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# Impacts of harvesting on brine shrimp (*Artemia franciscana*) in Great Salt Lake, Utah, USA

Selective harvesting on brine shrimp

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**Abstract.** Selective harvesting can cause evolutionary responses in populations via shifts in phenotypic characteristics, especially those affecting life history. Brine shrimp (*Artemia franciscana*) cysts in Great Salt Lake (GSL), Utah, USA are commercially harvested with techniques that select against floating cysts. This selective pressure could cause evolutionary changes over time. Our objectives are to (1) determine if there is a genetic basis to cyst buoyancy, (2) determine if cyst buoyancy and nauplii mortality have changed over time, and (3) to examine GSL environmental conditions over time to distinguish whether selective harvesting pressure or a trend in environmental conditions has caused changes in cyst buoyancy and nauplii mortality. Mating crosses between floating and sinking parental phenotypes with two food

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concentrations (low and high) indicated there is a genetic basis to cyst buoyancy. Using cysts harvested from 1991–2011, we found cyst buoyancy decreased and nauplii mortality increased over time. Data on water temperature, salinity, and chlorophyll *a* concentration in GSL from 1994 to 2011 indicated that although water temperature has increased over time and chlorophyll *a* concentration has decreased over time, the selective harvesting pressure against floating cysts is a better predictor of changes in cyst buoyancy and nauplii mortality over time than trends in environmental conditions. Harvesting of GSL *A. franciscana* cysts is causing evolutionary changes, which has implications for the sustainable management and harvesting of these cysts. Monitoring phenotypic characteristics and life-history traits of the population should be implemented and appropriate responses taken to reduce the impacts of the selective harvesting.

*Key words:* *Artemia franciscana*; *brine shrimp*; *buoyancy*; *cysts*; *Great Salt Lake, Utah, USA*; *selective harvesting*.

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## INTRODUCTION

Human harvesting and exploitation of wildlife has contributed to the decline and extinction of entire populations and species (Burney and Flannery 2005, Allendorf et al. 2008). Overharvesting can reduce population sizes and cause changes in phenotypic and life-history traits, which increase population extinction risk. When harvesting of wildlife populations is

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selective, and the trait targeted by harvesters possesses heritable variation, selective harvesting can cause evolutionary responses in populations (Ratner and Lande 2001). These evolutionary responses typically include shifts away from the trait targeted by harvesters, which results in reduced harvesting yields (Conover and Munch 2002), and undermines the long-term goals of sustainable harvesting (Allendorf and Hard 2009). Selective harvesting can also reduce genetic variation (Allendorf et al. 2008), which increases extinction risk by reducing the population's ability to adapt to changing environmental conditions (Frankham 2005).

Changes in phenotypic and life-history traits in response to harvesting have been observed in multiple organisms, including *Daphnia* (Edley and Law 1988, Spitze 1991), elephants (Jachmann et al. 1995), Atlantic cod (Olsen et al. 2004), and bighorn sheep (Coltman et al. 2003). Disentangling the environmental and genetic components of observed changes in phenotypes and life-history traits can be difficult. However, it is critical to know whether harvesting induces genetic changes, since evolved responses can lead to lower sustainable yields (Olsen et al. 2004) and can reduce a population's capability to recover from overharvesting (Walsh et al. 2006). A recent study by van Wijk et al. (2013) provides direct evidence of rapid phenotypic and genetic responses to size-selective harvesting over just a few generations. Not only does harvesting lead to phenotypic changes in harvested populations, but these phenotypic changes are typically more rapid than phenotypic changes in natural systems (Darimont et al. 2009). The reversal of evolutionary changes caused by selective harvesting is possible (Conover et al. 2009). However, recovery back to a population's original state can take more than twice as long as the period of selection (Conover et al. 2009). The evolutionary effects of selective harvesting, including effects on phenotypic and life-history traits, should be monitored in order

to effectively manage harvested populations (Conover and Munch 2002), especially because changes in phenotypic and life-history traits may have genetic underpinnings (Belgrano and Fowler 2013).

Brine shrimp (*Artemia* spp.) are an important organism that may be experiencing evolutionary changes due to the commercial harvest of their populations. Their life cycle includes a diapausing egg stage, called a cyst, which is commercially harvested and used as a highly nutritious food for commercially cultured larval fish and crustaceans (Belovsky et al. 2011). The Great Salt Lake (Utah, USA; GSL) contains one species, *Artemia franciscana*. The commercial harvest of cysts from GSL provides an annual harvest representing up to 90% of the brine shrimp cyst global trade (Ruebhart et al. 2008). Harvesting cysts from GSL began in the early 1950s and continues today. During the 1980s there was a switch from harvesting cysts from the shoreline to skimming cysts off the surface of GSL, which increased yield and improved cyst hatching quality (Lavens and Sorgeloos 2000). However, cysts differ in their buoyancy and can sink, float, or remain neutral in the water column (Belovsky, *unpublished data*). Therefore, by skimming cysts off the water's surface, harvesters selectively remove floating cysts.

Cyst harvesting has been a selective pressure on *A. franciscana* for over 30 years, and it is possible harvesting has affected the population in multiple ways (population size, phenotypes, life-history traits, and genetic variation). The Utah Division of Wildlife Resources (UDWR) manages yearly cyst harvesting from GSL and ends the harvesting season when the minimum number of cysts needed to repopulate the GSL in the spring is reached; this is currently estimated at 21 cysts/L (Belovsky, *personal communication*). Also, *A. franciscana* is a major food resource for the abundant waterbird populations that nest or migrate through GSL (Paul and Manning

2002). Although this fishery is managed for sustainable population sizes, the effects of harvesting on *A. franciscana* phenotypic and life-history traits have not been examined.

Due to their long harvesting history and the production of diapausing cysts, brine shrimp are a good model system to examine changes in phenotypic and life-history traits over time caused by harvesting. Especially since previous studies indicate selective harvesting effects manifest in as little as four generations (Conover and Munch 2002). We have historic samples of harvested cysts from 1991–2011 (intermittent) providing samples for 16 years. Using these historic cyst samples, we can determine if harvesting of *A. franciscana* cysts in Great Salt Lake, UT, has affected phenotypic and life-history traits over time.

*Objective 1.*—Our first objective is to determine whether cyst buoyancy has a genetic basis that can be selected upon, because selective harvesting can only cause evolutionary changes in a population if it acts upon a trait that has a genetic component and is heritable. Previous studies have estimated heritability (Shirdhankar et al. 2004) and environmental and genetic variance (Browne et al. 1984, 2002) for a variety of brine shrimp traits. However, cyst buoyancy was not examined. Since Browne et al. (2002) shows a genetic component for every trait examined, we hypothesize cyst buoyancy has a genetic basis.

*Objective 2.*—Our second objective is to determine whether cyst buoyancy and nauplii mortality have changed over time. Current harvesting techniques may select against floating cysts and selection on one trait can lead to evolution of a group of traits (Conover and Munch 2002). We suggest cyst buoyancy relates to nauplii mortality because first instar nauplii (<24

hours after hatching) do not feed and depend upon cyst energy reserves to survive (Benijts et al. 1976). Thus we hypothesize cyst buoyancy has decreased and nauplii mortality has increased over time.

*Objective 3.*—Abiotic conditions in the GSL are highly variable on both a seasonal and annual basis (Belovsky et al. 2011) and may influence cyst buoyancy and nauplii mortality. To distinguish between trends due to selective harvesting pressures and changes in environmental conditions over time, we examined water temperature, salinity, and chlorophyll *a* concentration (Chl*a*) of GSL from 1994 to 2011. We hypothesize the selective pressure due to harvesting is a better predictor of any observed changes in cyst buoyancy and nauplii mortality over time, rather than any observed trends in the GSL environmental factors.

#### MATERIALS AND METHODS

*Study organism.*—*Artemia* inhabit brackish and hypersaline inland lakes, coastal lagoons, and solar saltworks worldwide (Browne and MacDonald 1982). *Artemia franciscana* is a New World sexual species of brine shrimp (Browne and MacDonald 1982). Female *A. franciscana* can reproduce by ovoviviparity, producing nauplii that hatch in the ovisac, or oviparity, producing diapausing cysts. During the summer, the brine shrimp population in GSL grows primarily through ovoviparous reproduction. In the fall, females increase their production of diapausing cysts (oviparity), which can withstand cold water temperatures during the winter and hatch in the spring with warmer water temperatures (Belovsky et al. 2011).

*Historic cyst samples.*—Historic cyst samples were obtained from Great Salt Lake Brine Shrimp Cooperative (Mountain Green, Utah, USA). Samples include harvested cysts from 1991–2011 (intermittent) providing samples for 16 yr (Appendix A: Table A1). Some cyst samples have known collection dates from GSL (Appendix A: Table A1).

*Genetic basis of cyst buoyancy.*—To determine whether cyst buoyancy has a genetic basis, we set up mating crosses with two treatments: parental phenotype and food concentration. Parental phenotype was categorized as whether they came from floating or sinking cysts. This was determined by placing cysts in 60 parts per thousand (ppt) saltwater and separately collecting floating cysts and sinking cysts. Individuals from floating and sinking cysts were raised to the adult stage (Appendix B) and then separated by sex (males have claspers, females have ovisac). The two food concentrations used were 80 ug/L of Chla (high) and 10 ug/L of Chla (low).

Experimental trials ( $n = 10$ ) were mating crosses between floating males and floating females or between sinking males and sinking females. Each experimental trial contained five males and five females and was fed 400 mL of a feeding solution every third day. Feeding solutions were made of 60 ppt saltwater and *Dunaliella viridis* at the specific food concentration: low (10 ug/L of Chla) or high (80 ug/L of Chla). Experimental trials were checked once a week for the production of offspring and death of adult individuals. During weekly inspections, adult density was replenished to five males and five females per bottle, nauplii were removed, and cysts were counted and placed back into the trial. After five weeks, experimental trials were terminated and all cysts were collected and placed into test tubes with 50 mL of 60 ppt saltwater. After 1 h, the number of cysts floating and sinking was counted. Empty shells were not counted.

The proportion of cysts floating in 60 ppt in each experimental trial was used in statistical analyses.

*Cyst buoyancy.*—We determined the salinity at which 50% of cysts float/sink for each year of historic cysts. Using seven different salinities (0, 15, 30, 45, 60, 90, 120 ppt), we counted cysts that were floating and sinking after 1 h ( $n = 4$  test tubes). We sprinkled a tiny amount of dry cysts into a 50 mL test tube, added 50 mL of water, and waited 1 h before counting the cysts. Saltwater was pipetted onto the top of the water column in the test tube to break water surface tension and allow the cysts to distribute in the water column. Floating cysts were those in the top half of the water column and sinking cysts were those in the lower half of the water column.

*Nauplii survival experiments.*—For each year of historic cyst samples, cysts were hatched (Appendix B) and then forty nauplii were immediately placed into an experimental bottle ( $n = 5$ ) on Day 0 and their mortality recorded on Day 3 and Day 7. Nauplii were categorized as individuals that had not gone through metamorphosis and were not showing segmentation. Beginning on Day 0 for each experiment and continuing every other day, each experimental bottle was fed a solution of *Dunaliella viridis* at a concentration of 80 ug/L of Chl $a$ . See Appendix B for further details.

*Environmental factors.*—The Great Salt Lake Ecosystem Program provided us with a large dataset of abiotic and biotic conditions of Great Salt Lake from 1994 to 2011. Using this data set, we calculated mean values for temperature, salinity, and chlorophyll  $a$  concentration (Chl $a$ ) using the 1–2 months prior to when the cysts were harvested (Appendix A: Table A1), as we are only interested in maternal conditions that would affect cyst production. For samples without a

known collection date, we used the months August–October and September–October, since cyst samples with known collection dates were most often collected in October. Yearly averages from two months and one month prior to collection date were significantly correlated for temperature (Pearson's  $r = 0.95$ ), salinity (Pearson's  $r = 1.00$ ), and chlorophyll  $a$  (Pearson's  $r = 0.99$ ). Thus, the yearly means for two months prior to collection date were used in statistical analyses.

*Statistical Analyses.*—For the genetic basis of cyst buoyancy data, a general linear model with a quasibinomial distribution (overdispersion factor = 4.09) was used to test the effects of parental phenotype and food concentration on the proportion of floating cysts in 60 ppt saltwater.

For cyst buoyancy, a general linear model with a quasibinomial distribution (overdispersion factors  $> 1$ ) was used to fit the data for each year and the salinity at which 50% of cysts float/sink was calculated. A regression was used to test the relationship between year (1991–2011) and the salinity where 50% of cysts float/sink (cyst buoyancy). Nauplii mortality was calculated as the proportion of nauplii dead per day. A regression was used to test the relationship between year (1991–2011) and nauplii mortality. Cook's distance was used to check for outliers, and no outliers were detected for cyst buoyancy or nauplii mortality. Analyses were conducted in R 3.0.2 (R Development Core Team 2013).

Correlations of environmental factors against year were used to examine changes over time in GSL. Pearson's correlation matrix was used to examine correlation among the GSL environmental factors and with year. Since temperature and Chl $a$  are highly correlated with each other (Pearson's  $r = -0.679$ ), and year is highly correlated with both temperature (Pearson's  $r =$

0.797) and Chla (Pearson's  $r = -0.824$ ), multiple linear regression could not be used to examine whether environmental factors showing linear trends or selective pressure over time (year) best explained any observed change in cyst buoyancy or nauplii mortality. Instead, we used simple regressions and residuals analyses to compare the impacts of year or environmental factors on changes in cyst buoyancy and nauplii mortality over time. Statistical analyses were done in SYSTAT (version 13; Systat Software, Chicago, Illinois, USA).

## RESULTS

*Genetic basis of cyst buoyancy.*—There is a significant effect of parental phenotype (floater vs. sinker,  $F_{1,35} = 6.897$ ,  $P = 0.013$ ) and food concentration (low vs. high,  $F_{1,34} = 9.542$ ,  $P = 0.004$ ) on proportion of floating cysts. In addition, there is a significant interaction between parental phenotype  $\times$  food concentration on proportion of floating cysts ( $F_{1,33} = 5.199$ ,  $P = 0.029$ , Fig. 1).

*Cyst buoyancy.*—The salinity where 50% of cysts float/sink has significantly increased from 1991 to 2011 ( $F_{1,14} = 7.451$ ,  $R^2 = 0.347$ ,  $P = 0.016$ , Fig. 2).

*Nauplii mortality.*—There is a significant increase in nauplii mortality from 1991 to 2011 ( $F_{1,14} = 21.6$ ,  $R^2 = 0.607$ ,  $P < 0.001$ ; Fig. 3).

*Environmental factors.*—Yearly mean values for water temperature, salinity, and chlorophyll *a* (Chla) for Great Salt Lake from 1994 to 2011 are shown in Fig. 4. There is a significant increase in water temperature (Pearson's  $r = 0.65$ ,  $P = 0.003$ , Fig. 4A), no linear trend in salinity (Pearson's  $r = 0.20$ ,  $P = 0.44$ , Fig. 4B), and a significant decrease in chlorophyll *a* (Pearson's  $r = -0.57$ ,  $P = 0.03$ , Fig. 4C) from 1994 to 2011.

Great Salt Lake water temperature and Chl $a$  are highly correlated (Pearson's  $r = -0.679$ ), and year is highly correlated with both temperature (Pearson's  $r = 0.797$ ) and Chl $a$  (Pearson's  $r = -0.824$ ). Because of these high covariations and linear trends in GSL temperature and Chl $a$ , we used simple linear regressions to distinguish whether GSL environmental factors or selective pressure over time (year) best explained the observed changes in cyst buoyancy and nauplii mortality. For cyst buoyancy, the regression against year ( $R^2 = 0.301$ ,  $P = 0.016$ ) explains more of the variation than the regressions against water temperature ( $R^2 = 0.108$ ,  $P = 0.13$ ) or chlorophyll  $a$  ( $R^2 = 0.131$ ,  $P = 0.11$ ). Similarly, for nauplii mortality, the regression against year ( $R^2 = 0.579$ ,  $P = 0.0004$ ) explains more of the variation than the regressions against water temperature ( $R^2 = 0.203$ ,  $P = 0.052$ ) or chlorophyll  $a$  ( $R^2 = 0.302$ ,  $P = 0.024$ ). In addition, the residuals of the regressions against year were then analyzed against water temperature and Chl $a$  for cyst buoyancy and nauplii mortality. Residuals from the regression of cyst buoyancy against year were not significantly explained by temperature ( $R^2 < 0.001$ ,  $P = 0.96$ ) or Chl $a$  ( $R^2 < 0.001$ ,  $P = 0.94$ ). Residuals from the regression of nauplii mortality against year also were not significantly explained by temperature ( $R^2 = 0.002$ ,  $P = 0.86$ ) or Chl $a$  ( $R^2 = 0.002$ ,  $P = 0.87$ ).

## DISCUSSION

Our three objectives were to (1) determine if there is a genetic basis to cyst buoyancy, (2) determine if there has been a change in cyst buoyancy and nauplii mortality over time, and (3) compare any observed trends in cyst buoyancy and nauplii mortality over time to changes in environmental conditions (temperature, salinity, chlorophyll  $a$  concentration) in GSL.

There is a genetic basis to cyst buoyancy (Fig. 1). This is critical to know when examining whether the selective harvesting of floating cysts is causing evolutionary changes in

GSL *A. franciscana*. The heritability and environmental versus genetic components of cyst buoyancy have not been examined previously. Eimanifar et al. (2006) examined the mitochondrial diversity of *A. urmiana* from Urmia Lake in Iran and they observed significant genetic differentiation between floating and sinking cysts at three different regions in Urmia Lake. Our results indicate a clear relationship between the cyst buoyancy of the parents and their offspring for *A. franciscana* in GSL. Thus, it is possible genetic differentiation exists between floating and sinking cysts from *A. franciscana* in GSL. Although we did not determine actual heritability estimates of cyst buoyancy, the proportion of floating cysts is 211.3% higher from floater parents than sinker parents (Fig. 1). This indicates cyst buoyancy has a genetic component and can be selected upon. Furthermore, the selective harvesting of floating cysts could cause evolutionary changes in the *A. franciscana* in GSL.

Food concentration was also important in determining cyst buoyancy. The proportion of floating cysts is 368.6% higher when parents were fed the high food concentration compared to the low food concentration (Fig. 1, Appendix C: Table C1). Hence, there is an environmental component to cyst buoyancy and the food concentration the parents experience strongly influences the buoyancy of produced cysts. The significant interaction between parent phenotype and food concentration (Fig. 1) indicates parental phenotype is not as important in determining cyst buoyancy with low food concentrations. It appears poor nutrition always leads to more sinking cysts regardless of parental phenotype. Our results supports previous research which indicates food availability (ChlA) for adult female *A. franciscana* producing cysts can influence the cyst buoyancy and nauplii mortality of offspring (Belovsky, *unpublished data*). Thus, maternal effects, specifically food availability, influence cyst buoyancy, with less food leading to

more sinking cysts (Fig. 1). Overall, cyst buoyancy likely has both genetic and environmental components to its variance, which is expected since previous studies found both genetic and environmental components for all brine shrimp traits examined (Browne et al. 2002).

Our results support our hypothesis that cyst buoyancy has decreased over time (Fig. 2). Because we examined the salinity where 50% of cysts float/sink, an increase in this value indicates a decrease in cyst buoyancy. This is a strong indication that current harvesting techniques are selectively harvesting floating cysts and causing the population to shift toward more sinking cysts. Although we showed cyst buoyancy is influenced by both parental phenotype and food concentration, the direct mechanism behind cyst buoyancy is unknown. Abatzopoulos et al. (2006) measured cyst buoyancy of *Artemia urmiana* Günther and GSL *A. franciscana* cysts. *Artemia urmiana* cysts show very little floating capacity compared to GSL *A. franciscana* cysts (Abatzopoulos et al. 2006). After investigating the cyst chorion structure, Abatzopoulos et al. (2006) discovered the alveolar and fibrous layers differ between *A. urmiana* and *A. franciscana* cysts. Because *A. franciscana* cysts have a thicker alveolar layer and wider alveolae than *A. urmiana*, Abatzopoulos et al. (2006) hypothesize the alveolae shape and volume, since alveolae contain air, influence cyst buoyancy. It is possible some other mechanism influences cyst buoyancy within a brine shrimp species, such as carbohydrate or lipid content. However, these have not been compared between floating and sinking cysts for *A. franciscana*. Also, floating cysts have higher haplotype and nucleotide diversity than sinking cysts of *A. urmiana* (Eimanifar et al. 2006). If this is also the case for *A. franciscana* in GSL, then selective harvesting could cause reduced genetic diversity along with decreased cyst buoyancy over time.

In addition to cyst buoyancy, we also examined nauplii mortality, which shows a significant increase over time (Fig. 2). We suggest the increase in nauplii mortality is a result of the selective harvesting of floating cysts. Because harvesting in GSL selects upon cyst buoyancy, cyst buoyancy and nauplii mortality would need to be connected for harvesting to also affect nauplii mortality. If selective harvesting affects both cyst buoyancy and nauplii mortality, we would expect changes in nauplii mortality to reflect changes in cyst buoyancy over time. Cyst buoyancy and nauplii mortality show a significant correlation (Pearson's  $r = 0.6997$ ,  $P = 0.005$ , Fig. 5), which supports the idea that cyst buoyancy and nauplii mortality are related.

Currently, the relationship between cyst buoyancy and life-history traits of brine shrimp are unknown. However, previous studies indicate brine shrimp cysts store carbohydrates that are used as energy for continued development of the encysted embryo once diapause ends (Clegg 1964, 1965). Also, during the first instar, the nauplii do not feed and instead use the “yolk” from their cyst as energy (Benijts et al. 1976). This coincides with a 20% decrease in individual dry weight and a 26% decrease in total lipid content (Benijts et al. 1976). During starvation periods, nauplii use reserved fatty acids, a category of lipids, for energy production (Han et al. 2001). If harvesting selects against buoyant cysts and cyst buoyancy depends upon energy reserves, and if these energy reserves influence nauplii mortality, then decreased cyst buoyancy can lead to the observed increase in nauplii mortality.

Cyst storage and viability could potentially affect our cyst buoyancy and nauplii mortality results. Clegg (1976) observed decreased cyst viability with increased storage time, with only 0.8% of cysts viable after 15 years and no viable cysts after 28 years. However, we successfully

hatched brine shrimp from cysts stored for 23 years, since they were collected in 1991 and used for experiments in 2014. Also, we had  $40\% \pm 3\%$  (mean  $\pm$  SE) of 1991 cysts hatch after 72 hours and there was no decrease in cyst viability from 1991 to 2011 (S. Sura, *unpublished data*). Thus, it is unlikely cyst viability influenced our cyst buoyancy results. If, instead, storage time affects the life history of embryos that remain viable and do hatch when diapause is broken, we would expect to see increased nauplii mortality for cysts with longer storage time, and an overall decrease in nauplii mortality from 1991 to 2011. Instead our results indicate nauplii mortality has significantly increased over time. Overall, it is unlikely the length of time the cysts were in diapause contributed to our results for cyst buoyancy and nauplii mortality.

Using mean values of GSL environmental conditions during cyst production, we found a significant increase in water temperature and significant decrease in *Chla* from 1994 to 2011 (Fig. 4). Food availability (*Chla*) for adult female *A. franciscana* when producing cysts can influence the cyst buoyancy and nauplii mortality of offspring (Belovsky, *unpublished data*). Therefore, the decrease in GSL *Chla* over time could be driving the observed changes in cyst buoyancy and nauplii mortality. However, we also suspect that selective harvesting pressure against floating cysts over time (year) could be driving the observed decrease in cyst buoyancy and increase in nauplii mortality. It was important to distinguish whether these environmental conditions or selective harvesting over time (year) was better at explaining the changes in cyst buoyancy and nauplii mortality over time. Although year is highly correlated with both temperature and *Chla*, and despite the known response of cyst buoyancy and nauplii mortality to maternal food availability (Belovsky, *unpublished data*) our results indicate the selective

pressure (year) against floating cysts is the best predictor for the observed changes in cyst buoyancy and nauplii mortality over time, instead of temperature or Chla.

This is the first study to examine and provide evidence of directional shifts in phenotypic and life-history traits of *A. franciscana* in GSL. Decreasing cyst buoyancy is a major concern since this trait is targeted by the harvesting industry to harvest cysts. Increased nauplii mortality is also concerning because there is a conceivable connection between cyst buoyancy, energy content, and nauplii mortality, which suggests nauplii mortality is also impacted by commercial cyst harvesting. In addition, our historic cyst samples are cysts that were harvested from GSL, indicating they have characteristics allowing them to be harvested. Although this could have limited our ability to detect changes over time, the fact we did detect an increase in nauplii mortality and decrease in cyst buoyancy suggests even larger changes could be occurring in GSL. Since the sustainable harvesting of GSL *A. franciscana* is critical for both ecological and economic reasons, UDWR should monitor phenotypic and life-history traits over time. Also, the development of large scale harvesting techniques of cysts throughout the water column would increase harvesting of other species of brine shrimp cysts and reduce the selective harvesting impacts on *A. franciscana* in GSL.

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#### SUPPLEMENTAL MATERIAL

##### **Ecological Archives**

Appendices A–C are available online: <http://dx.doi.org/10.1890/15-0776.1.sm>

FIG. 1. Average proportion of floating cysts in 60 parts per thousand (ppt) saltwater produced from sinking or floating adult males and females in experimental bottles.

FIG. 2. The estimated salinity where 50% of cysts float/sink based upon a quasibinomial distribution for 16 yr between 1991 and 2011.

FIG. 3. Average proportion of nauplii dead per day ( $\pm$  SE) in a survival experiment lasting 7 d.

FIG. 4. Yearly average values for (A) water temperature, (B) salinity, and (C) chlorophyll *a* for Great Salt Lake from 1994 to 2011.

FIG. 5. Correlation between nauplii mortality and cyst buoyancy.







