BRINE SHRIMP POPULATION DYNAMICS

AND

SUSTAINABLE HARVESTING

IN THE GREAT SALT LAKE, UTAH

2001 PROGRESS REPORT

TO

THE UTAH DIVISION OF WILDLFE RESOURCES

SALT LAKE CITY, UTAH

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JUNE 1, 2002

INTRODUCTION:

This is a report on the seventh year of studies of the population dynamics of brine shrimp (*Artemia franciscana*) and phytoplankton in the Great Salt Lake ecosystem, and the mathematical modeling of these dynamics. Here we present:

1. the completed project on brine shrimp demography conducted in the laboratory;
2. further evidence on the importance of over winter survival of brine shrimp cysts to annual population numbers;
3. the forecast for Great Salt Lake brine shrimp harvests for 2002, based upon past modeling efforts.

These results are based upon work conducted in the past year and work referred to in previous annual reports.

BRINE SHRIMP DEMOGRAPHY:

Brine shrimp are the dominant phytoplankton grazers in the Great Salt Lake, the fourth largest terminal lake in the world. Also, they are a major source of food for the migrant shorebirds that visit the lake, which are >30% of all shorebirds in the Pacific flyway (Paton et al. 1992). Natural variation in water temperature, salinity, phytoplankton availability within and among years is very great, as is variation in brine shrimp numbers and productivity. For example, salinity has varied from 7 – 14% over the past 5 years and from 5 – 28% over the past 100 years (Stephens and Arnow 1987; Stephens 1990; Wurtsbaugh and Berry 1990) in the south arm of the lake. In addition, environmental factors are being modified by anthropogenic influences, especially as the surrounding watershed becomes urbanized. Mining of lake waters for minerals, diversion of inflows of freshwater and construction of causeways modify salinity. Diversion of inflows changes lake levels, which impacts water temperatures. Phytoplankton abundances are modified by salinity/temperature changes and nutrient inputs from sewage, agriculture, urbanization, and loss of surrounding wetlands. Therefore, documenting the impacts of different environmental factors (water temperature, salinity and food abundance) on brine shrimp (*Artemia franciscana*) from the Great Salt Lake is critical for developing comprehensive and sound management plans for this ecosystem and the economically important brine shrimp fishery (Sorgeloos 1980, Peterson 1992).

Correlating environmental conditions with population responses in the field is difficult, because a number of factors can change simultaneously. To overcome this difficulty, field data on population responses and environmental conditions often need to be obtained for a long time series so that very different combinations of environmental

factors are sampled. On the other hand, if experiments can be conducted which vary environmental factors independently so that a variety of combinations can be examined, then population responses can be compared with environmental factors more efficiently.

The difficult nature of sampling a sufficient range of environmental conditions in the field for correlation with brine shrimp population responses was evident in 1997, when brine shrimp stocks dramatically diminished (Stephens 1997*b*). This was particularly due to the poor transition of a very abundant supply of nauplii and juvenile life stages to the adult stage (Belovsky and Mellison 1997; Stephens 1997*b*). At this time, water temperature and salinity were declining. In addition, phytoplankton numbers declined and their relative composition dramatically changed; the chlorophyte *Dunaliella viridis* which comprised >80% dropped to < 20%, and centric diatoms correspondingly increased (Stephens 1997*a*, 1999). With so many factors changing simultaneously, different groups of individuals attributed the brine shrimp decline to one or more of several factors: water temperature, salinity, food availability, the high density of nauplii and juvenile shrimp, and overharvesting.

To overcome these problems, we initiated a set of experiments that varied water temperature, salinity and food availability to address their influence on brine shrimp population responses (survival rate, transition between life stages, reproductive rate, and reproductive allocation between ovoviviparity and oviparity) at different life stages (cyst, nauplii, juvenile and adult).

Methods:

The brine shrimp survival-reproduction studies rely upon replicated populations composed of individuals of a single developmental-category (nauplii: $\leq$ 5 mm, juvenile: > 5 mm and $\leq$ 9 mm, or adult: > 9 mm) (Heath 1924). Shrimp for the experiments were reared from cysts that were commercially obtained from the Great Salt Lake or from cysts/nauplii produced in the experiments. Experimental individuals reared from cysts were maintained in aquaria containing 40 l of the same hypersaline aqueous solution that was used in the experiment. Hypersaline solutions were made by dissolving Instant Ocean (35 g/l) in distilled water and increasing the salinity to the desired level by dissolving additional water softener salt. Because the water softener salt is obtained from the Great Salt Lake, the solution must be filtered to remove brine shrimp cysts. Aquaria were continuously aerated and the brine shrimp were fed a solution of dried baker's yeast every day (100 mg/aquaria). Juvenile-stage males and females were separated into different aquaria as appendage differences appeared (Halfer-Cervini et al. 1968).

Each experimental population was held in a 500 ml Nalgene bottle containing 400 ml of hypersaline solution that was continuously aerated. Once a week, half of the solution in each bottle was replaced with fresh hypersaline solution and sediments were removed. Every week, the bottles' walls were scrubbed with a sponge to remove deposits, prevent lethal pH levels from developing due to bacterial growth and limit the potential for algae and bacteria to serve as additional food.

Experimental populations for a particular developmental stage and combination of environmental conditions were maintained in an environmental chamber at 12h light: 12h dark. Because of the number of experimental populations (>1900), all experimental

combinations could not be conducted simultaneously due to space limits, and, more importantly, due to time limits for maintaining and censusing populations. Therefore, for expedience a single developmental stage/temperature/salinity combination was examined at a time (30 – 60 populations). The populations (bottles) were held in rectangular trays, treatments were randomly assigned to bottles, and trays were rotated 90° every 2 days to minimize any potential spatial effects in the environmental chamber (e.g., position relative to lights and fans).

Each population of a developmental-category was maintained at a constant density (20 individuals/400 ml of hypersaline solution), one of 5 - 6 food levels (see below), one of four water temperatures (10, 15, 20 or 28°C) and one of three salinity levels (45, 90 or 120 ppt). Food levels varied between the experiments conducted with different life stages, because the higher food levels for adults could not be cleared by nauplii and juveniles, which led to lethal pH levels. Adults received one of six food levels (0, 1, 2.5, 5, 10 or 15 mg of yeast/2 days or 0, 0.5, 1.25, 2.5, 5 or 7.5 ml of yeast suspension/2 days). The 0 level of food was included to assess the availability of phytoplankton and bacteria in the hypersaline water holding the population and was not examined at all temperature/salinity levels. Nauplii and juveniles received five food levels (1, 2.5, 5, 7.5, or 10 mg of yeast/2 days or 0.5, 1.25, 2.5, 3.75 or 5 ml of yeast suspension/2 days).

For each developmental stage, a factorial design was obtained for all temperature, salinity and food levels (excluding the 0 level for adults). Each combination of temperature/salinity/food levels was represented by 5 replicate populations of cysts,

nauplii, or juveniles and 10 replicates for adults. The maintenance and censusing of populations varied with the developmental stage.

Adults – Experimental populations were initiated with 10 individuals of each sex. Females had been kept isolated from males prior to the experiment so that all reproduction could be attributed to experimental conditions. Each population (bottle) was censused every 3 days for 4 weeks. At each census, dead adult males and females were replaced to maintain a constant population size. Nauplii and cysts were counted and removed.

Nauplii – Experimental populations were initiated with 20 individuals without regard to sex. Two types of experiments were conducted with nauplii:

1) nauplii from the adult experiments were used to stock populations at the same temperature/salinity/food as the adult experiment;
2) nauplii from commercially obtained cysts (see above) were used to stock populations for the range of temperature/salinity/food combinations.

Nauplii produced in the adult experiment were from ovoviviparity, rather than oviparity (cysts), because cysts did not have time to hatch before they were removed (3 days). Comparing results between the two nauplii sources at the same temperature/salinity/food levels provides some indication of potential demographic differences produced by each mode of reproduction. To maintain a constant density, nauplii were counted every 3 days for 4 weeks. Individuals that had become juveniles were removed. Dead nauplii and removed juveniles were replaced with nauplii from the same adult temperature/salinity/food combinations in experiment #1 or the same temperature/salinity in experiment #2.

Juveniles – Experimental populations were initiated with 20 individuals without regard to sex. All juveniles were reared from commercially obtained cysts (see above) from the Great Salt Lake. Juveniles were counted every 3 days for 4 weeks. Individuals that had become adults were removed and sexed. Dead juveniles and removed adults were replaced with juveniles raised under the same temperature/salinity combinations to maintain density.

Cysts – Cysts from adult populations for each temperature/salinity/food combination were pooled, allowed to dry and were frozen (-10°C) for 1 month. Five replicates of 50 cysts were placed in hypersaline solution (90 ppt) at 20°C and emerging nauplii were removed twice a day. After a week, the cysts were dried and frozen again for a month, when hatching was tried again. This was repeated a third time.

Census data were used to compute survival and reproductive rates, transition probabilities (e.g., probability of a nauplia becoming an adult), expected lifetime reproduction for a female and cyst hatchability for different temperature/salinity/food combinations. Observations were analyzed using ANOVA after appropriate transformations to obtain normality, e.g., arcsine transform for proportions. Loss of populations or insufficient numbers of nauplii or cysts from particular temperature/salinity/food combinations sometimes provided fewer replicate populations, and unbalanced ANOVAs or an incomplete factorial design had to be employed. All statistics were conducted using SYSTAT (version 10).

Results:

Adults – Survival rate (probability of surviving the experiment) was statistically significant for temperature, salinity, food availability, all 2-way interactions and the 3-way interaction (Table 1), explaining 87% of the observed variation in survival. Survival declined with increasing temperature (Fig. 1A.i). Survival was greatest at 90 ppt salinity (Fig. 1A.ii), except at 10°C, when it declined with increasing salinity. Survival asymptotically increased with food abundance (Fig. 1A.iii). The greatest survival was observed at 10°C and 45 ppt. Male and female survival exhibited similar patterns with temperature, salinity and food, but males generally survived relatively better than females at all conditions ($df = 1$, $F = 58.74$, $P < 0.0000001$), especially at lower food levels, 45 ppt salinity and 10°C.

Expected lifetime reproduction per female (total number of nauplii and cysts produced in a bottle/[number of females replaced + initial number of females]) was statistically significant for temperature, salinity, food availability, all 2-way interactions and the 3-way interaction (Table 2), explaining 79% of the observed variability in reproduction. Reproduction was always greatest at 20°C (Fig. 2A). Reproduction was greatest at 90 ppt salinity (Fig. 2B), except at 10°C, when it declined with increasing salinity and at the lowest food levels when it declined with salinity. Reproduction increased with all but the highest food level (Fig. 2C). The greatest reproduction was observed at 20°C, 90 ppt salinity and a food level of 7.5 ml/2 days.

Brine shrimp reproduce by oviparity (dormant cysts) and by ovoviviparity (eggs that hatch immediately in the brood sac so that nauplii are released). The proportion of reproduction due to oviparity versus ovoviviparity was affected by temperature and food

availability, and their interaction with salinity (Table 3), explaining 50% of the observed variability. The least reproduction by oviparity occurred at 15°C (Fig. 2A.i). At 10° C and 15°C, oviparity decreased with salinity, but at higher temperatures it increased with salinity. Oviparity always declined as food availability increased (Fig. 2B.iii), especially at 15°C. The least oviparity occurred at the highest food levels, 15°C and 120 ppt salinity.

Nauplii – Survival rate (probability of surviving the experiment) of nauplii from the adult experiments or reared from commercially obtained cysts did not differ ($F = 0.002$; $df = 1, 693$; $P < 0.97$), so the data were pooled. Survival rate was statistically significant for temperature, salinity, food availability, all 2-way interactions and the 3-way interaction (Table 4), explaining 53% of the observed variability in survival (32% for nauplii from adult experiments and 78% for nauplii reared from cysts). Survival declined with increasing temperature (Fig. 1B.i). Survival was lowest at 120 ppt salinity (Fig. 1B.ii), with nauplii surviving the best at 45 ppt salinity at all but 20°C when survival was substantially greater at 90 ppt salinity. Survival increased with food abundance (Fig. 1B.iii). Greatest survival was observed at 10°C and 90 ppt.

The probability of transition from a nauplia to a juvenile [number becoming juveniles/(number replaced + initial number)] for individuals produced from commercial cysts (0.10 ± 0.13) was statistically different from those obtained from the adult experiments (0.06 ± 0.08) ($F = 39.96$; $df = 1, 519$; $P < 0.0000001$). Temperature, salinity, food availability and some of the interaction terms were significant (Table 5), explaining 66% of the observed variability (77% for nauplii from cysts and 37% for nauplii from adult experiments). Both sources of nauplii responded similarly to

experimental conditions. Transition was always greatest at 20°C (Fig. 3A.i). Transition was lowest at 120 ppt salinity (Fig. 3A.ii) and tended to decline as salinity increased, except at 20°C when the greatest transition was at 90 ppt salinity. While the nauplii from the adult experiments did not respond as strongly to food availability as did nauplii from commercial cysts, transition always increased with food availability (Fig. 3A.iii). The greatest probability of transition occurred at the highest food levels at 20°C and 90 ppt salinity.

Juveniles – Survival rate (probability of surviving the experiment) was statistically significant for temperature, salinity, food availability, all 2-way interactions and the 3-way interaction (Table 6), explaining 91% of the observed variability in survival. Survival declined at the highest temperature (Fig. 1C.i). Survival was greatest at 90 ppt salinity (Fig. 1C.ii). Survival increased asymptotically with food abundance (Fig. 1C.iii). The probability of transition from a juvenile to an adult [number becoming adults/(number replaced + initial number)] was statistically significant for temperature, salinity, and food (Table 7), explaining 89% of the observed variability. Transition was slightly greater at 20°C than 15°C, but declined dramatically at 10°C and 28°C (Fig. 3B.i). Transition was greatest at 90 ppt salinity (Fig. 3B.ii). Transition increased asymptotically with food availability (Fig. 3B.iii).

Cysts – Proportion of cysts hatching that were produced in the adult experiments varied only with salinity (Table 8) and then very weakly, explaining only 4% of the observed variability. However, hatchability did not vary much between temperature/salinity/food combinations, averaging 34%.

Discussion:

Temperature explained the greatest amount of variation in expected lifetime reproductive output per adult female, with salinity second and food third in importance. Salinity explained the greatest variation in survival for adults and juveniles and transition between the juvenile and adult stages, with temperature second and food third. For nauplii, survival and transition to the juvenile stage were similarly affected by temperature and salinity, with food less important. Juveniles and adults were much more affected by salinity and temperature than nauplii, and all developmental stages were similarly affected by food abundance. Overall, juveniles were most sensitive to environmental factors, especially salinity and have demonstrated the greatest variability in survival and transition to the adult stage in the Great Salt Lake (Belovsky and Mellison 1997, 1998; Stephens 1997*a*, 1997*b*, 1999). However, the rankings of importance among the environmental factors in the experiments do not reflect which factor is most important for brine shrimp in the Great Salt Lake (e.g., food abundance generally could be very low in the lake), but indicates the brine shrimps' degree of sensitivity to changes in these factors.

Temperature – Survival for all of the developmental stages declined as temperature increased from 10 – 28°C. This is most likely due to reduced metabolic demands for the brine shrimp at lower temperatures, because survival at these low temperatures also increased with food availability. Unlike survival, expected lifetime reproduction per adult female was greatest at 20°C, which indicates that reproductive allocation requires higher water temperatures and this creates a trade-off between survival and reproduction. The same pattern also is observed for the probability of

transition from the nauplii to juvenile stage and from the juvenile to adult stage, with the greatest probability of transition occurring at 20°C. Therefore, a general trade-off in temperature response exists for brine shrimp between their survival and ability to allocate resources to growth and reproduction. Several populations of each developmental stage were examined at 5°C, and while individuals survived at levels comparable to 10°C, there was no reproduction among adults and no transition between developmental stages for nauplii and juveniles (unpubl. data).

Water temperatures in the Great Salt Lake are generally near 20°C in the summer and often approach 30°C in the late summer (Whelan 1973; Butts 1977), because of its shallowness and the high solar radiation. Temperatures generally fall below 10°C by November and do not exceed this level until April (Wurtsbaugh and Berry 1990), the period when brine shrimp either disappear from the lake or are at very low densities.

Salinity – For all developmental stages, survival rate was greatest at salinities between 45 and 90 ppt, as was the probability of transition to the next developmental stage and expected lifetime reproductive output for an adult female. Therefore, there was no apparent trade-off response for salinity between survival and growth/reproduction, as was observed for temperature. Many long-time brine shrimp harvesters claim that Great Salt Lake brine shrimp do better at salinities of 120 – 150 ppt, and recent reduced harvests were due to declining salinities in the south arm of the Great Salt Lake (60 – 90 ppt). While some research findings with *A. franciscana* and *monica* suggest a higher optimal salinity of 120 ppt (Wear and Haslett 1985; Lenz unpublished manuscript), other studies provide similar results to our findings (Dana and Lenz 1986; Dana et al. 1993).

Food – For all developmental stages, survival increased linearly or asymptotically with food availability, as did reproduction and transition probabilities between developmental stages. Phytoplankton availability in the Great Salt Lake has varied dramatically in recent years (Felix and Rushforth 1979; Rushforth and Felix 1982; Stephens 1997*a*, 1997*b*, 1999). By maintaining a constant density and varying food availability between treatments, the experiment examines exploitative intraspecific competition, because food abundance divided by shrimp density (per capita food availability) varies in the experiments. Therefore, different densities and food availabilities should respond similarly based on the per capita food availabilities examined here; this seems to be the case from a small number of additional experimental populations examined that had a constant food availability, but brine shrimp density was varied (unpubl. data).

Nauplii source – Nauplii reared from commercially harvested cysts and those obtained from the adult experiment did not differ in survival, but did differ in transition probabilities with nauplii reared from commercial cysts more likely to become juveniles. The nauplii from the adult experiments were produced by ovoviviparity, which may be nutritionally less costly to the mother (Browne 1980) and may mean that these young start life with less nutritional reserve. Greater nutritional reserves will reduce the time it takes to grow to the juvenile stage, which may make this transition more likely to occur before the nauplii die, regardless of the source of mortality. Furthermore, since the brine shrimp companies screen cysts for better hatching before packaging them for sale, it is possible that these cysts have even greater nutritional reserves. The importance of the nutritional reserve in the cyst is supported by the observation that nauplii from the adult

experiments (oviparity) could not approach the higher probabilities of transition for cyst-reared nauplii, even at the highest food levels. However, survival may not differ between these sources of nauplii, because far less nutrition is needed for maintenance than for growth.

Ovoviviparity versus oviparity – Adult females changed their reproductive mode with salinity and food abundance. Greater oviparity is expected at low water temperatures as a response to the onset of winter. We suggest that at higher temperatures, greater oviparity is a response to lower survival as temperature increases. Likewise, greater oviparity at low food abundances might be a response to decreasing survival. Therefore, while the increase in cyst production with cooler water temperatures is a regular response to the inevitable onset of winter, greater cyst production in years that are very warm and during which the phytoplankton are overgrazed is a response that will vary among years depending on annual conditions. Similar responses to food availability are reported in the literature (Amat et al. 1987; Berthelemy-Okazaki and Hedgecock 1987), but the response to temperature has not always been observed (Berthelemy-Okazaki and Hedgecock 1987; Barata et al. 1996).

Cyst hatchability – There were no strong environmental influences on cyst hatchability. This might be expected because the cyst is a "hedge" against an upcoming hostile environment and must have high survival. In this case, females may invest a more constant amount of resources per cyst and simply produce more or less cysts depending on resource availability.

Lifetime reproductive output – All of the temperature/salinity/food combinations can be examined to predict the expected reproductive output of a female at hatching

(probability of a nauplia becoming a juvenile X probability of a juvenile becoming an adult X the expected lifetime reproductive output of an adult) (Fig. 4). When all of these values are combined, the reproductive performance (fitness) was more than an order of magnitude greater at 20°C, 90 ppt salinity and at the highest food availabilities. Interestingly, the summers of 2000 - 2002 produced conditions near this combination of values for an extended period (July – September: Belovsky and Larson 2001) in the Great Salt Lake and these were years of very large reproductive output, especially of cysts.

Conclusion:

A number of studies have examined the responses of North American *Artemia* spp. to different temperature, salinity and food levels as single factors or in combination (e.g., Wear and Haslett 1985; Dana and Lenz 1986; Dana et al. 1993; Gliwicz et al. 1995; Barata et al. 1996; Lenz unpublished manuscript). None of these studies have examined the wide range of all three factors simultaneously that we have. Furthermore, our experimental design examines each developmental stage in isolation, examines the source of the individuals (oviparity vs. ovoviviparity), and maintains constant relationships between food and density. In our opinion, this provides a better ability to decipher the role played by each environmental factor.

Many of the environmental influences on demography observed in our experiments are counter to perceptions based on casual observation of the brine shrimp population in the Great Salt Lake and associations attributed to temperature and salinity. This should not be surprising, because the experiment varies each factor independently of other factors. However, in the lake, environmental factors often vary together. For

example, high salinities are often associated with high water temperatures, because salinity in part increases with evaporation, which depends on increased air temperature and solar radiation that also raise water temperature.

The simultaneous variation of environmental factors in the field is most troublesome in assessing the effect of food abundance on the brine shrimp in the Great Salt Lake (Cuellar 1990). We are conducting similar experiments that vary temperature/salinity/nutrient abundance combinations on assemblages and monocultures of phytoplankton species from the Great Salt Lake. Total phytoplankton abundance and the relative abundance of preferred species (*Dunaliella viridis* and *salina*) tend to increase with salinity and to decrease with temperature (Larson and Belovsky, in prep.). Therefore, one could attribute variation in the brine shrimp population to direct effects of temperature and salinity on the shrimp, when in fact it is variation in phytoplankton abundance and species composition that is most important. This may explain why higher salinity (120 ppt) is sometimes thought to be best for the brine shrimp (Wear and Haslett 1985; Lenz unpublished manuscript). We are also in the process of calibrating demographic responses reported here with yeast as the food to monocultures of different Great Salt Lake phytoplankton as the food.

Brine shrimp are the dominant consumer in the Great Salt Lake and provide an economically important fishery. Within and among year variability in water temperature, salinity and food availability in the Great Salt Lake is great and strongly influences brine shrimp numbers and productivity. These environmental factors are also being modified by human activity (e.g., water diversion, urbanization, agriculture, mining and wetland destruction). Therefore, our experimental results should provide a better understanding

of this ecologically important species in the simple ecosystem of the Great Salt Lake and insights for the better management of the Great Salt Lake ecosystem and its brine shrimp fishery.

Table 1. The balanced ANOVA results for adult survival.

Treatment:	**df**	**F**	**P**
Temperature	3	293.91	0.0000001
Salinity	2	758.84	0.0000001
Food	4	23.30	0.0000001
Temperature X Salinity	6	129.58	0.0000001
Temperature X Food	12	5.14	0.0000001
Salinity X Food	8	9.93	0.0000001
Temperature X Salinity X Food	24	4.27	0.0000001
Error	540		

Table 2. The balanced ANOVA results for expected lifetime reproduction per female.

Treatment:	**df**	**F**	**P**
Temperature	3	314.59	0.0000001
Salinity	2	147.76	0.0000001
Food	4	36.37	0.0000001
Temperature X Salinity	6	44.96	0.0000001
Temperature X Food	12	3.89	0.0000001
Salinity X Food	8	27.77	0.0000001
Temperature X Salinity X Food	24	6.06	0.0000001
Error	540		

Table 3. The balanced ANOVA results for proportion of reproduction by oviparity.

Treatment:	**df**	**F**	**P**
Temperature	3	88.20	0.0000001
Salinity	2	0.10	0.91
Food	4	2.56	0.038
Temperature X Salinity	6	19.57	0.0000001
Temperature X Food	12	2.40	0.005
Salinity X Food	8	4.58	0.00002
Temperature X Salinity X Food	24	3.22	0.0000001
Error	540		

Table 4. The unbalanced ANOVA results for nauplii survival rate, when individuals hatched from cysts and from adult experiments are pooled.

Treatment:	**df**	**F**	**P**
Temperature	3	63.01	0.0000001
Salinity	2	71.92	0.0000001
Food	4	22.52	0.0000001
Temperature X Salinity	6	34.12	0.0000001
Temperature X Food	12	3.02	0.0000001
Salinity X Food	8	4.04	0.0000001
Temperature X Salinity X Food	24	1.90	0.006
Error	639		

Table 5. The unbalanced ANOVA results for the probability of a nauplia's transition to a juvenile, when individuals were hatched from cysts.

Treatment:	**df**	**F**	**P**
Temperature	3	42.07	0.0000001
Salinity	2	42.28	0.0000001
Food	4	20.59	0.0000001
Temperature X Salinity	6	20.34	0.0000001
Temperature X Food	12	0.61	0.83
Salinity X Food	8	2.64	0.007
Temperature X Salinity X Food	24	1.19	0.24
Error	639		

Table 6. The incomplete factorial, unbalanced ANOVA results for juvenile survival rate.

Treatment:	**df**	**F**	**P**
Temperature	3	31.12	0.0000001
Salinity	2	1071.76	0.0000001
Food	4	8.18	0.0000001
Error	240		

Table 7. The incomplete factorial, unbalanced ANOVA results for the probability of a juvenile's transition to an adult.

Treatment:	**df**	**F**	**P**
Temperature	3	13.40	0.0000001
Salinity	2	374.32	0.0000001
Food	4	24.72	0.0000001
Error	240		

Table 8. The incomplete factorial, unbalanced ANOVA results for cyst hatchability.

Treatment:	**df**	**F**	**P**
Temperature	3	1.54	0.2
Salinity	1	4.49	0.035
Food	4	0.98	0.42
Error	307		

Figures:

Figure 1. ANOVA least square means for survival rates (probability of surviving the experiment) for adults (A), nauplii (B) and juveniles (C) are plotted with treatment levels for temperature (i), salinity (ii) and food abundance (iii). The bars represent standard errors.

Figure 2. ANOVA least square means for A) Expected lifetime reproduction per adult female [total number of nauplii and cysts produced during the experiment/(number of females replaced + initial number of females)] and B) the proportion of reproductive output that is due to oviparity (cysts) are plotted with treatment levels for temperature (i), salinity (ii) and food abundance (iii). The bars represent standard errors.

Figure 3. ANOVA least square means for the probability of transition (number attaining next developmental stage/[number replaced + initial number]) between the stages of A) nauplii and juveniles and B) juveniles and adults are plotted with treatment levels for temperature (i), salinity (ii) and food abundance (iii). The bars represent standard errors.

Figure 4. Lifetime reproductive output (probability of a nauplia becoming a juvenile X probability of a juvenile becoming an adult X the expected lifetime reproductive output of an adult female) is computed for the different temperature/salinity/food levels. The response surfaces were plotted using a distance weighted least squares (DWLS) smoothing function (SYSTAT: version 10).

Figure 1.

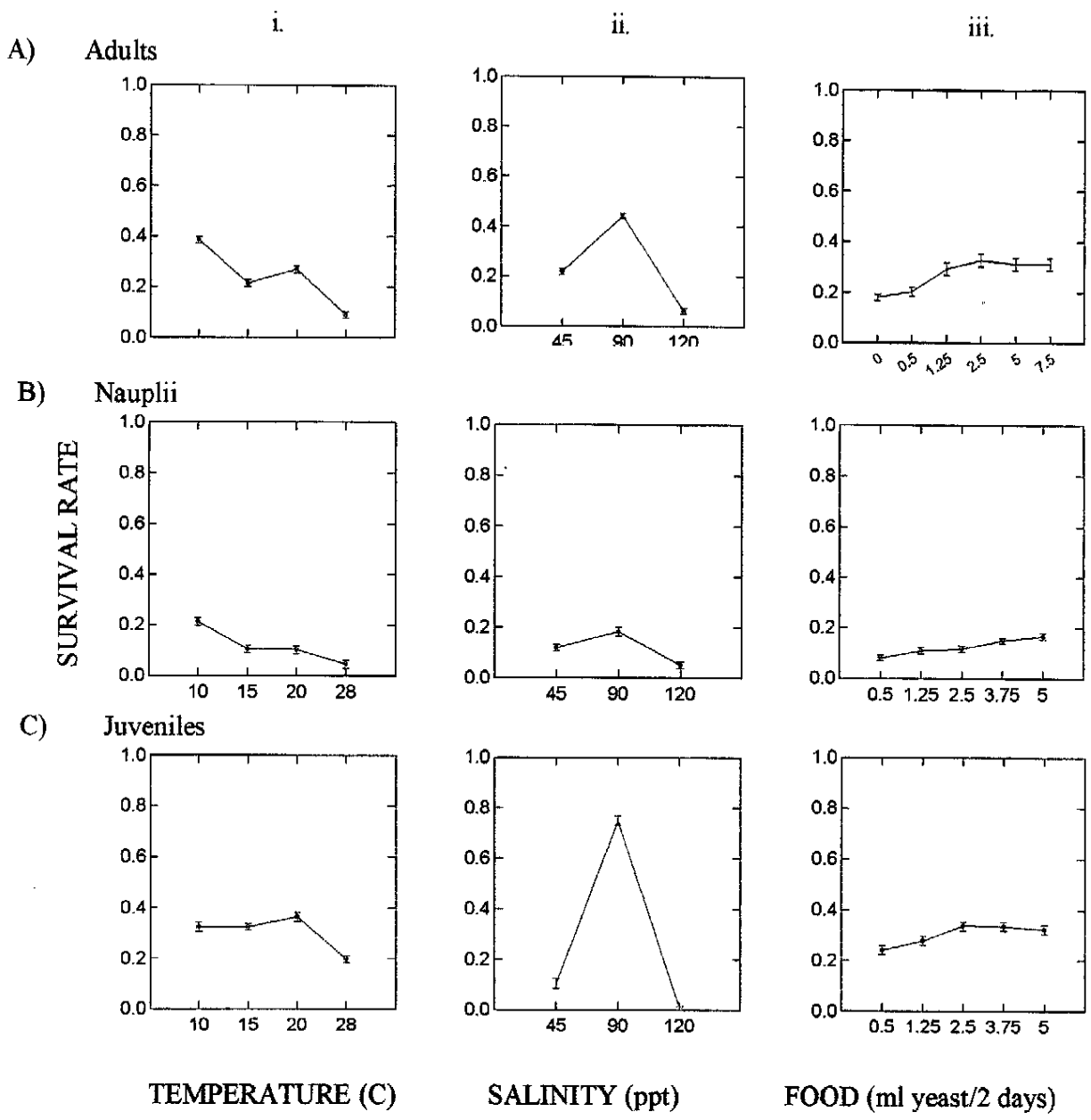

i.
ii.
iii.
A) Adults
B) Nauplii
C) Juveniles
SURVIVAL RATE
1.0
0.8
0.6
0.4
0.2
0.0
10 15 20 28
45 90 120
0 0.5 1.25 2.5 5 7.5
0.5 1.25 2.5 3.75 5
TEMPERATURE (C)
SALINITY (ppt)
FOOD (ml yeast/2 days)

Figure 2.

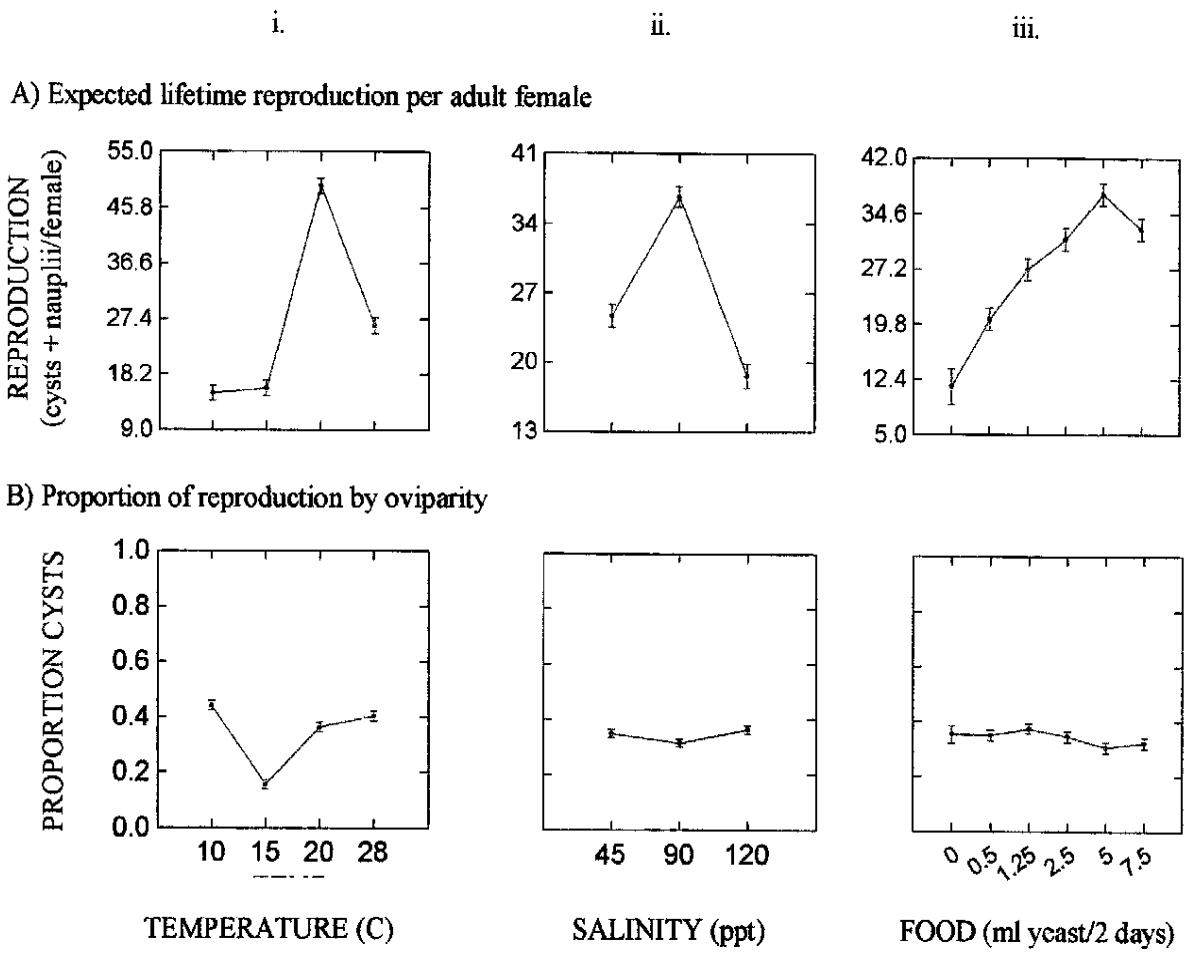

i.
ii.
iii.
A) Expected lifetime reproduction per adult female
REPRODUCTION (cysts + nauplii/female)
55.0
45.8
36.6
27.4
18.2
9.0
41
34
27
20
13
42.0
34.6
27.2
19.8
12.4
5.0
B) Proportion of reproduction by oviparity
PROPORTION CYSTS
1.0
0.8
0.6
0.4
0.2
0.0
10 15 20 28
45 90 120
0 0.5 1.25 2.5 5 7.5
TEMPERATURE (C)
SALINITY (ppt)
FOOD (ml yeast/2 days)

Figure 3.

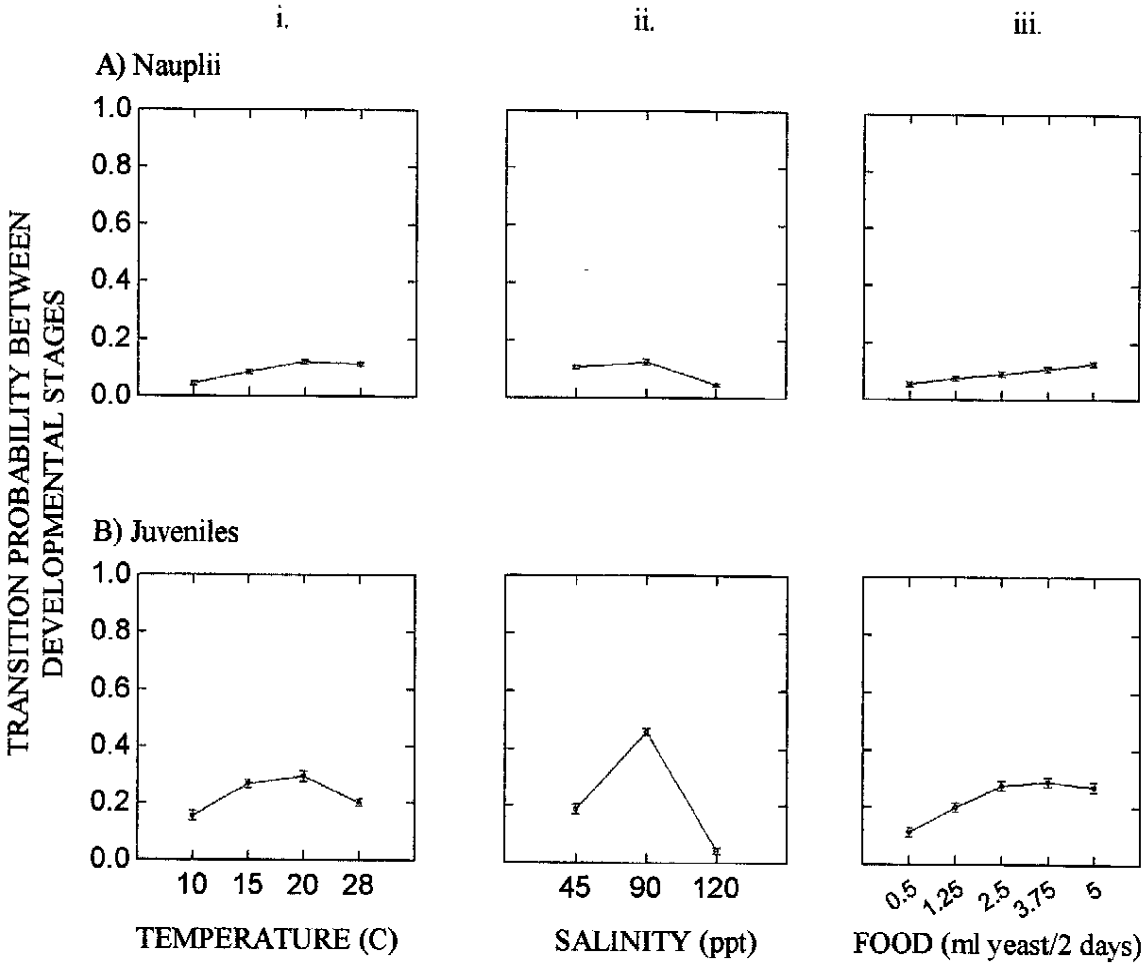
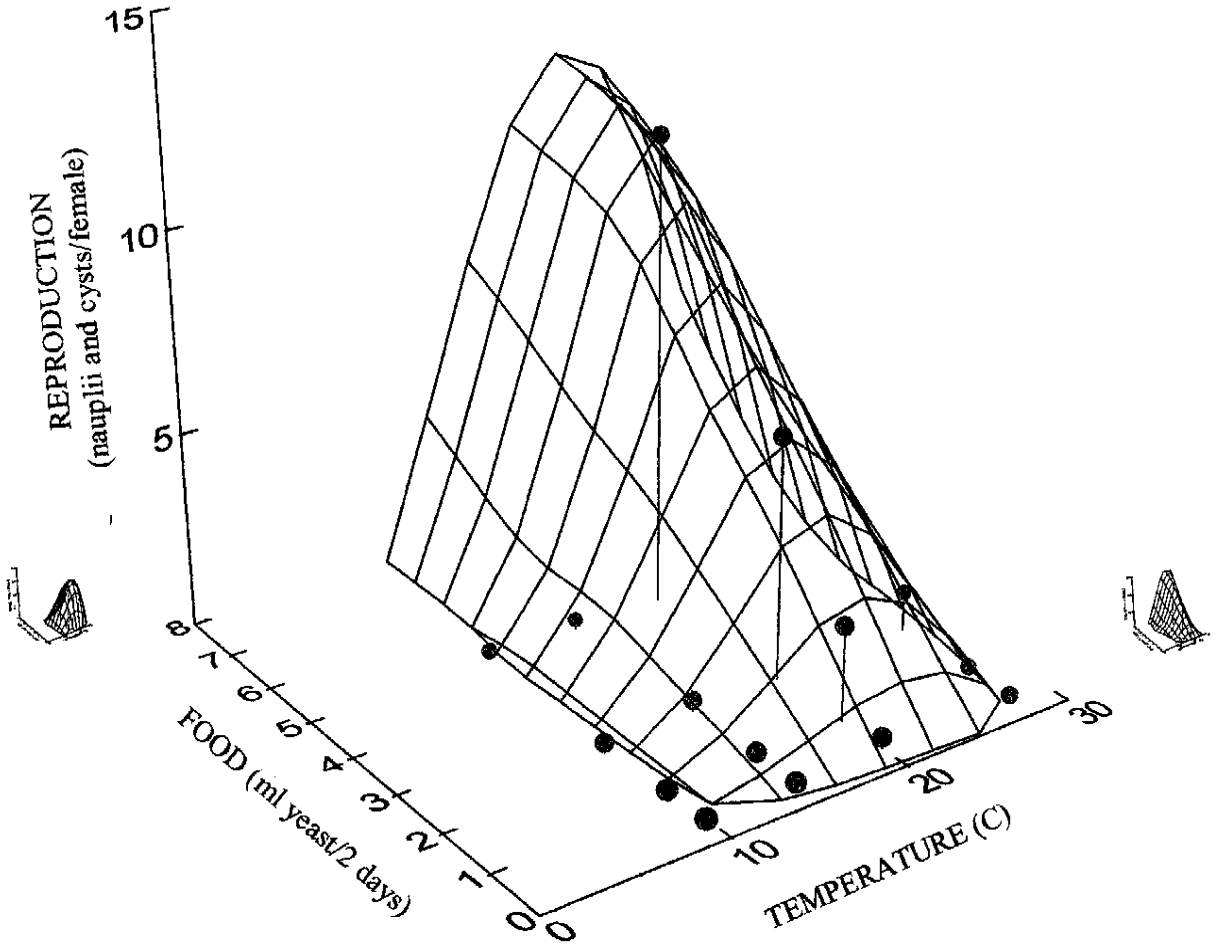

i.
ii.
iii.
A) Nauplii
B) Juveniles
TRANSITION PROBABILITY BETWEEN DEVELOPMENTAL STAGES
1.0
0.8
0.6
0.4
0.2
0.0
10 15 20 28
TEMPERATURE (C)
45 90 120
SALINITY (ppt)
0.5 1.25 2.5 3.75 5
FOOD (ml yeast/2 days)

Figure 4.



45ppt 90ppt 120ppt

OVERWINTER CYST SURVIVAL:

Species that produce a cryptobiotic life-stage to survive periodic harsh environments raise interesting evolutionary questions, because these stages exhibit unique physiological and developmental traits and are produced with the onset of specific environmental cues. It is often assumed that an individual of a cryptobiotic life-stage will either be viable or not (e.g., can hatch or not), and if the individual is viable (i.e., can hatch), then it will survive the harsh conditions for which it has been produced as long as these conditions do not persist too long (Halvorson 1961; Levins 1969; Hairston 1998). Therefore, seldom is information available on how well the cryptobiotic life-stage survives harsh environmental conditions, which would enable an assessment of the life-stage's ability to allow a population to recover when conditions once again become favorable for growth and reproduction.

The diapausing cysts of brine shrimp (Branchiopoda, Anostraca) are an extreme cryptobiotic life-stage, and some species of brine shrimp, like *Artemia franciscana*, that can produce broods of either live births (ovoviviparity) or cysts (oviparity) within a lifespan are unusual (Lavens and Sorgeloos 1987). Most of the interest in diapausing cysts has focused on how long cysts remain viable in dried lake beds (Lavens and Sorgeloos 1987). However, even the short-term viability of cysts can have consequences for some species, such as *Artemia franciscana* in the Great Salt Lake (Utah, USA), which annually survives winter as cysts to restart the spring population. This life history strategy has important management implications because cysts are commercially valuable and intensely harvested.

Measuring cyst survival is difficult in the field. One can measure the viability of cysts as they are produced by females, but later in the lake, it becomes problematic to

separate cysts between ones produced in the current year and older cysts and to account for the current year's cysts that are no longer present. Consequently, overwinter survival of *A. franciscana* cysts in the Great Salt Lake has not been measured, and estimates of cyst survival from the literature range from 10-90% (Lenz, unpublished report). In this study, we measured cyst survival over the winter in the Great Salt Lake using cysts in mesh bags that were placed in the lake and on the beaches.

Study Site:

The Great Salt Lake is the fourth largest hypersaline terminal lake in the world. In 1963, at its lowest elevation (1278 m), it covered 2470 km^2 and had a salinity of 280 ppt. In 1987, at its highest elevation (1292 m), it covered 5490 km^2 and had a salinity of 50 ppt. The lake is composed of two arms that became separated in 1959 by a railroad causeway through which some exchange occurs via two culverts, a breach and permeability of the causeway itself. The north arm has a salinity that is near saturation so that bacteria and cyanobacteria comprise most of the biota. The south arm has a lower salinity, because 95% of the lake's surface inflows are located here, and contains a much more diverse biota, including *A. franciscana*. Because it is a terminal lake, Great Salt Lake is eutrophic. Gwynn (2002) provides a detailed description of the lake's history, natural history and geology.

Methods:

Each year (1998 – 2001) in one week with the onset of cold weather (end of October to mid-December), *A. franciscana* cysts were obtained from the Great Salt Lake

by Utah Division of Wildlife Resources (UDWR) personnel. They collected plankton net samples at 5 different locations in the south arm. The cysts were pooled between locations and empty shells were discarded by flotation in a 50 ppt aqueous solution. These cysts were the stock used to assess overwinter survival. Control values were provided by a sample of these cysts that were hatched (see below) at the start of the experiment and at the end of the experiment (March) after being stored at 0°C in the lab.

Cylinders (3.5 cm X 20 cm) made of 153 μm plankton netting were used to hold cysts to be examined for survival. To construct the cylinders, the netting was folded and a seam was sewn with a sewing machine; this seam was sealed with tent seam-sealer to ensure that sewing needles and nylon thread did not increase mesh size and permit cysts to escape. From pilot studies we found that cysts could not pass through the mesh. Each cylinder was loaded with 200 cysts, and tests of our counts indicated that the actual number varied by $\pm$ 2 cysts. All cylinders containing cysts were kept at 0°C for no more than a week before being placed in the lake.

Before we placed the cysts in the cylinder, a 58 g lead fishing sinker coated with neoprene plastic was attached to each cylinder using a pocket sewn into the base of the cylinder. Then the cylinder, once loaded, was fixed by a plastic sleeve to a float (Fig. 5). The fishing sinker acted as a counter-weight so the cylinder remained suspended below the float and the float did not flip over in the lake. Floats were constructed of square blocks of redwood that were painted with bright yellow marine epoxy paint and sprinkled with silver plastic flakes to increase visibility. Two float sizes were employed: 20 cm X 20 cm square and 31 cm X 31 cm square. All floats were 4 cm thick.

We were interested in whether cyst survival varied between cysts remaining in the lake and those deposited on beaches.

1. To investigate the survival of cysts in the lake, 20 cm X 20 cm floats were anchored with nylon rope and a concrete block in the lake. Five random locations in the south arm near Antelope Island were selected and 5 floats were anchored at each site. We tried to retrieve one float at each location every two weeks, but this was not always possible. In the winter of 1999 - 2000, 10 floats were anchored at each site to allow more frequent sampling.
2. To investigate the beach survival of cysts, two methods were used. In 1998 – 1999, twenty-five 30 cm X 30 cm floats were equipped with small radio-transmitters. These were released at 17 lake sampling sites used by UDWR and 8 other randomly selected locations. Each float equipped with a radio-transmitter was accompanied by four 20 cm X 20 cm floats without radios. The hope was that these floats would stay together and wash up on beaches, providing information on lake-source locations of beach-deposited cysts. We tried to locate floats with a radio-receiver using a boat or walking the beach, but this did not work. We then used an airplane with a radio-receiver to determine a float's general location, travelled by air boat to the location and tried to find it by walking the beach with a radio-receiver. Only 25 floats were recovered (56% of ones equipped with a radio-transmitter and 11% of the accompanying floats). The first floats deposited on the beaches were retrieved 4 weeks after release and then every 2 weeks after that. This approach was too costly in time and money for the low return. Therefore, in

1999 – 2002, floats were anchored like the lake floats at five randomly selected beaches in the south arm. The same number of floats and frequency of recovery were used as in the lake.

Some floats were lost when they broke away from their anchor and some floats were not collected at the designated time due to inclement weather. Floats recovered after March 1 were not used in the experiment, because spring hatching sometimes begins by this date.

On retrieval, the mesh cylinders were removed from the floats and kept in a cooler until they were returned to the lab. The cylinders were stored at 0°C for a predetermined period (30 d). Upon removal from the freezer, the cylinders were examined for holes or enlarged mesh, and these were discarded, because cysts may have escaped or entered the cylinder . The numbers of cysts remaining in a cylinder could not be counted because most cylinders, especially those washing ashore, accumulated large numbers of broken cysts. Also, cylinders had to be washed to remove any cysts on the outside before hatching could be initiated. Hatching was conducted by cutting open the cylinder and placing it in 500 ml of hypersaline water (45 ppt) at 20°C. Nauplii were counted and removed after 24, 48 and 72 h. After 72 h, remaining cysts were frozen again for a month and hatching was tried again. This continued until no more nauplii emerged. Control samples of cysts were hatched in the same manner.

The percentage of cysts hatching from each cylinder was computed; this value relative to the percentage hatching from the year's control cysts measured survival. All percentages (proportions) were arcsine-transformed to assure a normal distribution. Unbalanced ANOVA and ANCOVA were required because sample sizes were not equal

due to lost floats and inability to recover floats at particular times due to inclement weather. All statistics were conducted using SYSTAT (version 10).

Results:

The percentage of cysts hatching (Figure 6A) declined over the winter (i.e., increasing week number); this percentage did not differ between floats from the beach versus in the lake; and the percentage varied significantly among years (Table 9). All further analyses pooled cysts from the beach and lake. Survival (% hatching from float/% hatching in control) declined exponentially with time since floats were released, which provided mortality rates between 7 and 22% per week (Fig. 6B). Hatchability declines were attributed to the lake environment, because control cysts hatched at the time of float release and those hatched after being kept in the lab at 0°C until the end of each year's experiment did not differ ($F = 0.04$; $df = 1,17$; $P < 0.85$).

Discussion:

Experimental results indicate that *A. franciscana* cysts, as a cryptobiotic life-stage, are not completely buffered from harsh winter conditions in Great Salt Lake. The importance of the overwinter decline in survival for the following spring's nauplii emergence is illustrated by comparing three values.

1. The viability (% hatching) of control cysts at the start of winter varied among years and ranged between 30.6 and 78.8% (Fig. 7A: $F = 27.75$; $df = 3, 34$; $P < 0.0001$).

2. The cysts in the floats at the end of the winter just prior to spring emergence of nauplii exhibited a survival (% hatching from float/% hatching in control) that significantly differed among years and ranged between 9.4 and 53.3% (Fig. 7B: $F = 29.06$; $df = 3, 71$; $P < 0.0001$).
3. The result was cyst viability (% hatching) at spring nauplii emergence that significantly differed among years and ranged between 6.9 and 24.1% (Fig. 7C: $F = 14.91$; $df = 3,67$, $P < 0.0001$).

Furthermore, significantly poorer survival occurred in years when cysts entering the winter period had high viability (Table 10); this tended to reduce differences in initial cyst viability.

Low overwinter survival of cysts and variability in survival among years indicates that measures of cyst viability or number of cysts at the onset of winter are not good predictors of nauplii cohort numbers emerging in spring. Low overwinter survival is in part due to embryonic death attributed to the rigors of winter in the Great Salt Lake. However, another factor for low survival is periodic warming during winter, which allows some nauplii to emerge without the potential to survive as water temperatures once again cool. This was particularly important for the low survival observed in 1998 – 1999, when nauplii, but no juveniles, were observed in the lake at every month during winter (P. Birdsey, pers. com., Doyle Stephens, pers. com.). This has also been observed for *A. monica* at Mono Lake, California (Dana et al. 1990).

While brine shrimp cysts resident in dried lake sediments for decades can still hatch (Lavens and Sorgeloos 1987), our mortality rates (7 – 22% per week) indicate that the few shrimp emerging from these sediments are not due to high cyst survival, but from

the large number of cysts deposited. Furthermore, our results indicate that managers must consider how many cysts remain after the commercial harvest to initiate the spring population, because many cysts will fail to survive the winter. It has been suggested by harvesters (pers. comm.) that overharvesting in one year may not be important, because there will be a large reservoir of cysts deposited in years when overharvesting did not occur. However, our results indicate that the viability of any reservoir may rapidly decline in nature.

Conclusion:

While our study indicates that cryptobiotic life-stages experience buffering from harsh environmental conditions which the other life-stages do not (e.g., few, if any, nauplii, juvenile or adult brine shrimp survive winter and they are unable to grow or reproduce), these buffered life-stages can still exhibit high mortality. Furthermore, although the timing of the production of cryptobiotic life-stages has received attention (Hairston and Olds 1984), the timing of emergence from these life-stages to ensure adequate conditions for growth and reproduction may be as or more important. The implications for the annual dynamics of the brine shrimp population in the Great Salt Lake are critical, especially because this population is intensively harvested and some birds rely upon the brine shrimp as a food resource for migration and reproduction.

Table 9. The unbalanced ANCOVA result for cyst hatchability, where week is a covariate.

Treatment:	**df**	**F**	**P**
Treatment	1	1.6	0.21
Year	3	4.65	0.004
Week	1	25.41	0.0001
Error	150		

Table 10. The unbalanced ANCOVA result for overwinter cyst survival, initial cyst viability is a covariate.

Treatment:	**df**	**F**	**P**
Year	2	11.92	0.0001
Initial viability	1	63.17	0.0001
Error	71		

Figure Captions:

Figure 5. The design of the floats used to measure cyst survival in the lake.

Figure 6. A) Viability of cysts (percent hatching $\pm$ 1 se) recovered from floats at different weeks during four winters. 1998-1999 points are red circles; 1999-2000 points are light blue squares; 2000-2001 points are green diamonds; 2001-2002 points are dark blue diamonds. B) Percent survival (100 X % hatching from float/% hatching from control $\pm$ 1 se) measured at each week since the float was released in the lake during four winters. Negative exponential functions fit by nonlinear regression to the average survival at each week during four winters are also presented. Statistics for each year are as follows: 1998-1999 (red circles), $100e^{-0.22t}$, $r^2 = 0.99$, N=5, P<0.01; 1999-2000 (light blue squares), $100e^{-0.07t}$, $r^2 = 0.64$, N=7, P<0.05; 2000-2001 (green diamonds), $100e^{-0.13t}$, $r^2 = 0.89$, N=5, P<0.01; 2001-2002 (dark blue diamonds), $100e^{-0.08t}$, $r^2 = 0.97$, N=5P<0.01, where t is week number.

Figure 7. A) Initial cyst viability (percent hatching $\pm$ 1 se) at start of winter (time of float release - control) in each year. B) Percent cyst survival (100 X % hatching from float/% hatching from control $\pm$ 1 se) for floats collected between February and the first week of March in each year. C) End of winter cyst viability (percent hatching $\pm$ 1 se) for floats collected between February and the first week of March in each year. Sample sizes are presented.

Figure 5.

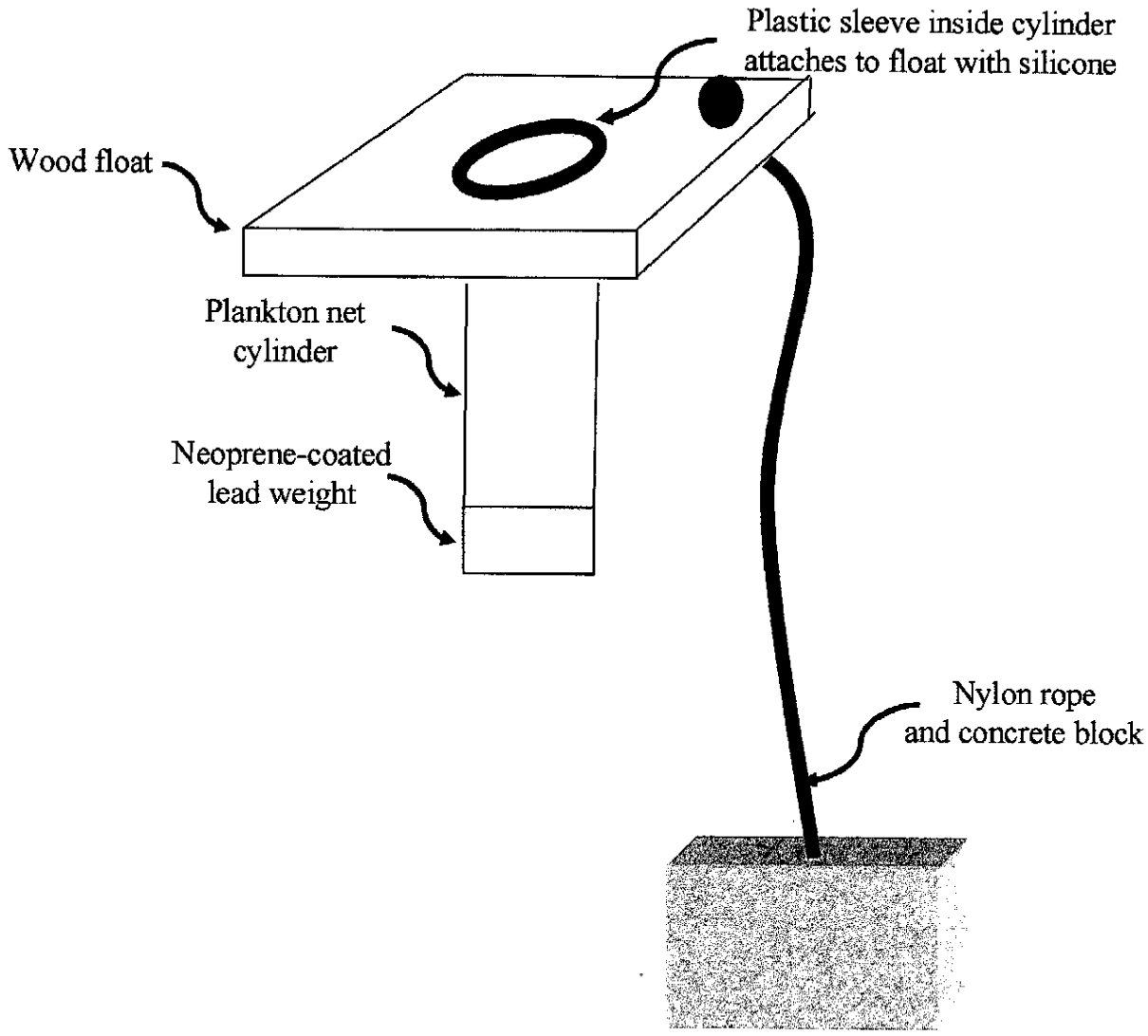

Plastic sleeve inside cylinder
attaches to float with silicone
Wood float
Plankton net
cylinder
Neoprene-coated
lead weight
Nylon rope
and concrete block

Figure 6.

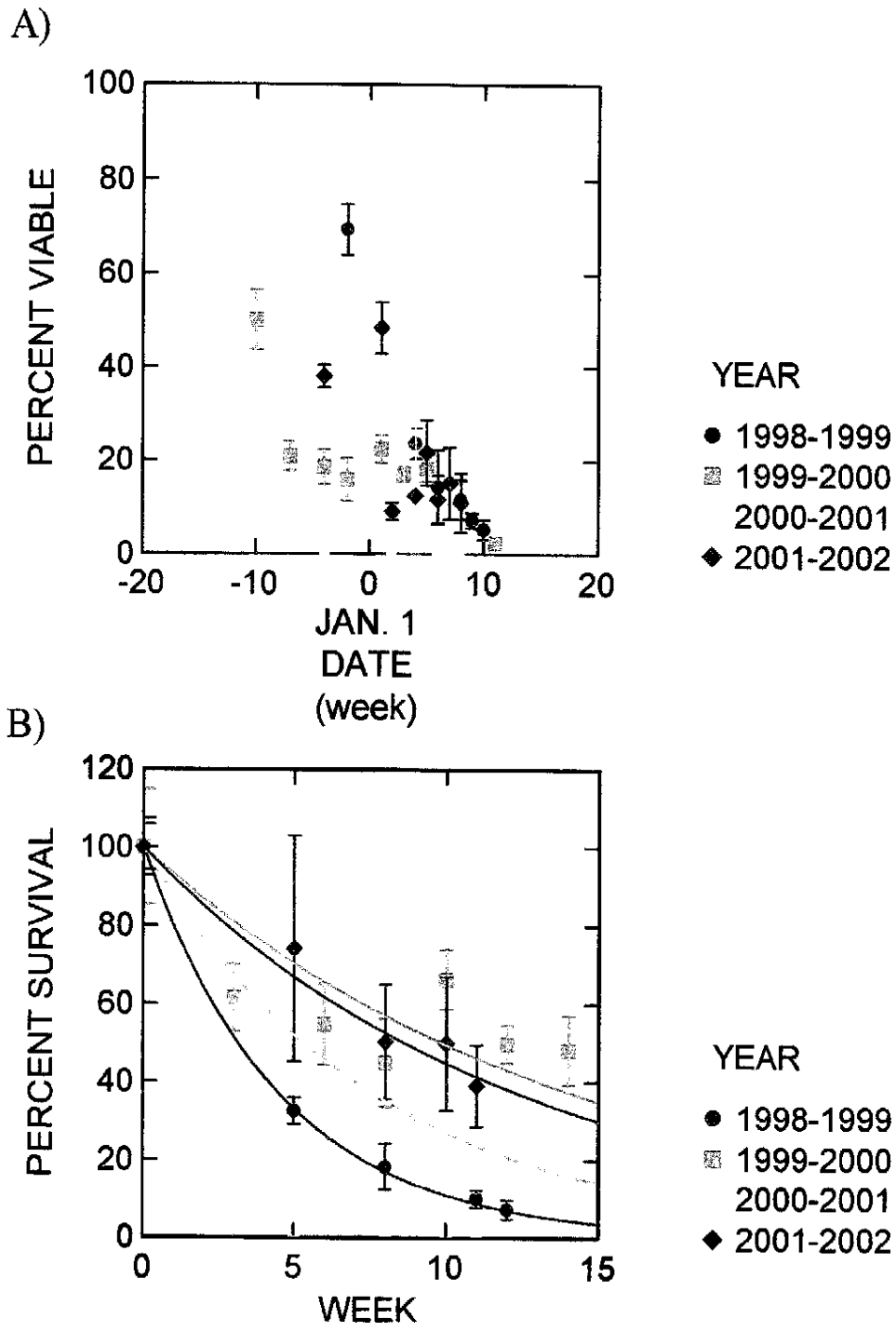
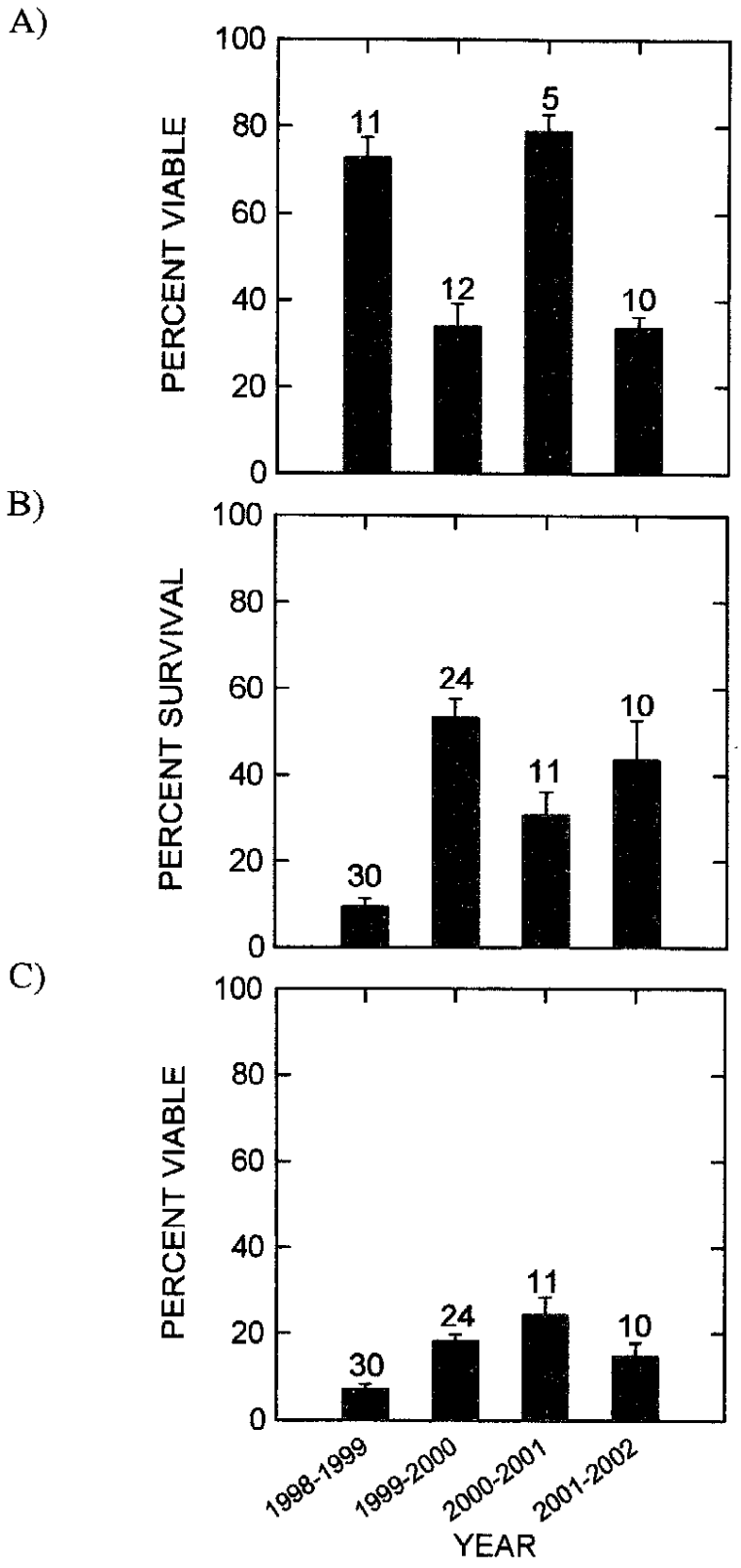

A)
PERCENT VIABLE
100
80
60
40
20
0
-20
-10
0
10
20
JAN. 1
DATE
(week)
YEAR
1998-1999
1999-2000
2000-2001
2001-2002
B)
PERCENT SURVIVAL
120
100
80
60
40
20
0
0
5
10
15
WEEK
YEAR
1998-1999
1999-2000
2000-2001
2001-2002

Figure 7.


A)
PERCENT VIABLE
100
80
60
40
20
0
11
12
5
10
B)
PERCENT SURVIVAL
100
80
60
40
20
0
30
24
11
10
C)
PERCENT VIABLE
100
80
60
40
20
0
30
24
11
10
1998-1999
1999-2000
2000-2001
2001-2002
YEAR

BRINE SHRIMP HARVEST FORECAST FOR 2002:

Belovsky et al. (1999) presented the empirical model and how it is used by UDWR to determine harvest levels in detail. Here we present the Fall, 2001 – Spring, 2002 population data to project the Fall, 2002 population, especially as it relates to potential harvesting levels.

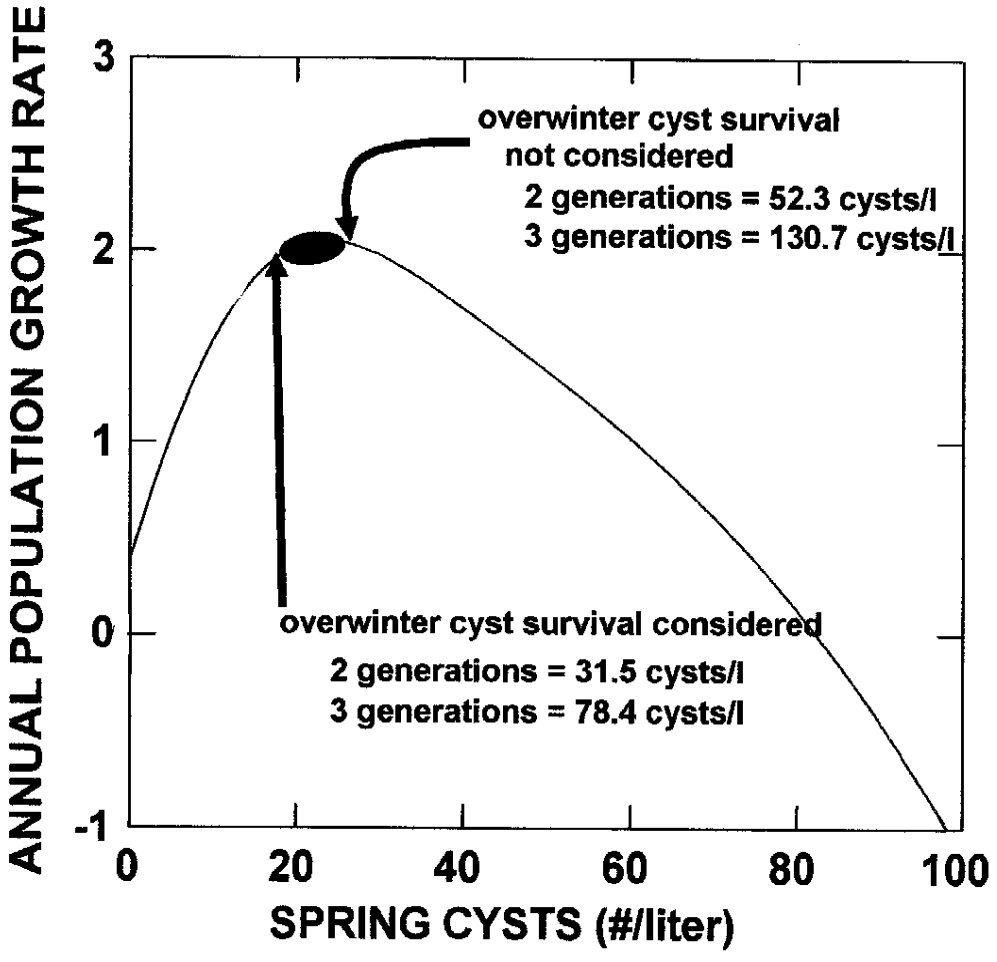
As a reminder, the model was developed using data from 1995 and 1996, two years of abundant cysts during the harvest season, as benchmarks. Abundant cysts allow the brine shrimp population to be initiated in the next year by many hatchlings, which allows the population to grow rapidly to large numbers. An abundant brine shrimp population provides ample food for the avian consumers of brine shrimp and a large production of cysts for the harvesters, two management objectives. *Therefore, a management objective is to provide harvesters repeated years of some of their previous best years for harvesting (1995 and 1996).*

When a curve is fit to the initial and final production densities of cysts for each year by distance weighted least squares (DWLS) techniques (red line, Fig. 8) (Wilkinson 1996), the slope of the line represents the rate of production (cysts produced/time) by the brine shrimp population for an initial (Spring) cyst density. The 2002 initial cyst density was plotted on this curve and the rate of cyst production for the 2002 season was extrapolated (Fig. 8). This was done assuming that all cysts hatched (over winter cyst survival not considered: Fig. 8) and that only some cysts hatched, based on the observed hatchability (over winter cyst survival considered: Fig. 8). This produces a range of values for the rate of cyst production and these values were converted into a range of

values for final cyst production assuming that the population has 2 or 3 generations in the 2002 season (black ellipse: Fig. 8).

If the population has two generations, the projections are for 31.5 – 52.3 cysts/l. However, if the population has 3 generations, the final cyst production is 78.4 – 130.7 cysts/l.

Figure 8. The plot of population growth rate versus initial (spring) cyst density. The line is fit by a DWLS smoothing function and forced through the origin.



Acknowledgements:

I wish to thank the Utah Division of Wildlife Resources (UDWR) for financial support to conduct this study, and the assistance of UDWR personnel Clay Perschon, Paul Birdsey and Don Archer. Help in caring for and censusing populations was provided by Summer Allen and Bryan Mahon.

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