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PRIMARY RESEARCH PAPER

Brine shrimp grazing and fecal production increase sedimentation to the deep brine layer (monimolimnion) of Great Salt Lake, Utah

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Abstract Great Salt Lake (Utah) has a monimolimnion with high concentrations of salts, particulate matter, nutrients, and mercury. To test the importance of brine shrimp (*Artemia franciscana*) grazing on particulate matter flux, we created salinity gradients in 160-cm high columns, reflecting the lake's gradient. Two experiments were performed in replicated columns with or without *Artemia*. Sediment traps were positioned at the bottoms of the mixolimnion (95 cm), chemolimnion (105 cm), or monimolimnion (140 cm). We hypothesized that because of the high salt densities of the monimolimnia, greater accumulation of sediments would be in the lower chemocline, than in the monimolimnia. The presence of *Artemia* significantly decreased chlorophyll, total nitrogen, and total phosphorus in the mixolimnion and increased particulate matter collected in sediment traps by 28–90%. As hypothesized, the largest increase of sedimenting material was at the top of chemocline, but only in the absence of *Artemia*. When present, the largest increase of collected matter was in the bottom traps. *Artemia* significantly decreased the molar TN:TP ratio of collected material, suggesting nitrogen-deficient fecal material. The experiments demonstrated the importance of *Artemia* grazing for increasing material flux from the mixolimnion to the bottom, and determining the stoichiometry of accumulated material.

Keywords *Artemia* · Excretion · Feces · Grazing · Sedimentation rate · Stoichiometry · Zooplankton

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Introduction

The cycling of nutrients is important for the sustenance of ecosystems (DeAngelis et al., 1989) and the role of planktonic animals in this process has long been recognized (e.g., Sterner, 1986; Elser & Urabe, 1999; Vanni, 2002). Zooplankton activity may affect the sedimentation rate and dissolved nutrient concentrations, as well as the stoichiometry of sediments and dissolved nutrients. All these processes have been studied extensively, particularly in marine and freshwater environments. Much less is known about these processes in saline lakes, despite being so common and ecologically and culturally relevant (Jellison et al., 2008).

Although the effect of zooplankton on the downward flux of organic matter and nutrients has been studied much more extensively in oceans than in

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freshwater lakes, a variety of processes responsible for the variability of this effect have been identified in both types of environments (e.g., Turner & Ferrante, 1979; Sarnelle, 1999; Turner, 2015). This effect may be influenced by a variety of biological, physical, and chemical processes, including the rate of microbial degradation (Lampitt et al., 1990; Hansen & Bech, 1996), ingestion (González & Smetacek, 1994; Pilati et al., 2004), and destruction (Noji et al., 1991) of fecal pellets by zooplankton. Sedimentation rates are also influenced by the size of phytoplankton cells (Dagg et al., 2014), the strength of thermal stratification (Alldredge et al., 1987; Evans et al., 1998), and many other factors (Rosa, 1985; Eadie et al., 1989; Evans et al., 1998; Hannides et al., 2009). Pitsch et al. (2012) also demonstrated that the effect of zooplankton on the nutrient loss from a lake's epilimnion is much stronger through sedimentation than through net incorporation into zooplankton biomass. Many studies in both marine and freshwater have found that zooplankton decreases the vertical flux of nutrients and organic matter (e.g., Bathmann et al., 1987; Ayukai & Hattori, 1992; Sarnelle, 1999; Yoshimizu & Urabe, 2002), which has been attributed to a high grazing rate of zooplankton on fecal material, the production of bacteria associated with zooplankton activity, and a high primary production. Other studies have reported an opposite relationship (Honjo & Roman, 1978; Bloesch & Bürgi, 1989; Andreassen et al., 1996; Pilati & Wurtsbaugh, 2003; Pitsch et al., 2012), which is mainly attributed to the presence of a great number of large zooplankton taxa, which produce fecal pellets that sink quickly and resist decomposition (e.g., copepods and euphausiids, Wotton & Malmqvist, 2001). Surprisingly, there have been only a few studies on the effects of zooplankton on the vertical particulate flux in saline lakes (Jellison et al., 1993, Jellison & Melack, 2001) and ponds (Bruce & Imberger, 2009), despite the fact that salinity (density) might have a large (direct and indirect) influence on sedimentation rates.

Great Salt Lake (Utah, USA) is a large, shallow, hypersaline, and highly productive lake with a monimolimnion (deep brine layer) that accumulates high concentrations of nutrients, organic matter and mercury (Wurtsbaugh & Berry, 1990; Jones & Wurtsbaugh, 2014). As in other hypersaline lakes, it contains a relatively simple community of halotolerant organisms, with *Artemia franciscana* Kellogg, 1906 as the only species of macrozooplankton. At least three arguments suggest that the role of *Artemia* in the downward flux in saline lakes would be greater than in marine and freshwater environments. First, *Artemia* is a much more efficient filterer compared to marine and freshwater zooplankton species. For instance, an adult individual (10 mm) can filter approximately 360 ml $\times$ day^{-1} (Wurtsbaugh, 1992), while *Daphnia* spp. average only 22 ml $\times$ day^{-1} (Lampert, 1987) and *Cyclopoida* (1.0 mm) filter even less (3.0 ml $\times$ day^{-1}) (Peters & Downing, 1984). Secondly, *Artemia* produce larger (up to 4 cm long) well-packed and fast sinking fecal pellets (personal observation). Finally, many saline lakes are shallow, at least in comparison to marine environments and to many deep lakes; thus, fecal material may quickly leave the mixolimnion (upper mixing layer of a meromictic lake) and reach the bottom before it decomposes. On the other hand, at least three arguments suggest that *Artemia* could reduce sedimentation rates. First, *Artemia* is able to feed on fecal pellets (personal observation). Secondly, the high density of saline water, particularly in the deep brine layer, may reduce sinking rates of particles. This prediction is supported by high concentrations of nutrients and organic matter in this layer of Great Salt Lake. Finally, Sarnelle (1999) predicted that the negative effect of zooplankton on nutrient sedimentation should be more likely in highly productive lakes (at least at high density of planktonic grazers).

The effects of zooplankton on the flux of organic mater and nutrients consist not only of a net loss of nutrients in the epilimnion through sedimentation and their incorporation into its biomass, but also of a net retention of dissolved nutrients in the upper layers, directly due to its nutrient excretion and indirectly due to its grazing on phytoplankton, which in turn result in a reduced uptake of nutrients by the phytoplankton. This effect is particularly well studied in freshwater environments (Den Oude & Gulati, 1988; Schindler et al., 1993; Sterner et al., 1995; Vanni, 2002; Bruce et al., 2006). For instance, Bruce et al. (2006) demonstrated that the excretion of nutrients by zooplankton in Lake Kinneret accounts for 3–58% of phytoplankton uptake of P and N, and that the high variability of this uptake depends on seasonal differences of stratification in the water column. Evidence of the effect of zooplankton on dissolved nutrient concentrations in saline lakes are scarce and only

indirect. For instance, Belovsky et al. (2011) found a positive correlation between the nutrient pool in the mixolimnion and *Artemia* density in the Great Salt Lake based on the long-term data, and attributed this correlation either to the decreased biomass of phytoplankton through grazing (thus a lower consumption of nutrients by phytoplankton) or to the excretion of nutrients by the *Artemia*. A similar positive correlation between the nutrient pool (dissolved inorganic nitrogen) and zooplankton (*Artemia monica* Verrill, 1869) density was found in Mono Lake (Jellison & Melack, 2001).

The presence of zooplankton may also affect the stoichiometric ratios of dissolved matter and seston (including phytoplankton), either directly (through grazing on phytoplankton) or indirectly through the retention of nutrients and carbon in different proportions (Elser et al., 2000; Vanni, 2002). According to ecological stoichiometric theory, ratios of nutrients in phytoplankton may alter those ratios in dissolved matter and both grazer and phytoplankton elemental composition are critical parameters influencing the rates and ratios of nutrients released by zooplankton (e.g., Elser & Urabe, 1999). Since primary production in the Great Salt Lake, as in other hypersaline lakes, is mainly limited by nitrogen rather that phosphorus (Stephens & Gillespie, 1976; Javor, 1989; Ogata et al., 2017), it could be expected that a decrease of phytoplankton biomass through grazing would increase the relative pool of dissolved nitrogen compared to phosphorus and carbon. Moreover, it could also be expected that a lower ratio of C:N in the seston than in *Artemia* body tissues would decrease the relative amount of N in the exudates, as well as in the sedimenting material. Although the literature apparently does not provide any evidence supporting these predictions for saline lakes, there is some evidence from studies of marine and freshwater environments. For instance, Olsen et al. (1986) showed that the rate of P release was strongly dependent on the P content of food, and DeMott et al. (1998) found that *Daphnia* retain P at intermediate levels relative to its deficiency in the seston. Moreover, Darchambeau et al. (2005) revealed that excess nutrients, i.e., P in the case of herbivorous copepods and N for cladocerans, are concentrated in sinking feces, while the zooplankton retain the deficient elements in their bodies.

The aim of this study was to test four hypotheses concerning the effect of *Artemia franciscana* on the rate of particulate matter flux to the deep brine layer, the stoichiometry of accumulated material and the concentrations of dissolved nutrients in the mixolimnion. Each hypothesis was tested in a column experiment in which the environmental conditions mimicked the natural conditions of the Great Salt Lake in spring, albeit at a diminished scale. The *first hypothesis* was that *Artemia* grazing increases the sedimentation rate of particulate matter to the top of the chemocline. The *second* hypothesis was that sedimentation rate and accumulation of particulate material, either in the presence or absence of *Artemia*, is greater at the top of the chemocline than in the monimolimnia. *Third*, that *Artemia* increases dissolved nutrient concentrations in the mixolimnion. *Fourth*, that nutrient export via *Artemia* feces alters the stoichiometric ratios of sediments.

Materials and methods

The approach

To analyze the effects of *Artemia* grazing on material flux and dissolved nutrients in a meromictic lake, we performed two column experiments in the presence and absence of *Artemia franciscana*. The first (preliminary) experiment was done in 4 columns (2 with *Artemia* and 2 without, referred to hereafter as control columns), whereas for the second (main) experiment we utilized 6 columns (3 with *Artemia* and 3 controls). Sampling ports allowed us to measure conditions throughout the column (Fig. 1). The preliminary experiment was started on 4 May 2015 and the main experiment on 22 May 2015: both lasted 5 days. To simulate the stratified water column of the lake, we utilized acrylic plastic columns (19.7 cm diameter and 156 cm high; a detailed description of columns is available in Jones & Wurtsbaugh, 2014). The upper mixed layer of each column was filled with lake water from Great Salt Lake with a salinity of 150 g $\times$ l^{-1}, and the deep brine layer (DBL, monimolimnion) was filled with a solution of NaCl and distilled water with a salinity of 189 g $\times$ l^{-1} (19.8%) that mimicked that of the actual lake in April 2015. We placed sediment traps at three different depths: at the bottom of the mixed layer (95 cm), at 110 cm near the bottom of the chemocline, and 140 cm in the DBL. We measured limnological and chemical parameters of the water, accumulating material in traps and *Artemia* at the

Fig. 1 Sampling deep brine layer water though a port near the bottom of the experimental columns. For this photo and for sampling, we removed the black plastic covering the bottom 50 cm of the columns

beginning and at the end of each experiment. At the beginning of each experiment, we filled each column with 46 l of water up to a level of 150 cm plus 0.5 l in the preliminary experiment and 1.0 l in the main experiment of mixed-layer water to offset water that would be extracted in our initial samples.

Field collections

We collected water from Great Salt Lake on 11 April 2015 for the preliminary experiment and on 20 May 2015 for the main experiment. On 11 April, water was taken near the Great Salt Lake Marina (40.736°N, −112.214°W), and on 20 May from the location near the deepest part (7.75 m) of Gilbert Bay (41.210°N, −112.671°W) where the deep brine layer (DBL) was present. We pumped experimental water from 2 m (mixed-layer) using a hand-powered diaphragm bilge pump with acid-washed vinyl tubing into 20 l polyethylene Cubitainers® that were washed before with HCl and rinsed three times with mixed-layer water. The tube and pump were also flushed extensively with the lake water prior to collecting water. Lake water was transported and then stored 23 days before the preliminary experiment in a cold room at 13°C, and one day before the main experiment at 25°C in Cubitainers® in 18:6 light:dark cycle at 150 μE m^{-2} s^{-1}. During storage, the water was shaken and vented daily.

On May 20th, we measured limnological parameters and took samples for chemical analyses of the lake water. We measured redox potential, specific conductivity, oxygen concentration, and pH with an In Situ Troll 9500 sonde (Denver, Colorado). We measured water transparency using a 20 cm Secchi disk. Salinity was measured using a refractometer. Water samples were collected at 0.2, 3, 5.5, 7.0, 7.25, and 7.5 m depths for analysis of salinity, chlorophyll *a*, ash-free dry weight (AFDW), total nitrogen (TN) and total phosphorus (TP), ^{15}N and ^{13}C isotopes, total dissolved nitrogen (TDN) and total dissolved phosphorus (TDP). Before samples were taken from a given depth, the tube, pump, and containers for samples were flushed with water from the appropriate depth. Samples for the analyses were transported in a cold room at 13°C. To assess the chlorophyll *a* concentration, samples (two replicates for each depth) were filtered on Gelman A/E filters (25 mm) with a nominal pore size of 1 μm, and subsequently analyzed using the Welschmeyer (1994) method with a Turner 10-AU fluorometer. To assess AFDW, two 80 ml subsamples for each depth were filtered with pre-weighed and ashed (during 2 h in 550°C) 25 mm Gelman A/E filters, placed into dried aluminum containers, dried overnight at 60°C and weighed. Samples were placed in desiccator and then combusted at 550°C and re-weighed. To asses TN and TP, 8 ml samples of unfiltered water from each depth were placed in acid-washed, 60 ml bottles, diluted with ca. 30 ml of deionized water to a final salinity 3.5%, and then stored at −20°C. To assess TDN and TDP, samples were filtered with acid-washed 47 mm Pall GF/F filter (Sigma-Aldrich Corp.) with a nominal pore size of 0.7 μm and placed in acid-washed and rinsed Nalgene bottles and diluted to 3.5% final salinity and frozen as described previously.

The Aquatic Biogeochemistry Laboratory at Utah State University analyzed nutrients. Organic nitrogen and phosphorus were digested using the persulfate method of Valderrama (1981). Following digestion, the samples were analyzed for nitrate + nitrite (cadmium reduction) and phosphate (ascorbic acid molybdenum reaction) using an Astoria autoanalyzer

(Astoria Pacific International, Portland OR). Respective TN/TDN and TP/TDP detection limits were 0.006 and 0.003 mg l^{-1}. To estimate the particulate nitrogen and carbon and their isotopic content, one sample for each depth was filtered through 25-mm-diameter Gelman A/E glass-fiber filters with a nominal pore size of 1 µm until the filters clogged. The filters were dried for 24 h at 60°C, encapsulated for subsequent isotopic analysis at the University of California Davis Stable Isotope Facility. These samples were analyzed with a Europa Scientific ANCA 2020 mass spectrometer linked with a CN analyzer. Results from the laboratory included mass of N and C and the delta values of each sample.

The experiments

Experimental columns

Three weeks before the start of each experiment, *Artemia franciscana* cysts (Brine Shrimp Direct®) were hatched and then placed in 60-l aquaria with 15% (165 g l^{-1}) salinity water (tap water mixed with 60% NaCl and 40% Instant Ocean® salts) with a high concentration of phytoplankton (primarily *Dunaliella* sp.). The day before each experiment, lake water from the Cubitainers (124 l in the preliminary experiment and 186 l in the main experiment) was homogenized and filtered through acid-washed 240-µm screen to remove *Artemia* and naupli. Unfortunately, in the main experiment, the smallest fraction of naupli passed through the net, therefore, a small fraction of juvenile *Artemia* was also present in the control treatment during the experiment. However, due to the low grazing rate of nauplii (<2 ml × ind.$^{-1}$ × day^{-1}; Wurtsbaugh & Berry, 1990), we assumed that their effect on grazing and sedimentation rates were negligible. Mixed-layer (31 l) water was first added to each column. Artificial water mimicking the salinity of DBL in the lake was prepared by mixing 19.8% NaCl with 100 mg l^{-1} Na_2S to create anoxic conditions. We then pumped 15 l of this DBL water at a rate of 285 ml min^{-1} through the bottom sampling port below the mixed-layer water using a peristaltic pump, giving a total depth of 150 cm in each column. The experiments were performed at a constant room temperature (23°C) with fluorescent lights behind the upper meter of the columns, which provided 310 µmol m^{-2} s^{-1} (within the range of the light intensity in the top part of the water column in the lake, e.g., Figure 4 in Belovsky et al., 2011) on a 16:8 L:D cycle, as a standard in studies on zooplankton depth selection, including *Artemia* (e.g., Jones & Wurtsbaugh, 2014) and other zooplankton taxa (Alekseev, 2004). A covering of black plastic was wrapped around the bottom 50 cm of the columns to simulate the light conditions in the deeper layers of the lake.

Sediment traps

Experiments were started the following day by hanging 9 sediment traps in each column with monofilament fishing line. Three replicate traps were located at three different depths (95, 105, or 140 cm). Each trap was composed of twin glass tubes (each 33 ml; 18 mm diameter × 130 mm long) glued together with silicone. In the preliminary experiment, the lower part (20 ml) of each trap was filled with a solution of 23.6% artificial NaCl water and 4.5% formalin in an attempt to preserve sedimenting material and to reduce *Artemia* grazing on the sedimented material. The upper part was filled with 21% solution of NaCl without formalin. Because *Artemia* entered the traps and possibly grazed on sediments during the preliminary experiment, the concentration of formalin in the lower part of each trap was increased to 14.5% in the main experiment, which resulted in a decrease in salinity to 22.8% compared to the preliminary experiment. Rhodamine dye placed in the bottom layer of the sediment traps provided a visual demonstration that in the final experiment, the differences in salinity prevented mixing the water between layers and between the water inside and outside traps.

At the end of each experiment, the sedimenting traps were gently removed from each column. In the first experiment, the volume of the twin trap (148 ml) was diluted to 240 ml, and then AFDW was assessed accordingly using the same procedure as for the lake water. In the second experiment, each volume of twin traps was diluted to 180 ml and then divided into three subsamples (each 60 ml) for AFDW, TN/TP or particulate N:particulate C (PN/PC), and isotopic analysis.

Artemia grazers

On the first day of each experiment, 92 adult *Artemia* (2 l^{-1}, that reflects spring conditions in the Great Salt

Lake, Wurtsbaugh & Gliwicz, 2001; Belovsky et al., 2011) raised in the laboratory were introduced into the treatment columns. The remaining columns were used as controls. Another 24 randomly chosen adult *Artemia* were taken for the assessment of initial body size and AFDW of their tissues. Mean length of *Artemia* was measured from the top of the eye to the base of the abdomen with a dissecting microscope fitted with a micrometer. Additionally, the proportion of gravid females was assessed. To assess AFDW, measured individuals were divided randomly into three equal groups, placed into aluminum container, dried overnight at 60°C, and weighed. Samples were placed in desiccator, ashed in 550°C, and weighed again. AFDW was assessed as a difference between ashed and ashed weight of the container with dried *Artemia*. Similar procedures were performed to asses the final body size, the proportion of adults with eggs, and AFDW of *Artemia* at the end of each experiment. At the end of the experiments, all *Artemia* were collected from each column by draining the contents of the columns through an acid-washed 100 mm sieve, counted in petri dishes, then anesthetized with 2% formalin, washed, measured, and dried.

During each experiment, *Artemia* distribution (in each 10 cm layer) was recorded 3–4 times either during the day or once during the night. The black plastic shields on the lower parts of the columns were removed for counting and subsequently replaced. A flashlight was used to illuminate the *Artemia* for the nighttime counts. Because *Artemia* were drawn to the focused light source, exact night distributions were difficult to obtain, but the attraction effect was minimized by measuring each interval quickly and randomly (not progressively) along each column.

Physical–chemical conditions

We measured salinity with a refractometer in 5 ml samples taken with syringe from sample ports at 11 different depths in the columns (1, 10, 50, 90, 95, 100, 105, 110, 120, 140, and 150 cm). We measured temperature and dissolved O_2 concentration between 16 and 19 h by taking 60 ml samples of water with a syringe from 9 different depths (1, 10, 50, 90, 95, 100, 105, 110, 150 cm) dispensed into a 100 ml graduated cylinder with a stir bar in the bottom and rapidly measured with an air-calibrated YSI 58 Portable Meter (Yellow Springs). The width of the sensor was only slightly smaller than the diameter of the graduated cylinder, thus minimizing water contact with the air during the measurement. Chlorophyll *a* concentration was measured in 10 ml samples at 8 depths (1, 10, 50, 90, 95, 105, 110, 150 cm) using the same method utilized for samples from the lake. To assess AFDW, we took 60 ml samples at 6 depths (10, 90, 95, 105, 110, and 140 cm) and analyzed as described previously. To assess TN and TP in the water, we took 10 ml samples from each column from depths of 10, 95, 105, and 140 cm with a syringe, placed in acid-washed vials, diluted to seawater salinity as described previously and frozen. Chemical analysis of samples was the same as for the field samples. Although the procedure during analysis of dissolved nutrients either at the beginning or at the end of each experiment was similar to that performed in the field samples, the analyses were more detailed with measurements of soluble reactive phosphorus (SRP), nitrate + nitrite (hereafter, NO^{3-}) and ammonia (NH^{4+}; sodium hypochlorite method) in each sample. These analyses were done on water from four depths (10, 95, 105, and 140 cm) that was diluted as described above. Isotopic PN (^{15}N) and PC (^{13}C) concentration was assessed by taking one sample from each column at 4 depths (10, 95, 105, and 140 cm) and analyzed as described above.

Data analysis

Statistical analyses were performed using Statistix 9. To compare the mean temperature, salinity, chlorophyll, oxygen, and AFDW concentrations in the presence and absence of *Artemia* of each of the three layers of the water column (mixed layer, $x < 95$ cm; chemocline, $95 \leq x \leq 105$ cm; and DBL, $x > 105$ cm), a two-way ANOVA with Tukey's post hoc was performed with depth as the covariate. The same statistical test was used to compare the mean temperature, salinity, chlorophyll, oxygen, and AFDW concentrations in the initial and final samples. A two-way ANOVA with Tukey's post hoc with depth as the covariate was also used to compare the mean TN, TP, PC, PN, ^{15}N, ^{13}C, N:P, C:P in the presence and absence of *Artemia* or in the initial and final samples of each of the three layers of the water column. A one-way ANOVA was performed to check the significance of the differences in the mean body length of *Artemia*, the number of individuals with eggs and the total biomass of *Artemia* at the beginning and

at the end of each experiment. The two-way ANOVA was performed to check the effect of *Artemia* (the difference between *Artemia* treatment and control), layer (the difference between chemocline and DBL), the interaction between these two factors on the accumulation rate of AFDW in Exp. I, the accumulation rate of AFDW, TN, TP, PC, PN, the proportion of ^{13}C to ^{12}C, the proportion of ^{15}N to ^{14}N in the accumulated material, the molar PC to PN, and the molar TN to TP in the accumulated material.

Results

Lake conditions

A multi-year drought prior to the experiment resulted in a low water level (7.75 m maximum depth) and an extremely thin DBL in the south arm of the lake (0.50–0.75 m, Fig. 2) in relation to earlier years (e.g., Fig. 3 in Jones & Wurtsbaugh, 2014). The salinity increased from 15% in the mixed layer to over 20% in the DBL (Fig. 2a) and daytime oxygen concentration decreased from 8.5 mg O_2 l^{-1} ± 1.5 in the mixed layer to 0.1 ± 0.0 mg O_2 l^{-1} in the DBL. AFDW, TN, and TP concentrations increased 110–130% in the DBL (Fig. 2c, d), whereas PN and PC levels increased over 280% in the deep layer of the lake (Fig. 2d).

Artemia distribution and size

During the day, *Artemia* were evenly distributed through the mixed layer of the columns with only minimal numbers in the chemocline or DBL (Fig. 3a, b). During the night, however, high densities were present in the chemocline and in the DBL (Fig. 3c, d).

Although the mean body length of *Artemia* was slightly greater at the end than at the beginning of Exp. I (7.3 ± 0.4 and 8.2 ± 0.3 mm), this difference was not apparent in Exp. II. The dry biomass of *Artemia* in the two experiments was high, ranging from 2.0 to 2.3 mg l^{-1} when calculated using the volume of the mixed layer. The number of gravid females increased 15% from the beginning to end of the experiment ($P < 0.031$). The total biomass of *Artemia* was also greater at the end of each experiment (>7 mg, $P < 0.042$). The stoichiometric ratio of C:N in the tissues of *Artemia* decreased significantly during Exp. II from 6.2 ± 0.0 to 5.2 ± 0.3 ($P < 0.032$); the ratio was not assessed in Exp. I).

Physical–chemical responses

Despite the fact that we stored the lake water before the preliminary experiment, which decreased the relative oxygen and chlorophyll concentration in the mixolimnion during the experiment in relation to the conditions in the main experiment (and possibly also to the lake conditions), the effect of *Artemia* on measured physical and chemical water parameters was very similar in both experiments. The temperature was constant in the water column in both Exp. I (23.2 ± 0.1 initial, and 23.2 ± 0.01 final) and Exp. II (22.1 ± 1.0 initial, and 22.9 ± 1.2 final) and did not differ significantly during the *Artemia* treatment or the control either at the beginning or at the end of each

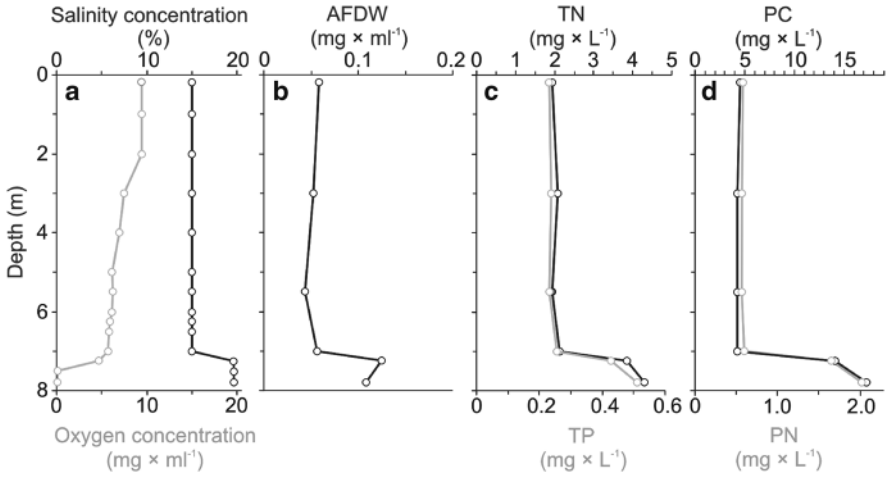

Fig. 2 Gradients of salinity and chemical (oxygen, ash-free dry weight, total nitrogen, total phosphorus, particular carbon) conditions of the water column near the deepest part of the Great Salt Lake on 20 May 2015

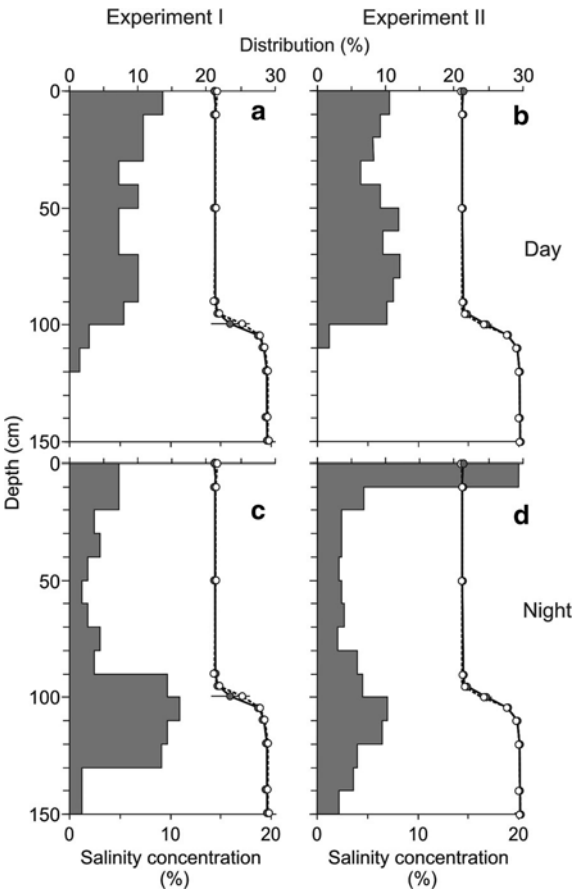

Fig. 3 Distribution of *Artemia* (*gray fields*) during the day (**a**, **b**) and night (**c**, **d**), and the mean salinity gradients in the presence (*continuous lines*, *gray circles*, mean ± 1SD) and absence (*dotted lines*, *white circles*, mean ± 1SD; SD, when greater than the width of a point) of *Artemia* in Exp. I (**a**, **c**) and Exp. II (**b**, **d**)

experiment (at $P > 0.05$, Two-way ANOVA, Table 1). The salinity gradient also was similar in the *Artemia* and control treatments, as well as at the beginning and at the end of each experiment (Table 1; Fig. 4a, d, g, i). Chlorophyll *a* (algal concentration) was high at the start of each experiment (12–29 μg l^{-1}). Chlorophyll was significantly reduced (23–38%) in the mixed layer and the chemocline during Exp. II in the presence of *Artemia* compared to the control, which also led to a significant reduction of daytime oxygen concentrations during this treatment by 37–95% (Table 1; Fig. 4). The greatest increase of chlorophyll *a* and the oxygen concentration during the experiments (particularly in the absence of *Artemia*) occurred in the chemocline, which may be attributed, at least partially, to the sedimentation of algae from the mixed layer.

Although the effect of *Artemia* on AFDW in the water column was not significant in Exp. I, the presence of *Artemia* significantly reduced AFDW (by 35%), TN (22%), TP (25%), PC (26%), PN (20%), and ^{15}N (10%) in the mixed layer in Exp. II (Table 2; Figs. 5, 6). *Artemia* presence did not affect the proportion of ^{13}C in the seston (Table 2; Fig. 6) nor the stoichiometric ratios (TN:TP, PC:PN) in any of the three layers of a water column (Table 2). The stoichiometric ratio of PC:PN at the beginning of Exp. II was 8.6:1; thus, it was slightly greater than in the body tissue of *Artemia*. There was also no significant effect of *Artemia* (at $P > 0.05$) on the level of dissolved nutrients (NH^{4+}, NO^{3-}, SRP) at the end of Exp. II in any of the three layers (two-way ANOVA, data not shown).

Artemia significantly increased the accumulation rates of AFDW in the traps during both experiments (Table 3; Fig. 5), and the increase was more apparent in the traps located in the DBL than in the chemocline (respectively, 48–90 and 28–40%). Similarly, the presence of *Artemia* also increased the accumulation rates of TN, TP, and PC, particularly in the DBL (Table 3; Figs. 5, 6). The accumulated material of the *Artemia* treatment in Exp. II contained a higher proportion of the ^{15}N isotope relative to the final control values (Table 3; Fig. 6). No such difference was observed for the ^{13}C isotope (Table 3; Fig. 6). *Artemia* significantly decreased the molar TN:TP ratio of accumulating material from 19:1 to 14:1 in the mixed layer and from 19:1 to 16:1 in the DBL, as well as the molar PC:PN ratio from 11:1 to 8:1 in the mixed layer and from 10:1 to 8:1 in the DBL (Table 3), both suggesting that the fecal material was nitrogen-deficient. The effect of *Artemia* on the particulate C:particulate phosphorus ratio in the accumulating material was negligible.

Discussion

The results of our study indicated that *Artemia* grazing reduced the algal concentration and in turn, the oxygen concentration in the mixolimnion. The results also revealed that *Artemia* grazing increases the material flux from the mixolimnion to the top of the chemocline, which was apparent in the majority of the

Table 1 Results of the two-way ANOVA with Tukey post hoc test for differences in mean temperature, salinity, chlorophyll, and oxygen concentrations in each of the four combinations of the two variables: the presence and absence of *Artemia*, as well as the initial and final samples of each of the three layers in the water column separately (mixed layer, chemocline, and DBL) in Exp. I or Exp. II

Exp. #	Layer	Comparison	Temp. (°C) Diff	Salinity conc. (%) Diff	Chl. *a* conc. (μg l^{-1}) Diff	Oxygen conc. (mg l^{-1}) Diff
I	Mixed layer	$Control_{initial}$ versus $control_{final}$	0.61 ns	0.24 ns	**4.23***	**1.52***
		$Artemia_{initial}$ versus $Artemia_{final}$	0.28 ns	0.23 ns	**3.98***	**0.95***
		$Control_{initial}$ versus $Artemia_{initial}$	1.00 ns	0.05 ns	0.15 ns	0.21 ns
		$Control_{final}$ versus $Artemia_{final}$	0.22 ns	0.06 ns	0.45 ns	0.78 ns
	Chemocline	$Control_{initial}$ versus $control_{final}$	0.36 ns	0.07 ns	**19.51***	4.96 ns
		$Artemia_{initial}$ versus $Artemia_{final}$	0.30 ns	0.52 ns	11.42 ns	2.76 ns
		$Control_{initial}$ versus $Artemia_{initial}$	0.62 ns	0.38 ns	0.57 ns	0.71 ns
		$Control_{final}$ versus $Artemia_{final}$	0.10 ns	0.20 ns	7.52 ns	1.50 ns
	DBL	$Control_{initial}$ versus $control_{final}$	0.26 ns	0.28 ns	3.73 ns	0.03 ns
		$Artemia_{initial}$ versus $Artemia_{final}$	0.55 ns	0.14 ns	6.51 ns	0.02 ns
		$Control_{initial}$ versus $Artemia_{initial}$	0.10 ns	0.14 ns	0.44 ns	0.00 ns
		$Control_{final}$ versus $Artemia_{final}$	0.11 ns	0.28 ns	2.35 ns	0.05 ns
II	Mixed layer	$Control_{initial}$ versus $control_{final}$	0.59 ns	0.12 ns	**5.43***	**1.98***
		$Artemia_{initial}$ versus $Artemia_{final}$	0.24 ns	0.18 ns	**10.76***	**3.95***
		$Control_{initial}$ versus $Artemia_{initial}$	0.44 ns	0.03 ns	0.99 ns	0.70 ns
		$Control_{final}$ versus $Artemia_{final}$	0.10 ns	0.03 ns	**6.32***	**5.23***
	Chemocline	$Control_{initial}$ versus $control_{final}$	0.89 ns	0.52 ns	**16.95***	0.95 ns
		$Artemia_{initial}$ versus $Artemia_{final}$	0.39 ns	0.53 ns	5.33 ns	**4.12***
		$Control_{initial}$ versus $Artemia_{initial}$	0.20 ns	0.16 ns	0.37 ns	0.08 ns
		$Control_{final}$ versus $Artemia_{final}$	0.30 ns	0.14 ns	**11.99***	**5.15***
	DBL	$Control_{initial}$ versus $control_{final}$	1.00 ns	0.26 ns	7.40 ns	0.00 ns
		$Artemia_{initial}$ versus $Artemia_{final}$	0.72 ns	0.20 ns	2.88 ns	0.025 ns
		$Control_{initial}$ versus $Artemia_{initial}$	0.34 ns	0.03 ns	0.29 ns	0.00 ns
		$Control_{final}$ versus $Artemia_{final}$	0.28 ns	0.03 ns	4.80 ns	0.01 ns

Ns no significance

Asterisk and bold type indicates significance at $P < 0.05$

measured parameters (AFDW, TP, TN and PC). The positive effect of *Artemia* grazing on the material flux from the mixolimnion to the top of the chemocline is most likely due to an increased sedimentation rate (due to the high filtration rate and production of large and fast sinking fecal pellets by *Artemia*), which overwhelm the sinking loss rate of phytoplankton due to *Artemia* grazing. Since we used a relatively low *Artemia* density in our experiment, this interpretation is consistent with the model prediction of Sarnelle (1999) that in highly productive lakes, a unimodal effect of zooplankton on sedimentation rate in relation to zooplankton density is expected, i.e., the effect is positive at a low and negative at a high density of planktonic grazers. Full confirmation of the model predictions would require additional experiments with *Artemia* densities at varying levels. A greater fraction of *Artemia* fecal material exiting the euphotic zone compared to the other zooplankton taxa, such as *Daphnia*, would explain the discrepancy between the result obtained in our study and the results obtained in some earlier studies in highly productive freshwater lakes and enclosures, in which zooplankton had a negative effect on the sedimentation rate, even at a low density of planktonic grazers (Sarnelle, 1999). The other possible effect responsible for this discrepancy

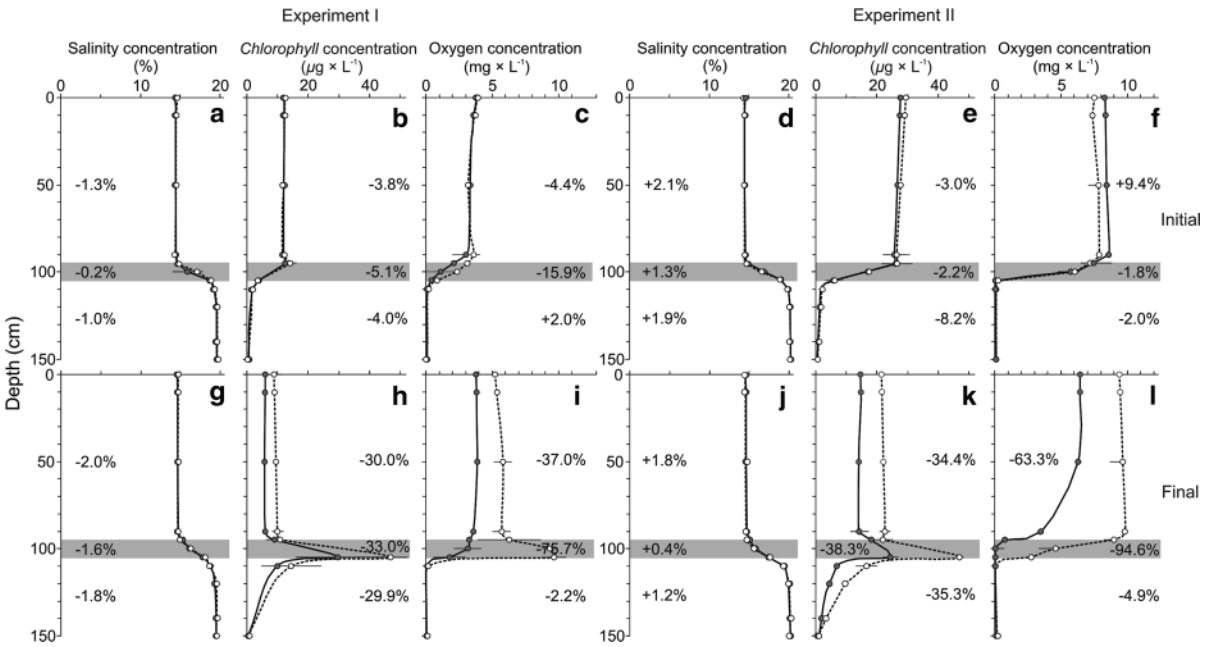

Fig. 4 Gradients of salinity, chlorophyll, and oxygen concentration at the beginning (*top row*: **a–f**) and at the end (*bottom*: **g–l**) of Exp. I (**a–c**, **g–i**) and Exp. II (**d–f**, **j–l**) in the presence (*continuous lines*, *gray circles*, mean ± 1SD) and the absence (*dotted lines*, *white circles*, mean ± 1SD) of *Artemia*. *Gray fields* show the depth ranges of the chemocline. The mean difference (%) in the concentration of each parameter between *Artemia* and the control is shown separately for the mixed layer, chemocline and DBL

would be a lower sinking loss rate of phytoplankton due to the higher density of water in hypersaline than freshwater lakes.

The positive effect of *Artemia* on the rate of the material flux from the mixolimnion to the top of the chemocline would support our first hypothesis that *Artemia* grazing increases the sedimentation rate to the top of the chemocline. However, another complementary explanation is possible: because *Artemia* migrated into the chemocline and monimolimnion at night they may have actively transported materials to the deeper layers. Such nighttime depth selection behavior could most likely be attributed to their willingness to feed on high concentrations of algae sedimented into the chemocline. This behavior is also consistent with observations that *Artemia* is resistant to hypoxic conditions (Vos et al., 1979). It is not clear why *Artemia* avoided the deep layers during the day if food levels were higher there. Conceivably, they chose to feed in the photic mixed layer during the day to capitalize on the ongoing primary production there. We were surprised that the *Artemia* utilized the top part of the hypoxic layers at night, because in a previous experiment utilizing the same experimental columns, the *Artemia* rarely entered the hypoxic layers (Jones & Wurtsbaugh, 2014). In that experiment, however, water from the DBL of the lake was used to fill the bottoms of the columns, in contrast to the artificial DBL we utilized. It is possible that high H_2S, anoxia and other characteristics of the lake's DBL cause *Artemia* to avoid that zone. Moreover, it should be noted that in our experiment, *Artemia* dwelled only in the upper portion of the DBL, and were constantly moving up and down, and therefore, individuals stayed in the hypoxic layers only for a short time period. Measurements of *Artemia* distribution in the lake during both day and night are needed to characterize their actual distribution in the lake, which would confirm that the inverse DVM observed in our study, particularly the selection of depths in the chemocline and in the top part of the DBL during the night, was not an experimental artifact.

According to our second hypothesis, the greatest sedimentation rate and accumulation of particulate matter would have been in the top of the chemocline. However, this occurred only in the Controls without

Table 2 Results of the two-way ANOVA with Tukey's post hoc test for differences in mean AFDW, total nitrogen, total phosphorus, N:P ratio, particular carbon, proportion of ^{13}C to ^{12}C, particular nitrogen, proportion of ^{15}N to ^{14}N in each of the four combinations of two variables: the presence and absence of *Artemia*, as well as the initial and final samples of each of the three layers in the water column separately (mixed layer, chemocline, and DBL) in Exp. II

Layer	Comparison	AFDW (g m^{-2} l^{-1}) Diff	TN (mg l^{-1}) Diff	TP (mg l^{-1}) Diff	N:P Diff
Mixed layer	$Control_{initial}$ versus $control_{final}$	0.008 ns	0.22 ns	0.027 ns	0.19 ns
	$Artemia_{initial}$ versus $Artemia_{final}$	**0.022***	**0.55***	**0.058***	0.78 ns
	$Control_{initial}$ versus $Artemia_{initial}$	0.001 ns	0.12 ns	0.029 ns	1.33 ns
	$Control_{final}$ versus $Artemia_{final}$	**0.013***	**0.50***	**0.059***	0.35 ns
Chemocline	$Control_{initial}$ versus $control_{final}$	0.013 ns	0.23 ns	0.021 ns	0.15 ns
	$Artemia_{initial}$ versus $Artemia_{final}$	**0.022***	0.18 ns	0.011 ns	1.15 ns
	$Control_{initial}$ versus $Artemia_{initial}$	0.001 ns	0.07 ns	0.024 ns	1.52 ns
	$Control_{final}$ versus $Artemia_{final}$	0.007 ns	0.48 ns	0.056 ns	0.22 ns
DBL	$Control_{initial}$ versusversus $control_{final}$	0.012 ns	0.12 ns	0.006 ns	0.75 ns
	$Artemia_{initial}$ versus $Artemia_{final}$	0.012 ns	**0.45***	0.036 ns	0.95 ns
	$Control_{initial}$ versus $Artemia_{initial}$	0.001 ns	0.19 ns	0.020 ns	0.12 ns
	$Control_{final}$ versus $Artemia_{final}$	0.001 ns	0.14 ns	0.011 ns	0.31 ns
Layer	Comparison	PC (mg C l^{-1}) Diff	^{13}C Diff	PN (mg C l^{-1}) Diff	^{15}N Diff
Mixed layer	$Control_{initial}$ versus $control_{final}$	0.81 ns	0.33 ns	0.00 ns	0.10 ns
	$Artemia_{initial}$ versus $Artemia_{final}$	**1.06***	0.39 ns	**0.29***	**0.79***
	$Control_{initial}$ versus $Artemia_{initial}$	0.13 ns	0.14 ns	0.05 ns	0.14 ns
	$Control_{final}$ versus $Artemia_{final}$	**1.75***	0.31 ns	**0.24***	**0.83***
Chemocline	$Control_{initial}$ versus $control_{final}$	1.08 ns	0.47 ns	0.07 ns	0.70 ns
	$Artemia_{initial}$ versus $Artemia_{final}$	0.26 ns	0.32 ns	0.07 ns	1.28 ns
	$Control_{initial}$ versus $Artemia_{initial}$	0.22 ns	0.19 ns	0.03 ns	0.16 ns
	$Control_{final}$ versus $Artemia_{final}$	1.56 ns	0.04 ns	0.17 ns	0.42 ns
DBL	$Control_{initial}$ versus $control_{final}$	0.28 ns	0.35 ns	0.05 ns	**0.91***
	$Artemia_{initial}$ versus $Artemia_{final}$	0.31 ns	0.33 ns	0.07 ns	**0.88***
	$Control_{initial}$ versus $Artemia_{initial}$	0.13 ns	0.31 ns	0.02 ns	0.09 ns
	$Control_{final}$ versus $Artemia_{final}$	0.14 ns	0.21 ns	0.03 ns	0.09 ns

Ns no significance

Asterisk and bold type indicates significance at $P < 0.05$

Artemia. In their presence, the accumulation rate of TP and TC was similar in the chemocline and in the DBL, and the accumulation rate of AFDW and TN was even slightly greater at the bottom of the DBL than in the chemocline. Although this observation contradicts the hypothesis, we are not able to prove that it is false, because this effect could be explained not only by the increased sedimentation rate through the DBL, but also by the 'active transport' of vertically migrating zooplankton. However, it should be noted that despite having only 1% of *Artemia* reach the bottom 10 cm of the columns at night, the accumulation of the material was much greater in the bottom traps in the presence of *Artemia* grazing than in the control, which indicated that fecal sedimentation and algal sedimentation were likely the dominant mechanism influencing the accumulation of matter in the DBL.

The results of our study also revealed that *Artemia* grazing did not significantly affect the stoichiometry of dissolved nutrients in the water column, but nutrient export via their feces alters the stoichiometric ratios of the accumulated material in the chemocline and DBL

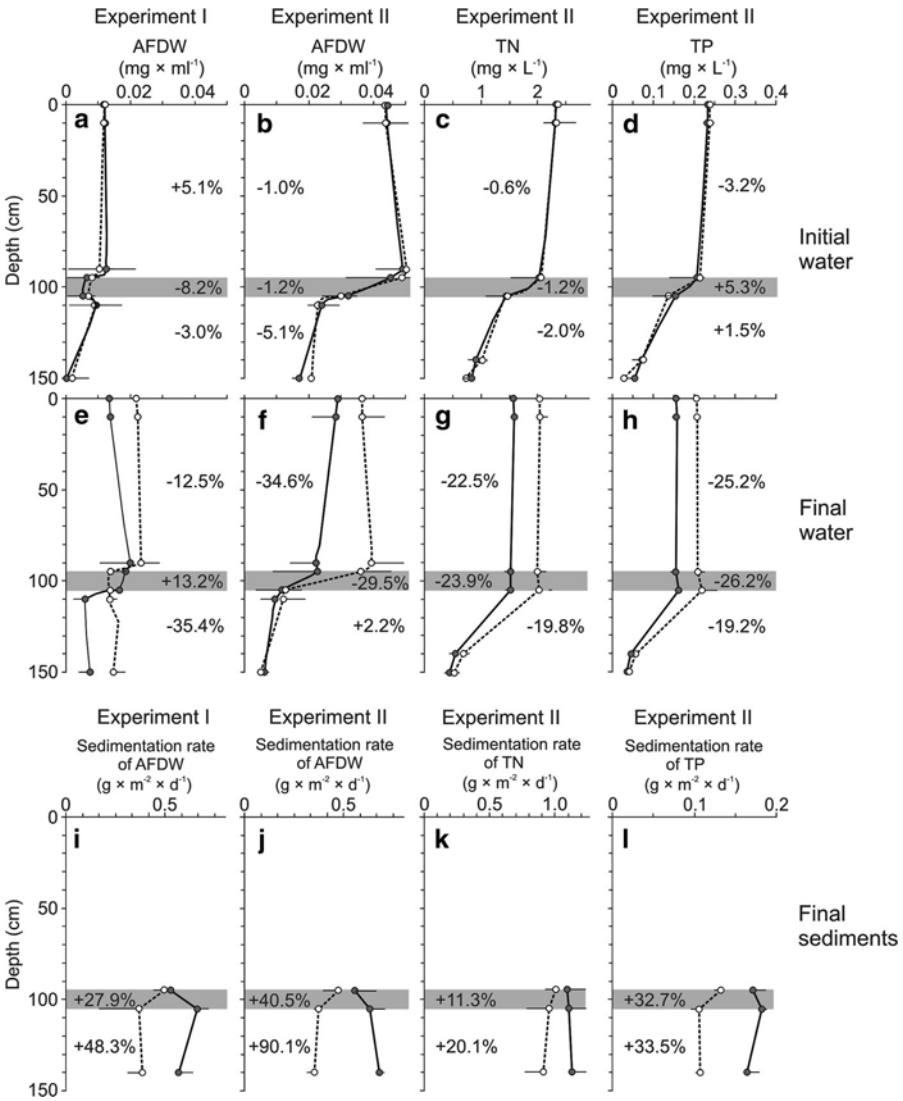

Fig. 5 Chemical parameters (AFDW, total N, total P) in the water column (mean ± 1SD) at the beginning (**a**–**d**) and end (**e**–**h**) of Exp. I and Exp. II, as well as the accumulation rate of AFDW (**i**, **j**), total N (**k**), total P (**l**) in the chemocline and DBL at the end of Exp. I and Exp. II in the presence (*continuous lines*, *gray circles*) and absence (*dotted lines*, *white circles*) of *Artemia*. *Gray fields* indicate the depth ranges of the chemocline. The mean difference (%) in the concentration of each parameter between *Artemia* and the control is shown separately for the mixed layer, chemocline and DBL

by decreasing the N:P ratio and increasing the C:N ratio, both suggesting that the fecal material was nitrogen-deficient. This observation is consistent with our fourth hypothesis. Moreover, the results of our study also revealed that the stoichiometric ratio of C:N in the tissues of *Artemia* decreased during the second experiment (this ratio was not assessed in the first experiment). The results are consistent with those of earlier studies about the effect of zooplankton on the stoichiometry of sediments in marine and freshwater environments (e.g., Pitsch et al., 2012) and with the stoichiometric theory, which states that the deficient elements (in this case N) are captured in the biomass and the excess elements are excreted or defecated. The analysis of the stable isotopes of nitrogen and carbon revealed other interesting results. For nutrients that are scarce, the 'enrichment' of the heavy isotope in an organism processing the element is expected, because the heavier isotope is processed with more difficulty than the lighter one. In turn, a decrease of that isotope in the excretions could be also expected. Ordinarily, with less limiting nutrients like carbon, there is less discrimination between the heavy and light isotopes, and consequently, less enrichment could be expected in the organism's tissues. Our data are consistent with these predictions. While the relative amount of ^{15}N in relation to ^{14}N decreased in the accumulated material of approximately $\delta - 1$ of the *Artemia* treatments

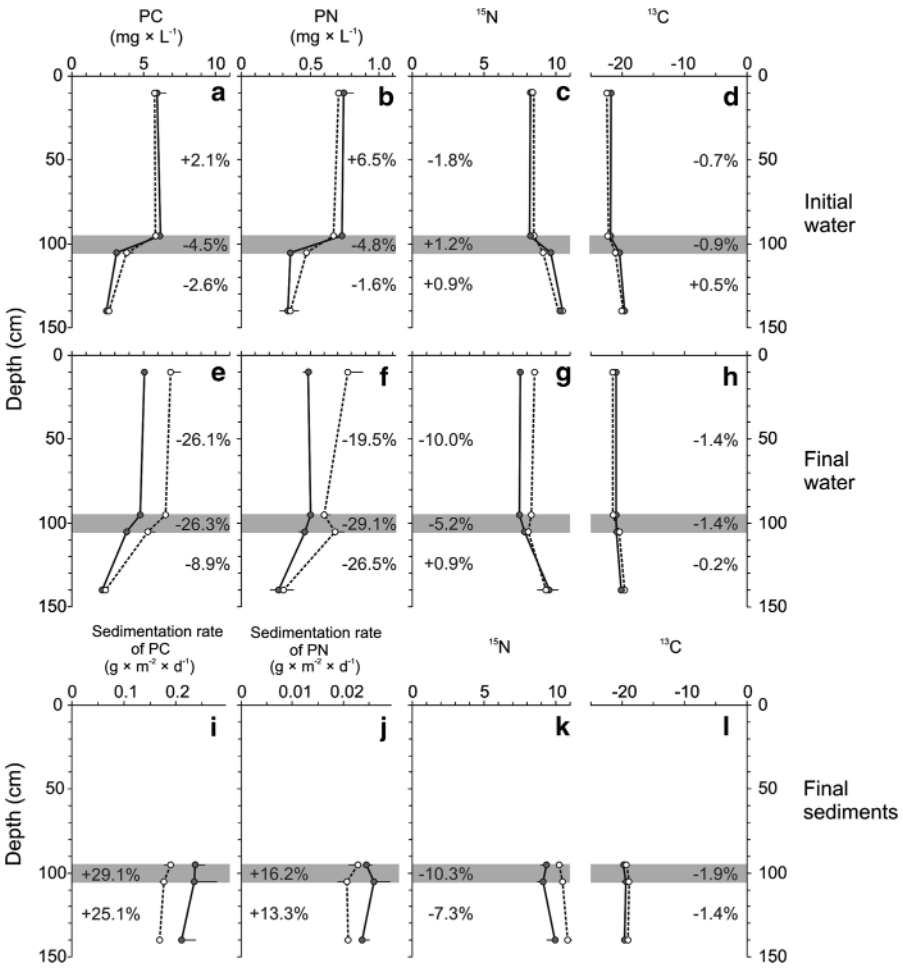

Fig. 6 Chemical parameters (particular C, particular N, proportion of ^{15}N to ^{14}N and ^{13}C to ^{12}C) in the water column at the beginning (**a–d**) and end (**e–h**) of Exp. I or Exp. II, as well as the accumulation rate of particular C (**i**), particular N (**j**) and the proportion of ^{15}N to ^{14}N (**k**) and ^{13}C to ^{12}C (**l**) in sediments in the chemocline and DBL at the end of Exp. I or Exp. II in the presence (*continuous lines*, *gray circles*, mean ± 1SD) and absence (*dotted lines*, *white circles*, mean ± 1SD) of *Artemia*. *Gray fields* indicate the range of the chemocline. The mean difference (%) in the concentration of each parameter between *Artemia* and the control is shown separately for the mixed layer, chemocline and DBL

relative to the final control values, the difference between ^{12}C and ^{13}C was not significant—neither in *Artemia* tissues at the beginning and at the end of the experiment nor in the accumulated material of the *Artemia* treatments relative to the final control values.

Contrary to the distinct effect of *Artemia* grazing on the material flux from the mixolimnion to the top of the chemocline and DBL and on the stoichiometry of the sediments, their effect on the level of dissolved nutrients (NH^{4+}, NO^{3-}, SRP) was not significant. This observation is not consistent with our third hypothesis and does not confirm the predictions of Belovsky et al. (2011), who claimed that the high amount of ammonia in the water of the GSL in summer is due to *Artemia* excretions. The observations of earlier studies in freshwater and marine environments on the role of zooplankton in increasing dissolved nutrients in the water of the epilimnion or the mixolimnion are also not confirmed (e.g., Den Oude & Gulati, 1988; Schindler et al., 1993; Jellison & Melack, 2001). Although the lack of a difference in soluble nutrients in our experiment could be an experimental artifact, it could also be the result of their rapid and much greater uptake by phytoplankton than their excretion by *Artemia*. Moreover, it should be noted that the real effect of *Artemia* on nutrient excretion in the lake could have been underestimated in our study due to the fact that although we controlled the density of adult individuals, this was not the case for the density of nauplii and juveniles. Although nauplii and small juveniles excrete less than 10% of that of adults, their relatively high density in the lake (1–6 ind. × l^{-1}, Fig. 9 in Belovsky et al., 2011) could have contributed to this process.

Table 3 The results of the two-way ANOVA (F, df and P, df in the subscripts) for the difference in the sedimentation rate of AFDW, total N, total P, particular C, particular N, particular nitrogen, proportion of ^{13}C to ^{12}C, and proportion of ^{15}N to ^{14}N in accumulated material in sediment traps, as well as molar particular C to particular N, and molar total N to total P in accumulated material between the *Artemia* treatment and the control, as well as the chemocline and DBL and the difference in the effect of *Artemia* in the chemocline and DBL in Exp. I or Exp. II

Exp. #	Factor	*Artemia* versus control		Chemocline versus DBL		Interaction	
		F_{df}	P	F_{df}	P	F_{df}	P
I	Sedimentation rate of AFDW	**5.20_1**	**0.037**	0.03_1	0.868	0.81_1	0.398
II	Sedimentation rate of AFDW	**39.06_1**	**<0.000**	0.02_1	0.894	3.62_1	0.081
II	Sedimentation rate of TN	**3.92_1**	**0.048**	0.06_1	0.817	0.25_1	0.624
II	Sedimentation rate of TP	**8.70_1**	**0.010**	2.61_1	0.128	0.56_1	0.468
II	Sedimentation rate of PC	**79.63_1**	**0.012**	**14.98_1**	**0.031**	1.07_1	0.409
II	Sedimentation rate of PN	7.56_1	0.111	1.00_1	0.422	0.11_1	0.775
II	^{13}C	2.39_1	0.262	0.00_1	0.969	0.06_1	0.823
II	^{15}N	**37.09_1**	**0.026**	**17.07_1**	**0.030**	0.82_1	0.461
II	PC:PN (molar)	**12.68_1**	**0.038**	2.67_1	0.244	0.04_1	0.860
II	TN:TP (molar)	**6.18_1**	**0.026**	3.88_1	0.069	2.35_1	0.147

Significant differences ($P < 0.05$) are presented in bold

The effect of zooplankton on the cycling of nutrients in pelagic ecosystems has usually been studied in the field. Among the techniques used to assess the sedimentation rate, the application of sediment traps has been most common (Evans et al., 1998; Turner, 2015), as well as sediment cores (e.g., Kimmel, 1979) and large volume filtration systems (e.g., Dagg et al., 2014). Other studies combined methods (Bathmann et al., 1987; Sarnelle, 1999; Bruce et al., 2006). For instance, Sarnelle (1999) used a combination of theoretical model predictions, a large-scale field experiment and descriptive data, while Bruce et al. (2006) used descriptive data and theoretical model predictions. Very few studies about the effect of zooplankton on the sedimentation rate have been carried out under strictly controlled laboratory conditions (e.g., Griffin, 2000). Among the most important advantages of our study was the possibility to precisely assess, using a variety of parameters, the effect of *Artemia* presence on the cycling of nutrients, which would be much more difficult in a field study. This was possible due to our ability to minimize the decomposition of the sedimented material and reduce *Artemia* grazing on the sediment material inside the traps. This was achieved by performing experiments of short duration with sediment traps in which the bottom part was filled with a solution of dense artificial NaCl water and formalin, as well as by eliminating all possible effects of local currents and turbulence occurring in the lake (Buesseler et al., 2007). The most important disadvantages of our study include the lack of a field experiment and the lack of considering some of the environmental variables that could modify the effect of *Artemia* grazing on nutrient cycling, such as temperature gradients and variation in sedimentation rates due to seasonal changes in brine shrimp density and life-stage composition. The other disadvantage was the inability to distinguish the effect of increased sedimentation and the effect of the 'active transport' by *Artemia* on the increased material flux from the mixolimnion in the presence of *Artemia*. Moreover, despite the inconsistency in the experimental design between experiments consisting of the fact that we stored the water only before the preliminary experiment, the effect of *Artemia* grazing on nutrient and particulate matter cycling was similar in both experiments.

To conclude, despite some disadvantages of the experimental design, our study clearly demonstrated the importance of *Artemia* grazing for nutrient and particulate matter cycling, especially on increasing the material flux from the mixolimnion to the bottom and regulating the stoichiometry of the sediments.

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References

Alekseev, V., 2004. Effects of diel vertical migration on ephippia production in *Daphnia*. Journal of Limnology 63: 1–6.

Alldredge, A. L., C. Gotschalk & S. MacIntire, 1987. Evidence for sustained residence of macrocrustacean fecal pellets in surface waters of Southern California. Deep-Sea Research 34: 1641–1652.

Andreassen, I., E.-M. Nothig & P. Wassmann, 1996. Vertical particle flux on the shelf off northern Spitsbergen, Norway. The Marine Ecology Progress Series 137: 215–228.

Ayukai, T. & H. Hattori, 1992. Production and downward flux of zooplankton fecal pellets in the anticyclonic gyre off Shikoku. Japan Oceanologica Acta 15: 163–172.

Bathmann, U. V., T. T. Noji, M. Voss & R. Peinert, 1987. Copepod fecal pellets: abundance, sedimentation and content at a permanent station in the Norwegian Sea in May/June 1986. Marine Ecology Progress Series 38: 45–51.

Belovsky, G. E., D. Stephens, C. Perschon, P. Birdsey, D. Paul, D. Naftz, R. Baskin, C. Larson, C. Mellison, J. Luft, R. Mosley, H. Mahon, J. Van Leuwen & D. V. Allen, 2011. The Great Salt Lake Ecosystem (Utah, USA): long term data and a structural equation approach. Ecosphere 2(33): 31–40.

Bloesch, J. & H. R. Bürgi, 1989. Changes in phytoplankton and zooplankton biomass and composition reflected by sedimentation. Limnology and Oceanography 34: 1048–1061.

Bruce, L. C. & J. Imberger, 2009. The role of zooplankton in the ecological succession of plankton and benthic algae across a salinity gradient in the Shark Bay solar salt ponds. Hydrobiologia 626: 111–128.

Bruce, L. C., D. P. Hamilton, J. Imberger, G. Gal, M. Gophen, T. Zohary & K. D. Hambright, 2006. A numerical simulation of the role of zooplankton in C, N and P cycling in Lake Kinneret, Israel. Ecological Modeling 193: 412–436.

Buesseler, K. O., A. N. Antia, M. Chen, S. W. Fowler, W. D. Gardner, O. Gustafsson, K. Harada, A. F. Michaels, M. Rutgers van der Loeff, M. Sarin, D. K. Steinberg & T. Trull, 2007. An assessment of the use of sediment traps for estimating upper ocean particle fluxes. Journal of Marine Research 65: 345–416.

Dagg, M. J., G. A. Jackson & D. M. Checkley, 2014. The distribution and vertical flux of fecal pellets from large zooplankton in Monterey bay and coastal California. Deep-Sea Research Part I: Oceanographic Research Papers 94: 72–86.

Darchambeau, F., I. Thys, B. Leporcq, L. Hoffmann & J.-P. Descy, 2005. Influence of zooplankton stoichiometry on nutrient sedimentation in a lake system. Limnology and Oceanography 50: 905–913.

DeAngelis, D. L., P. J. Mulholland, A. V. Palumbo, A. D. Steinman, M. A. Huston & J. W. Elwood, 1989. Nutrient dynamics and food-web stability. Annual Review of Ecology, Evolution, and Systematics 20: 71–95.

DeMott, W. R., R. D. Gulati & K. Siewertsen, 1998. Effects of phosphorus-deficient diets on the carbon and phosphorus balance of *Daphnia magna*. Limnology and Oceanography 43: 1147–1161.

Den Oude, P. J. & R. D. Gulati, 1988. Phosphorus and nitrogen excretion rates of zooplankton from the eutrophic Loosdrecht lakes, with notes on other P sources for phytoplankton requirements. Hydrobiologia 169: 379–390.

Eadie, B. J., H. A. Vanderploeg, J. A. Robbins & G. L. Bell, 1989. The significance of sediment resuspension and particle settling. In Tilzer, M. M. & C. Serruya (eds), Large Lakes: Ecological Structure and Function. Springer, Berlin: 196–209.

Elser, J. J. & J. Urabe, 1999. The stoichiometry of consumer-driven nutrient recycling: theory, observations, and consequences. Ecology 80: 735–751.

Elser, J. J., R. W. Sterner, A. E. Galford, T. H. Chrzanowski, D. L. Findlay, K. H. Mills, M. J. Paterson, M. P. Stainton & D. W. Schindler, 2000. Pelagic C:N: P stoichiometry in a eutrophic lake response to a whole-lake food-web manipulation. Ecosystems 3: 293–307.

Evans, M. S., B. J. Eadie & R. M. Glover, 1998. Sediment trap studies in southeastern Lake Michigan: fecal pellet express or the more traveled route? Journal of Great Lakes Research 24: 555–568.

González, H. E. & V. Smetacek, 1994. The possible role of the cyclopoid *Oithona* in retarding vertical flux of zooplankton faecal material. Marine Ecology Progress Series 105: 31–45.

Griffin, S. L., 2000. Influence of food type on the production and setting rate of faecal pellets produced by an estuarine copepod. Marine and Freshwater Research 51: 371–378.

Hannides, C. C. S., M. R. Landry, C. R. Benitez-Nelson, R. M. Styles, J. P. Montoya & D. M. Karl, 2009. Export stoichiometry and migrant-mediated flux of phosphorus in the North Pacific Subtropical Gyre. Deep-Sea Research I 56: 73–88.

Hansen, B. & G. Bech, 1996. Bacteria associated with a marine planktonic copepod in culture. I. Bacterial genera in seawater, body surface, intestines and fecal pellets and succession during fecal pellet degradation. Journal of Plankton Research 18: 257–273.

Honjo, S. & M. R. Roman, 1978. Marine copepod fecal pellets: production, preservation, and sedimentation. Journal of Marine Research 36: 45–57.

Javor, B. J., 1989. Hypersaline Environments. Microbiology and Biogeochemistry. Springer, Berlin.

Jellison, R. & J. M. Melack, 2001. Nitrogen limitation and particulate elemental ratios of seston in hypersaline Mono Lake, California, USA. Hydrobiologia 466: 1–12.

Jellison, R., L. G. Miller, J. M. Melack & G. L. Dana, 1993. Meromixis in hypersaline Mono Lake, California. 2. Nitrogen fluxes. Limnology and Oceanography 38: 1020–1039.

Jellison, R., W. D. Williams, B. Timms, J. Alcocer & N. V. Aladin, 2008. Salt lakes: values, threats and future. In Polunin, N. V. C. (ed.), Aquatic Ecosystems: Trends and Global Perspectives. Cambridge University Press, Cambridge: 94–112.

Jones, E. F. & W. A. Wurtsbaugh, 2014. The Great Salt Lake's monimolimnion and its importance for mercury bioaccumulation in brine shrimp (*Artemia franciscana*). Limnology and Oceanography 59(1): 141–155.

Kimmel, B. L., 1979. Recent sediment focusing in Castle Lake (California) using a volcanic ash layer as a stratigraphic marker. Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie 20: 393–400.

Lampert, W., 1987. Feeding and nutrition in *Daphnia*. In Peters, R. H. & R. de Bernardi (eds), Daphnia, Vol. 45. Memorie dell'Istituto Italiano di Idrobiologia Dott Marco, Pallanza: 143–192.

Lampitt, R. S., T. Noji & B. Von Bodungen, 1990. What happens to zooplankton faecal pellets? Implications for material flux. Marine Biology 104: 15–23.

Noji, T. T., K. W. Estep, F. MacIntyre & F. Norrbin, 1991. Image analysis of faecal material grazed upon by three species of copepods. Evidence for coprophagy, coprohexy and coprochaly. Journal of the Marine Biological Association of the UK 71: 465–480.

Ogata, E. M., W. A. Wurtsbaugh, T. N. Smith & S. L. Durham, 2017. Bioassay analysis of nutrient and *Artemia franciscana* effects on trophic interactions in the Great Salt Lake, USA. Hydrobiologia 788: 1–16.

Olsen, Y., A. Jensen, H. Reinertsen, K. Y. Borsheim, M. Heldal & A. Langeland, 1986. Dependence of the rate of release of phosphorus by zooplankton on the P: C ratio in the food supply, as calculated by a recycling model. Limnology and Oceanography 31: 34–44.

Peters, R. H. & J. A. Downing, 1984. Empirical analysis of zooplankton filtering and feeding rates. Limnology and Oceanography 29: 763–784.

Pilati, A. & W. A. Wurtsbaugh, 2003. Importance of zooplankton for the persistence of a deep chlorophyll layer: a limnocorral experiment. Limnology and Oceanography 48: 249–260.

Pilati, A., W. A. Wurtsbaugh & N. R. Brindza, 2004. Evidence of coprophagy in freshwater zooplankton. Freshwater Biology 49: 913–918.

Pitsch, M., V. Awassi, E. Susko & S. Hülsmann, 2012. Effects of zooplankton dynamics on epilimnetic phosphorus loss. Freshwater Biology 57: 704–715.

Rosa, F., 1985. Sedimentation and sediment resuspension in Lake Ontario. Journal of Great Lakes Research 11: 13–25.

Sarnelle, O., 1999. Zooplankton effects on vertical particulate flux: testable models and experimental results. Limnology and Oceanography 44: 357–370.

Schindler, D. E., J. F. Kitchell, X. He, J. R. Hodgson & S. R. Carpenter, 1993. Food web structure and phosphorus recycling in lakes. Transactions of the American Fisheries Society 122: 756–772.

Stephens, D. W. & D. M. Gillespie, 1976. Phytoplankton production in the Great Salt Lake, Utah, and a laboratory study of algal response to enrichment. Limnology and Oceanography 21: 74–87.

Sterner, R. W., 1986. Herbivores' direct and indirect effects on algal populations. Science 231: 605–607.

Sterner, R. W., T. H. Chrzanowski, J. J. Elser & N. B. George, 1995. Sources of nitrogen and phosphorus supporting the growth of bacterioplankton and phytoplankton in an oligotrophic Canadian shield lake. Limnology and Oceanography 40: 242–249.

Turner, J. T., 2015. Zooplankton fecal pellets, marine snow, phytodetritus and the ocean's biological pump. Progress in Oceanography 130: 205–248.

Turner, J. T. & J. G. Ferrante, 1979. Zooplankton fecal pellets in aquatic ecosystems. Bioscience 29: 670–677.

Valderrama, J. C., 1981. The simultaneous analysis of total nitrogen and total phosphorus in natural waters. Marine Chemistry 21: 109–122.

Vanni, M. J., 2002. Nutrient cycling by animals in freshwater ecosystems. Annual Review of Ecology, Evolution, and Systematics 33: 341–370.

Vos, J., F. Bernaerts, I. Gabriels & W. Decleir, 1979. Aerobic and anaerobic respiration of adult *Artemia salina* (L.) acclimated to different oxygen concentration. Comparative Biochemistry and Physiology, Part A 62: 545–548.

Welschmeyer, N. A., 1994. Fluorometric analysis of chlorophyll a in the presence of chlorophyll b and pheopigments. Limnology and Oceanography 39: 1985–1992.

Wotton, R. S. & B. Malmqvist, 2001. Feces in aquatic systems. BioScience 51: 537–544.

Wurtsbaugh, W. A., 1992. Food web modifications by an invertebrate predator in the Great Salt Lake (USA). Oecologia 89: 168–175.

Wurtsbaugh, W. A. & T. S. Berry, 1990. Cascading effects of decreased salinity on the plankton, chemistry, and physics of the Great Salt Lake (Utah). Canadian Journal of Fisheries and Aquatic Sciences 47: 100–109.

Wurtsbaugh, W. A. & Z. M. Gliwicz, 2001. Limnological control of brine shrimp population dynamics and cyst production in the Great Salt Lake, Utah. Hydrobiologia 466: 119–132.

Yoshimizu, C. & J. Urabe, 2002. Role of *Daphnia* in the decomposition of organic matter in the surface layer of Lake Biwa. Lakes and Reservoirs: Research and Management 7: 325–330.