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PRIMARY RESEARCH PAPER

Demographic responses of an extremophile crustacean to environmental factors: Great Salt Lake (Utah, USA) brine shrimp (*Artemia franciscana*)

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Abstract Hypersaline Great Salt Lake's (GSL: Utah, USA) pelagic food web is dominated by the herbivore, *Artemia franciscana*. *Artemia* demographic responses (survival, developmental transition, and reproduction) to GSL salinities, temperatures, common phytoplankton and yeast, and food levels were examined by factorial experiment. Survival across developmental stages was best at 90 ppt salinity, and decreased as temperature increased. Transition between life stages was best at 45 ppt salinity, and increased as temperature increased. Food was most important with both survival and transitioning responding similarly to food types and increasing with amount of food. *Artemia* reproduce in two ways (diapausing cysts – oviparity, live young – ovoviviparity): ovoviviparous and total reproduction were greatest at 90 ppt salinity and 20 °C, while oviparous reproduction was weakly affected by salinity and greatest at 20 °C. Oviparity was greatest at low food availability, while ovoviviparity and total reproduction increased with food availability, so reproduction shifted from oviparity to ovoviviparity as food increased. Maternal effects were observed for cyst hatchability, and ovoviviparous nauplii survival and transitioning to the juvenile stage. Combinations of salinity, temperature, food taxa and food amount strongly affect demography, making single factor studies of limited value. Results explain *Artemia* abundance in different parts of GSL and among years.

Keywords *Artemia franciscana* · Survival · Reproduction · Development · Great Salt Lake

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Introduction

Saline lakes represent 44% of the earth's lake water volume (Messager et al., 2016) and are rapidly disappearing as their freshwater inputs are diverted for human use (Wurtsbaugh et al., 2017). These terminal lakes are highly productive for phytoplankton and aquatic invertebrates, which can support large numbers of waterbirds. However, these lakes are understudied as their water is not potable and they have limited biodiversity. Hypersaline lakes represent an extreme class of saline lakes with very reduced biodiversity, but are often highly productive.

The Great Salt Lake (GSL: Utah, USA) is among the largest hypersaline lakes in the world and the largest in the western hemisphere (salinity = 60–250 ppt: Arnow & Stephens, 1990; Johnson et al., 2019). GSL has a simple pelagic food web: phytoplankton, that are often dominated by the chlorophytes, *Dunaliella viridis* Teodoresco and *D. salina* (Dunal) Teodoresco; essentially one herbivore, the filter-feeding brine shrimp (*Artemia franciscana* Kellogg, 1906); abundant waterbirds, many of which feed on brine shrimp (*e.g.*, Felix & Rushforth, 1980); and in the areas with low salinities, a corixid that feeds on brine shrimp. Brine shrimp vary dramatically in abundance between years in the lake's South Arm where they are most abundant in the lake (Belovsky et al., 2011) and their overwintering cysts are commercially harvested for the international aquaculture industry (Belovsky & Perschon, 2019). Because more than one-third of waterbirds in western North America migrate through the GSL and many are threatened/endangered, brine shrimp as food for these birds is a conservation concern.

Studies often examine how species inhabiting saline waters respond demographically (survive, grow, and reproduce) to salinity, but salinity is not the only environmental factor confronting these species (Browne & Wanigasekera, 2000). Brine shrimp (Crustacea, Branchiopoda), as extremophiles of highly saline waters, are often thought to be limited by salinity (Van Stappen, 1996; Abatzopoulos et al., 2002), yet other factors may also influence their demography. For example, temperature can be highly variable in shallow hypersaline lakes, which may directly affect brine shrimp demography, and also may lead to variation in phytoplankton species composition and abundance (Larson & Belovsky, 2013), which indirectly affects brine shrimp demography through food resources. Therefore, how salinity, temperature, and type and amount of food interact to affect brine shrimp development, growth and reproduction were examined using a factorial experiment. Offspring hatchability, survival and transitioning between stages also were examined for maternal effects of salinity, temperature, and food type and abundance. Results were used to address variation in GSL brine shrimp abundances between years and in different parts of the lake. This information is important for developing population models and management plans.

Methods

Brine shrimp were reared from GSL cysts or produced by these individuals in 40 L aquaria containing the same aerated hypersaline solution used for demographic treatments. They were fed, ad libitum, a solution of baker's yeast every day (100 mg/aquaria). Temperature was maintained at 20 °C. Developmental stages were nauplii: ≤ 5 mm, no segmentation; juveniles: > 5 mm and ≤ 9 mm, segmented without reproductive structures; adults: > 9 mm, reproductive structures (Heath, 1924). Juvenile males and females were separated into different aquaria to prevent reproduction as appendage differences appeared (Halfer-Cervini et al., 1968).

Experimental treatments included salinities, temperature, and food taxa and quantity.

Salinities were maintained at 15, 25, 45, 90, 120, 150 and 180 ppt. Salinities of 15–45ppt reflect the less than hypersaline bays that have been created via causeway construction where freshwater inflows occur (*e.g.*, Farmington Bay). Salinities of 45–150 ppt reflect the hypersaline South Arm of the lake that is most like historical conditions. The salinities (200 + ppt) of the North Arm created by a causeway across a bay without any major freshwater inputs were not examined, as brine shrimp are for all purposes absent. Salinities were attained by combining Instant Ocean (Spectrum Brands, Inc.) and Morton's Pure and Natural Water Softener Salts in a 2:3 ratio in RO water (Larson & Belovsky, 2013). Because the water softener salt is manufactured from Great Salt Lake, the solution was filtered to remove any potential brine shrimp cysts that might hatch in the experiment.

Finally, salinities in the experiments described below were maintained by weekly replacing the hypersaline water.

Temperatures were kept constant in an environmental chamber at 10, 15, 20 and 30 °C. 10 °C reflects onset and end of winter, 15 °C reflects spring and fall conditions, while 20–30 °C reflects summer (Belovsky et al., 2011).

Food taxa were typical for GSL and included chlorophytes (*Dunaleilla viridis*, *Carteria* sp.), bacillariophytes (pennate diatom: *Nitzschia epithemioides* Grunow, identified molecularly to genus and microscopically to species), cyanobacteria (*Euhalothece* sp., formerly *Coccochloris elabens* (Brébisson) F.E. Drouet & W.A. Dailey, identified molecularly to genus), and baker's yeast. Each phytoplankton taxon was isolated from GSL to provide lab cultures that were > > 90% pure. To obtain the high phytoplankton production needed to feed the *Artemia*, the culturing protocol included the following: nitrogen, the limiting nutrient for phytoplankton growth, was provided weekly at 0.64 mg/L in a Redfield ratio with phosphorus, *D. viridis* was kept at 120 ppt and 10 °C, while *Carteria* sp., *N. epithemioides* and *Euhalothece* sp. were kept at 25 ppt and 20 °C (Belovsky et al., submitted). Yeast was used to provide even higher food abundances, given difficulty in producing very high phytoplankton abundances.

Food quantities for brine shrimp were 0.5, 1.0, 2.0, 3.0, 7.0, 15.0, 30.0 and 45.0 µg chlorophyll-a/L/individual every 2 days. These values reflect food availabilities in the pelagic zone for brine shrimp (Belovsky et al., 2011). Chlorophyll-a, the most common measure of algal abundance, was measured using EPA Method 445 (Arar & Collins, 1997). Following extraction, the supernatant was pipetted into a non-acidic cuvette and measured with a fluorometer (sensitivity setting = 400–600 nm). Fluorometer readings were converted to µg chlorophyll-a/L using a curve based on standards with known chlorophyll-a concentrations. However, as yeast does not contain chlorophyll-a, yeast provided was converted to a chlorophyll-a equivalent by equating yeast mass to *Dunaliella* algal mass at a known chlorophyll-a measure. The yeast and algae were filtered on predried and weighed filters (Whatman GF/F, pore size = 1.1 µm), dried at 60 °C for 48 h, and weighed.

Experimental populations were maintained in 500 ml Nalgene bottles containing 400 ml of aerated saline solution and maintained at a temperature in an environmental chamber with a 12 h light:12 h dark regimen. Each population (bottle) was stocked with 20 individuals of a single developmental stage (nauplii, juvenile, or adult), regardless of sex, except for adults which were stocked with 10 ♀s and 10 ♂s. Every 3 days for 4 weeks, populations were censused. Censuses accounted for number surviving, number transitioning to next developmental stage (nauplii to juvenile, juvenile to adult), and reproduction by adults. Because the brine shrimp reproduce in two ways (oviparity – diapausing cysts, ovoviviparity – live young), numbers of each produced were counted. For nauplii and juveniles, dead and transitioned individuals were removed and replaced with individuals of the appropriate developmental stage. For adults, dead ♂ and ♀ individuals were replaced, and nauplii and cysts produced were removed. Replacement of dead and transitioned individuals maintains a constant density (20 individuals) with individuals reared identically, which addresses intraspecific competition for food. Replacement individuals have previously experienced the experimental salinity, but not always the same temperature, food factors and density. However, the generally high mortality of individuals previously comprising a population means that any potential effects due to combining individuals with no prior exposure to some of the experimental conditions with individuals already in the population should be minimized.

Given the number of treatments (4 temperatures, 7 salinities, 5 food types, 8 food levels, and 3 developmental stages), a very large number of treatment combinations were possible. Ten replicates (populations) were initially used with adults fed yeast to assess variation and thereafter, 5 replicates were employed (brine shrimp nauplii and juveniles with algae and yeast, and adults with algae). Given this large number of populations (bottles), limited environmental chamber space and maintenance and counting logistics, a complete factorial design was not feasible. At any one time, a single combination of developmental stage/temperature/food taxon at all amounts/1—2 salinities were examined providing 15–60 brine shrimp populations. Twenty (sometimes 5 or 10 if high mortality was expected) populations (4 X 5 array) were held in a tray, treatment combinations being examined were randomly assigned to bottles in a tray. Every 3 days, trays were rotated 90° to minimize possible spatial effects in a chamber (*e.g.*, position relative to lights

and fans). Weekly, inside walls of bottles were wiped with a sponge, sediments were removed, and the hypersaline solution was replaced to prevent lethal pH levels and remove any remaining food.

Three experiments were conducted:

1) Survival, transition (nymphs and juveniles) and reproduction (adults) were measured for each developmental stage–2788 populations. Sizes of individuals were not measured, as handling individuals could negatively affect survival and transition rates, the purpose of our demographic study. However, transition rates reflect maturation times and female size affects per capita reproductive rates (larger size increases per capita reproduction), which are measured in the experiment.
2) Maternal effects (salinity, temperature, and food type and amount) on cyst hatchability were measured. Cysts were kept frozen (−10 °C) for 1.5, 3, or 6 months to simulate diapause duration and winter temperatures, and nauplii emerging were counted and removed every 48 h until no nauplii emerged – 994 populations.
3) Maternal effects (salinity, temperature, and food type and amount) on ovoviviparous nauplii survival and transitioning were measured. Nauplii had a constant environment (90 ppt and 20 °C, and 2 µg chl_a/L/individual/2 days of *Dunaliella* if mothers were fed *Dunaliella* and 3 µg chl_a equivalent/L/individual/2 days of yeast if mothers were fed yeast) – 563 populations.

This resulted in a total of 4345 populations, which required 17 years to complete, given logistics (algal and brine production, experiment preparation and implementation).

Analysis of bottle counts addressed the following parameters:

- Survival = 1 – (# dying in bottle/total # in bottle over experiment),
- Transition = # transitioning in bottle/total # in bottle over experiment,
- Oviparous reproduction = total cysts produced in bottle/total females in bottle over experiment,
- Ovoviviparous reproduction = total nauplii produced in bottle/total females in bottle over experiment,
- Total reproduction = (total cysts + nauplii produced in bottle)/total females in bottle over experiment,
- Cyst hatchability = total nauplii emerging in bottle/total cysts stocked in bottle.

Survival, transitioning and cyst hatchability data were analyzed using generalized linear mixed models (GLMM) in R (ver. 4.2.3 © R Foundation, library: lme4, glmer command) with a binomial distribution and a logit link, where bottle was treated as a random variable, as these data represent alternative outcomes (*e.g.*, alive vs. dead, transitioned vs. not transitioned). All treatments were considered fixed variables and their significance was tested via a Type III Wald's χ^2 test. Multiple GLMM models were constructed given various combinations of each fixed variable and their 2-way interactions (higher order interactions could not be examined as the factorial design was not complete). The best fit model was selected based on the lowest BIC value (Anderson & Burnham, 2002). GLMM analyses using the complete range of experimental factors address the overall importance of factors for survival, transitioning and hatchability, while subsets of factors were used to address importance for different GSL areas.

Reproductive output was analyzed by GLM, as these data are continuous, not alternatives (*e.g.*, alive vs. dead), and all factors were considered fixed. Data were tested for normality by the Anderson–Darling Test and transformed if non-normal. Multiple GLM models were constructed by various combinations of each fixed variable and their 2-way interactions (higher order interactions could not be examined as the factorial design was not complete). The best fit model was selected based on the lowest BIC value (Anderson & Burnham, 2002). GLM analyses were conducted for the complete range of experimental factors to address the overall importance of different factors on oviparous, ovoviviparous, and total reproductive output. GLM analyses using the complete range of experimental factors address the overall importance of factors for reproduction, while subsets of factors were used to address importance for different GSL areas.

Results

Data are presented in Supplemental Table 1 (developmental stage survival, transitioning and reproduction), Supplemental Table 2 (maternal effects on cyst hatching), and Supplemental Table 3 (maternal effects on ovoviviparous nauplii survival and transitioning).

Survival and transitioning (nauplii to juveniles, juveniles to adults) of brine shrimp are summarized in Fig. 1 with respect to developmental stage (nauplii, juveniles, adults), salinity (15, 25, 45, 90, 120, 150, 180 ppt), temperature (10, 15, 20, 30 °C), food taxa (*Dunaliella*, *Carteria*, *Euhalothece*, *Nitzschia*, yeast), and food amount (0.5, 1.0, 2.0, 3.0, 7.0, 15.0, 30.0 and 45.0 µg chlorophyll-a/L/individual every 2 days).

The GLMM analyses of survival are presented in Table 1, indicating that all five main effects and four of ten two-way interactions are included in the best fit model based on BIC values. Two-way interaction terms for survival are not as important as main effects, increasing variance explained from 38 to 45% (Table 1). The GLMM results for transitioning are presented in Table 1, indicating that all five main effects and eight of ten two-way interaction terms are included in the best fit model based on BIC values. Two-way interaction terms for transitioning are not as important as main effects, but more important than for survival, increasing variance explained from 32 to 52% (Table 1). Three 2-way interaction terms appear in both the GLMM analysis of survival and transitioning (Table 1: developmental stage X food amount, developmental stage X temperature, food taxa X food amount), 1 only appears for survival (temperature X food amount), 5 only for transitioning (developmental stage X food taxa, developmental stage X salinity, temperature X food taxa, salinity X food taxa, salinity X food amount), and 1 for neither (salinity X temperature).

Main effects operate additively and their relative impacts can be envisioned in the examples presented in Fig. 2 for survival in relation to salinity. A comparison with salinity is examined, because salinity is often considered the most important determinant in hypersaline lakes (Van Stappen, 1996; Abatzopoulos et al., 2002). Not only does temperature, food taxa and amount of food first increase and then decrease survival when combined

Table 1 GLMM results for the best-fit models (lowest BIC) to *Artemia* survival, transitioning and reproduction. Analyses include all salinity, temperature, food taxa and food amount values for all developmental stages, except for reproduction which is restricted to adult data

Response	Variables	Statistics
Survival	Main effects: Taxa, Stage, Amount, Temperature, Salinity	$r=0.68$, BIC = 20262, $P \leq 0.0001$, N = 2788
	2-Way interactions: Stage X Taxa, Taxa X Amount, Stage X Temperature, Temperature X Amount	
Transition	Main effects: Taxa, Stage, Amount, Temperature, Salinity	$r=0.73$, BIC = 8359, $P \leq 0.0001$, N = 2788
	2-Way interactions: Stage X Taxa, Stage X Amount, Taxa X Amount, Taxa X Salinity, Temperature X Taxa, Stage X Salinity, Stage X Temperature, Salinity X Temperature	
Offspring/♀	Main effects: Temperature, Salinity, Amount, Taxa	$r=0.86$, BIC = 8234, $P \leq 0.0001$, N = 1005
	2-Way interactions: Temperature X Salinity, Salinity X Amount, Temperature X Taxa, Salinity X Taxa	
Eggs/♀	Main effects: Temperature, Salinity, Amount, Taxa	$r=0.86$, BIC = 7399, $P \leq 0.0001$, N = 1005
	2-Way interactions: Temperature X Salinity, Salinity X Taxa, Salinity X Amount	
Cysts/♀	Main effects: Temperature, Salinity, Amount, Taxa	$r=0.83$, BIC = 7539, $P \leq 0.0001$, N = 1005
	2-Way interactions: Temperature X Salinity, Salinity X Amount, Temperature X Taxa, Salinity X Taxa	
Proportion oviparity	Main effects: Amount, Salinity, *	$r=0.73$, BIC = 11728, $P \leq 0.0001$, N = 1005
	2-Way interactions: Amount X Salinity	
	*Taxa not included as the food *Nitzschia epithemioides* did not provide any reproduction (undefined due to division by zero)	

Table 2 Importance (% variance explained) of main effects based on GLMM for *Artemia* survival and transitioning. Results are presented for the overall experiment (salinities = 15 – 180 ppt), the range of salinities observed in GSL's South Arm (45 – 150 ppt) and the range of salinities observed in GSL's Farmington Bay (15–45 ppt)

	Survival			Transition		
Variable:	Overall	South Arm	Farm. Bay	Overall	South Arm	Farm. Bay
Stage	23	27	18	0	1	1
Taxa	29	30	42	34	35	36
Food Amount	18	16	18	30	35	38
Salinity	22	17	9	9	4	7
Temperature	7	11	13	27	25	18

with salinity, but the salinity providing the highest survival changes with food taxa and amount (Fig. 2 b, c). This indicates that examining salinity alone is not an adequate predictor of survival.

Main effects can be ranked by variance explained from most to least (Table 2):

1. Survival – Variance explained ranged from 29 – 7% with food taxa (yeast > *Dunaliella* > *Carteria* > *Euhalothece* > *Nitzschia*, Fig. 1d) > developmental stage (adults > juveniles ≃ nauplii, Fig. 1a) > salinity (best at 90 ppt, Fig. 1b) > food amount (increases with amount, Fig. 1e) > temperature (declines with temperature, Fig. 1c).
2. Transition – Variance explained ranged from 34 – 0% with food taxa (yeast ≃ *Dunaliella* > *Carteria* > *Euhalothece* > *Nitzschia*, Fig. 1d) > food amount (increases with amount, Fig. 1e) > temperature (increases with temperature, Fig. 1c) > salinity (best at 45 ppt, Fig. 1b) > > development stage (juveniles ≃ nauplii, Fig. 1a).

While food taxa rank the same for all developmental stages, juveniles transition better than nauplii on the larger-celled *Carteria* and *Nitzschia* (significant development stage X food taxa). In addition, amount of food increases in importance as brine shrimp grow larger (significant development stage X food amount). Finally, nauplii transition is least affected by salinity (significant development stage X salinity).

Importance of main effects across the complete experimental range may not convey their importance in different parts of the lake or years; therefore, analyses were conducted over the salinity range for different parts of GSL (South Arm: salinity = 45–150 ppt; Farmington Bay: salinity = 15–45 ppt) (Table 2).

1. Survival given South Arm conditions (mean = 30%) has effects ranked as food taxa > developmental stage > salinity ≃ food amount > temperature. Survival given Farmington Bay conditions (mean = 26%) has effects ranked as food taxa > developmental stage ≃ food amount > temperature > salinity. Both areas have survival affected more by food (taxa, amount) than abiotic effects (salinity, temperature).
2. Transitioning given South Arm conditions (mean = 7.2%) has effects ranked as food amount ≃ food taxa > temperature > salinity > developmental stage. Transitioning given Farmington Bay conditions (mean = 6.9%) has effects ranked as food amount ≃ food taxa ≃ temperature > salinity > developmental stage. Both areas have transitioning affected more by food (taxa, amount) than abiotic effects (salinity, temperature).

Reproduction per female (total, oviparous cysts, and ovoviviparous eggs) is summarized in Fig. 3 with respect to salinity (25, 45, 90, 120, 150, 180 ppt), temperature (10, 15, 20, 30 °C), food taxa (*Dunaliella*, *Carteria*, *Euhalothece*, *Nitzschia*, yeast), and food amount (0.5, 1.0, 2.0, 3.0, 7.0, 15.0, 30.0 and 45.0 µg chlorophyll-a/L/individual every 2 days).

Reproduction results from GLM analyses are presented in Table 1. Total offspring output per female is affected by all four main effects and four of the six two-way interaction terms in the best fit model based on BIC values. Two-way interaction terms for total offspring output per female are not as important as

the main effects, increasing the variance explained from 48 to 74% (Table 1). Oviparous cyst production per female is affected by all four main effects and four of the six two-way interaction terms in the best fit model based on BIC values. Two-way interaction terms for oviparous cyst production per female are not as important as the main effects, increasing the variance explained from 42 to 69% (Table 1). Ovoviviparous egg production per female is affected by the four main effects and three of the six two-way interaction terms in the best fit model based on BIC values. Two-way interaction terms for ovoviviparous egg production per female are not as important as the main effects, increasing the variance explained from 49 to 74% (Table 1). Three of the 2-way interaction terms appear in the GLM models for total, oviparous, and ovoviviparous output per female (salinity X temperature, salinity X food taxa, salinity X food amount), while results from GLM analyses for both total and oviparous output per female include the temperature X food taxa interaction term (Table 1).

Main effects can be ranked by variance explained from most to least (Table 3):

1. Oviparous production per female – Variance explained ranged from 32– 11% with food taxa (yeast > *Dunaliella* > *Euhalothece* > *Carteria* > *Nitzschia*: Fig. 3c) > temperature (maximum at 20 °C: Fig. 3b) ≃ amount of food (maximum at 2 µg chlorophyll-a/L/individual: Fig. 3d) > salinity (maximum at 90 ppt: Fig. 3a).
2. Ovoviviparous production per female – Variance explained ranged from 32 – 15% with temperature (maximum at 20 °C: Fig. 3b) > salinity (maximum at 90 ppt: Fig. 3a) > amount of food (increases as amount increases: Fig. 3d) > food taxa (*Dunaliella* > *Euhalothece* > *Carteria* ≃ yeast > *Nitzschia*: Fig. 3c).
3. Total reproduction per female – Variance explained ranged from 52 – 12% with temperature (maximum at 20 °C: Fig. 3b) > salinity (maximum at 90 ppt: Fig. 3a) > amount of food (peak at 2 µg chlorophyll-a/L/individual when oviparity dominates, then declines as oviparity shifts to ovoviviparity and finally increases again as food increases: Fig. 3d) > food taxa (yeast > *Dunaliella* > *Euhalothece* > *Carteria* > *Nitzschia*: Fig. 3c).

There is a dramatic shift from oviparity to ovoviviparity production when females are fed more than 2 µg chlorophyll-a/L/individual every 2 days, indicating that the two modes of reproduction are highly dependent on food availability (Fig. 4d, Table 1). Oviparity versus ovoviviparity is less affected by temperature and salinity, but both modes of reproduction decline as temperature and salinity increase (Fig. 4a, b), especially when they increase together (salinity X temperature interaction). Finally, food taxa were not included in the GLMM analysis (Table 1), because the diatom *Nitzschia* provided no reproductive output, an undefined value (division by zero); however, this further indicated the importance of food taxa (Fig. 4c).

Importance of each factor across the range of experimental conditions does not necessarily convey their importance in different parts of GSL or years; therefore, analyses also were conducted for the range of salinities in different parts of GSL (South Arm: salinity = 45–150 ppt; Farmington Bay: salinity = 15–45 ppt) (Table 3).

Table 3 Importance (% explained variance) of main effects based on GLM for *Artemia* reproduction (total, oviparity, and ovoviviparity) per female. Results are presented for the overall experiment (ALL, salinities = 15–120 ppt), South Arm salinities (SA, 45–150 ppt) and Farmington Bay salinities (FB, 15–45 ppt)

Variable:	Total			Cysts			Eggs		
	ALL:	SA:	FB:	ALL:	SA:	FB:	ALL:	SA:	FB:
Taxa	12	13	33	32	33	45	15	27	37
Food Amount	15	13	12	28	26	25	25	33	37
Salinity	21	17	3	11	6	15	28	12	2
Temperature	52	56	52	29	35	15	32	28	24

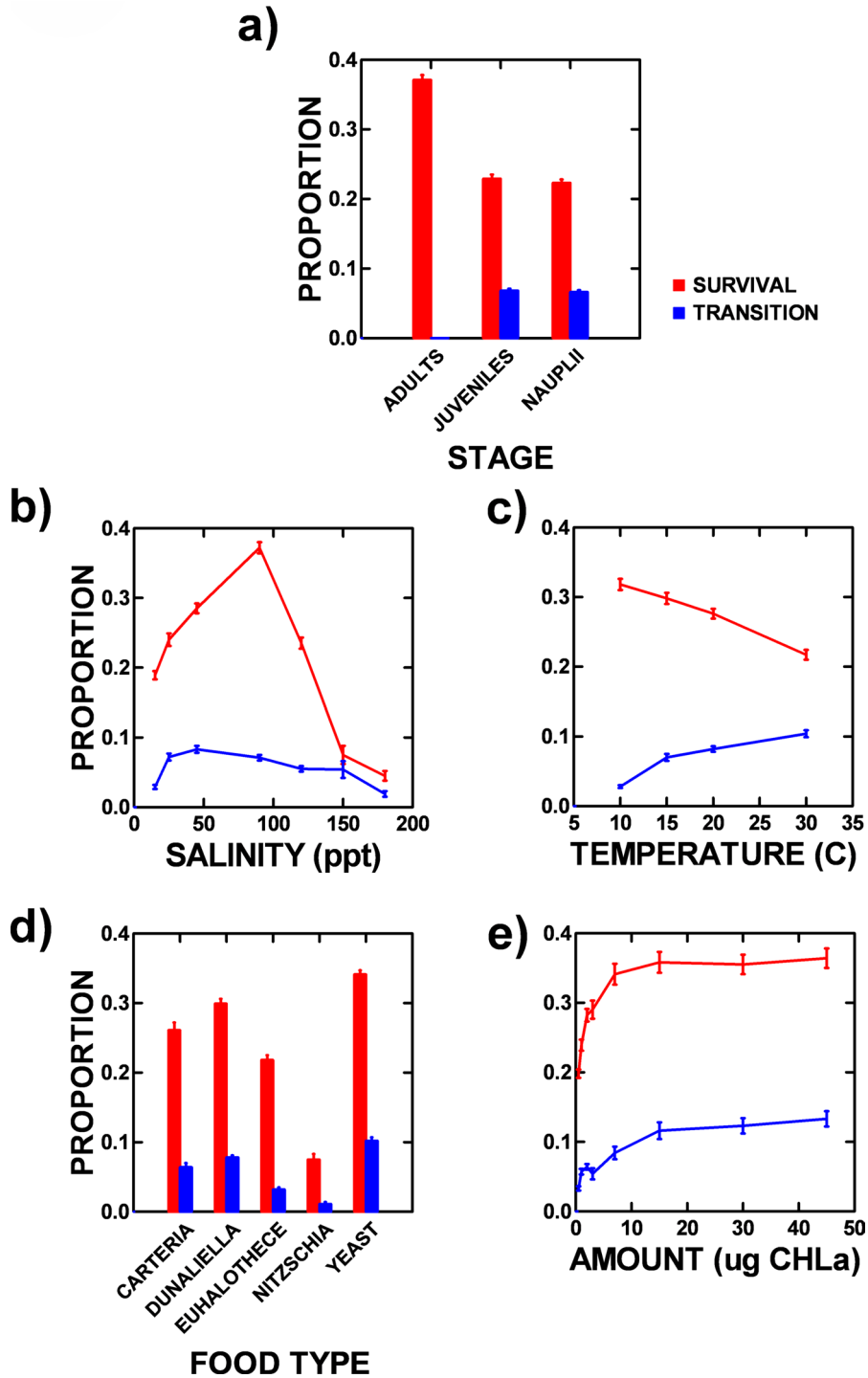

Fig. 1 *Artemia* fixed effects (±SE) for survival and transition in a multifactorial experiment (N = 2788) for **a** developmental stage, **b** salinity, **c** temperature, **d** food type, and **e** amount of food

1. Oviparous production per female for South Arm has the importance of effects ranked as temperature ≃ food taxa > food amount > salinity. For Farmington Bay, the ranking is food taxa > food amount ≥ temperature ≃ salinity. Both areas have food (taxa and amount) more important than abiotic effects (salinity and temperature), with food more important under Farmington Bay

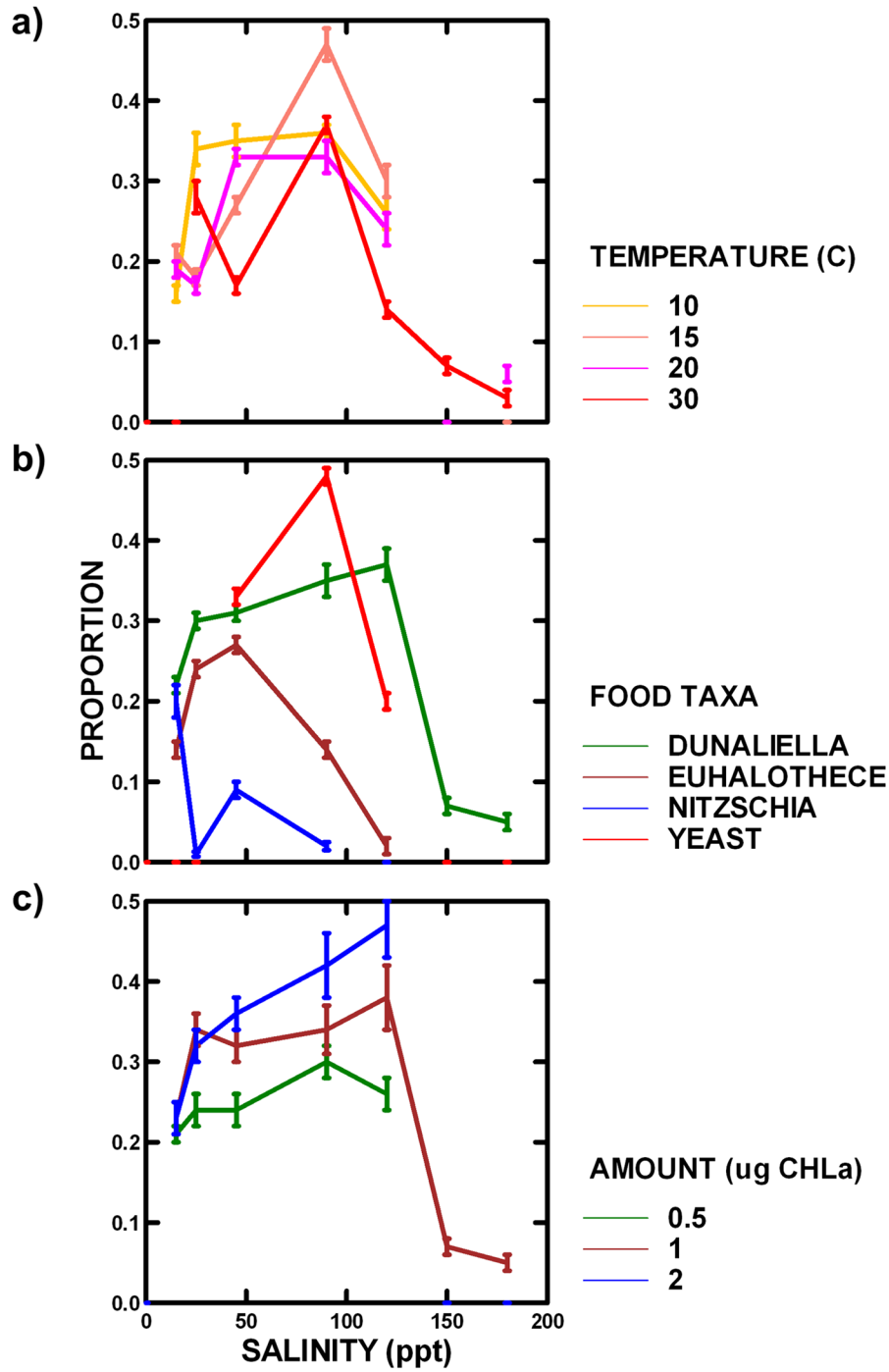

Fig. 2 Survival observed with the combination of salinity and **a** temperature; **b** food taxa; **c** food amount. Data for all developmental stages are employed in **a** (N = 2788), **b** limited data for *Carteria* as a food are excluded (N = 2638), and c) data is restricted to *Dunaliella*, the food with the greatest salinity data (N = 753)

than South Arm conditions. Oviparous production would be 8% greater under South Arm than Farmington Bay conditions (13.4 vs. 12.4 oviparous cysts per female).

2. Ovoviviparous production per female for South Arm has the importance of effects ranked as food amount > temperature ≃ food taxa > salinity. For Farmington Bay, the ranking is food amount ≃

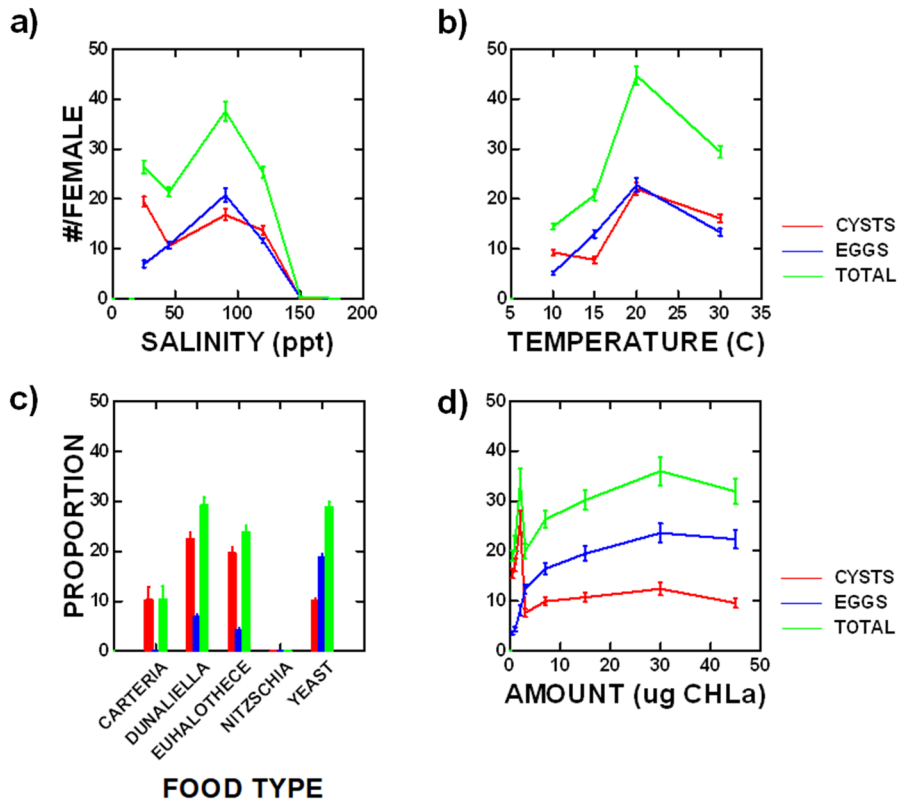

Fig. 3 *Artemia* adult fixed effects (± SE) for reproduction (cyst = oviparity, egg = ovoviviparity, total) in a multifactorial experiment (N = 1005) for all adult data for **a** salinity, **b** temperature, **c** food type, and **d** amount of food

food taxa > temperature > salinity. Both areas have food (taxa and amount) more important than abiotic effects (salinity and temperature), with food effects more important for Farmington Bay than South Arm. Ovoviviparous production would be 42% greater in the South Arm than Farmington Bay (14.2 vs. 10.0 ovoviviparous eggs per female).

3. Total reproduction per female for South Arm conditions has the importance of effects ranked as temperature > salinity > food taxa ≃ food amount. For Farmington Bay conditions, the ranking is temperature > food taxa > food amount > salinity. For South Arm and Farmington Bay conditions, abiotic effects (salinity and temperature) were more important than food (taxa and amount), with abiotic effects more important under South Arm conditions. This would lead to 23% greater total reproduction under South Arm than Farmington Bay conditions (27.6 vs. 22.4 offspring/female).

Maternal effects. Given adult experiments where enough cysts or ovoviviparous young were produced, maternal effects (temperature, salinity, and food amount, food taxa) on cyst hatchability (Fig. 5a–e), and nauplii survival and transition (Fig. 5f–h) were examined.

Results from GLMM analyses of cyst hatchability are presented in Table 4 with the combination of temperature, salinity, and food taxa statistically significant. The importance of each of these main effects based on variance explained was food taxa > salinity > temperature. Only one (food taxa X salinity) of the six two-way interactions was statistically significant. Time kept frozen (Months) did not affect hatchability.

The GLMM analyses of ovoviviparous nauplii survival and transition are presented in Table 4. All four maternal main effects of ovoviviparous nauplii survival and transitioning are statistically significant. The importance for survival based on variance explained is food amount ≃ salinity > temperature > food taxa, and for transitioning, temperature > salinity > food amount > food taxa. For both

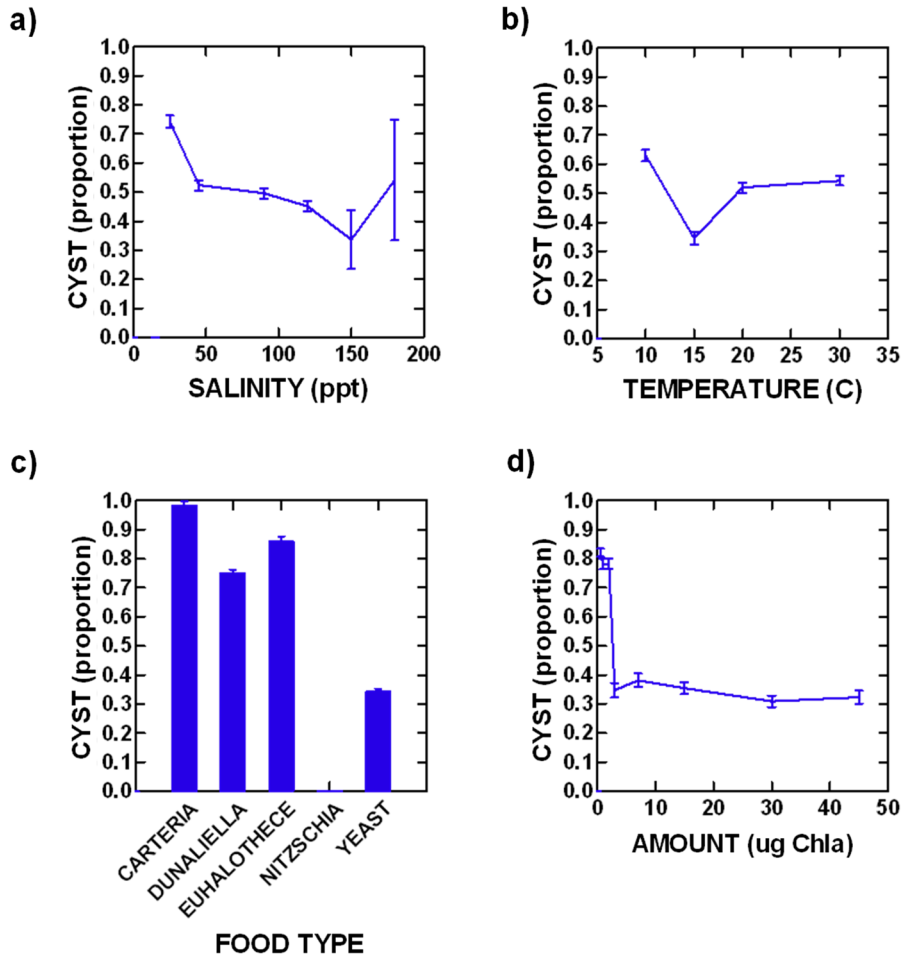

Fig. 4 *Artemia* adult fixed effects (±SE) for proportion of reproduction via cysts (oviparity) in a multifactorial experiment (N = 1005) for **a** salinity, **b** temperature, **c** food type, and **d** amount of food

survival and transitioning, the same four of the ten two-way interaction terms are significant based on BIC values. For survival, the interaction terms are more important than main effects, increasing variance explained from 17 to 52%, while for transitioning they are less important, increasing variance explained from 23 to 38% (Table 4).

Discussion

Our experiments addressed how the dominant (>>95%) hypersaline GSL pelagic herbivore (brine shrimp) survives, transitions between developmental stages and reproduces (both in total and apportioned between oviparity and ovoviviparity) in response to environmental conditions (salinity, temperature, food taxa, and food amount). Also, we examined how maternal environmental conditions affect offspring performance (oviparous cyst hatchability, ovoviviparous nauplii survival and transitioning to juveniles). Furthermore, combinations of environmental effects strongly affect demographic responses, which indicates that examining responses to any single factor is limited.

Our study indicates that salinity seldom (1/22 comparisons: total range of effects + South Arm conditions + Farmington Bay conditions) is the most important effect on demographic responses. This is counter to the common assumption that salinity should be most important because *Artemia* species inhabit hypersaline environments. Most laboratory studies with *Artemia* have examined salinity tolerances (minimum and maximum salinity) for survival over a short time (1–2 weeks), given a favorable temperature, and ad libitum food. Browne

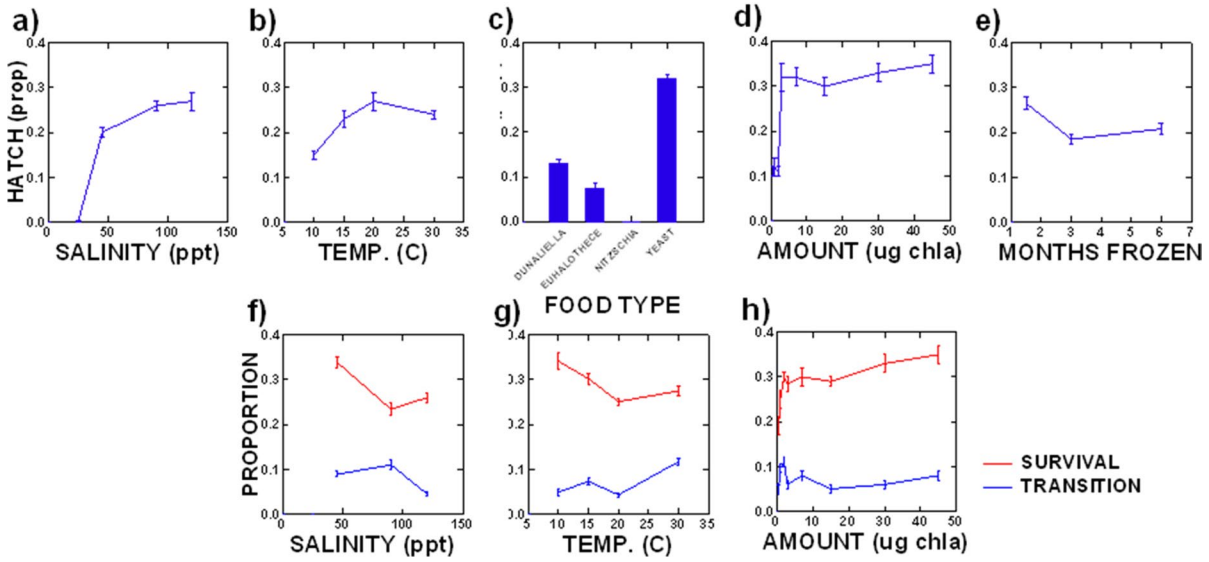

Fig. 5 *Artemia* maternal fixed effects for cyst proportion hatching (±SE) in a multifactorial experiment (N = 992) **a** salinity, **b** temperature, **c** food type, **d** amount of food, and **e** months kept frozen, and ovoviviparous nauplii survival and transition to juveniles (±SE) in a multifactorial experiment (N = 563) for **f** salinity, **g** temperature, and **h** amount of food

Table 4 GLMM results for the best-fit models (lowest BIC) to *Artemia* maternal effect on oviparous cyst hatchability (N = 993) and ovoviviparous nauplii survival and transition (N = 563). Analyses include all salinity, temperature, food taxa and food amount values

Response	Variable	Statistics
Cyst hatchability	Main effects: Taxa, Amount, Salinity, Temperature	$r = 0.53$, BIC = 7196, $P \leq 0.0001$, N = 993
	2-Way interactions: Taxa x Salinity	
Nauplii survival	Main effects: Taxa, Amount, Salinity, Temperature	$r = 0.72$, BIC = 4256, $P \leq 0.0001$, N = 563
	2-Way interactions: Taxa X Salinity, Taxa X Amount, Amount X Salinity, Salinity X Temperature	
Nauplii transition	Main effects: Taxa, Amount, Salinity, Temperature	$r = 0.62$, BIC = 2959, $P \leq 0.0001$, N = 563
	2-Way interactions: Taxa X Salinity, Taxa X Amount, Amount X Salinity, Salinity X Temperature	

and Wanigasekera (2000) point out that this limits the ability to attribute the importance of salinity on *Artemia* demography without multi-factor experiments. For example, Dana et al. (1993) found salinity explained 40 – 93% of survival and reproductive variability when salinity was examined by itself, while we found salinity to account for < 1 – 10% in our multi-factor experiment.

Comparing Artemia laboratory studies. Other studies with *A. franciscana* and its congeners find minimum salinity tolerances as 10–70 ppt, maximum tolerances as 140–180 ppt, and optimum salinity as 75–120 ppt (*e.g.*, Vanhaecke et al., 1984; Dana & Lenz, 1986; Wear & Haslett, 1986, 1987; Wear et al., 1986, Vanhaecke & Sorgeloos, 1989; Dana et al., 1993; Triantaphyllidis et al., 1995; Van Stappen, 1996; Browne & Wanigasekera, 2000; El-Bermawi et al., 2004; Irwin et al., 2007; Barnes & Wurtsbaugh, 2015), while Medina et al. (2007) report weak salinity effects. We estimate a minimum salinity at the lower end of the reported range, a maximum at the upper end of the range, and an optimum at ~ 90 ppt for survival (Fig. 1b).

Dana et al. (1993) found survival of immature individuals, especially nauplii, affected more by salinity, while we found juveniles to be more affected. While we found optimal survival for immature individuals at 90 ppt, their transitioning was optimal at 45 ppt

(Fig. 1b); however, transitioning at 90 ppt was only 14% less than at 45 ppt (7.1% vs. 8.3%). This difference was largely due to nauplii with a 23% decline from 45 to 90 ppt versus a 6% decline for juveniles. In part, this may explain why nauplii perform better in fresher-water lenses in GSL.

Temperature response studies for *Artemia* are fewer. Optimum temperatures for survival are reported at 22–30 °C (*e.g.*, Sorgeloos et al., 1986; Van Stappen, 1996; Abatzopoulos et al., 2003; Browne & Wanigasekera, 2000; Medina et al., 2007), while Vanhaecke et al. (1984) report little temperature effect. We did not observe an optimal temperature, but survival increased as temperature declined to 10 °C and transitioning increased with temperature to 30 °C, with temperature more important for transitioning than survival (Fig. 1c, Table 2). Studies varying temperature with salinity find a strong interaction where high salinities and temperatures lead to poorer survival (*e.g.*, Sorgeloos et al., 1976; Vanhaecke et al., 1984; Vanhaecke & Sorgeloos, 1989; Browne & Wanigasekera, 2000; Medina et al., 2007). However, Van Stappen (1996) reports weak interaction, and we observed no interaction for survival and weak interaction for transitioning.

Food effects on survival and transitioning are common and strong when studied (*e.g.*, Sick, 1976; Jaki et al., 1999; Caldwell et al., 2003; Lora-Vilchis et al., 2004; Seixas et al., 2009). *Artemia* are reported to perform better on chlorophytes than cyanobacteria (Sick, 1976; Jaki et al., 1999) or the bacillariophyte *Nitzschia* (Caldwell et al., 2003), as we found. Belovsky et al. (submitted) observed that *A. franciscana* in all 3 developmental stages consumed all of these phytoplankton in monoculture, but differentially selected among them in mixed cultures based on their survival value. Survival value was most dependent on ingestion rate (biovolume/h) of different phytoplankton species and their N:P content relative to *A. franciscana* developmental stage N:P body content, and less affected by cell biovolume. We also observed survival and transitioning to increase with more food (Fig. 1d, e).

Reproduction in our study was greatest at 90 ppt and 20 °C (Fig. 2a, b). Other studies report a decline as salinity increased (Dana & Lenz, 1986; Wear et al., 1986; Dana et al., 1993), while Abatzopoulos et al. (2003) observed maximum cyst production at 80 ppt and 22 °C, and Vartak & Joshi (2002) found maximum cyst production at 120 ppt. Vartak & Joshi (2002) report reproductive output to vary with type of food, and we found yeast and the chlorophyte *Dunaliella* led to the greatest output and the bacillariophyte *Nitzschia* to the lowest (*i.e.*, no) output (Fig. 3c). Browne (1982) found reproductive output to be largely driven by food availability, and we observed reproduction to peak, then decline and finally increase again as food increases, due to reproduction shifting from oviparity to ovoviviparity as food increases (Fig. 3d).

Shifts between oviparous and ovoviviparous reproduction in *Artemia* are interesting and can occur during a female's life with oviparity dominating as environmental conditions deteriorate (Godelieve et al., 2002). Salinity, temperature, and food have been suggested as possible stimuli (Godelieve et al., 2002). Increased temperature fostered ovoviviparity in some studies (Godelieve et al., 2002; Wang et al., 2019) and diminished it in others (Nambu et al., 2004). We observed little effect of temperature or salinity on this shift (Fig. 4a, b). Vartak & Joshi (2002) found food type important for this shift and Godelieve et al. (2002) reported that ovoviviparity dominated as food abundance increased, which our study supports (Fig. 4c, d). Finally, a maternal effect of better cyst hatching with better female nutrition and higher salinity was reported by Lavens & Sorgeloos (1987), as we observed (Fig. 5a–d). We also observed that ovoviviparous nauplii survival and transition improved with maternal nutrition (Fig. 5h). Maternal effects have been reported for other aquatic crustaceans and insects (Mikulski & Pijanowska, 2017; Coakley et al., 2018; Toyota et al., 2019).

Finally, studies examining a single environmental factor should be applied with caution, because we observed strong effects when factors were combined. Consequently, the impact of one factor can be increased or decreased when combined with other factors.

Comparing our laboratory studies with GSL field observations. Field and laboratory observations can be difficult to compare as multiple environmental factors covary in the field (*e.g.*, salinity may affect food taxa and food abundance). We analyzed subsets of our laboratory findings to salinity ranges that reflect two major areas within the lake: South Arm (salinity = 45–150 ppt, most typical of historic conditions) and Farmington Bay (salinity = 15–45 ppt,

anthropogenically created). However, these two areas also vary in terms of their phytoplankton species composition, which must be considered (South Arm dominated in most years by *Dunaliella*, and Farmington Bay in most years dominated by cyanophytes and bacillariophytes, with no *Dunaliella*: Wurtsbaugh, 1992; Marcarelli et al., 2006; Wurtsbaugh & Marcarelli, 2006; Wurtsbaugh et al., 2012).

South Arm brine shrimp observations from 1994–2018 (Belovsky et al., 2011, 2019; Belovsky & Perschon, 2019) in many ways reflect our laboratory projections for this area. In the laboratory and field, salinity and temperature tend to be less important than food resources (food abundance and species) for survival, transitioning, and proportion of reproduction by ovoviviparity. For example, in the laboratory and in this portion of the lake, chlorophytes (primarily *Dunaliella*) had a positive effect on demographic parameters, and in the field, while for years with the worst performing brine shrimp populations, cyanophytes and bacillariophytes tended to be relatively more abundant (Belovsky et al., 2011). Finally, a maternal nutrition effect was observed in the field and in the laboratory (Belovsky & Perschon, 2019) for cyst hatchability.

Farmington Bay brine shrimp densities are 30—38Xs lower than in the South Arm (Wurtsbaugh, 1992; Wurtsbaugh & Marcarelli, 2006). Laboratory projections based solely on salinity suggest that Farmington Bay brine shrimp abundances should be 2.2Xs less than the South Arm (Table 5). If food differences are included (South Arm – salinity: 45 – 150 ppt, food species = *Dunaliella*; Farmington Bay – salinity ≤ 45, food species ≠ *Dunaliella* or yeast), Farmington Bay brine shrimp abundances should be 33.6Xs less than the South Arm (Table 5). Therefore, the direct effect of salinity may be less important than food in producing differences in brine shrimp abundances. Furthermore, this low productivity of the *Artemia* population may make it more susceptible to competition from other zooplankton and corixid predators that can exist at the lower salinity (Wurtsbaugh, 1992).

North Arm of GSL (salinity > 200 ppt) essentially has no brine shrimp. Given our laboratory data at a salinity of 180 ppt, the brine shrimp population here is predicted to be $1.6X10^7$Xs less than in the South Arm.

Our laboratory experiments help to explain observed GSL brine shrimp demography by disentangling covarying abiotic and biotic environmental parameters. However, relying on laboratory studies based solely on abiotic factors (*e.g.*, salinity and temperature) must be used with caution when attempting to explain field observations, because under certain levels of the abiotic factors, food effects in the field

Table 5 Comparison of GSL South Arm (salinity = 45–150 ppt, food = *Dunaliella*) and GSL Farmington Bay (salinity ≤ 45 ppt, food ≠ *Dunaliella* or yeast) *Artemia* demographics based on laboratory experimental results. TOTAL PRODUCT is obtained my multiplying all of the ratios above

	Farmington Bay		South Arm		Ratio (South Arm/Farmington Bay)	
	Salinity only	Salinity and Food	Salinity only	Salinity and Food	Salinity only	Salinity and Food
Cyst Hatching (%)	19.5	13.9	25.3	20.1	1.3	1.45
Survival (%) of Nauplii	26.0	20	24.4	24.8	0.94	1.24
Transition (%) to Juveniles	6.9	3.5	7.5	8.7	1.09	2.50
Survival (%) of Juveniles	26.0	20	23.5	22.7	0.90	1.14
Transition (%) to Adults	6.9	3.5	6.9	6.1	1.00	1.74
Survival (%) of Adults	26.0	20	38.5	46.7	1.48	2.34
Reproduction (#/♀) by Adults	22.4	20.04	27.6	32.2	1.23	1.61
Total product					**2.2**	**33.6**

may be more critical for projections. Likewise, correlations between field abiotic conditions and field biotic observations can be misleading. For example, if GSL phytoplankton species and their abundance (food effects) change with salinity, then observed changes in brine shrimp demography under certain salinity levels could be attributed to salinity when changes in food may be driving brine shrimp responses.

Managing Great Salt Lake. Our multifactor laboratory experiments help forecast future changes in GSL. Given these results, Barrett & Belovsky (2020) predict that projected climate change for the GSL watershed (warmer and wetter) will increase South Arm brine shrimp, but this is accompanied by greater ovoviviparity and less oviparity. This would negatively affect the lucrative commercial harvest of brine shrimp cysts for aquaculture.

If more water is diverted from GSL inflows for agriculture, urban use, and mineral extraction, then South Arm salinity will increase, which decreases brine shrimp survival and transitioning. However, survival and transitioning declines may be ameliorated, if nitrogen also is concentrated, which increases phytoplankton (Belovsky et al., 2011; Barrett & Belovsky, 2020). Therefore, covariation among factors is a critical consideration. However, while this may have ameliorated the effects of increasing salinity observed in recent years on *Artemia* populations, once salinity exceeds certain levels (> 120–150 ppt in our experiments), this compensation diminishes.

The current poor suitability of Farmington Bay for brine shrimp will not improve without increased salinity and restoring abundant *Dunaliella* as food; however, reduced freshwater inflows cannot increase salinity as inflows are already limited, rather better water exchange with the more saline South Arm through the existing auto causeway may be needed. Furthermore, restoring the North Arm for brine shrimp requires reduced salinity; however, this can only be accomplished by greater exchange with the South Arm through the existing railroad causeway. The South Arm is already experiencing increased salinity and thus greater exchange with the North Arm will increase South Arm salinity and stress the brine shrimp. Therefore, management responses can be counter to each other, complicated by the current long-term drought and increasing anthropogenic demand for freshwater inflows.

The above analyses for GSL provide approximate boundaries for *Artemia* populations' performance in different regions of the lake. More detailed analyses (weekly and monthly responses within a year and among years) are near completion using an ecosystem model that examines experimental responses to environmental conditions for phytoplankton growth and carrying capacity (Belovsky et al., submitted), *Artemia* demography (these data) and avian populations that feed on *Artemia* (Caudell & Conover, 2006; Conover & Caudell, 2010).

Saline lake environments. Studies of other aquatic crustacea and insects found that they respond similarly to salinity and temperature, but at different values than *Artemia* (*e.g.*, Galat & Robinson, 1983; Galat et al., 1988; Herbst & Bradley, 1989; Hammer & Forro, 1992; Herbst & Blinn, 1998; Marcarelli et al., 2006; Devreker et al., 2009; Smith et al., 2010; Ladhar et al., 2015; Afonina & Tashlykova, 2018), and these studies seldom consider combined effects with food (except Herbst 2023 for the alkali fly, *Cirrula hians* (Say, 1830)). This led Williams (1998), in a classic paper, to claim that saline lakes, like GSL, have limited species diversity because salinity imposes osmoregulatory stress on organisms, which established the idea that saline lakes are harsh environments and species' performances (survival, productivity, etc.) must be low, and often are only overcome by the absence of competitors and predators. However, saline lake species are euryhaline and halotolerant, while species in fresh and low saline environments are stenohaline (Galat & Robinson, 1983; Javor, 1989; Williams, 2001; Schapira et al., 2010). Saline lake salinity varies considerably over time and resident species perform best at moderate salinities that are beyond most aquatic species' tolerances (Williams et al., 1990). Therefore, saline lakes are not harsh to species adapted to the range of salinities there (Sanders, 1969; Slobodkin & Sanders, 1969; Hammer, 1986; Barrett & Belovsky, 2020), and they are highly productive, which accounts for their high waterbird abundances and diversity.

Conclusion

Our study examines brine shrimp (*A. franciscana*) responses (survival, transition between developmental stages, reproductive output, oviparity vs.

ovoviviparity, and maternal effects) to a number of factors (developmental stage, salinity, temperature, food taxa, and food amount) in a multifactorial laboratory experiment. Temporal (annual) and spatial (areas within lake) conditions that enhance or diminish brine shrimp numbers were identified. Results indicate how future climate change and water diversions will affect the brine shrimp (Barrett & Belovsky, 2020), which has important economic consequences for the commercial harvest of brine shrimp (Belovsky & Perschon, 2019) and conservation, as many of the lake's abundant waterbirds depend on brine shrimp for food (Frank & Conover, 2019).

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Author contributions Gary E. Belovsky – experimental design, data collection, analysis, writing, Chad Larson – data collection, Heidi Mahon – data collection, Chad Mellison – data collection, Andrea Stumpf – data collection, writing, Anghy Ramos Valencia – data collection.

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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 competing interests to declare that are relevant to the content of this article.

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