



Artemia selective grazing: survival value and nutritional intake

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Abstract Grazing experiments were conducted for the zooplankton *Artemia franciscana* on three of its most common Great Salt Lake (Utah: USA) phytoplankton species (> 80–90% of phytoplankton biovolume: a chlorophyte, *Dunaliella viridis*; a cyanobacterium, *Euhalothece* sp., and a bacillariophyte, the pennate diatom *Nitzschia epithemioides*). For each *Artemia* developmental stage (nauplii, juveniles and adults), grazing rates (same phytoplankton abundances, temperatures, and salinities) are reported along with grazing preferences for the phytoplankton species in mixes of species pairs and all three species together. Each *Artemia* developmental stage exhibited different preferences for the phytoplankton species. Preferences measured for each species pair were consistent with preferences when all three species were together and were correlated with the phytoplankton's

survival value for each *Artemia* developmental stage. Survival values were positively related to the ingestion rate for each phytoplankton species (biovolume/individual/h), likely a function of cell size, and its nutritional quality treated as a function of phytoplankton N:P relative to *Artemia* developmental stage N:P.

Keywords *Artemia franciscana* · Great Salt Lake · Zooplankton grazing · Food value

Introduction

Artemia franciscana Kellogg, 1906, a pelagic filter-feeder, is the principal phytoplankton consumer in the Great Salt Lake (GSL: Utah, U.S.A.). GSL is among the largest saline lakes in the world and the largest in North America. Like most saline lakes, GSL lake levels have declined with anthropogenic water diversions and climate change (Wurtsbaugh et al., 2017). GSL *Artemia* constitute a major food resource for waterbirds in western North America, many of which are threatened/endangered, and *Artemia* overwintering eggs are commercially harvested for the world aquaculture industry. *Artemia* GSL populations are food-limited (Belovsky et al., 2011), so that a changing lake may affect their food resources and feeding behavior with important conservation and economic consequences.

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A wide-array of filter-feeding animals exist—sponges to zooplankton crustaceans to fish to flamingoes to whales, and filter-feeders can influence their food's abundance and ecosystem dynamics (e.g., Sautour & Castel, 1993; Levine et al., 1999; Meyer-Harms et al., 1999; Branco et al., 2018; Stukel et al., 2019; Rong et al., 2021). These animals are often considered to be non-selective in their ingestion of plankton (e.g., Bogdan & McNaught, 1975; DeMott, 1982; Onandia et al., 2015). When selection is observed, it is often based on size and shape of the plankton that meet the physical limits of the filtering structures that enable capture (e.g., Frost, 1972; Vanderploeg & Scavia, 1979; Bogdan & Gilbert, 1984; Hartmann & Kunkel, 1991; Sautour & Castel, 1993; Levine et al., 1999; Kmet' & Straškraba, 2004; Yin et al., 2010; Onandia et al., 2015; Conley et al., 2018; Feng et al., 2020).

Physical limits to filter-feeding are used in foraging models, especially for zooplankton (e.g., Lehman, 1976; Price, 1988; Kmet' & Straškraba, 2004; Sailley et al., 2015). However, there is evidence that filter-feeders can be selective beyond plankton physical traits, selecting additionally for plankton taxa and nutritional value (e.g., stoichiometry, toxicity, etc.) (e.g., Gophen et al., 1974; Bogdan & McNaught, 1975; Vanderploeg & Scavia, 1979; Roman & Rublee, 1981; DeMott, 1982; Richman & Dodson, 1983; Knisely & Geller, 1986; Demott, 1988; Lampert, 1987; Sierszen & Frost, 1990; Levine et al., 1999; Meyer-Harms et al., 1999; Arifin & Bendell-Young, 2000; Teegarden & Campbell, 2001; Sterner & Elser, 2002; Meunier et al., 2016; Branco et al., 2018; Conley et al., 2018; Pauli et al., 2021; Qiao et al., 2022). Therefore, as GSL and its phytoplankton change, (1) can filter-feeding *Artemia franciscana* compensate by selective feeding, and (2) what phytoplankton characteristics might influence selectivity?

We examined the above hypotheses for selective filter-feeding using laboratory experiments with different developmental stages (nauplii, juveniles, and adults) of *Artemia* and monocultures and mixes of three GSL phytoplankton species. Selective filter-feeding was examined, even though non-selective feeding has been reported previously in studies using phytoplankton species that are not sympatric with GSL *Artemia* (Provasoli & Shiaishi, 1959; Reeve, 1963b; Sick, 1976; Makridis & Vadstein, 1999; Evjemo & Olsen, 1999; Mohebbi, 2010; Riisgård

et al., 2015; Sánchez et al., 2016; Provasoli & Shiaishi, 1959; Sánchez et al., 2016).

Study system

Abbreviations and variables are defined in the Glossary (Table 1).

Three of the most common endemic GSL phytoplankton are a chlorophyte, *Dunaliella viridis* Teodoresco (DUN); a cyanobacterium, *Euhalothece* sp. (EUH: formerly *Coccochloris elabens* (Brébisson) F.E. Drouet & W.A. Dailey), and a bacillariophyte, the pennate diatom *Nitzschia epithemioides* Grunow (NIT). GSL phytoplankton counts for 1994–2022 (10 different research groups: Belovsky et al., submitted) report the following relative abundances based on biovolumes: chlorophytes averaged 67% for 1994–2022 and 94% in the past decade, with DUN accounting for >90% of chlorophytes; cyanobacteria averaged 16% for 1994–2022 and 2% in the past decade with EUH accounting for >90% of cyanobacteria, and diatoms averaged 17% for 1994–2022 and 4% in the past decade with NIT accounting for >15% of diatoms. NIT was selected as the pennate diatom because it is smaller (446 μm^3) than many GSL pennate diatoms (e.g., *Amphiprora* sp. ~11,719 μm^3 , *Navicula* sp. #1 ~4836 μm^3 , *Amphora* sp. ~1,588 μm^3 , *Navicula* sp. #2 ~1200 μm^3) that may be too large for *Artemia* to consume, especially if they form clumps. Therefore, *Artemia* grazing experiments with these phytoplankton should reflect GSL phytoplankton availability.

Methods

Organisms

All organisms were maintained and grazing trials conducted in water of known salinity, made by dissolving Instant Ocean (Spectrum Brands, Inc.) and Morton's Pure and Natural Water Softener Salts in a 40:60 ratio in reverse osmotic purified water (Larson & Belovsky, 2013; salinity was determined with a temperature-compensating refractometer (ATAGO PAL-03S). Because the water softener salt is from GSL, the solution was filtered to remove any potential *Artemia* cysts that might hatch.

Table 1 Glossary

Study system
GSL = Great Salt Lake
DUN = <i>Dunaliella viridis</i>
EUH = <i>Euhalothece</i> sp.
NIT = <i>Nitzschia epithemioides</i>
Measurements
RO = reverse osmotic purified water
Chl _a = chlorophyll-a (µg/L)
FSU = fluorescence signal unit; sensitivity = 400–600 nm
Initial Chl _a = µg/L at start of experiment
Δ Control = average of 3 control tube changes in µg Chl _a /L (end - start) in the experiment
Average # Shrimp = (# Initial Shrimp + # Final Shrimp)/2 in experiment
GLM = General Linear Model statistical analysis
C _{i,i} = initial pooled cell count for plankton species i in the control tubes
C _{F,i} = final pooled cell count for plankton species i in the control tubes
G _{i,i} = initial pooled cell count for plankton species i in the grazing tubes
G _{F,i} = final pooled cell count for plankton species i in the grazing tubes
E _i = expected final proportion of species i grazing tubes

Artemia were separated among three different development stages (nauplii: ≤ 5 mm, no segmentation; juveniles: > 5 mm and ≤ 9 mm, segmented without reproductive structures; adults: > 9 mm and reproductive structures: Heath, 1924). *Artemia* were reared by first hatching cysts harvested from GSL in a 1-L flask containing an aerated 45 ppt saline solution at 30 °C, and then transferring them to and maintaining them in 30 L aquaria containing the same aerated saline water as the grazing trial, kept at 20 °C, and fed, ad libitum, a solution of baker's yeast every other day (10 mg/aquaria). Juvenile males and females were separated to prevent reproduction as appendage differences appeared (Halfer-Cervini et al., 1968). The N:P values for freeze dried samples of each developmental stage were analyzed for N via elemental analyzer (©Costech) and P via microwave digestion and ICP-OCS (©Perkin-Elmer).

Phytoplankton cells of DUN, EUH (both identified microscopically), and NIT (identified molecularly to genus using DNA metabarcoding of 18S SSU rRNA genes and microscopically to species: Barrett, 2020) were isolated from the GSL South Arm to provide monocultures that were $> 95\%$ pure. To obtain high phytoplankton production for feeding, culturing was conducted in 3 -L glass jugs with a 12 h light–dark cycle, where DUN was maintained at a salinity of 120 ppt and a temperature of 10 °C, and EUH and NIT

were maintained at a salinity of 25 ppt and a temperature of 20 °C. As nitrogen is the limiting nutrient for GSL phytoplankton (Belovsky et al., 2011), each jug was weekly provided with 0.64 mg/L of nitrogen ($\text{NH}_4\text{NO}_3 = 49.6\%$, $\text{CaNO}_3 = 46.8\%$, $\text{N-NO}_3 = 3.5\%$) at the Redfield ratio (16:1 molar, Elser & Hassett, 1994) with phosphorus ($\text{P}_2\text{O}_5 = 69.6\%$, $\text{KH}_2\text{PO}_4 = 30.4\%$). Chlorophyll-a concentration (µg Chl_a/L) values for each species were measured using standard methods (Arar & Collins, 1997) and related to fluorometer readings (FSU, fluorescence signal unit; sensitivity = 400–600 nm: Turner Design TD-700 fluorometer), which differed among species ($r^2 = 0.81\text{--}0.99$). Also, each species' cell count per µg Chl_a/L was measured microscopically in a Palmer cell at 250–400×, where the well contained 1 ml of culture, and biovolume/cell is known (Larson & Belovsky, 2013). Finally, N:P values were analyzed from freeze dried samples of each phytoplankton species with N measured via elemental analyzer (©Costech) and P measured via microwave digestion and ICP-OCS (©Perkin-Elmer).

Grazing trials

Artemia grazing trials were conducted from 2019 to 2021, given pilot work and experimentation. Trials were conducted in 50-ml glass test tubes containing

40 ml of known salinity water and Chl_a concentration ($\mu\text{g/L}$) of phytoplankton species either alone or in mixes. Tubes held 1 female adult, 2 juveniles or 10 nauplii to attain approximately comparable and measurable consumption. Only female adults were used because they are larger and consume more than males. We minimized size differences within a developmental stage across trials by using individuals hatched at the same time and within a few days of transitioning to the needed developmental stage. Therefore, size differences within a developmental stage in a trial should reflect variability in individual growth rates, as individuals were reared identically, and this variation should not affect the order in which trials with a developmental stage were conducted. Finally, individuals were not reused among trials.

Grazing trials took place for 1 h to prevent food depletion (food reduced by: $<3 \pm 0.1\%$ for nauplii, $<12 \pm 0.3\%$ for juveniles, and $<18 \pm 0.6\%$ for adults) which would reduce grazing rates. Furthermore, depletion would prevent observation of selective grazing among phytoplankton species in mixtures, because feeding on less preferred species would be increased when food is low. A grazing trial consisted of 5 tubes containing *Artemia* of a developmental stage and 3 control tubes (no *Artemia*) at a salinity, temperature, and phytoplankton Chl_a concentration and species composition. Tubes were kept in an environmental chamber at a constant temperature and in the dark (no lights on and each tube wrapped in tin foil) to minimize phytoplankton growth. Protocols follow those reported by Sura et al. (2017) for studying DUN and EUH alone, except we starved *Artemia* for 12 h prior to a trial to ensure that individuals were hungry and therefore, more likely to feed, especially on phytoplankton species that otherwise might be avoided. With starving, no juvenile or adult mortality was observed in grazing trials, and nauplii had 12% mortality, which compared with 8% mortality without starving.

- (1) *Grazing on NIT*. Saline water at 45 and 90 ppt was used, because NIT does not survive well at higher salinities (Anderson et al., 2020; Belovsky et al., submitted), even though Sura et al. (2017) also used a salinity of 120 ppt in their grazing study with DUN and EUH. Temperatures of 10, 20, and 30 °C were used, while

Sura et al. (2017) did not examine grazing on DUN and EUH at 30 °C. Chl_a levels of 5, 20, or 40 $\mu\text{g/L}$ were employed, the same levels used by Sura et al. (2017) for DUN and EUH. Our NIT feeding solution was prepared by first passing the NIT culture through a 52 μm Nitex filter to remove clumped cells, the solution's higher Chl_a value was measured using the Chl_a regression with fluorometer readings (see above), and then the solution was diluted with the amount of saline water necessary to attain the desired Chl_a and salinity level for the trial. Finally, the experimental values are within the range of conditions observed in South Arm GSL where *Artemia* are abundant (Belovsky et al., 2011).

The experiment had a full factorial design with four treatments: three developmental stages (nauplii, juveniles, and adults), two salinities (45 and 90 ppt), three temperatures (10, 20, and 30 °C), and three food levels (5, 20, and 40 $\mu\text{g/L}$), with each treatment combination represented by 8 tubes with *Artemia* and 3 without *Artemia* (controls), which leads to 594 tubes. After an hour, surviving *Artemia* were counted and removed from the tube (juveniles and adults by pipette, nauplii by filtering for expedience). Control tubes for nauplii treatments were also filtered for consistency. As some NIT can adhere to tubes, tubes were scraped with an autoclaved glass rod 7–10 times (separate rod/tube), and the tube's feeding solution was shaken before taking fluorometer readings to use in the Chl_a regression (see above). Grazing rate ($\mu\text{g Chl}_a$ removed/individual/hr) was computed as

$$\frac{((\text{Initial Chl}_a + \Delta \text{ Control} - \text{Final } \mu\text{g/L Chl}_a) / (\text{Average \# Shrimp})) \times 0.04 \text{ L},$$

where 0.04 L converts $\mu\text{g Chl}_a/\text{L}$ to absolute $\mu\text{g Chl}_a$ consumed. Results for NIT alone were examined using SYSTAT 13 for GLM if data or transformations are normally distributed, and Mann–Whitney tests if data cannot be normalized. Results were then compared to Sura et al.'s (2017) results for DUN and EUH alone.

- (2) *Grazing on mixes of phytoplankton*. This experiment largely follows the protocols described in #1; however, only a single temperature (20 °C), salinity (90 ppt), and phytoplankton abundance

(40 $\mu\text{g Chl}_a/\text{L}$) in four mixtures of phytoplankton species (DUN-EUH, DUN-NIT, EUH-NIT, DUN-EUH-NIT) were employed. Each species in the mixture was equally abundant ($\mu\text{g Chl}_a/\text{L}$). While total consumption ($\mu\text{g Chl}_a$ removed/individual/hr) can be measured, this cannot be used to examine selective grazing by *Artemia* on different species, which requires counting the cells of each species in a known volume of the feeding medium at the start and end of the experiment. Therefore, upon adding the 40 ml of feeding solution to each tube and before adding any *Artemia*, the solution was mixed, and 1 ml was removed with a drop of 10% formalin-sugar added (60 ml formalin, 40 g sugar, 540 ml RO water) for preservation, and refrigerated for later cell counts. At experiment end, *Artemia* were removed as in #1, 1.7 ml of the 10% formalin-sugar solution was added to the tube, the tube was capped and refrigerated for later cell counts. Cell counts for tubes from the end of the experiment first had their sides scraped to free any cells adhering to the sides and mixed by shaking (see #1) before 1 ml was removed. Cell counts on a tube's 1 ml of medium from before and after the experiment were placed in a Palmer Cell well, and 3 transects were examined across the middle of the well at 400 $\times$ magnification, and all cells were counted and identified to species.

Each grazing trial had 5 tubes with *Artemia* and 3–5 control tubes for each developmental stage, which required cell counts on 28 tubes before and after. On occasion a tube (*e.g.*, broken or spilled) or a transect count was lost (*e.g.*, drying of Palmer cell well, or tally counter not cleared). First, control tube cell counts at the start ($C_{L,i}$) and end ($C_{F,i}$) of each trial can be used to measure a phytoplankton species' (i) proportional increase or decrease ($C_{F,i}/C_{L,i}$), which requires the number of transect counts for each tube at the start and end to be equal (overall experiment=242 control transects). Second, grazing tube cell counts at the start ($G_{L,i}$) and end ($G_{F,i}$) of each trial measure relative changes in phytoplankton species (i), which does not require an equal number of transect counts for each tube at the start and end (overall experiment=374 grazing transects). With transect counts, proportional changes in phytoplankton species can be used to assess whether *Artemia* preferentially

graze on a species (decrease in frequency) or avoid grazing on a species (increase in frequency) using χ^2 analyses ($P < 0.05$), as the species are categories and their cells are discrete counts. This can be done in two ways. First, $G_{L,i}$ and $G_{F,i}$ can be directly compared in two-way ^{2} tables. Second, if some species increase and others decrease in frequency in the control ($C_{L,i}$ vs. $C_{F,i}$), then changes in grazing frequencies ($G_{L,i}$ and $G_{F,i}$) must be adjusted. In this case, the expected final grazing value for species i (E_i) is

$$E_i = \Sigma G_{F,i} \times [(C_{F,i}/C_{L,i}) \times G_{L,i}] / \sum [(C_{F,i}/C_{L,i}) \times G_{L,i}],$$

and E_i is related to $G_{F,i}$ by χ^2 Goodness of Fit.

- (3) *Basis for grazing preferences.* If preferences are observed, ranked preferences can be compared to ranked phytoplankton–experimental traits using Kruskal–Wallis tests, and preference magnitudes can be related to phytoplankton–experimental traits and feeding responses using GLM and Best Subset Regression (SYSTAT 13).

Results

- (1) *Grazing on NIT.* Data are provided in SUPPLEMENTAL TABLE 1 and summarized in Fig. 1. Grazing rates ($\mu\text{g Chl}_a$ removed/individual/hr) on NIT for adults and juveniles are normally distributed, but nauplii rates were not normally distributed due to the large number of tubes in which no grazing of NIT was observed. Therefore, intake by developmental stage had to be compared using nonparametric tests.

Grazing rates increase with developmental stage (Fig. 1d, Table 2). Adult rates were 266% higher than for juveniles and 3245% higher than for nauplii, while juvenile grazing rates were 1218% higher than for nauplii. All developmental stages increase grazing rate with temperature (Fig. 1b, Table 3): averaging 151% higher at 30 °C than at 20 °C, 203% higher at 30 °C than at 10 °C, and 134% higher at 20 °C than at 10 °C. Nauplii grazing was not significantly affected by salinity, but juveniles and adults decreased grazing: averaging 62% less at 90 ppt than at 45 ppt

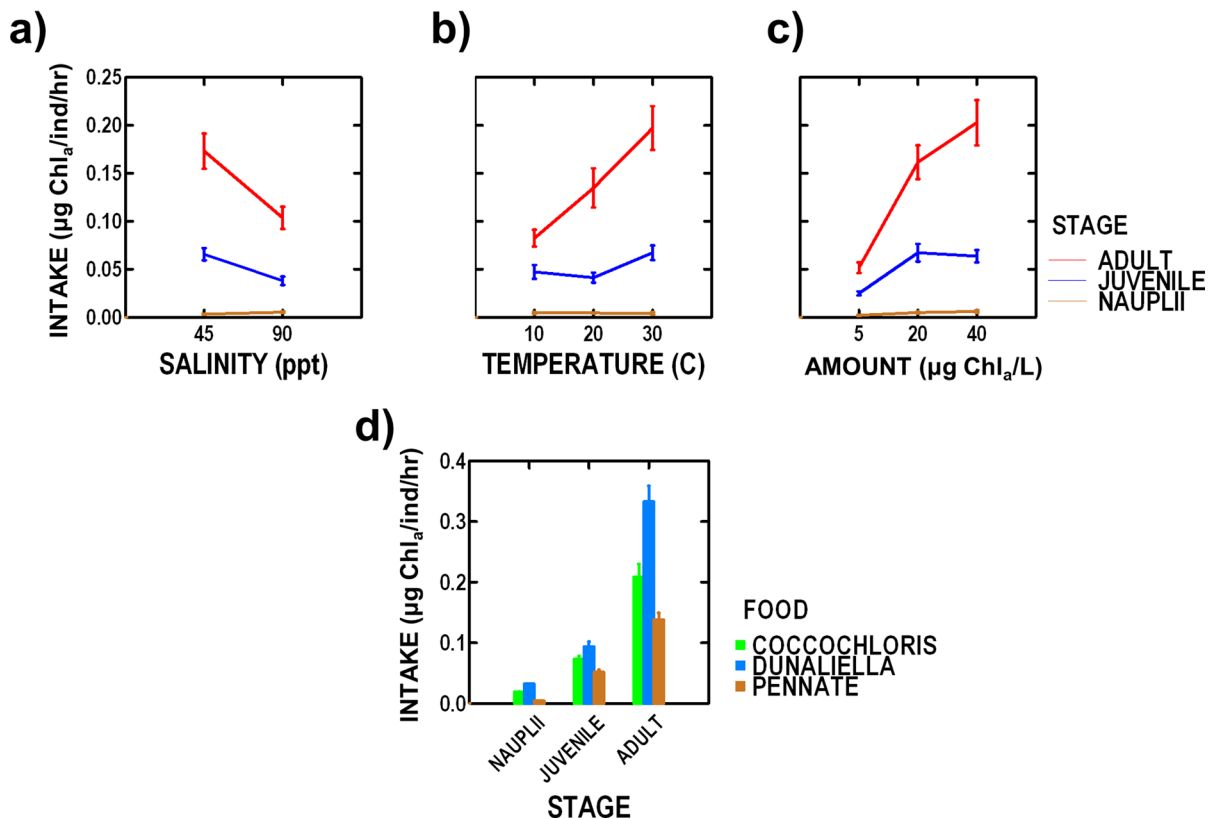


Fig. 1 *Artemia* grazing rate main effects for **a** salinity, **b** temperature, **c** abundance, and **d** developmental stage, with our NIT results compared to Sura et al.'s (2017) results for DUN and EUH

Table 2 *Artemia* intake rates of NIT for developmental stages (adult, juvenile, and nauplii) are not normally distributed (Kruskal-Wallis test: $\chi^2 = 192.01$, $DF = 2$, $P < 0.00001$), and are pairwise compared by Dwass-Steel-Critchlow-Fligner post hoc tests

	χ^2	DF	P
Adult–juvenile	8.13	1	0.00001
Adult–nauplii	16.64	1	0.00001
Juvenile–nauplii	15.91	1	0.00001

(Fig. 1a, Table 3). Grazing rate increased with NIT abundance for all developmental stages (Fig. 1c, Table 3): averaging 118% higher at 40 $\mu\text{g Chl}_a/\text{L}$ than at 20 $\mu\text{g Chl}_a/\text{L}$, 352% higher at 40 $\mu\text{g Chl}_a/\text{L}$ than at 5 $\mu\text{g Chl}_a/\text{L}$, and 298% higher at 20 $\mu\text{g Chl}_a/\text{L}$ than 5 $\mu\text{g Chl}_a/\text{L}$. NIT abundance was most important for juveniles and adults, while temperature was least

important. For nauplii, temperature was most important, and salinity least important.

For juveniles and adults, all pairwise interaction terms were statistically significant (Table 3) and similar, and they improved explanatory power by 36% for juveniles and 26% for adults. The strongest interaction was between temperature and salinity, where grazing rate increases more with temperature at lower salinities (45 vs. 90 ppt). In addition, grazing rates increase more with temperature at higher amounts of NIT (5 to 40 $\mu\text{g Chl}_a/\text{L}$), and decrease more with salinity as NIT decreases (5 to 40 $\mu\text{g Chl}_a/\text{L}$). Finally, interaction terms for nauplii could not be examined, given that their grazing rates had to be examined non-parametrically, as they are not normally distributed.

NIT results agreed with Sura et al.'s (2017) DUN and EUH results. The main effects of developmental stage, food abundance, temperature, and salinity were statistically significant and similarly affected grazing

Table 3 ANOVA results for *Artemia* adult and juvenile NIT intake rates, and Kruskal–Wallis tests for nauplii

Stage factor	Adult			Juvenile			Nauplii		
	F	DF	P	F	DF	P	χ^2	DF	P
Temperature (Temp)	39.17	2, 125	0.00001	19.46	2, 124	0.00001	12.33	2	0.002
Salinity (Sal)	45.29	1, 125	0.00001	64.17	1, 124	0.00001	2.92	1	0.09
Amount (Amt)	74.12	2, 125	0.00001	56.16	2, 124	0.00001	6.24	2	0.04
Temp $\times$ Sal	19.33	2, 125	0.00001	69.72	2, 124	0.00001			
Temp $\times$ Amt	14.66	4, 125	0.00001	14.35	4, 124	0.00001			
Sal $\times$ Amt	21.31	2, 125	0.00001	20.27	2, 124	0.00001			

rate. Sura et al.'s (2017) pairwise interactions, except salinity $\times$ temperature ($P < 0.07$), were statistically significant and operated similarly to our NIT results.

- (2) *Grazing on mixes of phytoplankton.* Cell counts for this experiment are presented in Supplemental Table 2. Based on comparisons of $G_{I,i}$ with $G_{F,i}$ values with two-way χ^2 tables (Table 4: W/O GROWTH), the usual assessment of selectivity (Reeve, 1963b), 7 of 12 trials exhibit selectivity (χ^2 test, $P < 0.05$), which is not different from random ($\chi^2 = 0.33$, $df = 1$, $P < 0.56$). Furthermore, selectivity indices for each phytoplankton species ($1 - G_{F,i}/G_{I,i}$; + = preferred, – = avoided) by each *Artemia* developmental stage are not consistent when results for 2-way and 3-way mixes are compared. Therefore, selective grazing is not supported, as claimed by Reeve (1963b). However, this assessment of selectivity is not appropriate, because control cell counts ($C_{I,i}$ and $C_{F,i}$) for the phytoplankton species indicate that some species increased, and others decreased over a trial, so that phytoplankton frequencies changed in the absence of grazing ($\chi^2 = 105.78$, $df = 2$, $P < 0.000001$), and $C_{I,i}$ and $G_{I,i}$ frequencies were different ($\chi^2 = 128.84$, $df = 2$, $P < 0.000001$).

In control tubes, DUN increased, EUH tended to be unchanged, and NIT decreased ($C_I/C_F \pm SE$, $N = 9$: respectively 1.26 ± 0.09 , 1.02 ± 0.03 , 0.77 ± 0.05). Therefore, $G_{I,i}$ must be corrected for the growth (changes) of each species in controls (E_i value in the Methods). χ^2 Goodness of Fit Tests (Table 4: W/GROWTH) indicate selectivity in 11 of 12 trials (χ^2 test, $P < 0.05$), which is unlikely to be a random result ($\chi^2 = 8.33$, $df = 1$, $P < 0.004$). Furthermore, all three *Artemia* developmental

stages demonstrate strong selectivity ($1 - G_{F,i}/E_i$; + = preferred, – = avoided) in the 3 phytoplankton species mix ($P < 0.00002$ – 0.000001) and even though DUN is always preferentially selected, the strength of selectivity among species changes with *Artemia* developmental stage: nauplii – DUN > EUH > NIT, juveniles – DUN > EUH > NIT, and adults – DUN > NIT > EUH. Therefore, *Artemia* selective grazing is indicated, which indicates the method used to measure selectivity is critical.

- (3) *Basis for grazing preferences.* Phytoplankton–experimental traits and *Artemia* grazing responses are presented in Table 5. Selectivity rankings for each *Artemia* development stage presented above are compared with the rankings of phytoplankton–experimental traits, a frequently applied qualitative approach. Filter-feeder selectivity is often thought to depend on phytoplankton biovolume, which is observed ($P < 0.04$), with small (EUH) and large (NIT) biovolumes selected less than intermediate biovolumes (DUN) ($P < 0.09$). Cell and biovolume abundances are equally related to selectivity as is cell biovolume, because they depend on cell biovolume. This analysis is crude, as the number of phytoplankton species is limited, but a more rigorous analysis using selectivity strength can be conducted. Using selectivity strength in a GLM, cell biovolume is no longer statistically significant ($P < 0.20$, $F = 2.14$, $df = 2, 6$). When selectivity strength is related to *Artemia* grazing responses using Best Subset Regression, only *Artemia* developmental stage survival, when consuming these phytoplankton species individually (Belovsky et al., 2024), is positively

Table 4 *Artemia* (nauplii, juveniles, adults) selective grazing on three GSL phytoplankton species (SELECT: + = preferred, – = avoided), W/O GROWTH presents the standard analysis (Reeve, 1963b), where phytoplankton growth is not considered, while W/GROWTH considers phytoplankton growth measured in controls

Selectivity W/O growth:					Selectivity W/growth:							
df	χ^2	P	SELECT	$(1 - G_{Fi}/G_{Fj})$	GROWTH	G _{Fi}	E _i	G _{Fj}	df	χ^2	P	SELECT
					(C_{Fi}/C_{Fj})					$(E_i \text{ vs. } G_{Fj})$		$(1 - G_{Fi}/E_i)$
NAUPLII												
DUN/EUH												
DUN			− 0.07		1.83	230	395.97	286				0.28
EUH	1	3.04	0.08	0.01	1.09	3723	3838.03	3948	1	33.69	0.00001	− 0.03
DUN/NIT												
DUN			− 0.07		1.02	866	1164.18	1119				0.04
NIT	1	31.60	0.00001	0.12	0.60	674	534.82	580	1	5.57	0.02	− 0.08
EUH/NIT												
EUH			− 0.01		1.07	3866	3432.14	3414				0.01
NIT	1	0.35	0.56	0.03	0.92	247	187.86	206	1	1.85	0.17	− 0.10
DUN/EUH/NIT												
DUN			− 0.16		1.30	277	376.91	328				0.13
EUH			0.04		0.81	2947	2487.77	2421				0.03
NIT	2	36.70	0.00001	− 0.19	0.73	232	177.32	293	2	83.6	0.00001	− 0.65
JUVENILES												
DUN/EUH												
DUN			0.02		1.12	372	360.77	327				0.09
EUH	1	0.36	0.55	− 0.01	1.05	3301	3011.23	3045	1	3.54	0.06	− 0.01
DUN/NIT												
DUN			− 0.10		1.20	826	949.08	917				0.03
NIT	1	40.30	0.00001	0.25	0.50	430	203.92	236	1	6.13	0.01	− 0.16
EUH/NIT												
EUH			0.01		1.07	4369	2256.54	2228				0.01
NIT	1	0.40	0.52	− 0.04	0.92	279	123.46	152	1	6.96	0.008	− 0.23
DUN/EUH/NIT												
DUN			0.09		1.09	887	937.96	755				0.20
EUH			− 0.05		1.10	1741	1854.76	1998				− 0.08
NIT	2	29.29	0.00001	0.07	0.80	338	260.28	300	2	52.81	0.00001	− 0.15
ADULTS												
DUN/EUH												

Table 4 (continued)

	Selectivity W/O growth:				Selectivity W/growth:				SELECT (1 - G _{Fi} /E _i)	P	χ ² (G _{Fi} vs. G _{Fi})	df	G _{Fi}	df	χ ² (E _i vs. G _{Fi})	P	SELECT (1 - G _{Fi} /E _i)
	df	χ ²	(G _{Fi} vs. G _{Fi})	P	SELECT (1 - G _{Fi} /G _{Fi})	GROWTH (C _{Fi} /C _{Fi})	G _{Fi}	E _i									
DUN					0.05	1.27	513	515.11	0.29				368				0.29
EUH	1	1.99	0.16		-0.01	0.98	7757	5997.89	-0.02	0.00001	45.62	1	6145	1	45.62	0.00001	-0.02
DUN/NIT																	
DUN					-0.04	1.03	923	1007.05	0.05				957				0.05
NIT	1	9.97	0.002		0.08	0.68	549	393.95	-0.13	0.003	8.85	1	444	1	8.85	0.003	-0.13
EUH/NIT																	
EUH					-0.07	1.07	3600	3312.94	-0.01				3352				-0.01
NIT	1	13.40	0.0003		0.15	0.92	340	268.06	0.15	0.01	6.15	1	229	1	6.15	0.01	0.15
DUN/EUH/NIT																	
DUN					-0.12	1.49	443	650.85	0.15				552				0.15
EUH					0.01	0.97	6007	5720.44	-0.02				5852				-0.02
NIT	2	20.16	0.00004		0.11	0.92	303	273.71	0.12	0.00002	21.95	2	241	2	21.95	0.00002	0.12

related to selectivity strength (Fig. 2a: $r=0.71$, $AIC=-0.21$, $N=9$, $P<0.03$).

Survival in food-limited populations like GSL *Artemia* (Wurtsbaugh & Gliwicz, 2001; Belovsky et al., 2011) should be related to the quantity of food ingested and its quality. Sterner & Elser (2002) suggest that a food's quality depends on its molar N:P similarity with the consumer, which is proportional to

$$1/\left\{\frac{\text{abs(phytoplankton species N : P - Artemia development stage N : P)}}{\text{Artemia development stage N : P}}\right\}$$

and calculated values are presented in Table 6. *Artemia* biovolume intake ($\mu\text{m}^3/\text{individual}/\text{h}$: Table 5) combined with the above computed food quality (Table 6), and again including cell volume (Table 5) comprise the Best Subset Regression for survival (Fig. 2b: $r=0.95$, $AIC=56.91$, $N=9$, $P<0.006$).

Discussion

Grazing rates of Great Salt Lake *Artemia* developmental stages respond to phytoplankton abundance, temperature, and salinity with the diatom *Nitzschia* in a comparable manner to Sura et al.'s (2017) observations with the chlorophyte *Dunaliella* and cyanobacterium *Eubacterium*, all common Great Salt Lake phytoplankton. For all of the phytoplankton, nauplii exhibit a weaker response than juveniles or adults. However, grazing rates on *Nitzschia* by *Artemia* developmental stages were 86, 45, and 58% lower, respectively, for nauplii, juveniles, and adults than observed for *Dunaliella* and *Eubacterium* (Fig. 1d), at the same phytoplankton abundances (Chl_a $\mu\text{g}/\text{L}$), temperatures, and salinities. Grazing rates (Chl_a $\mu\text{g}/\text{h}$), while different among developmental stages, still rank the same, *Dunaliella* > *Eubacterium* > *Nitzschia*, which is not related to the phytoplankton cell size rank *Nitzschia* > *Dunaliella* > *Eubacterium* or cell abundance rank *Eubacterium* > *Dunaliella* > *Nitzschia* (Table 5). These results differ from studies that claim that *Artemia* grazing rates on phytoplankton are negatively related to phytoplankton cell biovolume and positively related to cell abundance (Provasoli & Shiaishi, 1959; Reeve, 1963a, b; Sick, 1976; Makridis & Vadstein, 1999; Evjemo & Olsen, 1999; Mohebbi, 2010; Riisgård et al., 2015; Sánchez et al., 2016), which would lead

Table 5 Phytoplankton cell and experimental characteristics in grazing trials

	DUN	EUH	NIT
TRAITS			
Cell biovolume (μm^3) ^a	147	19	446
Chl _a abundance ($\mu\text{g/L}$) ^a	39	39	39
Cell abundance (#/L) ^a	1.15E+07	3.67E+07	6.11E+06
Biovolume abundance ($\mu\text{m}^3/\text{L}$) ^a	1.68E+09	6.97E+08	2.72E+09
ARTEMIA RESPONSES			
Chl _a intake rate ($\mu\text{g/h}$) ^{a,b}			
Adult	0.33	0.21	0.14
Juvenile	0.094	0.073	0.052
Nauplii	0.033	0.02	0.004
Cell intake rate (#/h) ^{a,b}			
Adult	9.69E+04	1.97E+05	2.19E+04
Juvenile	2.76E+04	6.86E+04	8.14E+03
Nauplii	9.69E+03	1.88E+04	6.26E+02
Biovolume intake rate ($\mu\text{m}^3/\text{h}$) ^{a,b}			
Adult	1.42E+07	3.75E+06	9.78E+06
Juvenile	4.06E+06	1.30E+06	3.63E+06
Nauplii	1.42E+06	3.57E+05	2.79E+05
Survival (%) ^c			
Adult	42.30%	25.50%	28.10%
Juvenile	25.60%	22.30%	5.00%
Nauplii	26.70%	17.40%	8.10%

(a) This study

(b) Sura et al. (2017)

(c) Belovsky et al. (2024)

to a grazing intake rank of *Euhalothece* > *Dunaliella* > *Nitzschia*. These results suggest that *Artemia* filter-feeding may be optimal on intermediate-sized phytoplankton, such as *Dunaliella*.

However, rather than focusing on grazing rate alone, selective feeding by *Artemia* may be better addressed with grazing observations on mixes of phytoplankton. Selectivity is exhibited (Table 4), when at the end of the trial, the frequencies of some phytoplankton species decrease (preferred) and others increase (avoided) compared to expected ending frequencies without grazing. When provided with a mix of the three phytoplankton species, all *Artemia* developmental stages exhibited selective grazing. Selectivity is correlated with the survival value of each phytoplankton species when consumed by each *Artemia* developmental stage (Fig. 2a), which

is consistent with a filter-feeding zooplankton optimizing nutritional intake (Lehman, 1976).

Survival value of each phytoplankton species is positively correlated with nutritional intake: quantity eaten (intake rate = biovolume/individual/h) and quality of food (N:P molar similarity between the phytoplankton and *Artemia* body composition). In addition, survival was negatively related to phytoplankton cell size, which probably is due to increased handling time for large cells reducing intake rate. All *Artemia* developmental stages have the greatest preference for *Dunaliella*, which provides the greatest survival and nutritional intake. However, preference for and survival on *Nitzschia* increases for juveniles and adults, which is consistent with small zooplankton exhibiting poor survival on diatoms (Liu et al., 2016), while larger zooplankton exhibit better survival on diatoms (Knisely

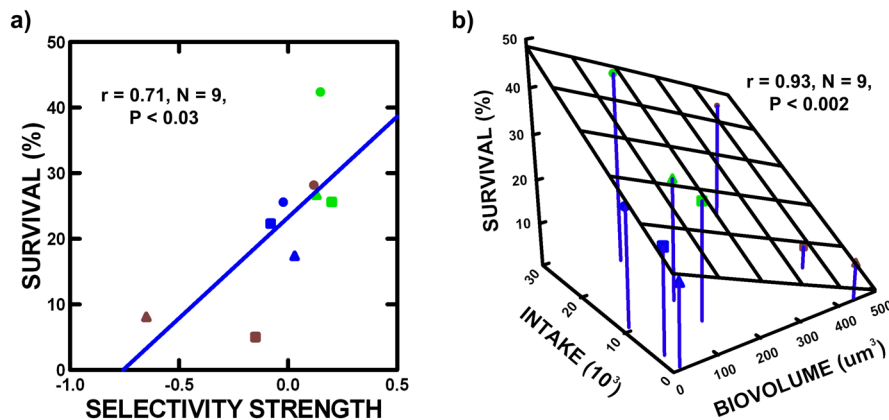


Fig. 2 **a** The relationship between grazing selection strength on different phytoplankton species (DUN = green, EUH = blue, NIT = brown) and survival by *Artemia* developmental stages (adults = circle, juveniles = square, nauplii = triangle). **b** The

relationship between survival and grazing rate based on nutritional intake (see text: biovolume intake $\times$ nutritional quality), and phytoplankton species' cell biovolume

& Geller, 1986). Thus, *Artemia*'s grazing preferences are certainly influenced by the physical limits set by cell size, and may be influenced by their ability to assess the survival value of foods (Knisely & Geller, 1986; Lampert, 1987; Meunier et al., 2016); however, to truly assess this, a greater array of phytoplankton species would need to be tested.

Filter-feeding zooplankton often have the ability to reduce phytoplankton abundance and productivity, and thereby, affect ecosystems (e.g., Sautour & Castel, 1993; Levine et al., 1999; Meyer-Harms et al., 1999; Branco et al., 2018; Stukel et al., 2019). This impact can intensify if zooplankton selectively forage, because they will graze down preferred species more before switching to less preferred species. For example, sometimes in Great Salt Lake, diatoms and cyanobacteria can comprise >90% of abundance (biovolume), replacing *Dunaliella*, which is normally >85% of abundance (Belovsky et al., 2011). This shift is probably due to temporally varying

temperature, salinity, and wind conditions (Belovsky et al., submitted); however, *Artemia* still strongly reduce *Dunaliella* abundance, even though grazing on diatoms and cyanobacteria increases. Selective grazing by *Artemia* maintains the impact on *Dunaliella*, which should lead to better *Artemia* survival than expected given the increase in diatom and cyanobacteria abundance.

Our observed selective grazing is counter to claims that *Artemia* do not preferentially graze, except perhaps by cell size and abundance (Provasoli & Shai-shi, 1959; Reeve, 1963a, b; Sick, 1976; Makridis & Vadstein, 1999; Evjemo & Olsen, 1999; Mohebbi, 2010; Riisgård et al., 2015; Sánchez et al., 2016). These claims center on one study (Reeve, 1963b), where 15 selectivity trials never had a χ^2 result with $P < 0.28$ (our computations), because

- (1) Reeve's trials, although using a similar *Artemia* density to our study (1 adult/68 ml vs. 1

Table 6 Molar N:P measurements for the phytoplankton species and *Artemia* developmental stages measured in the grazing experiments, and the similarity of phytoplankton to *Artemia* values computed using the equation in the text

Phytoplankton species	<i>Artemia</i> stage		
	Nauplii (9:1)	Juveniles (24:1)	Adults (23:1)
DUN (10:1)	9.00	1.72	1.75
EUH (15:1)	1.49	2.63	2.86
NIT (15:1)	1.49	2.63	2.86

adult/40 ml), were conducted over 14–20 h vs. our 1 h trials. A longer time leads to food depletion, unlike our trials, forcing consumption of less preferred species, which obscures preferences.

- (2) Phytoplankton populations change (grow or decline) in our controls (no *Artemia*), which has to be accounted for in assessing preference in feeding trials. Therefore, as we show, simply comparing phytoplankton frequencies at the start and end of the grazing trial as reported by Reeve is inappropriate.
- (3) Phytoplankton employed by Reeve did not include species that *Artemia* coevolved with in Great Salt Lake, except for *Dunaliella*, but Reeve's culture was from a marine source.

These concerns were raised by Vanderploeg & Scavia (1979) for studying filter-feeding zooplankton preferences.

Conclusions

Our study suggests that *Artemia franciscana*, the dominant Great Salt Lake filter-feeding zooplankton, selectively grazes among three Great Salt Lake phytoplankton species based not only on their cell size relative to the size of the *Artemia* developmental stage, but also possibly on their survival value. How *Artemia* might assess a food's survival value is unknown; however, we observed that survival was correlated with nutritional intake (product of food intake rate and its nutritional quality). While we observed this across all three *Artemia* developmental stages (nauplii, juveniles and adults) on three phytoplankton species, a greater array of survival and nutritional intake values is needed to address whether *Artemia* are able to select these food traits. Finally, we also observed that phytoplankton large cell size, a physical characteristic often considered a basis for selective grazing by filter-feeding zooplankton, also reduced survival value by reducing food intake rate.

Selective grazing by filter-feeding zooplankton can have important impacts on ecosystems (Sailley et al., 2015). First, selective grazing can affect phytoplankton abundance and production, especially by influencing phytoplankton species composition, which could impact interspecific competition among

phytoplankton. Second, filter-feeding zooplankton abundances are controlled by phytoplankton abundance and predation. However, phytoplankton species composition combined with zooplankton selective feeding may strongly affect zooplankton abundances through nutritional intake, which directly impacts zooplankton survival, and may also impact the importance of predation (*e.g.*, predation may have a greater impact on prey already experiencing low survival). Therefore, the species of phytoplankton present, as they affect zooplankton survival through selective grazing, need to be considered to better understand ecosystem dynamics.

Our findings presented here for Great Salt Lake *Artemia* and phytoplankton may help to understand Great Salt Lake trophic dynamics, that have been observed within and among years (Belovsky et al., 2011). But increasing threats to the lake due to urbanization, water diversion, and climate change (Wurtsbaugh et al., 2017) are expected to change phytoplankton abundances, and possibly species composition, which will impact *Artemia* survival given the selective grazing observed here. Changes in *Artemia* abundance have important economic impacts through the commercial harvest of *Artemia* diapausing eggs for the world aquaculture industry, and for conservation, given the abundant waterbirds, some of which are threatened, that reside in or migrate through Great Salt Lake and consume *Artemia*.

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Data availability The authors declare that the data supporting the findings of this study are available within the paper, and its supplementary information files.

Declarations

Conflict of interest The authors have no relevant financial or non-financial interests to disclose. The authors have no compet-

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