampling conducted between 1994 and 2006. Preliminary nonrandom sampling was conducted from June 1994 through June 1995 by Wurtsbaugh (1995) and Gliwicz et al. (1995) for UDWR; these data, which were published by Wurtsbaugh and Gliwicz (2001), are included in our analysis to increase the time series. Furthermore, when available, earlier observations found in the literature were added to the database to assess whether our observations are consistent with earlier observations and to assess whether major changes in the lake have taken place.

Sampling sites

Fig. 1 presents our 1995–2006 sampling sites in the South Arm of Great Salt Lake that were located by GPS. Initial sampling in 1994 employed 10 sites that were more or less uniformly distributed over the South Arm of the lake with four sites in the shallow littoral zone, four sites in the deepest areas (>7.9 m), and two sites at intermediate depths (Gliwicz et al. 1995, Wurtsbaugh 1995, Wurtsbaugh and Gliwicz 2001). With this initial sampling, a power analysis

indicated that 10 sites were adequate to ensure standard errors no greater than 25% of the mean at most times (Gliwicz et al. 1995).

We decided to further reduce standard errors by sampling more than 10 sites starting in fall of 1995, which still met logistical limits to sampling. In addition, the initial sampling had indicated that standard errors could be reduced even more by stratifying the lake into two regions: $<$ and ≥ 4 m depth, even though this constrained analyses based on depth. Consequently, we randomly selected 14 sites within the two strata using a square kilometer grid system: seven sites were at depths <4 m; seven sites were at depths ≥ 4 m. In addition to the 14 random sites, one site north of Fremont Island was selected nonrandomly to be near the major inflow of freshwater (Bear River), a region exhibiting high variability. In 1997, two additional sites were nonrandomly added: one east of Fremont Island to better sample the Bear River estuary and one in Farmington Bay to examine the inflow of freshwater (Jordan River) and urban sewage there. In 1998, four additional random sites were added (DWR 1–4), because four original sampling sites were discontinued when decreasing lake levels prohibited access to shallow areas (Sites 2433, 2636, 3641, 3954): this maintained the sampling of 17 random sites since 1997.

Sampling frequency

In 1994, 2–4 week sampling was employed depending on weather to develop the power analysis. From 1995–1996, each site was sampled monthly. After 1996, each site was sampled monthly from February–March, bimonthly from April–September, and sometimes weekly from October–January (monitoring for regulation during the commercial harvest season for cysts). This sampling regimen was not always achieved due to inclement weather, which made it unsafe to be on the lake; however, all sites were sampled within three days of each other, weather permitting. All measurements were averaged for all sites and days within a weekly sampling period to provide an average for that week. All weekly averages within a month of a year were averaged to provide a monthly average value for that year.

Measurements

At each site the following measures were

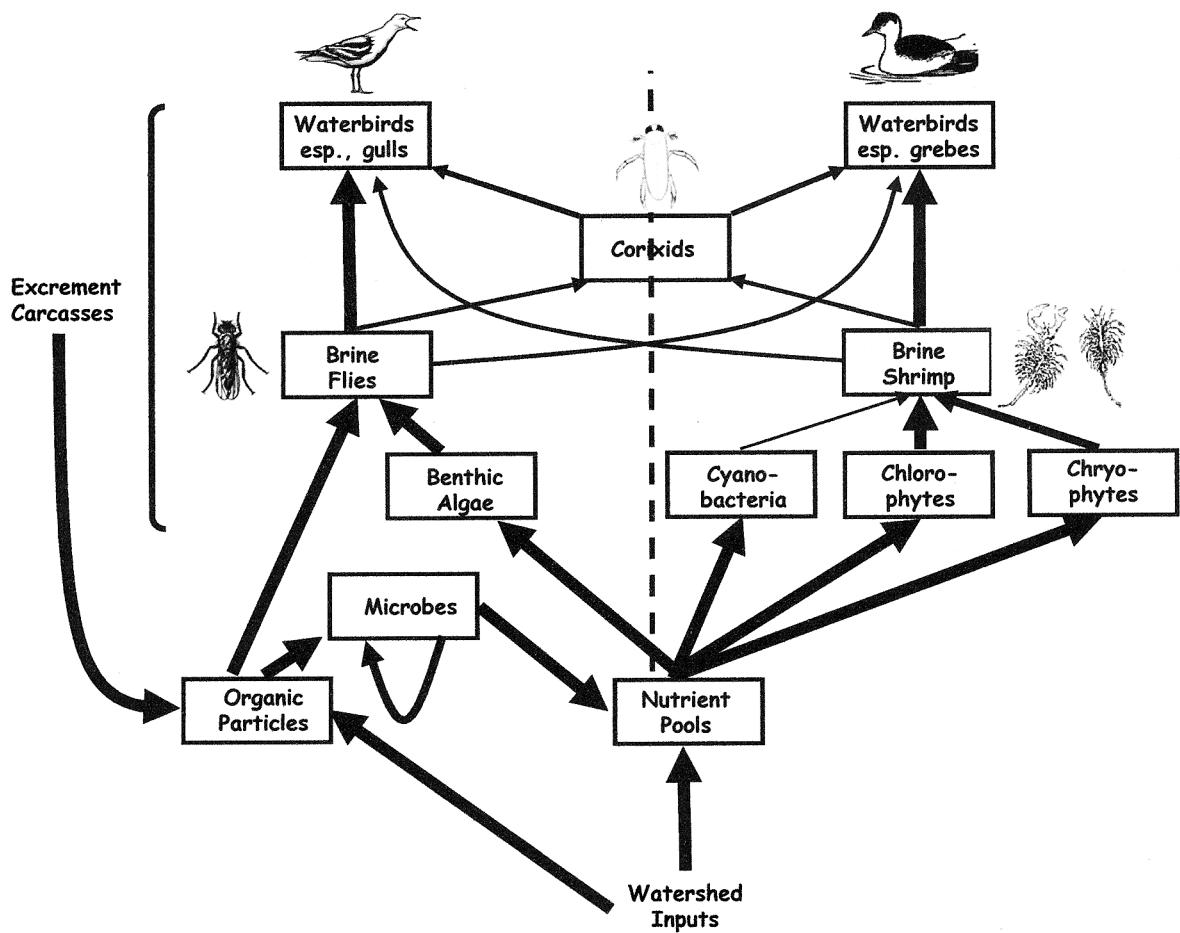


Fig. 2. Our hypothesized simple food web diagrams for the Great Salt Lake South Arm are presented. Two food webs are proposed: a phytoplankton-based web (right of dashed line) and an organic particle/benthic algae web (left of dashed line). Arrow thickness represents suspected relative interaction strengths. The phytoplankton-based web was examined here.

made.

1. *Lake elevation* was obtained from the USGS gage at Saltair Marina on Great Salt Lake.

2. *Physical measures* were collected at various depths at each site. Salinity was measured at 1 m below the surface and 1 m above the bottom using an optical refractometer specific for NaCl at 20°C. Salinity measures were corrected for water temperature using a regression developed in the laboratory using a hydrometer. Photosynthetically active radiation (PAR) was measured using a LiCor LI-193SA spherical quantum sensor in the air at the water surface and at 1-m intervals from 1995–2000. Depth profiles of water temperature and dissolved oxygen were mea-

sured at 1-m intervals using a YSI Model 59. Secchi disc measures were taken at each site.

3. *Nutrient concentrations* were measured from water samples taken at 5–11 sites on each sampling date using a pump at 1 m below the surface and 1 m above the bottom. At each depth, two 500 ml samples were taken, filtered through 0.45 µm filters and frozen. This provides 1 m values for all sites sampled and >4 m values only for sites deeper than 4 m. The water was analyzed for ammonia, nitrite, nitrate (DIN) and total dissolved phosphorus (TDP) at the USGS National Water Quality Laboratory using methods modified for high salinity (Fishman and Friedman 1989), because hypersaline conditions

can distort chemical analyses (Fishman and Friedman 1989).

4. *Phytoplankton abundance* were made using two 500 ml water samples collected at 1 m below the surface and passed through 153 μm mesh to remove brine shrimp. One bottle was used to measure chlorophyll concentration by fluorometry and the other to measure phytoplankton species composition by cell count. These samples were collected from 4–9 sites on each date.

To measure chlorophyll with fluorometry (Turner Designs, Model 10AU), each 500 ml water sample was filtered through a 0.8 μm glass fiber filter (Whatman GF/F) and extraction was conducted following Wetzel and Likens (1979) with methanol in 1994–1995 (Gliwicz et al. 1995, Wurtsbaugh 1995) and thereafter, with acetone. Prior to 1999, concentrations of chlorophyll-*a* (Chla) were corrected for phaeophytin-*a* utilizing the acidification procedure (Wetzel and Likens 1979), and after 1999, chlorophyll-*a* was directly measured (Welschmeyer 1994). Chlorophyll measures were unavailable for large portions of 2001–2002 and 2003.

To enumerate and identify phytoplankton taxa, the second sample was immediately preserved using Lugol solution in 1994 (Gliwicz et al. 1995); however, concern that Lugol solution was less effective at the high salinities of Great Salt Lake led Wurtsbaugh (1995) to employ 5% sugar-formalin as a preservative in 1995. After 1995, Stephens and others kept the sample refrigerated and in the dark, and enumeration occurred within several days. Samples were filtered through a 1.2 μm Millipore filter and algal cells on the filter were re-suspended in 5 ml of distilled water. If the sample was not immediately enumerated, the distilled water re-suspension was preserved in Lugol solution. Aliquots of the sample were removed and placed in a Palmer counting chamber for enumeration (Palmer and Maloney 1954). Algal cells in the Palmer cell were identified and counted along one or two transects at 400 \times , rather than 160 \times , magnification under a microscope with interference phase contrast. Counting at higher magnification (400 \times) facilitates species identification, especially for Bacillariophytes, and provides a more representative suite of the phytoplankton from the pumped water sample than from plankton net samples. The mean counts per

transect were converted to cells per liter using the appropriate Palmer cell multiplication factor. Cell counts were available for 1995–2002 and 2005–2006, as conducted by the laboratories of Dr. S. Rushforth at the Botany Department of Brigham Young University (1995–1999), of Dr. G. Belovsky at the Department of Fisheries and Wildlife, Utah State University or Department of Biology, University of Notre Dame (1999–2002), or Great Salt Lake Ecosystem Project Laboratory (GSLEP), UDWR (2005–2006). Cell counts were converted to phytoplankton biovolume based on cell shape and dimensions.

5. *Brine shrimp* were sampled using a 0.5 m diameter \times 2 m plankton net (153 μm mesh). This was the largest net size that could be employed by hand; a large net is needed given times of the year when brine shrimp are not very abundant and a large net reduces sample variation (Wiebe and Holland 1968). Previous studies of brine shrimp in Great Salt Lake and other hypersaline lakes have used 80–250 μm mesh (larger number is coarser mesh: Dana et al. 1990, Wear and Haslett 1987, Wurtsbaugh and Berry 1990, Wurtsbaugh and Marcarelli 2004). Quality control results indicated that a 153 μm mesh did not lose any nauplii or cysts, while a 183 μm mesh lost up to 6%.

The net was lowered to the lake bottom and raised vertically to the surface at a rate of approximately 1 m/s. The depth of the lake bottom was recorded and was used to compute the volume of water sampled (depth \times net mouth area). Three tows were made at each site. The computed volume was calibrated in 1995 using a non-reversing TSK Model 901 flow meter, indicating a sampling efficiency of 87% by volume and this did not change between the first and third tow. Therefore, as expected using a net with a 4:1 length to mouth ratio and relatively large mesh size, little sampling loss due to back pressure was indicated.

Each tow's brine shrimp sample (500ml) was preserved in buffered formalin in the field and then transferred to 70% ETOH until they could be counted. Numbers of brine shrimp were counted in 10 ml subsamples under a dissecting microscope. Subsamples were examined until a minimum of 50 adults and juveniles were counted. Cysts (unhatched and hatched) and nauplii were counted in a single 5 ml subsample.

Nauplii were defined as ≤ 1.5 mm; juveniles were > 1.5 mm that were not sexually mature (females without ovisac and males without claspers); adults were sexually mature (> 6 thoracopods). Adult females were examined to determine whether they had eggs or cysts in their ovisac. Counts were extrapolated to numbers per liter based upon each tow's volume. This was repeated three times for each tow and the values were averaged. In addition, brine shrimp biomass was computed in terms of adult equivalents (nauplii = 0.13 adults, juveniles = 0.63 based on live-mass).

6. *Other taxa* were identified incidentally in the phytoplankton (protozoans, dinoflagellates, nematodes, rotifers, copepods and cladocerans) and plankton net samples (brine fly larvae and corixids) when encountered.

7. *Eared Grebe populations* were estimated in the fall of all years (except 2002) using a photo survey of transects of the Great Salt Lake to project the population for the entire lake (Paul et al. 1999a, b). Transects were flown with a Cessna 185 using in-plane GPS and altimeter to gauge area size covered by photos. Grebes were identified in photos and enumerated to account for density.

8. *Brine shrimp cyst commercial harvesting* (metric tons per year) was estimated by UDWR using random surveys of harvest boats returning to harbor and legally mandated reports filed by the harvest companies.

Statistics

All analyses were conducted using the monthly average values for each year using SYSTAT (version 13), Systat Software, Inc., Chicago, Illinois, USA. Proportions were arcsine-square root transformed to obtain normality and heteroscedascity was minimized using \log_{10} -transforms when necessary. Temporal variations in survey data were analyzed using GLM to assess whether observed inter- (among year) and intra-(monthly) annual fluctuations were statistically significant, where month and year were treated as blocks. Specific hypotheses were tested using t-test and regression.

Dynamics of the phytoplankton-based food web were investigated using structural equation modeling with our survey data (Grace 2006, Hampton and Schindler 2006, Shipley 1999).

Structural equation modeling is more powerful than standard multiple regression or path analysis approaches that attempt to fit unspecified linear models to observations (Shipley 2000). Structural equation modeling is accomplished by first hypothesizing relationships, then depicting the relationships in an equation, and finally using regression methods to fit the equations to data to determine whether the proposed hypotheses may be operating. Inclusion of an independent variable required its partial correlation to have a $p < 0.15$ tolerance, and the Akaike Information Criteria index for the model including the variable must be less than the model without it. Both linear and non-linear equations were employed, depending on the specific hypothesized relationship. Least square and robust (least median square) functions were employed to minimize error, and both were examined for consistency. Robust regressions were used, because least square regressions are sometimes strongly impacted by outliers (Gotelli and Ellison 2004), and outliers were often evident in our data.

RESULTS

Here we summarize our Great Salt Lake dataset (Supplement) and examine inter- and intra-annual patterns. This database is the foundation necessary for testing specific hypotheses regarding the phytoplankton-based food chain as developed in the *Discussion*.

Abiotic measures

Depth profiles in temperature and salinity at the same time in two years are presented for a deep and shallow site as an example (Fig. 3). These data were selected because they represent typical patterns observed across all sites. The deep site (Site 3510) in both years demonstrated temperature stratification (i.e., thermocline) and demonstrated salinity stratification (i.e., chemocline) in 2005, but not in 2006. The shallow site (Site 2935) did not demonstrate a chemocline or thermocline in either year (2005, 2006); however, a weak thermocline can be seen to be developing in 2006, which may be a diel condition due to calm waters. Average PAR with depth is presented for March (peak phytoplankton abundance) and June (lowest phytoplankton abundance) in 1998

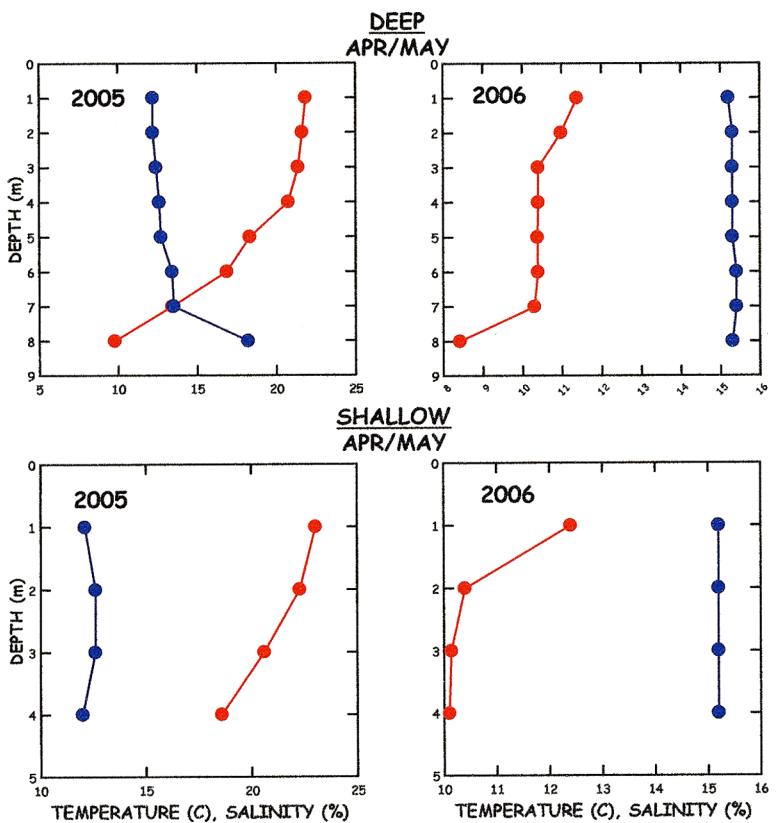


Fig. 3. Plots of water temperature (red) and salinity (blue) with depth in the Great Salt Lake South Arm are presented for a deep and shallow site in April/May for two years (2005, 2006). In 2005, the deep site exhibits the deep brine layer (chemocline), but not in 2006. Both years exhibit a thermocline at the deep site, but never at the shallow site.

(Fig. 4A, B). PAR at both times was reduced to less than $200 \mu\text{E m}^{-2} \text{s}^{-1}$, the light intensity required for good algal growth (Horne and Goldman 1994), at a depth between 3–5 m; therefore, the photic zone may be generally defined as the first 4 m of the water column.

Within year (Fig. 5A, B, and C) and among year patterns (1994–2006: Fig. 5D, E, and F) of lake elevation, water temperature (1 m), and salinity for Great Salt Lake are presented. While lake elevation varied both within (GLM: $F = 18.20$, $\text{df} = 11, 132$, $p < 0.001$) and among years (GLM: $F = 252.01$, $\text{df} = 12, 132$, $p < 0.001$), among year variation was far more variable than within year variation. Annually, lake elevation was greatest from April through June. While salinity varies both within (GLM: $F = 6.85$, $\text{df} = 11, 117$, $p < 0.001$) and among years (GLM: $F = 137.39$, $\text{df} = 12, 117$, $p < 0.001$), among year variation was far more

variable than within year variation. Mean annual salinity during the study varied from 8.8–16.3%. Annually, salinity is lowest from May–July during spring runoff. While water temperature at 1 m varied both within (GLM: $F = 269.76$, $\text{df} = 11, 118$, $p < 0.001$) and among years (GLM: $F = 3.74$, $\text{df} = 12, 118$, $p < 0.001$), within year variation was far more variable than among year variation. Mean surface water temperatures varied by 7.6°C among years. Annual mean water temperature was greatest in July–August (25.8°C) and lowest in January–February (1.5°C).

PAR measurements were only available for 4 full years (1996–1999). There was no significant annual variation in PAR at the surface (GLM: $F = 1.34$, $\text{df} = 3, 28$, $p < 0.28$); however, there was significant variation among months (GLM: $F = 3.11$, $\text{df} = 11, 28$, $p < 0.008$) with October through January receiving the least PAR. Annually, 73%

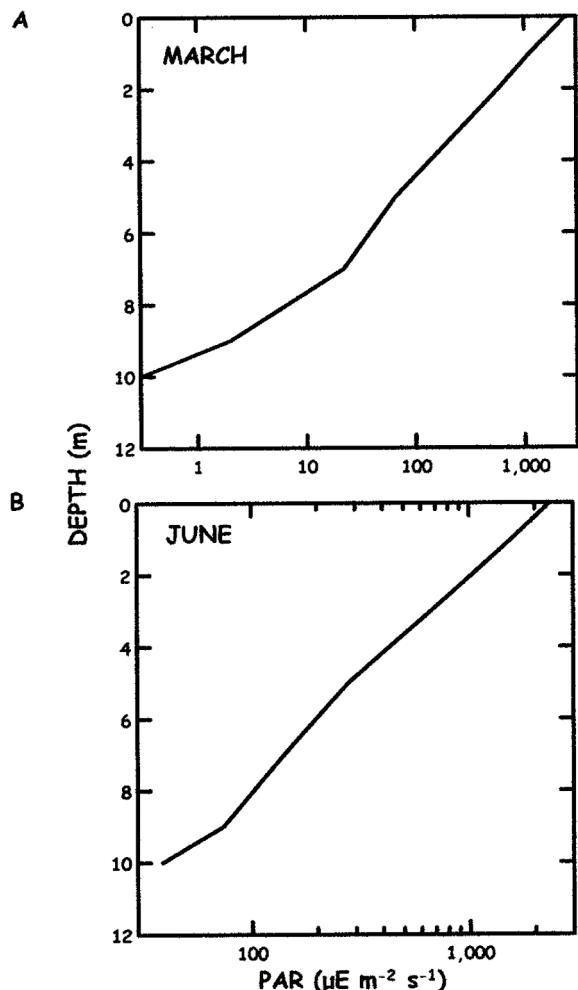


Fig. 4. Plots of average photosynthetically active radiation (PAR: $\mu\text{E m}^{-2} \text{s}^{-1}$) with depth in 1998 for March (peak phytoplankton abundance) and June (lowest phytoplankton abundance).

of maximum PAR is received and during October through January, 65% is received. Light availability/turbidity as measured by Secchi depth transparencies (Fig. 6A, D) varied both within (GLM: $F = 14.73$, $df = 11, 103$, $p < 0.001$) and among years (GLM: $F = 4.50$, $df = 12, 103$, $p < 0.0001$). Secchi transparencies were greatest in July (averaging 3.4 m) and least in January (averaging 1.5 m).

Nutrient measures

Photosynthesis occurs year-round in Great Salt Lake, in fact, peak phytoplankton abundances occur in late fall to early spring when brine

shrimp grazing is absent. When phytoplankton are at their lowest abundances (summer), nutrients are tied up in the shrimp population. Therefore, measures of lake nutrient concentrations do not represent nutrient pools, but unused nutrients available to phytoplankton and benthic algae.

Within year patterns of lake nutrient concentrations (dissolved inorganic N: DIN and total dissolved P: TDP) at shallow (1 m) and deep (>4 m) depths are presented in Fig. 6B and C. Among year patterns (1994–2006) of lake nutrient levels (DIN and TDP) at shallow (1 m) and deep (>4 m) depths are presented in Fig. 6E and F. Nitrate and nitrite values of N were always below detection values and therefore, ammonia was the principal form of inorganic N. Shallow DIN did not vary significantly within years (GLM: $F = 1.36$, $df = 11, 58$, $p < 0.21$), but varied among years (GLM: $F = 7.38$, $df = 9, 58$, $p < 0.001$). Deep DIN varied within years (GLM: $F = 3.27$, $df = 11, 47$, $p < 0.011$) and among years (GLM: $F = 82.69$, $df = 9, 47$, $p < 0.001$). Deep DIN was lowest from February through May. Shallow TDP did not vary within years (GLM: $F = 0.75$, $df = 11, 54$, $p < 0.69$), but varied among years (GLM: $F = 4.72$, $df = 8, 54$, $p < 0.001$). Deep TDP did not vary within years (GLM: $F = 1.15$, $df = 11, 43$, $p < 0.35$) or among years (GLM: $F = 3.12$, $df = 8, 43$, $p < 0.007$). Nutrient measures under hypersaline conditions can be distorted and require special techniques (Fishman and Friedman 1989), which were employed; nonetheless, we still view the values as relative, rather than absolute, changes over time.

Dissolved oxygen

Dissolved oxygen measures are difficult to make in hypersaline water and DO correction tables for salinity are only available up to 67,000 $\mu\text{S/cm}$ (Lewis 2006). Therefore, sensor measures were viewed as relative rather than absolute values and were not as regularly taken as other parameters (Fig. 7). For the same sites and dates reported for temperature and salinity depth profiles, DO (% saturation: Fig. 7A, C) declined with depth as expected and approached anoxia only at greatest depths, especially in 2005 when a chemocline re-emerged at Site 3510. Average DO measures for all sites on a given date (Fig. 7B, D) varied within years (GLM: $F = 3.36$, $df = 10, 12$, p

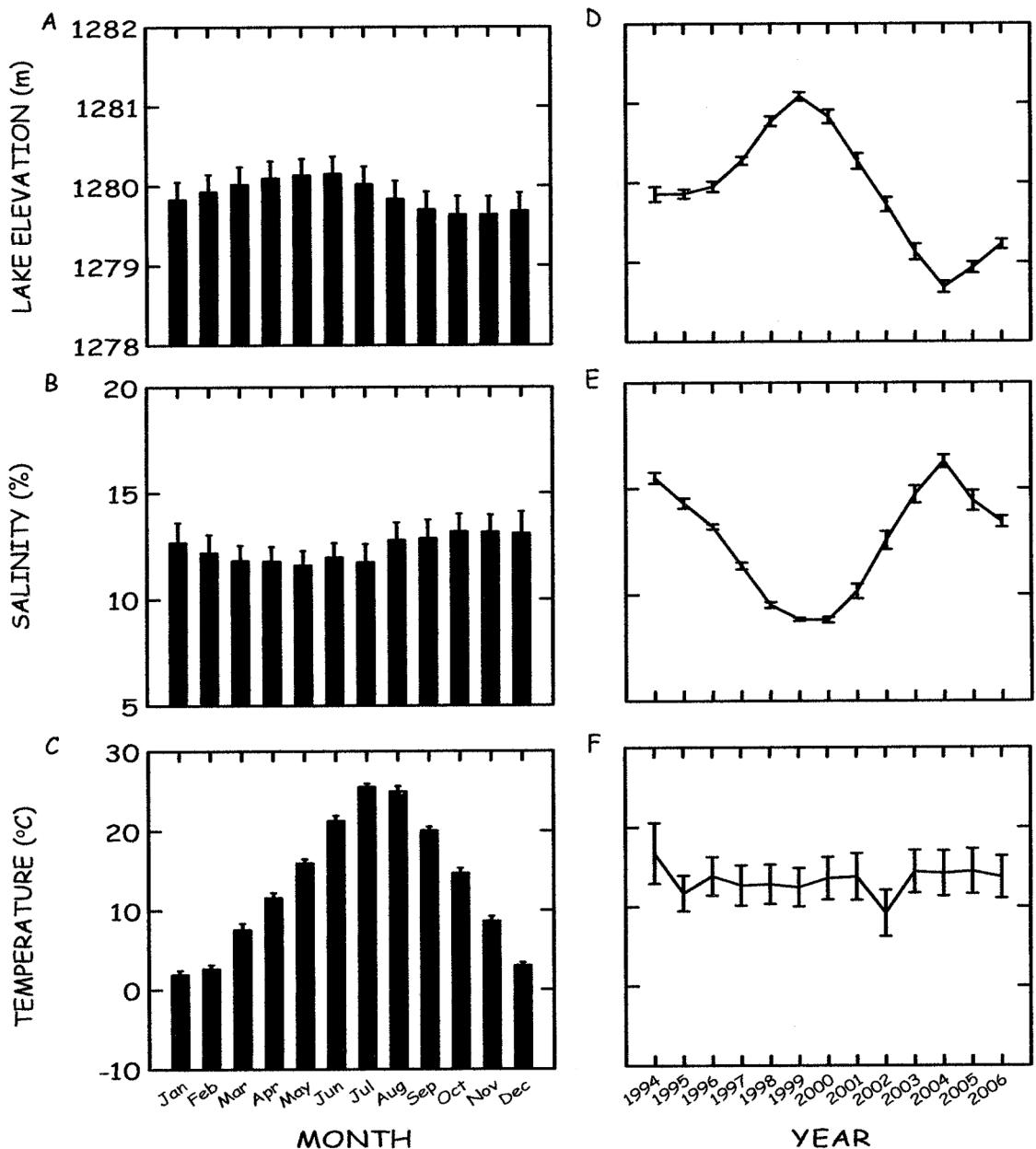


Fig. 5. Basic physical measurements of the Great Salt Lake South Arm are presented for variations within year (intra-annual) by month and among years (inter-annual). Average lake elevation (A, D), salinity (B, E), and water temperature (C, F) observations are presented for the period of our study (1994–2006) along with standard errors.

< 0.025) and among years (1994–2004, GLM: $F = 7.41$, $df = 5, 12$, $p < 0.002$).

Biotic measures

Phytoplankton.—Abundance of Chla (Fig. 8A, C) varied approximately to an equal degree

within years (GLM: $F = 3.77$, $df = 11, 93$, $p < 0.001$) and among years (GLM: $F = 2.54$, $df = 12, 93$, $p < 0.006$). Chla was greatest between November and April, with January–February providing peak levels. Peak Chla levels were greatest in 1998 ($228 \mu\text{g/l}$), more than seven times

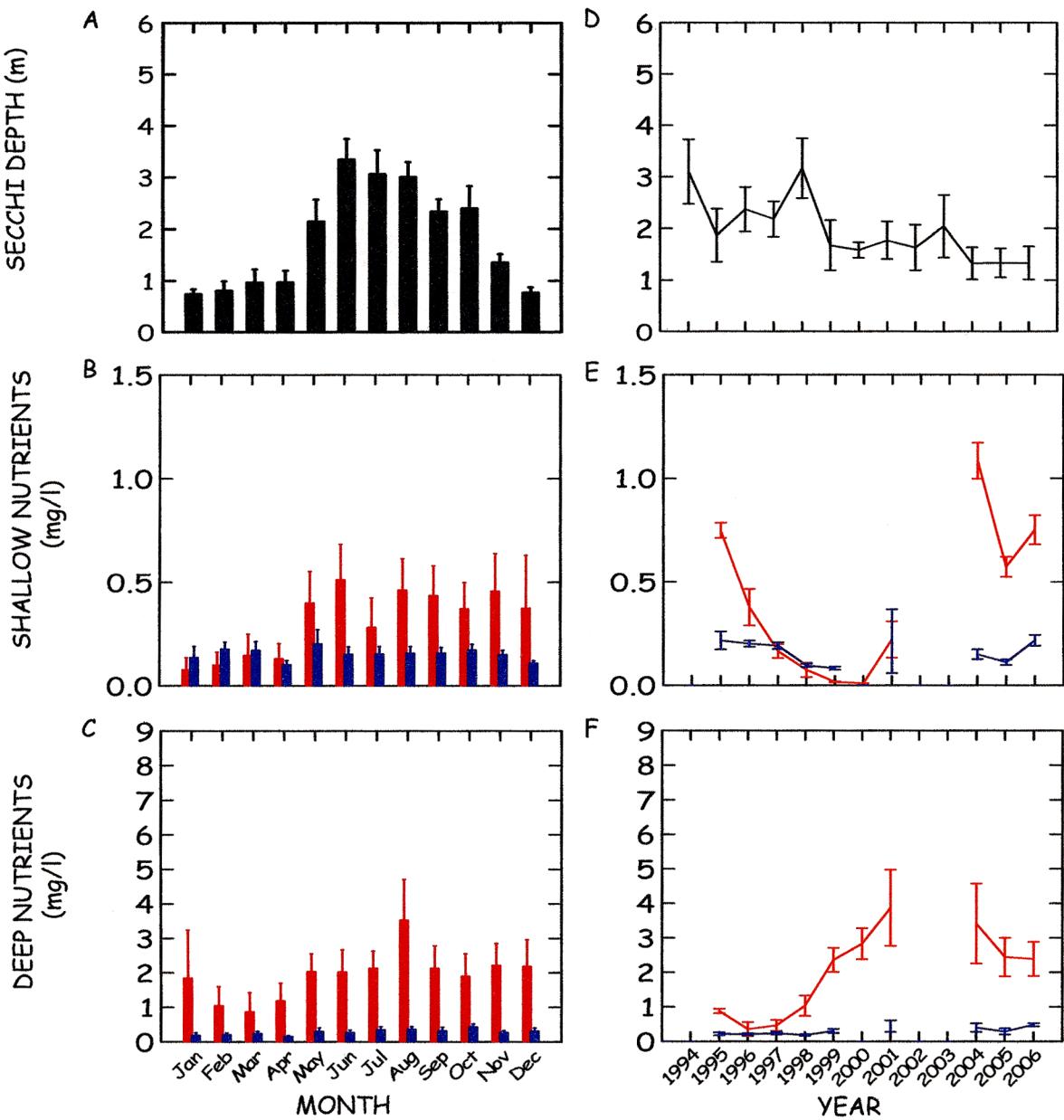


Fig. 6. Measures related to phytoplankton resource requirements in the Great Salt Lake South Arm are presented for variation within year (intra-annual) by month and among years (inter-annual). Average transparency (Secchi Depth: A, D), photic zone (1 m) DIN (red) and TDP (blue) concentrations (B, E) and deep (>5 m) DIN (red) and TDP (blue) concentrations (C, F) are presented for the period of our study (1994–2006) along with standard errors.

greater than in 1995, 2000, 2002 and 2003. The next highest Chla levels occurred in 1997 ($114 \mu\text{g/l}$).

Phytoplankton composition for all years except 2003–2004, when enumeration was discontinued

by UDWR, (Chlorophyta, Bacillariophyta, Cyanophyta: Fig. 8B, D) did not vary within years (GLM respectively: $F = 1.09$, $\text{df} = 11, 49$, $p < 0.39$; $F = 1.41$, $\text{df} = 11, 49$, $p < 0.20$; $F = 0.70$, $\text{df} = 11, 49$, $p < 0.74$), but varied dramatically among years

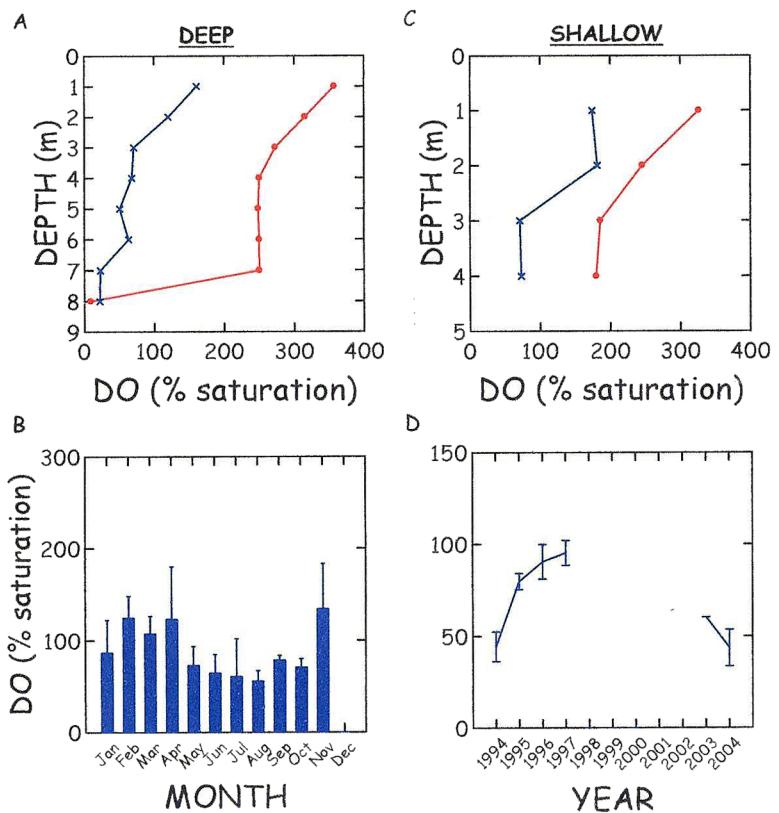


Fig. 7. Dissolved oxygen (DO: % of saturation) measures in the Great Salt Lake South Arm are presented. Plots of DO with depth at two sampling sites for April in two years (red, 2005; blue, 2006) are presented in (A) for a deep site and (C) for a shallow site. DO values for variations are presented within year by month (intra-annual) in (B) and among years (inter-annual) in (D) for the period of our study (1994–2006) along with standard errors.

(GLM respectively: $F = 5.88$, $df = 10, 49$, $p < 0.000009$; $F = 1.41$, $df = 10, 49$, $p < 0.000002$; $F = 4.58$, $df = 10, 49$, $p < 0.0001$). Lowest Chlorophyte abundances occur from July through November, lowest Bacillariophyte abundances occur from March through June, and Cyanophytes were lowest from November through March. Chlorophytes dominated in 2001, 2002, and 2006, Bacillariophyta dominated in 1996, 1997 and 2005, and Cyanophyta dominated in 1998–2000. Chlorophyta and Bacillariophyta were equally dominant in 1995. All three taxa were approximately equal in 1994. Therefore, the phytoplankton was far more diverse and variable than previously reported (Wirick 1972, Felix and Rushforth 1977, 1979, 1980, Rushforth and Felix 1982) and more than 60 species were identified during our study as compared to previous reports ≤ 20 species (Felix and Rush-

forth 1977, 1979, 1980, Rushforth and Felix 1982).

Brine shrimp.—Brine shrimp generally hatch from overwintering cysts in March/April and largely disappear during December, a period marked with water temperatures $<4^{\circ}\text{C}$ (Fig. 9A, B and C). Nauplii and juvenile densities varied within years (Fig. 9A, B, GLM respectively: $F = 10.39$, $df = 11, 120$, $p < 0.001$; $F = 4.57$, $df = 11, 120$, $p < 0.009$) and among years (Fig. 9D, E, GLM respectively: $F = 2.43$, $df = 12, 120$, $p < 0.007$; $F = 3.02$, $df = 12, 120$, $p < 0.001$). Nauplii and juvenile densities peaked in May and then declined over the summer and fall with nauplii diminishing more rapidly than juveniles. The highest nauplii densities were observed in 2000 (56.4 nauplii/l) and the lowest densities (25 times lower) occurred in 1994. The highest juvenile densities were observed in 1997 (9.4 juveniles/l) and the lowest densities (three times lower)

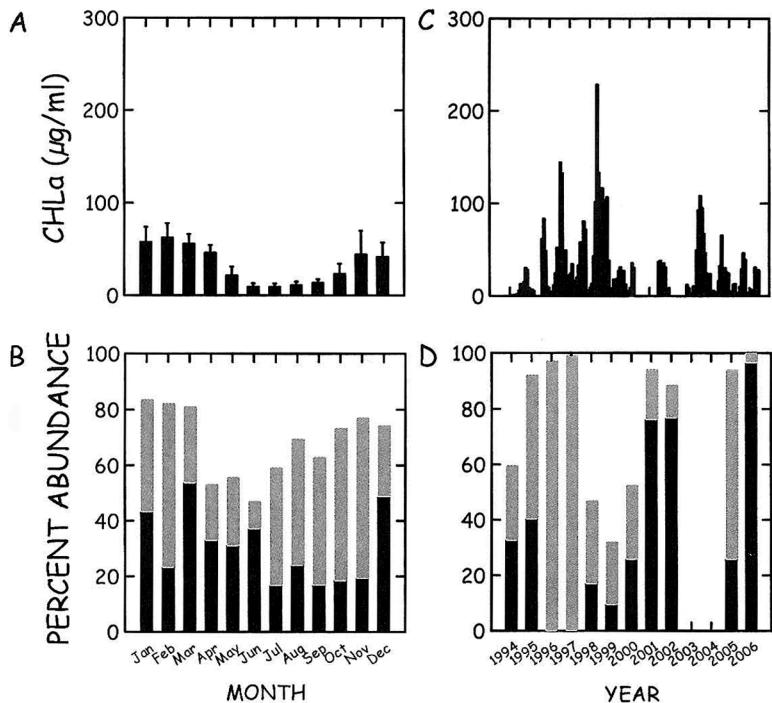


Fig. 8. Phytoplankton measures in the Great Salt Lake South Arm are presented for variations within year (intra-annual) by month and among years (inter-annual). Average chlorophyll-*a* concentrations (A, C: no measures for large portions of 2000–2001, 2003), and phytoplankton relative composition by taxa (Chlorophytes, black; Bacillariophytes, gray; Cyanophytes, the difference from 100%; B, D: no counts for 2003–2004) are presented for the period of our study (1994–2006) along with standard errors.

occurred in 1995. Adult densities varied within years (Fig. 9C, GLM: $F = 11.32$, $df = 11, 120$, $p < 0.001$), but did not vary among years (Fig. 9F, GLM: $F = 0.73$, $df = 12, 120$, $p < 0.72$). Adult numbers peak in May or June and then slowly decline. Lack of significant differences among years arises from the great variability in adult numbers within a year. However, adults densities were observed to be highest in 2004 (5.82 adults/l) and the lowest densities (2.07 adults/l or 2.8 times lower) occurred in 1995. Given the large numbers of nauplii relative to juveniles in May, nauplii survival is low. However, the survival of juveniles to adults is much greater.

Densities of cysts, the diapausing life stage which overwinters and initiates each year's population, (Fig. 10A, E) approached significant variation within years (GLM: $F = 1.62$, $df = 11, 109$, $p < 0.10$), but did vary significantly among years (GLM: $F = 3.18$, $df = 11, 109$, $p < 0.001$). One would expect significant within-year variation, because cysts are primarily produced prior

to winter as the diapausing life stage. However, cysts were found at relatively high abundances throughout the year, especially in May. This occurs for two reasons that particularly apply to May counts: 1) counting of broken cysts after they hatch (up to 90% broken on occasion); 2) appearance of cysts re-entering the lake with rain, wind or rising water levels from shoreline deposits. To compensate for this, May was excluded from analyses and within year variation was then observed to be significant (GLM: $F = 1.93$, $df = 10, 109$, $p < 0.04$). Peak densities of cysts were observed from September–November, as expected for a diapausing life stage. The highest cyst densities were observed in 1995 (249 cysts/l) and the lowest (> eight times lower) occurred in 1999, neither of these values occurred in May. Because adult density did not vary among years to the extent that cyst densities did, production of the overwintering cysts was not likely due to variation in adult densities as much as to variation in per capita reproductive output.

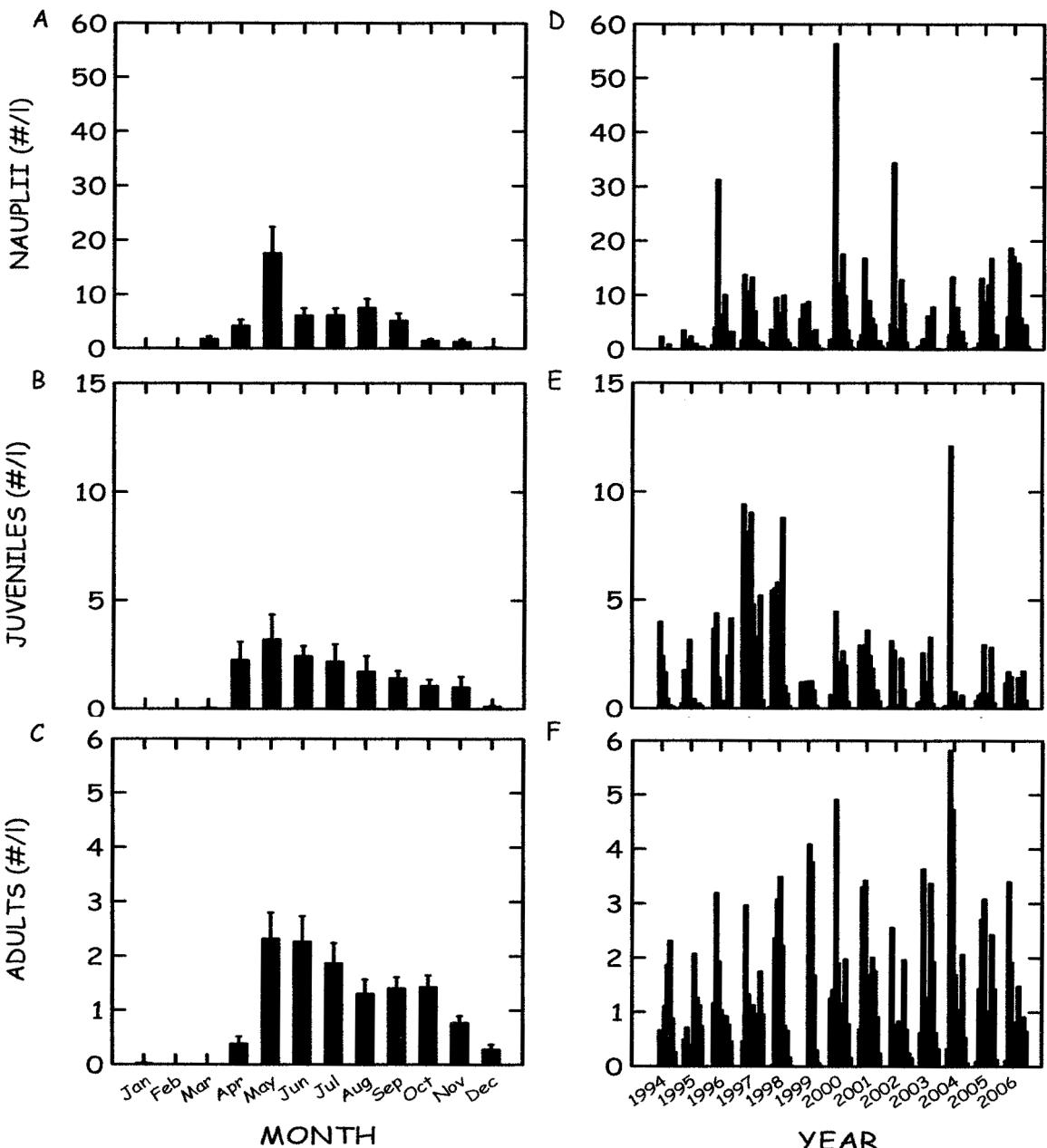


Fig. 9. Brine shrimp developmental stage abundances in the Great Salt Lake South Arm are presented for variations within year (intra-annual) by month and among years (inter-annual). Average nauplii (A, D), juvenile (B, E) and adult (C, F) densities are presented for the period of our study (1994–2006) along with standard errors.

There are a number of ways that per capita reproductive output might vary. First, the adult sex ratio might be skewed in favor of males (Fig. 10B, F). Sex ratios were observed to be skewed for some months within years (GLM: $F = 1.90$, $df = 10, 85$, $p < 0.05$), but not among years (GLM: F

= 1.44, $df = 12, 85$, $p < 0.16$). Sex ratios were skewed in favor of males only at hatching time (April) which suggests that cysts containing males hatch earlier, while from September–December, females predominated which suggested that females survive better than males.

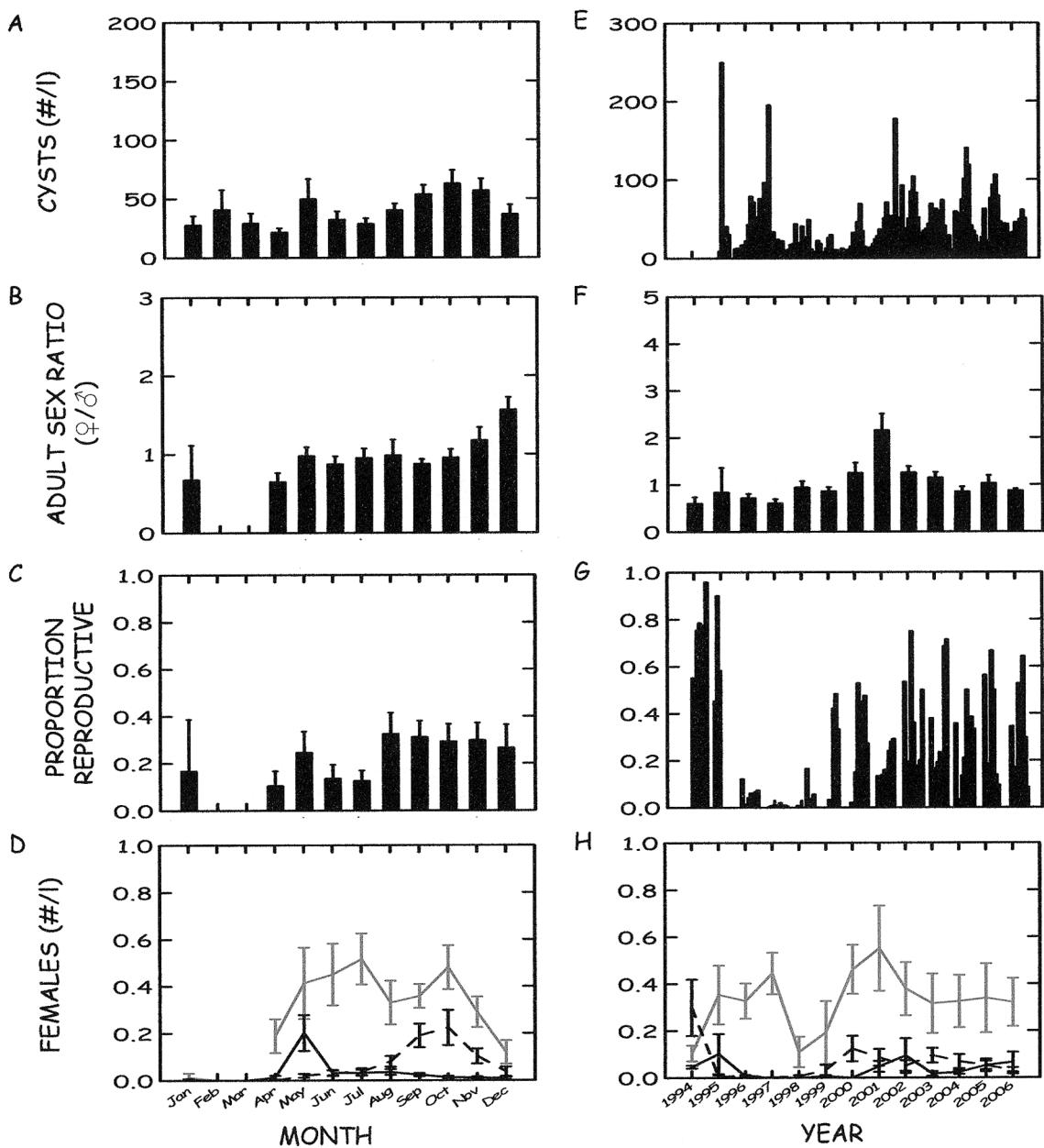


Fig. 10. Brine shrimp population attributes in the Great Salt Lake South Arm are presented for variations within year (intra-annual) by month and among years (inter-annual). Average cyst density (A, E), adult sex ratio (B, F), proportion of adult females that are reproductive (C, G), and density of females that reproduce via ovoviparity (black) and oviparity (gray) (D, H) are presented for the period of our study (1994–2006) along with standard errors.

Second, the proportion of females that are reproductive might vary. Proportion of reproductive females (Fig. 10C, G) varied within years (GLM: $F = 3.53$, $df = 10$, 85 , $p < 0.001$), and

among years ($F = 11.62$, $df = 12$, 85 , $p < 0.001$). The proportion of reproductive females was lowest in April, June and July. However, variability in this proportion was greater among

years than within years, with the greatest value (0.90) in 1995 and the lowest value (0.02) in 1997, a 45-fold difference.

Per capita reproductive output by females is complicated further because brine shrimp can reproduce in two ways: ovoviparity (eggs that hatch in the ovisac) and oviparity (diapausing cysts). Density of females reproducing by ovoviparity and oviparity (Fig. 10D, H) differed within years (GLM respectively: $F = 6.62$, $df = 11, 116$, $p < 0.001$; $F = 8.79$, $df = 11, 116$, $p < 0.001$) and among years (GLM respectively: $F = 2.12$, $df = 12, 116$, $p < 0.02$; $F = 6.22$, $df = 12, 116$, $p < 0.001$). Ovoviparity peaked in May and then declined, while oviparity peaked in September–October, which indicated reproductive mode shifted after the period of low reproduction in June and July. Some years had more females reproducing via ovoviparity (1995, 2002, 2006), but in most years oviparity dominated (1994, 1999–2001, 2003, 2004). Therefore, reproductive output depends on the proportion of females that are reproductive, and the shift from ovoviparity to oviparity.

Predators of brine shrimp.—There are three potentially important predators of brine shrimp: corixids that consume brine shrimp, grebes that consume brine shrimp and their cysts, and humans that commercially harvest brine shrimp cysts. Corixid densities in plankton tows (Fig. 11D, H) were never great and did not vary within years (GLM: $F = 1.52$, $df = 11, 45$, $p < 0.16$), but did vary among years (GLM: $F = 2.37$, $df = 6, 45$, $p < 0.05$). Corixids were most abundant at the same times of the year as brine shrimp (April–December), and appeared to exhibit two generations each year (April, July). Over the six years of measurements, corixid densities varied from an annual mean approaching $0/m^3$ to $1.46/m^3$. Grebe numbers in the fall varied dramatically among years (Fig. 12A). The commercial harvest of brine shrimp cysts (Fig. 12B) averaged 4597 ± 892 metric tons/yr and varied considerably among years. Grebe and harvest numbers could not be statistically examined for within and among year variability, because they were based on point samples by UDWR (respectively, single lake survey and sum of commercial harvest records).

Other taxa.—Several taxa were occasionally encountered (protozoans, dinoflagellates, copepods and brine fly larvae), all but brine fly larvae

were exceedingly rare at most times of the year. Protozoans (primarily ciliates, but also amoebae) and dinoflagellates (primarily *Glenodinium* sp., but occasionally *Ceratium* sp.) were only abundant from December–March (Fig. 11A, E). Copepods (Fig. 11B, F) were only abundant at the time of spring inflows to Great Salt Lake (March–July) and varied by more than 2800-fold over six years; however, neither within year (GLM: $F = 1.35$, $df = 11, 45$, $p < 0.23$) nor among year (GLM: $F = 1.43$, $df = 6, 45$, $p < 0.23$) variation were significant. Also, rotifers and nematodes were occasionally encountered.

Brine fly larvae (Fig. 11C and G) in the water column were abundant, but not as abundant as brine shrimp, and exhibited both within year (GLM: $F = 2.85$, $df = 11, 33$, $p < 0.01$) and among year variation (GLM: $F = 5.55$, $df = 3, 33$, $p < 0.003$). Brine fly larvae were sampled starting in 2003. They were most abundant at the same times of year as brine shrimp (April–December), but their populations exhibit two-annual peaks: April–May and August–October, which may reflect two distinct annual generations. Over four years, brine fly larvae densities varied by more than 2.7-fold.

DISCUSSION

Using our Great Salt Lake survey data, the dynamics of the phytoplankton-based food web can be investigated (right of dashed line in Fig. 2) using structural equation modeling. Our initial premise for the structural equation modeling is that there are two distinct times of the year that need to be examined separately: without brine shrimp present (December–February) and with brine shrimp present (March–November). The ecosystem's inter-annual variation is most strongly exhibited when brine shrimp are absent (e.g., annual peak phytoplankton abundance), which suggests that the strong effect of brine shrimp can mask annual differences in abiotic influences. On the other hand, intra-annual variation is most strongly exhibited when brine shrimp are present, because brine shrimp abundance is highly variable among months.

Our initial hypotheses about the food web included the following:

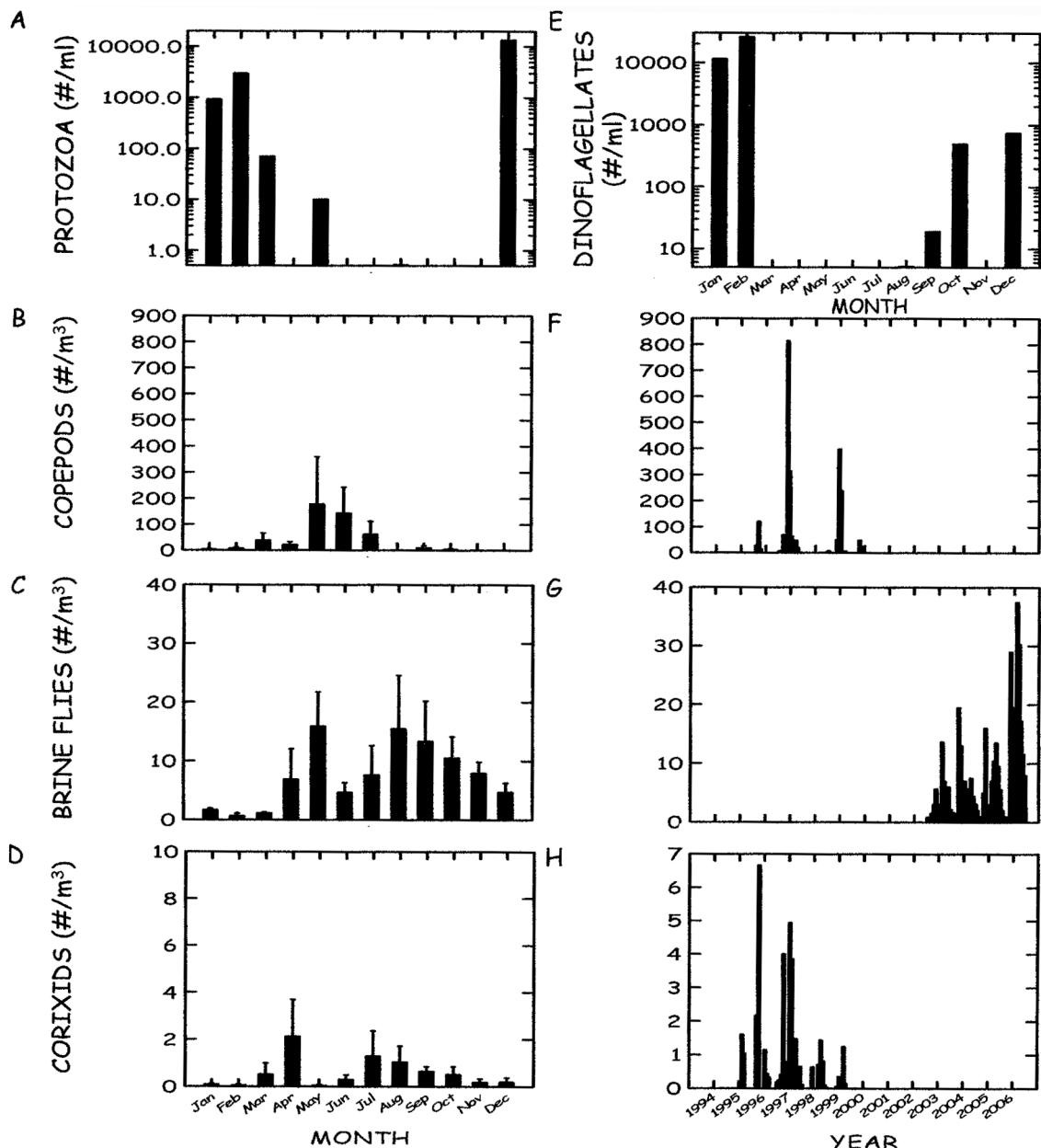


Fig. 11. Abundances of other biota in the Great Salt Lake South Arm are presented. Average densities for protozoans (A) and dinoflagellates (E) are presented by month, because they were only measured for two years (1994, 2000). Copepod density (B, F), brine fly density (C, G), and corixid density (D, H) for variations within year (intra-annual) by month and among years (inter-annual) are presented along with standard errors, because 4–5 years had been sampled.

1. In the absence of brine shrimp, maximum annual phytoplankton abundance is primarily determined by nutrient availability. Nutrient availability should be strongly affected by abiotic factors, but these relationships were

unknown. Two alternative starting points were considered: variation in watershed inflows of nutrients or variation in lake volume changing nutrient concentration of a fixed nutrient quantity already in the lake.

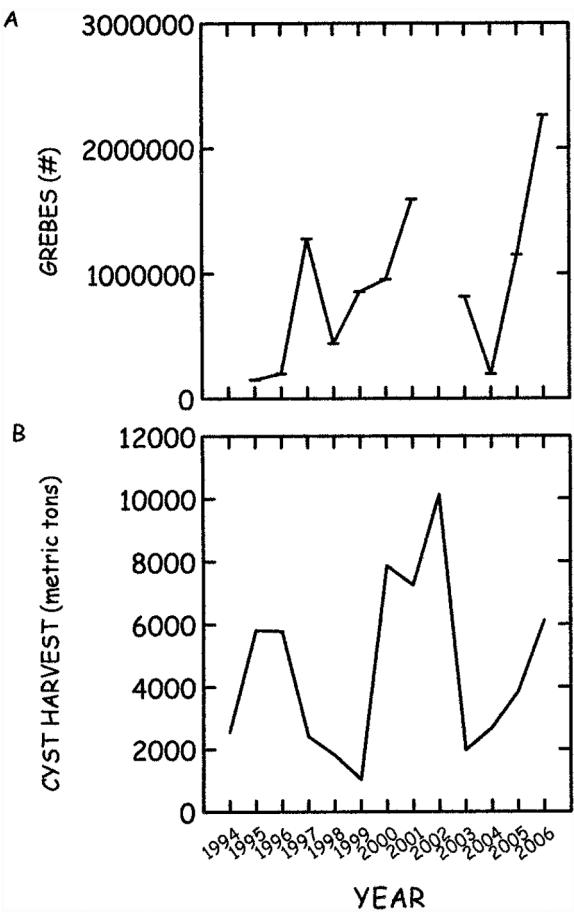


Fig. 12. Annual fall Eared Grebe population numbers (A) and commercial cyst harvest (B) in the Great Salt Lake are presented for the period of our study (1994–2006).

2. With brine shrimp, phytoplankton abundance should depend on its annual maximum in the absence of brine shrimp, intensity of brine shrimp grazing, and its ability to recover after grazing. Therefore, brine shrimp abundance is critical and we hypothesized that brine shrimp populations were ultimately limited by phytoplankton availability.
3. Brine shrimp, we hypothesized, strongly affected the annual abundances of Eared Grebes, but these birds did not significantly impact brine shrimp numbers.
4. We suspected that other species in Great Salt Lake as depicted in the food web (Fig. 2) exert little influence on phytoplankton, brine shrimp or Eared Grebes, and vice versa.

Each of these initial predictions will be addressed.

Nutrient availability

We established that most nutrients did not come from watershed inflows. First, annual watershed inflow to the lake was not significantly correlated with nutrient concentrations (DIN or TDP at 1 m: respectively, $p < 0.72$ and $p < 0.36$). Second, nutrient concentrations at 1 m for sites near watershed inflow sources (Sites 2267, 2336, 2583, and 2963) were not greater than at sites farther from inflows (Sites 2935, 3641, 3510 and 3954) (paired t-test: DIN, $t = -0.19$, $df = 16$, $p = 0.25$; TDP, $t = 0.56$, $df = 7$, $p < 0.60$). Finally, nutrient concentrations at 1 m actually increased with salinity, and salinity increases as inflow diminishes. This is not to say that watershed inputs of nutrients are unimportant, but this change occurs at decadal time scales (recent measures indicate only 8% of annual inputs come from watershed inflows: D. Naftz, *unpublished data*). Finally, DIN dynamics were more strongly affected by salinity than TDP dynamics.

Another source of nutrients might be atmospheric deposition. Maximum annual atmospheric input can be estimated using the maximum surface area of Great Salt Lake and maximum DIN deposition values for the region (NADP 2000). This indicates that atmospheric deposition accounts for less than 1.5% of DIN, again, a minor annual input.

The above observations indicate that interannual variation in nutrients is primarily a dilution of an endogenous pool. However, we originally hypothesized that nutrients would be well mixed in Great Salt Lake, because the lake's shallow depth and high surface to depth ratio would permit winds to easily mix the waters (Baskin 2005, 2006, Baskin and Allen 2005, Baskin and Turner 2006). However, mixing and the effect on nutrient concentrations were more complicated. For example, much greater concentrations of DIN (principally ammonia) at greater depths were observed (Fig. 13A, paired t-test: $t = 8.90$, $df = 66$, $p < 0.001$). Although TDP concentrations were far less different with depth, they also increased with depth (Fig. 13A, paired t-test: $t = -7.59$, $df = 61$, $p < 0.001$). Therefore, nutrients appear to accumulate at greater depths.

Greater nutrient concentrations with depth,

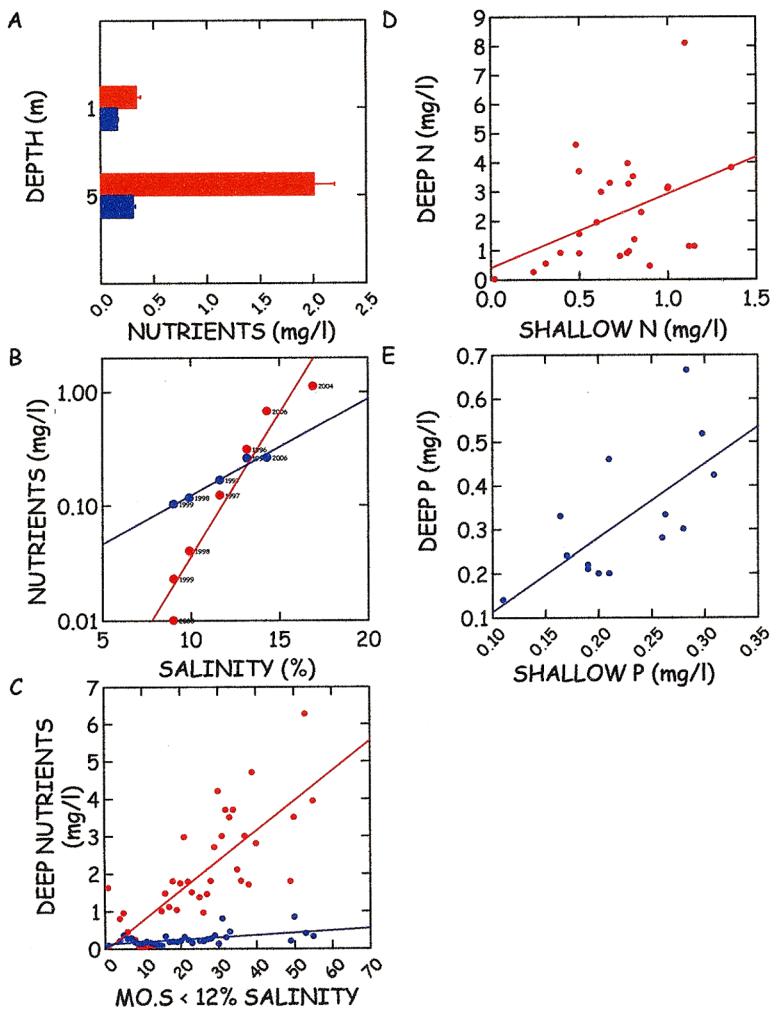


Fig. 13. Relationships between shallow and deep DIN and TDP in the Great Salt Lake South Arm are presented. (A) Average concentrations of DIN (red) and TDP (blue) at shallow (1 m) and deep (>5 m) depths. (B) Relationship between shallow salinity and DIN (red) and TDP (blue) concentrations. (C) Monthly DIN (red) and TDP (blue) at deep sites in relation to the number of months since average lake salinity was below 12%. (D) Relationship between monthly shallow and deep DIN in months when salinity is greater than 12%. (E) Relationship between monthly shallow and deep TDP in months when salinity is greater than 12%.

especially N in ammonia, are typical of eutrophic lakes. Terminal lake systems with large water-sheds, like Great Salt Lake, generally are hyper-eutrophic, as they accumulate nutrients. This explanation is based on high biotic activity in eutrophic lakes which exhausts shallow nutrients and produces products (e.g., excrement, carcasses, etc.) that sink and accumulate in deep layers until mixing occurs. However, several other nutrient patterns emerge with depth that complicates this simple explanation.

As expected, when shallow DIN or TDP increase, then their deep pools respectively increase, but shallow and deep pools are weakly coupled, especially for DIN (regression: DIN, $r^2 = 0.06$, $n = 67$, $p < 0.049$; TDP, $r^2 = 0.23$, $n = 62$, $p < 0.001$). Also, as expected, when shallow or deep DIN increase, then shallow or deep TDP respectively increase, but DIN and TDP pools are weakly coupled, especially at shallow depths (regression: shallow, $r^2 = 0.05$, $n = 72$, $p < 0.06$; deep, $r^2 = 0.38$, $n = 61$, $p < 0.001$). Weak linkages

between shallow and deep nutrient pools, and DIN and TDP pools at the same depth indicate that they are partially distinct. This would occur if Great Salt Lake does not mix as thoroughly as we originally hypothesized.

Frequent mixing is indicated for shallow portions (<4 m) of the lake, because they never exhibited a chemocline or a thermocline, except possibly a diel thermocline with calm conditions. However, deep portions (>4 m) always exhibited a thermocline between five and 7 m, and exhibited a chemocline in some years. The chemocline is termed the “deep brine layer” and it is always present at the deepest sites, but expands into shallower areas as salinities decline ($\sim <12\%$). It expanded for a 7–8 year period and again for two years at the end of our 13-year study. When a deep brine layer is present at a site, it was always below the thermocline. This creates complex patterns of mixing in the lake with the waters above the thermocline being well mixed by wind/wave action, the waters between the thermocline and chemocline periodically mixing with spring and fall turnover, and the waters below the chemocline mixing only in some years when salinities are high and wind/wave action is great.

The more complicated pattern of mixing may explain the accumulation of nutrients at greater depth and the weak linkage between shallow and deep nutrient pools, as oligomixis reflects the expansion and contraction of a “deep brine” layer (Lin 1976a, b, Stephens 1976, Stephens and Gillespie 1976). Oligomixis, rather than meromixis, occurs because at greatest depths, a deep brine layer never disappears, a deep brine layer may appear periodically at intermediate depths, and a deep brine layer may never appear in the shallowest areas ($>74\%$ of volume, Baskin 2005, 2006, Baskin and Allen 2005, Baskin and Turner 2006). Therefore, explaining the pattern of increasing N and P with depth is complicated and dynamic, and we propose the following scenario.

Deep (>5 m) nutrients.—We start with deep nutrients, because we hypothesize that: 1) the deep pool sequesters nutrients from the shallows as oligomixis intensifies and releases nutrients as oligomixis diminishes, and 2) being below the photic zone, biotic influences will be weak.

A key factor is identifying when nutrients are

sequestered in the deep layer of the lake versus when nutrients are released. To do this, we employed piecewise regression to identify a breakpoint in salinity when deep DIN or TDP were correlated with shallow DIN or TDP at higher salinities (mixing) or independent at lower salinities (very limited mixing). A breakpoint was observed at 12% salinity and no significant correlations were ever observed with the previous or current months’ abundance of phytoplankton or brine shrimp. At salinities $< 12\%$, deep nutrients were uncorrelated with shallow nutrients (DIN: $r^2 = 0.023$, $n = 40$, $p < 0.99$; TDP: $r^2 = 0.016$, $n = 30$, $p < 0.57$), and deep nutrients increased as the number of months since salinity had been $<12\%$ increased (Fig. 13C, N: $r^2 = 0.62$, $n = 40$, $p < 0.001$; TDP: $r^2 = 0.27$, $n = 30$, $p < 0.002$). At salinities $\geq 12\%$, deep nutrients were correlated with shallow nutrients (Fig. 13D, E, N: $r^2 = 0.21$, $n = 27$, $p < 0.016$; TDP: $r^2 = 0.46$, $n = 16$, $p < 0.008$).

Shallow nutrients.—We proposed three hypotheses for nutrient pools in shallow regions: 1) they will increase as lake volume decreases (salinity rises) and concentrates the endogenous nutrient pool; 2) they will increase as the presence of a “deep brine” layer diminishes (salinity rises) and releases nutrients, or decrease as the “deep brine” layer increases in extent (salinity declines) and sequesters nutrients, and 3) they will increase as biotic activity (phytoplankton and brine shrimp abundance) decreases and fewer nutrients are used.

Hypothesis 2 was already supported above in discussion of deep nutrients. Hypothesis 1 was supported, as nutrient concentrations were positively correlated with the current salinity, but hypothesis 3 was not supported, because nutrient concentrations were not negatively correlated with the current or previous months’ phytoplankton abundance and the previous month’s brine shrimp abundance was positively, not negatively, correlated with nutrients (DIN: $r^2 = 0.74$, $n = 71$, $p < 0.001$, Salinity, $p < 0.001$, Shrimp, $p < 0.013$; TDP: $r^2 = 0.55$, $n = 55$, $p < 0.001$, Salinity, $p < 0.001$, Shrimp, $p < 0.007$). The biotic relationships will be discussed further below, but it appears that when brine shrimp are present they can influence nutrients through their consumption of phytoplankton and releasing the consumed nutrients through excrement,

especially by production of ammonia. At times of the year when brine shrimp were absent (brine shrimp biomass < 0.1 adult equivalent/l), hypothesis 1 dominates and phytoplankton still exhibit no influence (Fig. 13B, DIN: $r^2 = 0.92$, $n = 7$, $p < 0.001$; TDP: $r^2 = 0.95$, $n = 5$, $p < 0.005$).

In summary (Fig. 14), DIN and TDP dynamics in Great Salt Lake appear to reflect two pools: the shallow or photic zone and a deep zone. The deep zone increases and decreases as a nutrient sink due to oligomixis with nutrients settling into the deep brine layer. When the deep brine layer diminishes as salinity increases, mixing of the photic and deep zones occurs with wind/wave action and results in a single nutrient pool. During portions of the year when brine shrimp are present, they make nutrients available in the photic zone through their excrement.

Phytoplankton

Even though phytoplankton abundance ($Chla$) was negatively correlated with Secchi depth (Fig. 15A: $r^2 = 0.42$, $n = 100$, $p < 0.001$), there is no indication that light limits phytoplankton production, because PAR was very high, averaging 73% of maximum, and the photic zone was always at least 4 m deep. We also know from laboratory studies with Great Salt Lake phytoplankton that reduced production is exhibited at higher salinities and lower temperatures (Herbst and Bradley 1989, Larson 2004). Therefore, we hypothesize that phytoplankton abundance is primarily limited by nutrients and brine shrimp grazing with smaller effects of temperature and salinity.

Phytoplankton growth appeared to be limited by N availability, as reflected by the Redfield Ratio. The ratio of N:P in phytoplankton based on particulate organic N and P in many aquatic ecosystems (Redfield Ratio) tends to approach a value of 16. Consequently, optimal phytoplankton growth should occur when inorganic sources of N and P approach a ratio of 16 in the ecosystem (Redfield 1934, 1942, 1958, Redfield et al. 1963, but see Sterner et al. 2008 for exceptions). Inorganic N:P ratios less than 16 indicate N limitation for phytoplankton and values greater than 16 indicate P limitation. Observed inorganic N:P ratios were always less than 16 for shallow and deep nutrient pools, indicating N limitation (Fig. 15B and C). These

ratios did not vary within years (GLM: shallow, $F = 1.28$, $df = 11, 52$, $p < 0.27$; deep, $F = 1.04$, $df = 11, 41$, $p < 0.43$), but did vary among years (GLM: shallow, $F = 43.49$, $df = 8, 52$, $p < 0.001$; deep, $F = 3.31$, $df = 8, 41$, $p < 0.005$). N limitation is supported by previous laboratory studies of phytoplankton reared in water from the South Arm of Great Salt Lake (Stephens and Gillespie 1976, Wurtsbaugh 1988).

If N is limiting, we would expect to observe annual peak phytoplankton abundances ($Chla_{peak}$) to be greater in years when DIN concentrations are greater. These peak abundances occur in months when brine shrimp are absent, because brine shrimp grazing is very intense. Therefore, we hypothesize the following relationship:

$$Chla_{peak} = (DIN_{pho})(k_1 - k_2 \text{Salinity} + k_3 \text{Temperature})$$

where k_1 , k_2 and k_3 are constants. Temperature had no significant effect, because observed winter water temperatures when brine shrimp were absent only varied by a few degrees among years. As expected, phytoplankton abundance ($Chla_{peak}$) diminished as salinity increased ($p < 0.005$). However, DIN in the photic zone (DIN_{pho}) had a slightly larger effect (53% of variance) as hypothesized (Fig. 15D: nonlinear regression: $r^2 = 0.88$, $n = 9$, $p < 0.001$).

When brine shrimp are present, we hypothesize that phytoplankton abundance by month ($Chla_{mo}$) depends on the preceding winter's peak phytoplankton abundance ($Chla_{peak}$), which reflects that year's nutrient limitation, its reduction by brine shrimp grazing and observed effects of temperature and salinity from the laboratory:

$$Chla_{mo} = (Chla_{peak})(k_4 - k_5 \text{Salinity} + k_6 \text{Temperature} - k_7 Shrimp_{t-1})$$

where k_4-k_7 are constants, and $Shrimp_{t-1}$ is the brine shrimp biomass in the previous month (nonlinear regression using robust LMS to achieve convergence: $r^2 = 0.76$, $n = 85$, $p < 0.001$). Brine shrimp biomass dominated the decrease in $Chla_{mo}$ ($p < 0.001$) from that year's $Chla_{peak}$, increasing salinity had a smaller effect in decreasing $Chla_{mo}$ ($p < 0.001$), and temperature had no effect ($p < 0.17$). Therefore, we conclude that the annual availability of DIN sets a maximum phytoplankton abundance and this is strongly reduced by brine shrimp grazing with

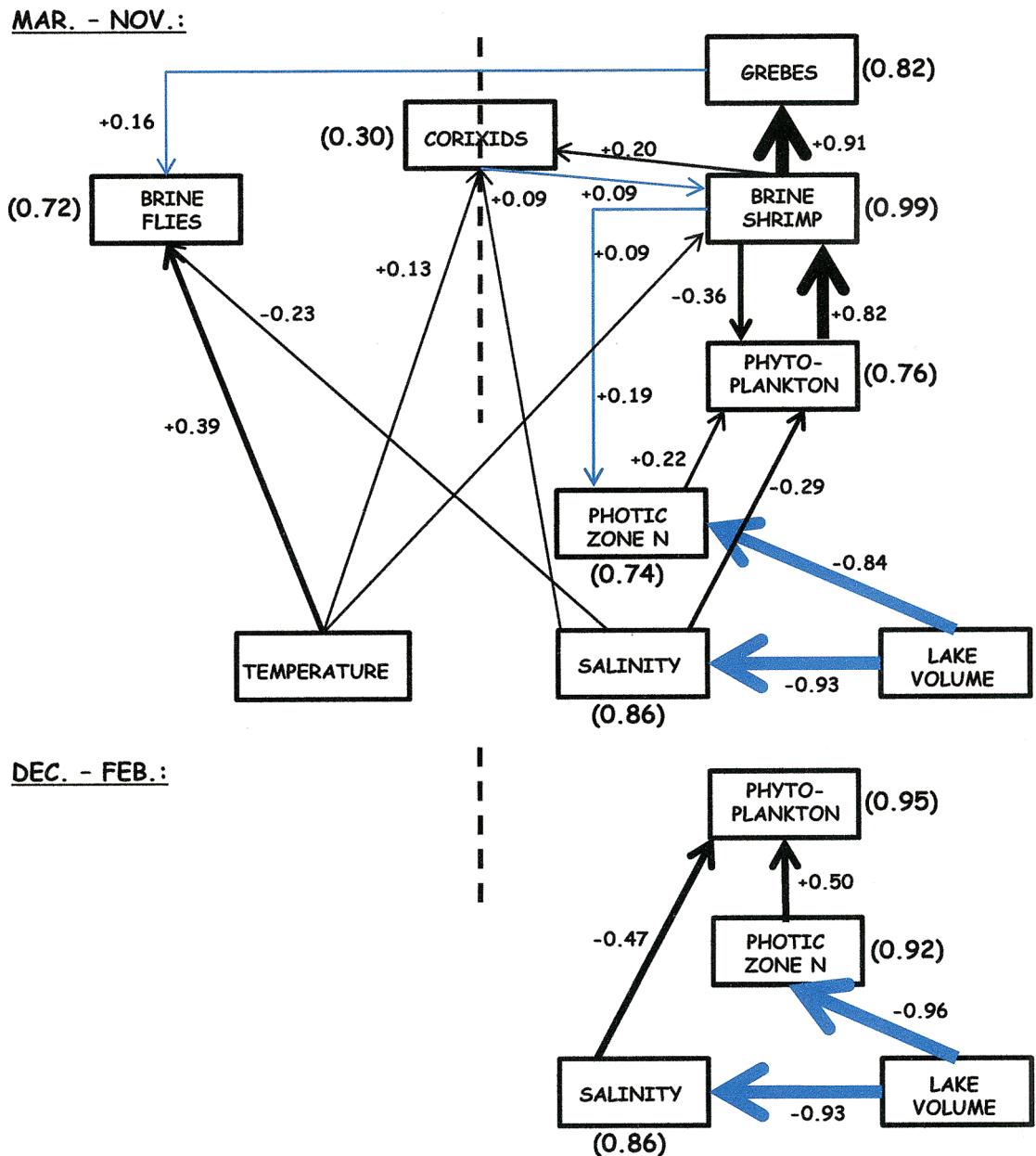


Fig. 14. The phytoplankton-based food web in the Great Salt Lake South Arm is summarized for periods when brine shrimp are present (March–November) and absent (December–February). Arrow size reflects interaction strength, with blue arrows indicating indirect interactions and black arrows indicating direct interactions. Beside the arrow is its partial correlation coefficient and each factor's r^2 is in parentheses.

little or no effect of salinity or temperature on the phytoplankton.

Phytoplankton dynamics are more than changes in overall abundance, but also include considerable annual and monthly variation in

taxa composition (Fig. 8B, D: Chlorophyte, Bacillariophyte, and Cyanophyte). We hypothesize that taxa relative abundances in the lake should respond similarly to observations in laboratory experiments with Great Salt Lake

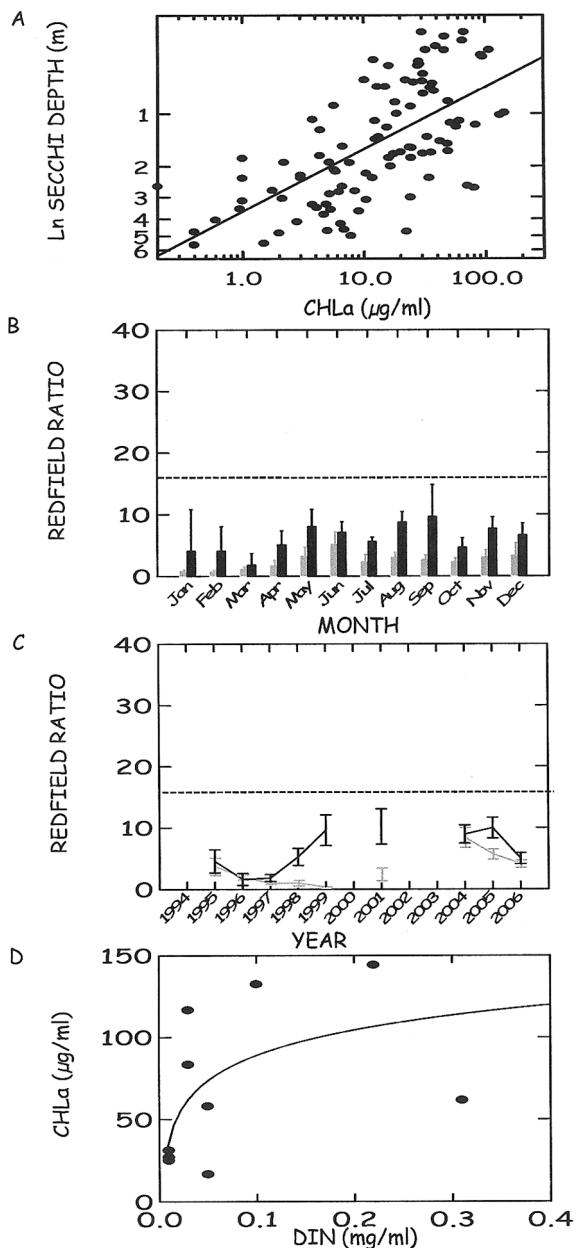


Fig. 15. The relationship between phytoplankton abundance (Chla) and Secchi Depth in the Great Salt Lake South Arm is presented (A). Monthly (B) and yearly (C) inorganic N:P ratios ($\pm \text{SE}$) are presented for the photic zone (1 m) (gray) and deeper levels ($>5 \text{ m}$) (black). The dashed line represents the 16:1 N:P ratio (Redfield Ratio). The relationship between photic zone DIN and phytoplankton abundance (Chla) is presented (D) when brine shrimp are absent.

phytoplankton, as salinity, temperature, overall phytoplankton abundance (surrogate for nutrient availability) and abundances of other taxa are changed (Larson 2004). Using backward stepwise regression, the annual and intra-annual relative abundances of each phytoplankton taxa were examined with salinity, temperature, $\text{Chla}_{\text{peak}}$ (surrogate for nutrients), and absolute abundances of other taxa (Table 1) to assess whether laboratory and field observations agree.

Chlorophyte relative abundance in the laboratory increases as salinity increases, as temperature declines, as nutrients increase, and as Bacillariophyte absolute abundance declines (competition) (Larson 2004). In the lake, annual variation in Chlorophyte relative abundance only was negatively correlated with Bacillariophyte abundance ($r^2 = 0.58$, $n = 10$, $p < 0.01$), while intra-annual variation in relative abundance was positively correlated with salinity, and negatively correlated with temperature, $\text{Chla}_{\text{peak}}$ (nutrient abundance), and Bacillariophyte abundance ($r^2 = 0.52$, $n = 51$, $p < 0.001$). These results were consistent with laboratory observations, except for the negative relationship with $\text{Chla}_{\text{peak}}$. We suggest that the unanticipated $\text{Chla}_{\text{peak}}$ result may reflect the concurrent Bacillariophyte increased abundance (competition) as described below, which prevents Chlorophytes from responding in the field.

Bacillariophyte relative abundance in the laboratory increases as Chlorophyte and Cyanophyte absolute abundances decrease (competition), but it was not very sensitive to salinity, temperature or nutrient availability (Larson 2004). In the lake, annual variation in Bacillariophyte relative abundance was negatively correlated with salinity, temperature and Chlorophyte abundance ($r^2 = 0.87$, $n = 10$, $p < 0.01$), while intra-annual variation in relative abundance was positively correlated with salinity and $\text{Chla}_{\text{peak}}$ but negatively correlated with Chlorophyte and Cyanophyte abundances ($r^2 = 0.49$, $n = 51$, $p < 0.001$). The consistently strong negative responses to Chlorophyte and Cyanophyte abundances were expected from the laboratory. The mixed annual and intra-annual results for temperature and salinity might be expected, given their weak effects in the laboratory. Finally, the positive response to $\text{Chla}_{\text{peak}}$ cannot be explained from laboratory results, but

Table 1. Significant partial correlation signs for inter- and intra-annual relative abundances of phytoplankton taxa.

Period	Salinity	Temperature	Peak Chla	Absolute Abundance			r^2	N
				Chlorophyte	Bacillariophyte	Cyanophyte		
Inter-annual								
Chlorophyte	–	–	–	–	–	–	0.58	10
Bacillariophyte	–	–	–	–	–	–	0.87	10
Cyanophyte	–	–	–	–	–	–	0.51	10
Intra-annual								
Chlorophyte	+	–	–	–	–	–	0.58	10
Bacillariophyte	+	–	–	–	–	–	0.87	10
Cyanophyte	–	–	–	–	–	–	0.51	10

variation in laboratory nutrients far exceeded field variation and Bacillariophytes may be particularly sensitive to low nutrient availability.

Cyanophyte relative abundance in the laboratory increases as salinity declines and as temperature increases (Larson 2004). In the lake, annual variation in Cyanophyte relative abundance was negatively correlated with salinity ($r^2 = 0.51$, $n = 10$, $p < 0.02$), while intra-annual variation in relative abundance was negatively correlated with salinity, temperature, $Chla_{peak}$ and Chlorophyte and Bacillariophyte abundance ($r^2 = 0.60$, $n = 51$, $p < 0.001$). The very strong negative response to salinity is expected from laboratory observations. We were surprised that temperature did not produce a strong positive effect in the field. A negative competitive effect of Chlorophyte and Bacillariophyte abundances was unexpected from laboratory studies. This, however, may be consistent with the observed negative effect of $Chla_{peak}$ (nutrients), because many of the Cyanophytes can fix nitrogen, unlike Chlorophytes and Bacillariophytes; therefore, Cyanophytes do better when nutrients are less abundant because they can fix their own nutrients and low nutrients reduce competition from other taxa.

In summary (Fig. 14), among years, peak phytoplankton abundance ($Chla_{peak}$) occurred when brine shrimp were absent (December–February) and was primarily limited by photic zone DIN concentrations. Within a year (month) when brine shrimp were present, phytoplankton abundance primarily depended on the year's $Chla_{peak}$ and brine shrimp grazing. The relative abundances of phytoplankton taxa varied with $Chla_{peak}$, salinity, temperature and competition

with other taxa. Phytoplankton abundance and composition were highly variable among and within years as DIN and biotic interactions among phytoplankton taxa varied.

Brine shrimp

Brine shrimp did not appear to be restricted by dissolved oxygen (% saturation) except at depths well below the photic zone (>5–7 m, Fig. 7A), even though DO declined with temperature ($p < 0.001$) and salinity ($p < 0.001$) as expected (regression: $r^2 = 0.68$, $n = 28$, $p < 0.001$). Studies in other lakes indicate that different *Artemia* species do better at higher values within the range of salinities and temperatures observed in our study (e.g., Dana and Lenz 1986, Dana et al. 1993, 1995, Wear and Haslett 1986, Wear et al. 1986). The positive effect of temperature is expected because brine shrimp are more productive in warmer water and consume more phytoplankton. From our results presented above, we also know that brine shrimp increase photic zone DIN through their excretion (ammonia), which increases phytoplankton abundance, but decrease phytoplankton abundance through grazing. Therefore, we hypothesized that brine shrimp abundance is primarily limited by phytoplankton abundance. We also examined whether the availability of different phytoplankton taxa differentially affected brine shrimp abundance. This was accomplished using backward stepwise regression to compare brine shrimp abundance with phytoplankton abundance, salinity, temperature and the abundances of phytoplankton taxa.

Assessing whether phytoplankton abundance limits brine shrimp abundance is not straightforward, because phytoplankton abundance peaks

at times of the year when it is too cold for brine shrimp to persist in the Great Salt Lake (winter/spring) and phytoplankton recover (increase) after grazing as the brine shrimp population declines due to cooler water temperatures in the fall (Fig. 16). Consequently, the role of phytoplankton abundance on brine shrimp abundance (#/l) was examined in two ways: inter-annually using each year's average shrimp abundance (#/l) from April–October, and intra-annually using monthly brine shrimp abundances of each developmental stage (#/l) from April–October.

Inter-annual average brine shrimp abundance is hypothesized to follow the relationship:

$$\text{Shrimp Abundance} = k_8 \text{Chla}_{\text{peak}} + k_9 \text{Temperature} + k_{10} \text{Shrimp} + k_{11}$$

where k_8 – k_{11} are constants and *Shrimp Abundance* is the average #/l from April–October during a year, *Temperature* is the maximum water temperature during a year, and *Salinity* is the maximum salinity during a year. Shrimp Abundance was positively correlated with annual maximum phytoplankton abundance ($\text{Chla}_{\text{peak}}$: $\mu\text{g/ml}$, $p < 0.021$) and maximum annual water temperature ($p < 0.043$) (Fig. 17A: $r^2 = 0.71$, $n = 14$, $p < 0.013$). $\text{Chla}_{\text{peak}}$ accounted for 80% of the explained variance. There was no significant effect of the maximum annual salinity. The analysis included data from years prior to our study (1970, 1971,

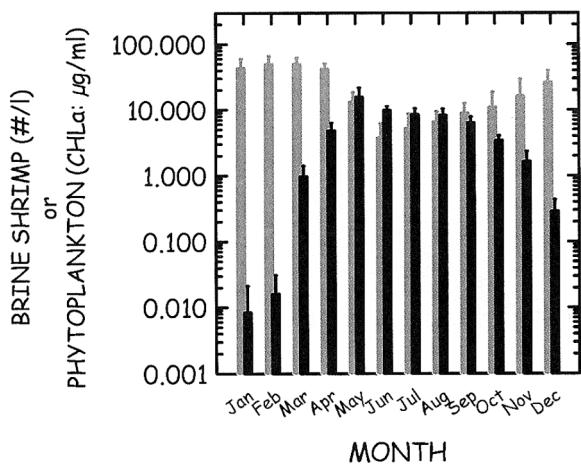


Fig. 16. Comparison between average monthly phytoplankton (gray) and brine shrimp (black) densities in the Great Salt Lake South Arm are presented along with standard errors.

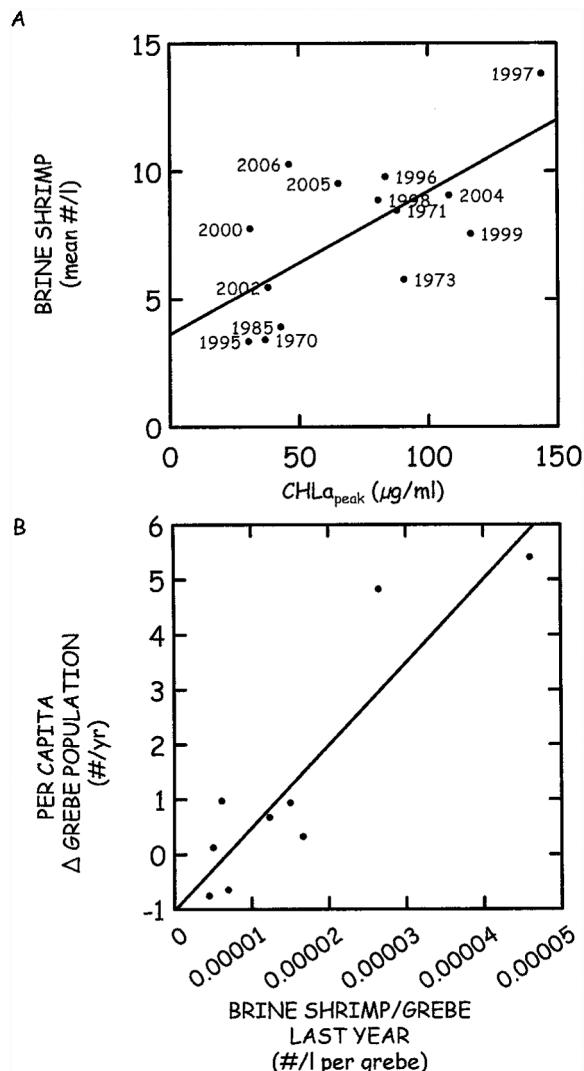


Fig. 17. The relationship between peak annual phytoplankton abundance (Chla) and brine shrimp density is presented with the year for the Great Salt Lake South Arm (A). The relationship between last year's brine shrimp density per grebe and the per capita change in grebe numbers between the previous and current year is presented (B).

1973, 1985: Stephens and Gillespie 1976, Wirick 1972, Wurtsbaugh and Berry 1990, Wurtsbaugh 1992, Wurtsbaugh and Gliwicz 2001), which indicates that current and past brine shrimp dynamics may be similar. Therefore, we conclude that brine shrimp are primarily food-limited among years.

Absence of a salinity effect was surprising

given results for other *Artemia* species (e.g., Wear and Haslett 1986, Wear et al. 1986, Dana and Lenz 1986, Dana et al. 1993, 1995, Gliwicz et al. 1995, Barata et al. 1996a, b, Williams 1998, Browne and Wanigasekera 2000). We suggest that the correlations with salinity observed in these studies may reflect the negative effects of salinity on phytoplankton production reported above (*Discussion: Phytoplankton*), not necessarily the direct effect of salinity on brine shrimp. Furthermore, from laboratory studies with Great Salt Lake brine shrimp (Belovsky and Larson 2002), salinity only exhibited negative population effects at very low (4.5%) and very high (12%) salinities, which were seldom observed in our study (8.8–17.4%).

One can question our conclusion that brine shrimp are food-limited given predation by corixids (Wurtsbaugh and Berry 1990, Wurtsbaugh 1992) and the abundant Eared Grebes (Caudell and Conover 2006) might limit brine shrimp. However, when corixid and Eared Grebe numbers were correlated with the residuals of the above relationships or were included in the relationships, predator impacts were not negative as expected if it is limiting, but exhibited a weak positive effect for corixids ($p < 0.02$) and no effect for Eared Grebes ($p < 0.24$). Previous claims that corixids might limit brine shrimp arise, because the studies were conducted in littoral areas, not open water, and in years and regions of the lake (e.g., Farmington Bay with its causeway and inflows) where salinities were very low (~5%) so that corixid numbers were 50 times higher than observed in our whole lake samples. Mellison's (2000) study of corixids in littoral areas of Farmington Bay when salinities were between 3–9% found that they did not limit brine shrimp even though their densities were 141–241 times greater than our average value, which supports our conclusion. Finally, we suspect that Eared Grebe numbers, although large, are not large enough to decrease the high abundance and reproduction of brine shrimp.

For the smaller number of years (8 vs. 14) when the abundances of the three phytoplankton taxa ($Chla_{peak}$ multiplied by taxa average relative abundances) are known, the backward stepwise regression was repeated with these values substituted for $Chla_{peak}$, which provides a better fit ($r^2 = 0.95$, $n = 8$, $p < 0.005$). Again maximum

summer water temperature was positively correlated with average brine shrimp abundance ($p < 0.005$), maximum annual salinity had no effect, and phytoplankton abundances accounted for the majority of variation explained (82%). Chlorophyte abundance had no significant effect ($p < 0.77$), Bacillariophyte abundance had a significant positive effect ($p < 0.002$) and Cyanophyte abundance had a significant negative effect ($p < 0.06$). The absence of a Chlorophyte effect was surprising because this is assumed to be the principal food for brine shrimp; however, Chlorophyte abundance did not vary appreciably among years, which weakens its influence in the regression, while Bacillariophyte and Cyanophyte abundances vary much more among years.

Intra-annual (monthly) brine shrimp abundance (#/l) changes ($\Delta Shrimp$) with survival and reproduction during the period after cysts hatch in the spring (April–November). Because inter-annual brine shrimp abundance was food-limited and increased with water temperature, we expect that survival and reproduction, and thereby intra-annual $\Delta Shrimp$, also should be food-limited and increase with temperature. Because nauplii, juveniles and adult brine shrimp require different amounts of food, differ in survival, and only adults reproduce, each stage must be accounted for separately in assessing $\Delta Shrimp$. Therefore, we hypothesize the following relationship which can be examined via backward stepwise regression:

$$\begin{aligned} \Delta Shrimp = & k_{12} Chla_{t-1} - k_{13} Nauplii_{t-1} \\ & - k_{14} Juveniles_{t-1} - k_{15} Adults_{t-1} \\ & + k_{16} Temperature_{t-1} + k_{17} Salinity_{t-1} \\ & + k_{18} \end{aligned}$$

where k_{12} – k_{18} are constants, $\Delta Shrimp$ is the change in brine shrimp density between months, and $t - 1$ refers to the value from the previous month. The function reflects intraspecific exploitative competition for food (i.e., density dependence) so that as phytoplankton abundance in the previous month ($Chla_{t-1}$) increases relative to brine shrimp energetic requirements then $\Delta Shrimp$ will become positive, and as $Chla_{t-1}$ decreases relative to brine shrimp energetic requirements then $\Delta Shrimp$ will become negative (Schoener 1973).

As hypothesized, $\Delta Shrimp$ was positively correlated with the previous month's phyto-

plankton abundance ($Chla_{t-1}$) ($p < 0.007$) and temperature ($p < 0.003$), but negatively correlated with the previous month's density of nauplii ($p < 0.001$) and juveniles ($p < 0.018$) ($r^2 = 0.78$, $n = 79$, $p < 0.001$). Density of adults did not have a significant effect ($p < 0.29$). Significant influence of nauplii and juvenile densities on $\Delta Shrimp$ is due to their large numbers, while the insignificant influence of adult density is due to their relatively small numbers. This is not to say that adult densities are unimportant, because adults produce nauplii. As with inter-annual brine shrimp abundance, salinity had no effect and any limitation by corixid or Eared Grebe predation was not indicated. Finally, a more detailed examination using phytoplankton abundance by taxa did not contribute to the correlation. Therefore, monthly changes in shrimp numbers arise from competition for food and increased survival at warmer temperatures, and explain the observed annual pattern of phytoplankton abundance and brine shrimp (Fig. 16).

Demography's importance is emphasized by the intra-annual function, which reflects characteristics of a complex stage-dependent matrix population model, where monthly changes depend on food and temperature. Brine shrimp demography is critical to the population's production and can be tracked through the annual life cycle (Table 2). Understanding biotic and abiotic factors influencing crustacean populations is not well understood (Twombly et al. 2007), and our brine shrimp data can contribute to a better understanding.

1. *Spring (March–April) nauplii*, as they hatch from cysts, constitute the onset of the annual cycle. The peak density of spring nauplii is highly correlated with the density of cysts present in the spring (average of January–March), as expected because cysts are the stage that permits brine shrimp to survive winter's cold (Table 2: $r^2 = 0.75$, $n = 11$, $p < 0.001$).

2. *Changes in nauplii density* after the March–April hatching are important because these are the source of adults. Nauplii density should increase primarily from adult females producing live young via ovoviparity, but some nauplii may emerge from cysts, which is the change in cyst density ($\Delta Cysts$). Nauplii density should decrease as some die or transition into juveniles, and lower water temperatures and salinity should

decrease survival and reproduction. Finally, the abundance of phytoplankton per shrimp should increase nauplii through greater reproduction, but decrease it through increased transition to juveniles; the net effect should be positive, because reproduction exceeds transition. We hypothesize the following relationship which can be examined via backward stepwise regression:

$$\begin{aligned}\Delta Nauplii = & k_{19} Reproductive Females_{t-1} \\ & + k_{20} \Delta Cysts_{t-1} - k_{21} Nauplii_{t-1} \\ & + k_{22} Temperature_{t-1} + k_{23} Salinity \\ & + k_{24} \left(\frac{Chla_{t-1}}{Shrimp_{t-1}} \right) + k_{25}\end{aligned}$$

where k_{19} – k_{25} are constants. The hypothesized relationship is supported (Table 2: $r^2 = 0.76$, $n = 19$, $p < 0.001$), except salinity again is found to have no effect. Food is the dominant limiting factor and examining it by taxa did not improve correlations.

3. *Density of reproductive adult females* is a critical aspect of $\Delta Nauplii$ and depends on density of adult females and the proportion that are reproductive. Density of reproductive females should be a function similar to $\Delta Shrimp$ presented above with $Adults_{t-1}$ replaced by $Adult Females_{t-1}$:

$$\begin{aligned}Adult females_{t-1} = & k_{26} Nauplii_{t-1} \\ & + k_{27} Juveniles_{t-1} \\ & + k_{28} Adult females_{t-1} \\ & + k_{29} Chla_{t-1} \\ & + k_{30} Temperature_{t-1} \\ & + k_{31} Salinity + k_{32}\end{aligned}$$

where k_{26} – k_{32} are constants. As for $\Delta Shrimp$, salinity has no effect, but all other hypothesized relationships are observed (Table 2: $r^2 = 0.65$, $n = 27$, $p < 0.001$), and again food is the principal limiting factor and examining it by taxa did not improve correlations.

The proportion of adult females that are reproductive (producing eggs via ovoviparity or cysts via oviparity) should increase with food availability, decline due to intraspecific competition for food (brine shrimp biomass), and salinity was not considered important given the above results. Given our earlier inter-annual results, we hypothesize that food abundance should primarily be defined by Chlorophyte and Bacillario-

Table 2. Significant multiple regressions obtained for brine shrimp demography (partial correlations in parentheses).

Life Stage	Independent Variables	r^2	N	P
1) Peak spring nauplii density (Mar or Apr)	Spring cyst density	0.75	11	<0.001
2) $\Delta Nauplii$ (ovoviparity production: May–Jun)	Adult females w/eggs _{t-1} (+0.28) Per capita phytoplankton _{t-1} (+0.08) $\Delta Cysts$ (+0.07) Nauplii _{t-1} (-0.39) Temperature _{t-1} (-0.05)	0.76	19	<0.001
3) Adult female density (May–Nov)	Nauplii _{t-1} + Juveniles _{t-1} (+0.68) Adult females _{t-1} (+0.09) Per capita phytoplankton _{t-1} (+0.02) Temperature _{t-1} (+0.02)	0.65	27	<0.001
Proportion of females reproducing (May–Nov)	Chlorophyte abundance _{t-1} (+0.40) Cyanophyte abundance _{t-1} (-0.28) Brine shrimp biomass _{t-1} (-0.28)	0.91	27	<0.001
4) Proportion of reproducing females producing nauplii (May–Nov)	Chlorophyte abundance _{t-1} (+0.43) Cyanophyte abundance _{t-1} (-0.28) Temperature _{t-1} (-0.20)	0.83	27	<0.001
5) $\Delta Cysts$ (oviparity production: Jul–Nov)	Adult females w/cysts _{t-1} (+0.31) Per capita chlorophytes _{t-1} (+0.28) Per capita cyanophytes _{t-1} (-0.01) Nauplii _{t-1} (-0.08) Temperature _{t-1} (+0.03)	0.53	27	<0.001
6) Spring cyst density (Dec–Mar)	Peak fall cyst density (+0.87) Winter salinity (± 0.09)	0.77	11	<0.001

phyte abundances, while Cyanophyte abundance should have a negative effect:

$$\begin{aligned} \text{Proportion Females Reproductive} \\ = & k_{33} \text{Chlorophytes}_{t-1} + k_{34} \text{Bacillariophytes}_{t-1} \\ & - k_{35} \text{Cyanophytes}_{t-1} \\ & - k_{36} \text{Brine Shrimp Biomass}_{t-1} \\ & + k_{37} \text{Temperature}_{t-1} + k_{38} \end{aligned}$$

where k_{33} – k_{38} are constants. The relationship is supported with food again the dominant limiting factor (considering taxa instead of $Chla_{t-1}$ improved the correlation), except that Bacillariophyte abundance and temperature were not significant (Table 2: $r^2 = 0.91$, $n = 27$, $P < 0.001$).

4. Brine shrimp reproduction is more complex than the proportion of females that are reproductive, because reproduction can occur through ovoviparity (eggs hatch in the female's egg sac) and oviparity (diapausing cysts). While reproduction occurs via both modes throughout the annual cycle, there is a strong seasonal pattern with ovoviparity dominating early in the cycle and oviparity dominating late. From laboratory studies, we know that the switch from ovoviparity to oviparity is triggered by low food abundance and increased temperature (Gliwicz et al. 1995, Belovsky and Larson 2002). We hypothesize the following relationship:

$$\begin{aligned} \text{Proportion Ovoviparity} = & k_{39} \text{Chlorophytes}_{t-1} \\ & + k_{40} \text{Bacillariophytes}_{t-1} \\ & - k_{41} \text{Cyanophytes}_{t-1} \\ & + k_{42} \text{Temperature}_{t-1} \\ & + k_{43} \end{aligned}$$

where k_{39} – k_{43} are constants. The function is supported with food being the dominant limiting factor, but again Bacillariophytes are not significant (Table 2: $r^2 = 0.83$, $n = 27$, $p < 0.001$). Proportion oviparity is 1 minus proportion ovoviparity.

5. Change in cyst density ($\Delta Cysts$) is important because it reflects accumulation of cysts (diapausing eggs) that permit the population to survive winter (December–February) and initiate the next year's population. This should increase as the density of adult reproductive females producing cysts increases, as food increases and as temperature increases, but it should decrease if cysts hatch. We hypothesize the following relationship:

$$\begin{aligned} \Delta Cysts = & k_{44} \text{Chlorophytes}_{t-1} \\ & + k_{45} \text{Bacillariophytes}_{t-1} \\ & - k_{46} \text{Cyanophytes}_{t-1} + k_{47} \text{Temperature}_{t-1} \\ & + k_{48} \end{aligned}$$

where k_{44} – k_{48} are constants. The function is supported, but again Bacillariophytes are not

significant (Table 2: $r^2 = 0.53$, $n = 27$, $p < 0.001$).

6. Spring cyst density (average of January–March) completes the annual cycle (see above: *Discussion: Brine Shrimp: Demography: 1. Spring (March–April) nauplii*). Obviously, spring cysts should increase with the peak fall density. Lower overwinter salinities should decrease the spring cysts, because at lower salinities cysts can break diapause and hatch during brief warm periods, but these nauplii die as it is too cold to feed. Furthermore, at lower salinities cysts can sink, temporarily being lost in the deep brine layer and sediments. However, at higher overwinter salinities, spring cysts also decline as greater cyst buoyancy allows winds and waves to deposit more of them on beaches, where they are temporarily lost until washed back into the lake. Warmer temperatures might decrease spring cysts if diapause breaks at lower salinities as discussed above. We hypothesize the following relationship:

$$\begin{aligned} \text{Spring Cysts} = & k_{49}\text{Peak Fall Cysts} + k_{50}\text{Salinity} \\ & - k_{51}\text{Salinity}^2 \\ & - k_{52}\text{Average Winter Temperature} \\ & - k_{53} \end{aligned}$$

where k_{49} – k_{53} are constants. This is supported, but temperature is not significant because it may not vary enough among years (Table 2: $r^2 = 0.77$, $n = 11$, $p < 0.001$).

In summary (Fig. 14), brine shrimp density and demography are primarily food-limited as expected from our bottom-up hypothesis for this food web. Temperature has a less important effect, while salinity and predation exert no effect. Our observation of food-limitation is consistent with Wurtsbaugh and Gliwicz's (2001) suggestion based on a single year (1994) from our dataset. Our more comprehensive dataset also indicates that phytoplankton taxa differ in suitability as foods for brine shrimp.

Predators

Even though we found that corixids and Eared Grebes did not exert a negative effect on brine shrimp populations, we still expected corixid and Eared Grebe numbers to increase with brine shrimp density, given our bottom-up hypothesis for this food web.

Corixid density should not be a simple function of brine shrimp density, because we know that

corixids exhibit no preference for nauplii due to their small size, avoid adults due to their large size, but prefer juveniles (Belovsky and Mellison 1998). Salinity should exhibit a negative effect on corixids, because they cannot tolerate salinities approaching 9%, and prefer salinities between 2–6% (Mellison 2000). Temperature may exhibit a positive effect, because corixids are restricted to shallows where water temperatures are highest (Hayes 1971, Mellison 2000). We hypothesize the following relationship:

$$\begin{aligned} \text{Corixids} = & k_{54}\text{Juveniles}_{t-1} - k_{55}\text{Adults}_{t-1} \\ & - k_{56}\text{Salinity}_{t-1} + k_{57}\text{Temperature}_{t-1} \\ & - k_{58} \end{aligned}$$

where k_{54} – k_{58} are constants. Corixid density was poorly explained by this relationship ($r^2 = 0.12$, $n = 62$, $p < 0.03$). As expected from corixid feeding behavior, density is not correlated with nauplii ($p < 0.57$), is negatively correlated with adults ($p < 0.02$), and is positively correlated with juveniles ($p < 0.01$). Temperature is positively correlated with density as predicted ($p < 0.06$). However, salinity unexpectedly exhibits a positive effect ($p < 0.04$) for which we have no explanation except that there may be some other environmental variable important to corixids that is positively correlated with salinity. A weak relationship between brine shrimp and corixid densities is not surprising, as corixids are not restricted to Great Salt Lake, but can fly between the lake and surrounding brackish waters where they have abundant alternate prey (Hayes 1971). Also, we suspect that substrate in the shallows may exert strong limits to corixids.

Grebe numbers should exhibit a per capita change between years that is positively correlated with the abundance of brine shrimp (all developmental stages) in the previous year, because more food should lead to greater survival and reproduction. Grebes consume large amounts of brine shrimp and their cysts in the South Arm (as much as 95% of diet: Caudell 2001, Conover and Caudell 2009, Conover et al. 2009). This relationship emerges (Fig. 17B: $r^2 = 0.81$, $n = 9$, $p < 0.001$), indicating the dependence of grebes on brine shrimp. Because Great Salt Lake is primarily a staging area for spring and fall grebe migration (most grebes reproduce and all winter elsewhere), this indicates that migratory success is critical to grebe populations.

A brine shrimp density of 5.85/l is predicted by the above regression to provide no net change in grebe numbers. Jehl (1988, 2007) concluded that Eared Grebe migration from Mono Lake in California was influenced by comparable brine shrimp densities. In contrast, a smaller value of 0.04–1.0/l was estimated to provide basal and foraging energetic needs for Eared Grebes in Great Salt Lake (Caudell 2001, Caudell and Conover 2006, Conover and Caudell 2009), but this does not include the greater demands of migration, survival in the wild, and reproduction. Finally, our estimated minimum brine shrimp density for maintenance of grebe populations (5.85/l) is not much smaller than average observed brine shrimp density during our study (6.97/l), which suggests that grebe numbers may be sensitive to brine shrimp populations.

In summary (Fig. 14), corixids were not closely coupled with the nutrient/phytoplankton/brine shrimp food web in the Great Salt Lake's South Arm, while grebe populations were.

Anthropogenic impacts: brine shrimp harvesting

Commercial harvests of brine shrimp cysts are consistently large (4597 ± 892 metric tons/yr (SE)), averaging $61 \pm 11\%$ (SE) of peak fall cyst densities and with some years approaching >90%. This might influence the nutrient/phytoplankton/brine shrimp food web, because spring cysts, which initiate the brine shrimp population, are in part the fall peak cyst density less the harvest. However, no significant correlation could be detected between annual harvest and the following year's brine shrimp population ($r^2 = 0.01$, $n = 11$, $p < 0.70$). First, we might not expect to observe an impact, because starting in 1997, UDWR limited harvests to levels projected to prevent a negative impact on brine shrimp population production. Second, to detect harvest effects, one needs a better understanding of overwinter cyst survival and how spring hatching numbers subtly impact brine shrimp age structure and reproduction. This is the subject of additional papers on an experimental study of overwinter cyst survival and the State of Utah's development of cyst harvest regulations (G. Belovsky et al., *unpublished manuscript*; G. Belovsky and C. Perschon, *unpublished manuscript*).

Other Great Salt Lake biota

A number of other species were incidentally encountered in our phytoplankton and brine shrimp sampling. Brine fly larvae were frequently encountered and abundant, but most species were rarely encountered and at low densities compared to other aquatic systems (protozoans, dinoflagellates, copepods, cladocerans, nematodes and rotifers). For example, cladocerans were encountered only twice in 13 years and probably reflect high freshwater inflows to Great Salt Lake. However, some of the less abundant species (protozoans, dinoflagellates and copepods) were encountered frequently enough to have their densities analyzed. Many of these species are not part of the phytoplankton-based food web discussed in this paper (right of dashed line in Fig. 2), but the organic particle/benthic algae-based food web (left of dashed line).

Brine fly larval densities were positively correlated with brine shrimp densities ($r^2 = 0.24$, $n = 48$, $p < 0.001$), which indicates that both species similarly respond to the environment. Therefore, we hypothesized that brine fly larvae should respond, like brine shrimp, positively with phytoplankton abundance and water temperature, and negatively with salinity:

$$\text{Brine Fly Larvae} = k_{59}\text{Chla}_{t-1} + k_{60}\text{Temperature}_{t-1} - k_{61}\text{Salinity}_{t-1} + k_{62}$$

where k_{59} – k_{62} are constants. The hypothesized relationship was observed ($r^2 = 0.70$, $n = 41$, $p < 0.001$) with water temperature dominating ($p < 0.001$). We suspect that Chla is not a better predictor of brine fly larval density ($p < 0.04$), because the larvae primarily consume organic particles (detritus) and benthic algae, not phytoplankton like brine shrimp, and this correlation reflects benthic algae and phytoplankton both increasing with greater nutrients (DIN). Brine shrimp density is not correlated ($p < 0.20$) with the residuals of this relationship, indicating the absence of strong interspecific competition as also found in the laboratory (Belovsky and Mellison 1997). Grebe numbers were positively correlated with the residuals ($p < 0.001$), indicating no negative effect of grebe predation, and corixid predation could not be examined because they were sampled in different years. Results support the ecosystem depiction in Fig. 2 where two weakly linked food webs comprise

the Great Salt Lake's South Arm.

Protozoan and *dinoflagellate* densities only responded to abiotic conditions. Protozoans, principally ciliates, were negatively correlated with water temperature and salinity ($r^2 = 0.59$, $n = 10$, $p < 0.05$). Dinoflagellates were negatively correlated with temperature ($r^2 = 0.51$, $n = 7$, $p < 0.07$). Increased density with lower temperature reflects both taxa's presence only in winter.

Copepod densities are positively correlated with phytoplankton abundance ($p < 0.09$) and temperature ($p < 0.002$), and negatively correlated with salinity ($p < 0.12$) and brine shrimp biomass ($p < 0.004$) ($r^2 = 0.41$, $n = 42$, $p < 0.009$). Copepods are most abundant when salinity is low, but their ability to respond to low salinities may be curtailed by competition with brine shrimp. However, the residuals of the relationship for brine shrimp density were not correlated with copepods ($p < 0.76$), indicating that copepods have no competitive effect on brine shrimp.

CONCLUSION

Our 17 years of data through 2006 for the Great Salt Lake's South Arm and continued monitoring represents one of the most extensive and long term studies of a large hypersaline lake, since most long term studies are from much smaller shallow (e.g., Lake Grassmere, NZ: Wear and Haslett 1986, 1987, Wear et al. 1986) or deeper (e.g., Mono Lake, USA: Dana et al. 1990, 1993, 1995) hypersaline lakes that present very different environmental patterns. In general, there are few long term aquatic data sets (e.g., Lake Washington, USA: Hampton and Schindler 2006, Hampton et al. 2006; Peter and Paul Lakes, USA: Carpenter et al. 2001, Carpenter 2003; Lake Tahoe, USA: Goldman et al. 1993; Mirror Lake: Likens 1985; North American Great Lakes: numerous researchers).

The Great Salt Lake ecosystem is not complex, but it is not as simple as often portrayed (e.g., Jordan 1889, Pack 1919, Wirick 1972, Post 1975, 1980, Stephens 1974, Stephens and Gillespie 1976). While containing fewer species than most lakes, Great Salt Lake has more species (~100) than expected for salinity levels of 10–20% (~8 species expected: Williams 1978, Williams et al. 1990, see Boetius and Joye 2009 for a counter

view). Yet, Great Salt Lake's ecosystem is simple enough that its food web dynamics may be examined in entirety, as we present for one of the lake's two food webs: nutrient-phytoplankton-zooplankton-avian consumers (Fig. 2 and 14). For this food web, we are able to quantify how different abiotic and biotic factors operate (Fig. 14), and use these findings to examine several ecological concepts and provide some management projections for Great Salt Lake (Menge et al. 2009).

General ecological insights

Extreme environments.—Ecologists have long debated the relative importance of abiotic factors in controlling populations (Andrewartha and Birch 1954, 1984). The importance of abiotic factors has been particularly emphasized for extreme environments and there is no question that the hypersaline conditions of Great Salt Lake are extreme (Williams 1998). Nonetheless, Great Salt Lake is highly productive with dissolved inorganic nitrogen and salinity about equally limiting phytoplankton production when brine shrimp are not present, but the effect of salinity diminishes considerably when brine shrimp are grazing. A major impact of salinity on phytoplankton production does appear through its effect on phytoplankton taxa composition. We found little or no direct effect of salinity on brine shrimp density, but the above effect of salinity on phytoplankton abundance and taxonomic composition constitutes an indirect effect, because brine shrimp are food limited. The predators of brine shrimp were either unaffected (Eared Grebes) or weakly affected (corixids) by salinity. Therefore, salinity did not appear to dominate this food web's dynamics, supporting the idea that extreme environments are not extreme to species adapted to live there (Sanders 1969, Slobodkin and Sanders 1969).

Food web dynamics.—Ecologists for many years have debated whether food webs are primarily controlled by productivity (bottom-up control) or by consumption (top-down control) (Lindeman 1942, Hairston et al. 1960, Slobodkin et al. 1967, Fretwell 1977, Oksanen et al. 1981, Carpenter et al. 1985, Schmitz 1992, Carpenter and Kitchell 1993, Hairston 1989, Hairston and Hairston 1993). The above distinctions have been built upon simple food chain/web models that closely

resemble the Great Salt Lake food web examined by us. Using these simple models, some argue that top-down control should become stronger as primary production increases (e.g., Oksanen et al. 1981), while others argue that top-down control diminishes as primary production increases (e.g., Schmitz 1992). Our Great Salt Lake study supports the latter hypothesis, as bottom-up control is observed in this highly productive ecosystem.

Another possibility is that food webs are neither top-down nor bottom-up controlled, rather they are a mix of the two, and the relative importance of each can vary (Strong 1992, Chase 2000, Hunter and Price 1992, Schmitz 1992, Vanni and De Ruiter 1996, Schmitz et al. 2000). It has been suggested that top-down control decreases in relative importance at higher trophic levels, because predators are more likely to be food-limited, and this should result in greater reduction in food populations (next lower trophic level) as one moves up the food web (Menge and Sutherland 1987). The first part of this hypothesis is supported by our study as the partial correlation between food and consumer abundances increases from nutrients and phytoplankton (+0.22) to phytoplankton and brine shrimp (+0.82) to brine shrimp and grebes (+0.91). However, the second part is not supported, because Eared Grebe and corixid predation exerted no limits on brine shrimp density. The absence of predators reducing brine shrimp densities means that trophic cascades cannot emerge (Polis and Winemiller 1996).

Food web structure.—Ecologists using mathematical models have hypothesized that ecosystems should be composed of weakly linked food chains, making the ecosystem more stable, resilient and resistant (Pimm 2002, Pimm et al. 1991, Polis and Winemiller 1996, Teng and McCann 2004). While we only examined in detail the South Arm of Great Salt Lake's nutrient/phytoplankton/brine shrimp/Eared Grebe food web (right of dashed line in Fig. 2), there is another simple food web for which we have some information (organic particles/benthic algae/brine fly larvae/gulls: left of dashed line in Fig. 2). The two food webs are potentially cross linked in three ways: 1) phytoplankton and benthic algae competing for common nutrients, 2) brine shrimp and brine fly larvae competing

for phytoplankton and benthic algae, and 3) corixids and Eared Grebes preying on both brine shrimp and brine fly larvae. We measured the last two potential cross links and found them to be either very weak or nonexistent, supporting the idea that ecosystems may be composed of weakly cross linked food webs.

Nutrient dynamics.—Some ecologists consider that nutrient availability to autotrophs in an ecosystem is constant and independent of consumers, which simplifies food web dynamics (Hairston et al. 1960, Slobodkin et al. 1967, Fretwell 1977, Oksanen et al. 1981, Hairston 1989, Hairston and Hairston 1993). Others argue that nutrient availability is not constant, but modified by consumers, which complicates food web dynamics (e.g., Porter 1976, Porter et al. 1996, DeAngelis 1992, Pace 1993, Wetzel 1983, Wardle 2002, Weisser and Siemann 2004). The latter perspective is supported by our study, as brine shrimp increase nutrient availability to phytoplankton through their consumption of phytoplankton and re-release of nutrients through excrement. Similar observations have been reported for the simple ecosystems found in the harsh environment of desert streams (Grimm 1987, Grimm and Fisher 1989).

Highly variable annual nutrient availability to autotrophs also emerges in Great Salt Lake with the expansion and contraction of a deep brine layer creating oligomixis. Over years as the deep brine layer expands and oligomixis increases with lower salinities, more nutrients are lost to greater depths and the recycling of nutrients by consumers gains in importance until lake mixing increases and the deep brine layer contracts with higher salinities. Similar complexities have been reported for Mono Lake, another hypersaline lake (Melack and Jellison 1998, Carini and Joye 2008, MacIntyre et al. 2009), and lakes with higher salinity due to mine runoff (Pieters and Lawrence 2009).

Management implications

The Great Salt Lake is a unique ecosystem, especially for North America, but it is increasingly being threatened as the surrounding region (Salt Lake, Davis and Tooele Counties, Utah: Fig. 1) becomes more impacted by anthropogenic activities. Our study helps to identify potential anthropogenic threats, many of which have not

previously been fully recognized.

Commercial harvesting of brine shrimp cysts affecting waterbird populations by reducing their brine shrimp food base was the original concern motivating UDWR to fund our study. Even with the harvest removing annually an average of 61% (some years >90%) of cysts, our database did not identify a negative effect of harvesting on shrimp numbers. However, since 1997 (all but three years of our 13 year study), UDWR regulated harvests based on experimental and modeling studies that were funded by this project. The criteria for regulation requires that the harvest be stopped when cyst densities are reduced to a level where maximum brine shrimp production, as a waterbird food base, is assured, and harvesting is not allowed if cyst densities are below this value at the start of the harvest season. The basis and development of these regulations will be presented elsewhere (G. Belovsky and C. Perschon, *unpublished manuscript*). However, implementation of these regulations by UDWR requires careful and frequent monitoring of cyst densities to terminate harvesting at the appropriate level.

Water diversion of Great Salt Lake inflows by agriculture, industry and urbanization is increasing, because continued economic growth depends on water. The sum of current proposed projects to impound and divert freshwater that otherwise would flow into Great Salt Lake already exceeds the annual inflow (Great Salt Lake Planning Team 1999, 2000). Mining of minerals in Great Salt Lake water would further reduce water. Obviously, less water decreases. Our study indicates that this will increase water temperatures and salinity, which will strongly affect nutrient availability, phytoplankton abundance and composition, brine shrimp and Eared Grebes (Fig. 14). Given Great Salt Lake's oligomixis, salinity increases will enhance mixing, which releases nutrients from depths to the photic zone. This will increase phytoplankton production, but this will be short term, because phytoplankton abundance will diminish as salinity continues to increase. Changes in phytoplankton taxa composition are very complex and not as easily predicted. Nonetheless, the outcome will be lower brine shrimp abundances, a critical food base for many waterbirds.

Nutrient additions from agricultural fertilizers

and sewage are expected to increase and these will accumulate in this terminal lake. We already know that N concentrations are much greater in Farmington Bay, where the inflow of Salt Lake and Davis County sewage is located, and this leads to dramatically higher phytoplankton productivity and a different taxa composition than the South Arm (Marcarelli et al. 2006, Wurtsbaugh and Marcarelli 2004, 2006). Our study indicates that effects of nutrient additions may be masked by the lake's oligomixis during periods when the deep brine layer is extensive and long lasting, which can lead to complacency about pollutants. During these periods of lower salinity, nutrients can be sequestered at depths having little effect on phytoplankton production and composition; then as the deep brine layer is reduced in periods of higher salinity, nutrients will be released from the depths and phytoplankton production and composition will change dramatically. This means that the lake can appear to be unaffected by nutrient additions for long periods and then their effects can suddenly be manifested; water diversions (see above) changing salinity could help to suddenly release nutrients and other substances by diminishing the deep brine layer. Finally, cumulative N additions may lead to P replacing N as the limit to phytoplankton production.

Anthropogenic climate change with its increased temperatures and reduced precipitation and runoff in the lake's drainage (Wagner 2003, Knowles et al. 2006, Stewart et al. 2005, Wagner and Adrian 2009) could further exacerbate the effects of water diversion and nutrient addition. Climate change will reduce lake volume, increase salinity and temperature, and make oligomixis less important so that all of the concomitant effects described above could emerge sooner and be exacerbated. Finally, the more frequent mixing will increase the incidence of gas releases (e.g., sulfides) from lake sediments that are annoying to people today, making public complaints more frequent and intense (Reese and Anderson 2009).

Great Salt Lake is a unique ecosystem in North America with high biological production, wildlife and commercial value that may be threatened by anthropogenic pressures. This should be a conservation concern, and our study begins to provide ecological understanding of this unique system and how to protect it. This simple system

also informs us about ecological concepts that may be more difficult to address in more complex ecosystems. But it provides only a start, because it illustrates how little we know about nutrient availability and phytoplankton responses, dynamics in another major food web (organic particles, bacteria, benthic algae, brine fly larvae and their avian consumers), and how dynamics in specific areas of the lake may differ with depth, current, wind, inflows and proximity to anthropogenic influences. Our program is addressing these additional questions.

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SUPPLEMENT

Monthly data for the 13 years of our study (*Ecological Archives* C002-005-S1).