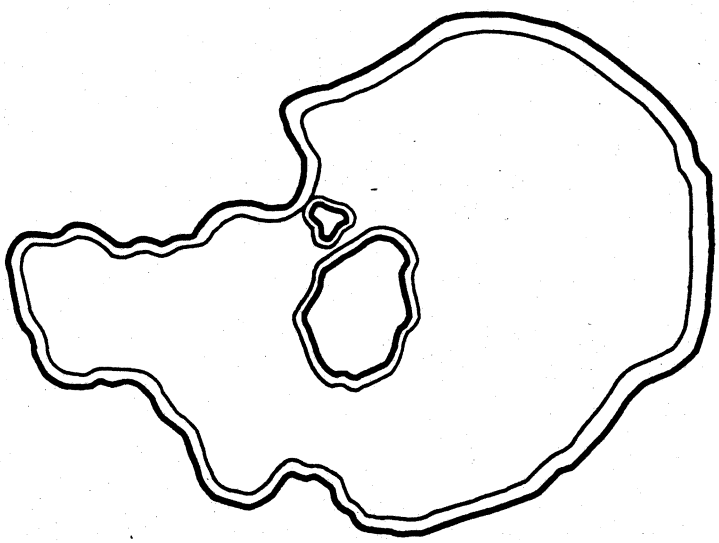
An Auxiliary Report
Prepared for the

MONO BASIN WATER RIGHTS EIR

Functional Relationships between *Artemia* Life History Characteristics and Salinity



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Mono Basin EIR Auxiliary Report No. 12

An Auxiliary Report
Prepared for the
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This auxiliary report was prepared to support the environmental impact report (EIR) on the amendment of appropriative water rights for water diversions by the City of Los Angeles Department of Water and Power (LADWP) in the Mono Lake Basin. Jones & Stokes Associates is preparing the EIR under the technical direction of the California State Water Resources Control Board (SWRCB). EIR preparation is funded by LADWP.

SWRCB is considering revisions to LADWP's appropriative water rights on four streams tributary to Mono Lake, Lee Vining Creek, Rush Creek, Parker Creek, and Walker Creek. LADWP has diverted water from these creeks since 1941 for power generation and municipal water supply. Since the diversions began, the water level in Mono Lake has fallen by 40 feet.

The Mono Basin water rights EIR examines the environmental effects of maintaining Mono Lake at various elevations and the effects of possible reduced diversions of water from Mono Basin to Owens Valley and the City of Los Angeles. Flows in the four tributary creeks to Mono Lake and water levels in Mono Lake are interrelated. SWRCB's decision on amendments to LADWP's water rights will consider both minimum streamflows to maintain fish populations in good condition and minimum lake levels to protect public trust values.

This report is one of a series of auxiliary reports for the EIR prepared by subcontractors to Jones & Stokes Associates, the EIR consultant, and contractors to LADWP. Information and data presented in these auxiliary reports are used by Jones & Stokes Associates and SWRCB, the EIR lead agency, in describing environmental conditions and conducting the impact analyses for the EIR. Information from these reports used in the EIR is subject to interpretation and integration with other information by Jones & Stokes Associates and SWRCB in preparing the EIR.

The information and conclusions presented in this auxiliary report are solely the responsibility of the author.

Copies of this auxiliary report may be obtained at the cost of reproduction by writing to Jim Canaday, Environmental Specialist, State Water Resources Control Board, Division of Water Rights, P.O. Box 2000, Sacramento, CA 95810.

Report to California State Water Resources Control Board

and Jones and Stokes Associates, Inc.

FUNCTIONAL RELATIONSHIPS BETWEEN *ARTEMIA* LIFE HISTORY CHARACTERISTICS AND SALINITY

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Abstract

The functional relationships between *Artemia monica* life history characteristics and salinity were determined using salinity bioassay data from four published studies and three experiments presented here. Salinity uniformly affected ten life history characteristics and explained 40 to 93 percent of the variation of these traits. Reductions in hatching success, survival, length, weight, ovigery, and brood size were observed as salinity increased from 76 to 168 g l^{-1}. Mean day of hatch, mean day of first brood production, and inter-brood duration were protracted as salinity was elevated. Salinity effects on life history characteristics were gradual and continuous rather than exhibiting particular salinity thresholds. The one exception was naupliar survival, which was constant between 76 and 133 g l^{-1} followed by a decrease above 133 g l^{-1}. These results show maintenance of osmotic homeostasis in elevated salinities has energetic costs which lower survival, growth, and reproduction in *A. monica*.

Introduction

The brine shrimp *Artemia* is well known for its ability to inhabit saline environments over a wide range of salinities (Persoone & Sorgeloos, 1980). *Artemia* is able to accommodate large changes in salinity by hyposmotic regulation whereby the osmotic pressure of the haemolymph is maintained relatively independent of the external medium (Croghan, 1958a). Hyposmotic regulation is accomplished in adult shrimp by active transport of ions and water through the gut into the haemolymph, and active excretion of ions across the branchiae into the external medium (Croghan, 1958b; Copeland, 1967; Smith, 1969). Naupliar osmoregulation is mediated by a distinct neck organ that actively transports and secretes salts (Conte *et al.*, 1972).

The continuous and active transport of ions against large concentration gradients requires expenditure of energy that increases at higher external salinity. There is evidence shrimp change the partitioning of available energy between ion transport and protein

synthesis in response to elevated salinity, rather than increase energy production (Conte *et al.*, 1973). Energy dependent processes such as growth and reproduction are likely to be lower in higher salinities as more energy is required for solute regulation in the maintenance of osmotic homeostasis.

Research on *Artemia monica* Verrill, a brine shrimp species endemic to Mono Lake, California, supports the hypothesis that there is an energetic trade-off between osmoregulation and other *Artemia* life history processes as a function of salinity. Short-term bioassays on adult *A. monica* show survival decreases, respiratory functions are lost, and internal solute homeostasis breaks down above 200 g l^{-1} (Herbst & Dana, 1977; 1980). Osmotic homeostasis is maintained and survival is high in salinities ranging 25 to 160 g l^{-1}. Naupliar stages are apparently more sensitive to salinity since survival decreases significantly above ca. 140 g l^{-1} (Dana & Lenz, 1986). Salinity effects on *A. monica* survival are generally consistent with studies on other *Artemia* species (for a review, see D'Agostino, 1980). Long-term salinity bioassays on *A. monica* corroborate the findings of short-term studies in that survival and hatching are lowered in elevated salinities (Dana & Lenz, 1986).

A. monica is similar to other *Artemia* species with regard to its hatching success as a function of osmolality, although its diapause requirements are atypical, being terminated by cold temperatures rather than the usual desiccation required by most *Artemia* species (Dana, 1981; Drinkwater & Crowe, 1987). Hatching is an osmotic process that is ultimately constrained at higher salinities by biophysical properties of the cyst. As external salinity increases so does the synthesis of glycerol, resulting in increased turgor pressure that ruptures the cyst wall (Clegg, 1964; 1976). In elevated salinities, hatching success lowers and onset of hatch is delayed in *A. monica* (Dana, 1981; Dana & Lenz, 1986; Drinkwater & Crowe, 1987; 1991; Thun & Starrett, 1987), as well as in other *Artemia* species (Jennings & Whitaker, 1941; Clegg, 1964; Royan, 1975). Hatching is completely eliminated at high salinities due to inadequate cellular water that is necessary for metabolic

processes (Clegg, 1964), and this occurs within the salinity range 140 to 160 g l^{-1} of Mono Lake water for *A. monica* (Drinkwater & Crowe, 1991).

Salinity effects on *A. monica* are of environmental concern because diversion of inflowing streams to Mono Lake since 1941 has caused salinity to nearly double to 98 g l^{-1}. Continued changes in salinity are possible, depending on the outcome of pending litigation and state regulatory activities. Changes in *A. monica* production are of interest not only because of its endemic status but also because of its importance as a food for thousands of nesting and migratory birds (Patten *et al.*,1987).

Here, we combine data from previous studies with new results and quantify the functional relationship between *A. monica* life history characteristics and salinity. Our analysis shows nearly all aspects of the life cycle of the brine shrimp are affected as salinity is increased. We bring these results into an ecological context and address the relative importance of physiological constraints and ecological factors as salinity increases.

Methods

Data Sources

As many sources as possible were utilized to examine the effects of salinity on ten different *A. monica* life history characteristics. The primary published source was the long-term salinity bioassay of Dana & Lenz (1986). This study evaluated salinity effects on life history characteristics over the entire life cycle of *A. monica*. Dana & Lenz (1986) raised shrimp from nauplii in seven salinity treatments ranging from 76 to 179 g l^{-1} of Mono Lake water. Nauplii were hatched from overwintering cysts in a lower salinity and transferred directly into each treatment with no acclimation, and all treatments were run concurrently. Shrimps were incubated in culture vials at 20°C with three replicate sets of 20 vials per salinity treatment. Shrimps were fed a whey-bran-*Spirulina* food mixture assumed to be saturating. Further methodological details can be found in Dana & Lenz

(1986). Published short-term bioassays (e.g., Herbst & Dana, 1977; 1980) were not used in the present analysis because full life cycle bioassays better reflect actual salinity effects.

Three other published studies were incorporated into this analysis, all of which evaluated salinity effects on hatching: Drinkwater & Crowe (1991), Thun & Starrett (1987), and Dana (1981). All three studies were conducted in culture systems at constant temperatures. We only utilized data from these studies in which cysts had been subjected to the obligatory dormancy period of at least 90 days at ca. 5°C. In two of the studies (Thun & Starrett, 1987; Drinkwater & Crowe, 1991) cysts originated from females collected from Mono Lake while in the third study (Dana, 1981) cysts were collected from Mono Lake sediments. Hatching was monitored at 4°C in four salinities ranging 50 to 125 g l^{-1} of Mono Lake water in Drinkwater & Crowe (1991) and at 10°C in four salinities ranging 97 to 157 g l^{-1} of Mono Lake water in Thun and Starrett (1987). Dana (1981) measured hatching at four temperatures in the 5 to 20°C range at one salinity, 94 g l^{-1} of Mono Lake water.

New unpublished results include data from three experiments. Experiment 1 was a long-term multiple generation salinity bioassay conducted on *A. monica* in 1985 by M. Rho, G. Starrett, and W. Perry (Los Angeles Department of Water and Power) in which hatching, survival, growth, and reproduction were monitored. Experiments 2 and 3 were conducted in 1982 by G. Dana and P. Lenz (University of California, Santa Barbara) in which temperature and salinity effects on *Artemia monica* hatching were evaluated.

In Experiment 1, shrimp were raised at 25°C in five successively higher concentrations of Mono Lake water ranging 97 to 192 g l^{-1}. Each generation of ovoviviparously produced nauplii were transferred to the next higher salinity, thus allowing for acclimation. Experiment 1 was initiated by hatching *A. monica* nauplii from cysts that had been obtained from females collected from Mono Lake. Cysts were incubated in 4°C anoxic water to satisfy dormancy requirements, and hatched at 15°C in oxygenated water.

Nauplii were raised in test tubes containing 10 ml Mono Lake water at a density of one per ml. As the nauplii developed, the density was reduced to one nauplius per 2 ml at ten days and further reduced to one nauplius per 5 ml at 15 days. Culture water was changed at five-day intervals at which time salinity was increased by 25% until the target salinity was reached at 20 days. In this way nauplii were slowly acclimated to each salinity treatment. Survival was monitored on a subset of 60 nauplii. Growth was monitored on a different subset of 100 nauplii after narcotizing with chloroform (Lochhead & Lochhead, 1941). Total body length was measured as the distance from the anterior margin of the head to the base of the caudal furca. Instar stage was identified according to Heath (1924). Nauplii measured for growth were not used in the reproductive phase of the experiment. Shrimp were fed a solution of powder rice bran-whey-*Spirulina* mix and Mono Lake water throughout the experiment, the concentration of which was adjusted as the shrimp developed.

Male and female shrimp were paired upon sexual maturity, and placed in four flow-through raceways of 4-5 liter capacity. Each raceway contained 24 pairs separated from each other with 100 μm Nitex screen. Three of the raceways were used to monitor reproduction and mortality and the fourth to measure growth rates. Length was measured as described above for nauplii. Reproductive parameters were monitored for 30 days and included time to first brood production, reproductive state (ovigerous versus non-ovigerous), reproductive mode (ovoviviparous versus oviparous), number of broods per female, brood size, and the time interval between broods. Broods were counted and removed daily. Cyst broods from 12 pairs of shrimp per salinity were placed in anoxic 4°C water for a minimum of 90 days. From these, hatching success was evaluated in oxygenated water at 15°C over a two-week period.

In Experiments 2 and 3 hatching success and rates were measured as a function of temperature and salinity respectively. In both experiments, cysts were collected in March from Mono Lake sediments using a tall model Birge Ekman grab sampler. From the

surface of these samples 2 ml cores were withdrawn with a 1 cm diameter 5 ml plastic syringe. We assumed these cysts had already experienced the appropriate dormancy conditions over the winter months. Experiments were terminated after peak hatching had occurred and the hatching rate had fallen to low values. At 10°C this occurred in ca. 15 days and at 2.5°C in ca. 60 days.

In Experiment 2 hatching success and rates were measured at two temperatures, 2.5°C and 10°C. Each treatment consisted of four replicates, each receiving 0.1 ml of Mono Lake sediments taken from the same sediment core. The density of cysts was 980 ml^{-1} as determined by counting subsamples of cysts from the same 2 ml sediment core from which the samples were taken. Cysts were incubated with associated sediments in 15 ml of Mono Lake water (97 g l^{-1}) in covered plastic containers.

In Experiment 3, hatching success and rates were measured at four salinities ranging 50 to 97 g l^{-1} of Mono Lake water. Each treatment consisted of five replicates containing 25 cysts each. Cysts were separated from the sediments by sieving through 120 μm Nitex mesh and incubated at 10°C in 5 ml of Mono Lake water in plastic petri dishes.

The studies described here used different temperatures and salinity units. Salinity of the various studies was presented either in grams per liter or parts per thousand. To standardize among studies, parts per thousand was converted to grams per liter using the equation, grams per liter = -11.06 + (1.196 x parts per thousand) (r^2, 0.999), which was derived from data presented in Thun & Starrett (1987). Life history-salinity regressions presented here utilized data up to 168 g l^{-1}. Although data from 179 and 192 g l^{-1} were available, they were not used because Drinkwater & Crowe (1991) demonstrated cysts reach a critical hydration level at a salinity between 140 and 160 g l^{-1}. They concluded *A. monica* will cease to exist within this range, and Dana & Lenz (1986) corroborated this finding. Life history data was obtained at 192 g l^{-1} in Experiment 1 by inoculating higher salinity treatments with nauplii ovoviviparously produced at lower salinities. Dana & Lenz

(1986) obtained life history data at 179 g l^{-1} by inoculating this salinity treatment with nauplii hatched from overwintering cysts at a lower salinity. The highest salinity used in the present analysis, 168 g l^{-1}, was included in the regressions because it is close to the upper limit described by Drinkwater & Crowe (1991). Temperature varied among the studies utilized in the present analysis. For example, Experiment 1 was conducted at 25°C while Dana & Lenz's (1986) study was conducted at 20°C. Analyses involving rate functions, including mean day of hatch, mean day of first brood production, and inter-brood duration, were standardized to a common temperature using derived or published equations.

Regression analyses were used to derive salinity response curves of each life history character. While both linear and curvilinear (exponential, multiplicative, and reciprocal) models were applied to the data, only the best-fit models are presented here. Tests for comparisons among means (ANOVA and Kruskal-Wallis tests) were applied when significance among treatment means was of interest (e.g., in the analyses on brood size, ovoviviparity, and naupliar survival)

Hatching

In assessing salinity effects on percent hatch we utilized only those experiments in which cysts were collected from females (Dana & Lenz, 1986; Thun & Starrett, 1987; Drinkwater & Crowe, 1991; Experiment 1). Females were collected from Mono Lake, placed in containers in the lab and left until cysts were released. Thun & Starrett (1987) used only indented cysts since they found significantly higher viability in indented compared to completely spherical cysts. Cyst shape was not considered in the other three studies. Since we were comparing results from different studies, those in which cysts were collected from lake sediments (e.g. Dana, 1981; Experiment 3) were not utilized because the histories of these eggs are unknown and factors other than salinity could affect their viability. For example, cysts collected from the top centimeter of sediment could be up to 10 years old, with older cysts having reduced viability, or high concentrations of

substances within the sediment could cause decreased viability. Experimental temperatures from the different studies ranged from 5 to 15°C. Hatching success has been positively related to temperature (G. Starrett, personal communication), negatively related to temperature (Dana, 1981), and unaffected by temperature (Drinkwater & Crowe, 1991). Given the conflicting data we assumed temperature effects on percent hatch were not significant over the range of temperatures considered here. Only data in which the dormancy period was 90 days or greater were used here since optimal hatching success only occurs after a minimum of 90 days of dormancy in suitable conditions (Dana, 1981; Thun & Starrett, 1987). Extending dormancy beyond 90 days does not significantly increase hatching success.

Mean day of hatch was calculated by fitting a normal distribution to the hatch versus time curves. Time zero was the day when the cysts were taken out of dormancy conditions (usually anoxic to prevent hatching) and placed in the hatching treatment. Mean day of hatch was temperature corrected to 10°C by using a regression of mean day of hatch on temperature based on four studies (Dana, 1981; Dana & Lenz, 1986; Thun & Starrett, 1987; Experiment 2). At a constant salinity (94-97 g l^{-1}) mean day of hatch decreased from 46 days to 3 days as temperature increased from 2.5 to 20°C (Fig. 1). Ninety-three percent of the variation in mean day of hatch was explained by the regression equation:

$$\text{Mean Day of Hatch} = 139 \times \text{Temperature}^{-1.317} \qquad (1)$$

In the assessment of salinity effects on mean day of hatch we used experiments in which cysts were collected from females or the sediments (Dana, 1981; Dana & Lenz, 1986; Thun & Starrett, 1987; Experiment 3). We assumed while percent hatch (i.e. viability) would be affected by the history of the cysts within the sediments, hatching rate and mean day of hatch would not be significantly influenced if the cyst was still viable. Only data in which the dormancy period of the cysts was 90 days or greater were used here for reasons stated earlier.

Survival

The effects of salinity on survivorship of naupliar stages (instars 1-8) of *A. monica* were addressed in Dana & Lenz (1986) and Experiment 1. In the present study, survival to instar 8 was chosen as an indication of naupliar survival because it represents survival over all naupliar stages. Dana & Lenz (1986) presented survival data as a time function (percent survival on a given day). Because instar stage information was available for each time step, we reanalyzed their data. The day at which all shrimp in a replicate reached instar stage 8 was determined and the percent survival was recorded. This method of estimating percent survival to the 8th instar stage slightly underestimates survivorship since there is some mortality of shrimp which reach instar 8 prior to the time all shrimp in a replicate have attained this stage. However, because mortality was low at the time of juvenile growth, the error is slight (See Fig. 1A in Dana & Lenz, 1986).

Adult survival in Experiment 1 was calculated for male and female pairs over a thirty day period. A death of a pair meant either the female or the male died, and the survivor of the pair was not monitored for survivorship. Although this is not an ideal measure of adult survivorship, it approximates the true response to salinity. Percent survival of adult pairs was also calculated from Dana & Lenz (1986) because it was not included in their publication. In their experiment, survival was monitored until one of the pair died, or until the third brood was produced. This is different from Experiment 1 in which pairs were monitored for a set time of thirty days. Percent survival was calculated by dividing number of pairs surviving by the number pairs total.

Length and weight

Dana & Lenz (1986) presented length data as length on each day of observation. However, paired length-instar data were available and instar-specific lengths were calculated for each salinity treatment. Adult length was calculated as an average of ten female and ten male lengths. In Experiment 1 length data for naupliar and juvenile stages were pooled over replicates since replicate information was not available. Therefore, a

mean and standard error were calculated over all the individual length measurements within a salinity treatment. Mean adult length was calculated by averaging 24 male and 24 female lengths over all dates in each salinity treatment. ANOVAs were done on each instar stage on $\log_{10}$ transformed data to determine if there was a significant effect of salinity on length. This analysis could be done only on Dana & Lenz's (1986) data because replicate data were not available for Experiment 1. Length-salinity regressions were done when there were significant differences in length within an instar stage.

There were no studies from which to directly assess salinity effects on weight of *A. monica*. From instar-specific lengths calculated in the present study, weight can be calculated using a weight-length regression derived from experiments on *A. monica* development rates (Dana & Jellison, unpublished data).

$$\text{Dry Weight (mg)} = .0057 \times \text{Length}^{2.296} \qquad (r^2, 0.68) \qquad (2)$$

Data for this regression were pooled from three experiments, each representing different food and temperature conditions. We assume this relationship holds true regardless of salinity based on Gilchrist's (1958) work that showed no difference in the weight-length relationship of adult male *Artemia* in salinities of 35 ppt and 140 ppt. Regressions of weight on salinity were then applied to those instar stages for which a significant effect of salinity on length was found.

Reproduction

Dana & Lenz (1986) assessed the effects of salinity on the onset of reproduction by comparing cumulative distribution curves of the time course from hatching to first brood production. Shrimp raised in 159 g l^{-1} took significantly longer to produce the first brood than those raised in salinities between 76 and 133 g l^{-1}. Data from Dana & Lenz (1986) and Experiment 1 were analyzed to generate cumulative distributions of number of females with first brood over time for each treatment with time referenced from day of hatch. Only data in which a female and male were paired for greater than seven days were included in the analysis to insure a female had adequate time with a male to become

fertilized. Data from all replicates were pooled so the cumulative number of females with first brood on each date was the total of all the replicates. Mean day of first brood production was calculated by fitting a normal distribution to the distribution of days at which the first brood was produced.

Data from Experiment 1, collected at 25°C, were corrected to 20°C to be consistent with the data of Dana & Lenz (1986). We derived an exponential temperature coefficient based on two treatments: time to first brood at 20°C, 97 g l^{-1} (Dana & Lenz, 1986) and at 25°C, 97 g l^{-1} (Experiment 1). The resulting regression was used to correct Experiment 1 data at 25°C to 20°C:

$$Time_{20\,°C} = Time_{25\,°C} \times (1.1079)^{(25-20)} \qquad (3)$$

The mean percentage of ovigerous females was calculated from Dana & Lenz (1986) and Experiment 1. Although Dana & Lenz (1986) did not evaluate salinity effects on percentage of ovigerous females, it was possible to calculate this population attribute from their data. Only females that did not produce a brood, and lived the entire experiment were considered infertile, while the total female population were those which had been paired with a male greater than seven days for the reason stated earlier.

The mean number of days between broods was calculated from Dana & Lenz (1986) and Experiment 1. Dana and Lenz (1986) did not present this life history characteristic in their publication, however it could be calculated from their data. Only pairs that survived seven days past pairing were considered in the analysis. Mean inter-brood duration from Experiment 1, measured at 25 °C, was adjusted to 20°C with the equation (Dana *et al.*, 1990):

$$IBD_{20°C} = IBD_{25°C} \times 0.9024^{(20-25)} \qquad (4)$$

where IBD is the inter-brood duration.

Mean brood size was calculated for each of the first three (Dana & Lenz, 1986) or four (Experiment 1) broods produced by a female. An ANOVA was done to determine

whether there was a significant difference in brood size among broods. This information was then used to determine whether the broods could be pooled in regression analysis.

Percent ovoviviparity was calculated for each of three broods from the data of Dana & Lenz (1986) and Experiment 1. A Kruskal-Wallis test was conducted on the data from both studies to determine whether there was a significant difference in ovoviviparity among broods. Data were pooled over broods for the regression analysis if no difference was found.

Results

Hatching

Percent of cysts that did not hatch increased from 10 to 100 % as salinity increased from 50 to 159 g l^{-1} (Fig. 2A). An exponential regression on salinity described 68% of the variation in percent non-hatching cysts (Table 1). Percent non-hatching cysts varied significantly among studies. At salinities of 97 to 100 g l^{-1}, a salinity range common to the four studies considered here, non-hatching cysts ranged 10 to 47 %. Salinity also affected the timing of the hatch with mean day of hatch (at 10°C) increasing from ca. 5 to 16 days as salinity increased 50 to 159 g l^{-1} (Fig. 2B). An exponential regression of mean day of hatch on salinities 50 to 159 g l^{-1} explained 77 % of the variation (Table 1).

Survival

Naupliar survival remained constant at about 80 % between salinities of 76 and 133 g l^{-1} (Fig. 2C). Above 133 g l^{-1}, percent survival dropped to 33 % at 159 g l^{-1}. Agreement between the two studies was reasonable, although survival in Experiment 1 was always higher than in Dana & Lenz (1986) for a given salinity. Survival did not differ significantly among treatments in the 76 to 133 g l^{-1} salinity range in Dana & Lenz's (1986) study (ANOVA and Scheffe's test), and in the 97 to 121 g l^{-1} range in Experiment 1 (ANOVA and Duncan's test). Above 121 g l^{-1} in Experiment 1 and 133 g l^{-1} in Dana & Lenz (1986), survival decreased and all differences in survival between salinity treatments

were statistically significant ($p<0.001$). A linear regression on salinities from 118 to 168 g l^{-1} explained 71 % of the variation in naupliar survival (Table 1).

Adult survival was consistently higher in Experiment 1 than in Dana & Lenz (1986) (Fig. 2D). However, a linear trend (r^2, 0.40) of lower survival at higher salinities was observed in both studies (Table 1). A regression of survival on salinity using only Experiment 1 data resulted in a greater effect of salinity (slope, -0.806) and a higher r^2 (0.96). Using only Dana & Lenz's (1986) data resulted in a lesser salinity effect (slope, -0.436) and a lower r^2 (0.77).

Length and weight

Adult length decreased as salinity increased in both studies evaluated (Figs. 3A & B). Juvenile length decreased at elevated salinities in Dana & Lenz (1986, Fig. 3A), but did not change significantly in Experiment 1 (1985, Fig. 3B). Regressions of length on salinities 76 to 168 g l^{-1} were significant for adults (Fig. 2E, $p=0.0004$), juveniles ($p=0.0044$), instar 7 ($p=0.0078$), and instar 6 ($p=0.033$), and explained 89, 66, 61 and 45 % of the variation respectively (Table 1). Regressions for instars 1-5 were not significant.

Mean weights of instars 6 through adults were calculated from length using the equation presented earlier (eq. 2). A linear regression of adult weight on salinities 76 to 168 g l^{-1} fit the data well with an r^2 value of 0.91 (Fig. 2F, Table 1). Individual linear regressions on juveniles, instar 7, and instar 6 resulted in lower r^2 values: 0.66, 0.62, and 0.48, respectively (Table 1). The slope of the regression of weight on salinity decreased with earlier instars, consistent with the relative instar weights. The percent weight change was nearly constant; at 100 g l^{-1} the relative decrease in weight associated with a 10 g l^{-1} increase in salinity was 8.1, 8.4, 7.7, and 7.2 % for instars 6, 7, juveniles, and adults, respectively.

Reproduction

Mean day of first brood production increased from ca. 42 to 70 days as salinity increased from 76 to 168 g l^{-1} (Fig. 2G). An exponential regression on salinity explained 84 % of the variation in mean day of first brood production (Table 1).

Percentage of ovigerous females decreased from 98 to 6 % as salinity increased 76 to 159 g l^{-1} (Fig. 2H) and the data from the two studies agreed well. We chose to eliminate from the regression the anomalous value at 168 g l^{-1} (Experiment 1) because an increase in ovigery at very high salinities was unlikely and probably a result of low sample size or individuals dying before the end of the experiment. A regression of percent ovigerous females on salinities 76 to 159 g l^{-1} explained 92 % of the variation (Table 1).

There was a trend of longer intervals between broods with increased salinity (Fig. 2I). At salinities of ca. 130 g l^{-1} and below, the data from the two studies agreed well. However, inter-brood duration at 159 g l^{-1} in Dana & Lenz's (1986) study was about 1-2 days less than observed at about the same salinity in Experiment 1. An exponential regression of inter-brood duration on salinities 76 to 168 g l^{-1} explained 61 % of the variation. The poor fit of the model is primarily due to the large disparity of points at the higher salinities, which may be related to the extrapolation of the temperature correction at higher salinities.

Brood size decreased as salinity increased in both Dana & Lenz (1986) (Fig. 4A) and Experiment 1 (Fig. 4B). An ANOVA done separately on the data from the two studies showed that up to ca. 150 g l^{-1}, the first brood was significantly smaller than subsequent broods ($p<0.02$). Subsequent broods were not significantly different from each other. Above 150 g l^{-1} the differences between the first brood and later broods were not significant. Due to the disparity of the first brood from other broods, separate regressions were done for the first brood and for subsequent broods pooled. Brood size in Experiment 1 was generally larger than in Dana & Lenz (1986) but differences between the two studies were smaller for the first brood. Salinity explained 85 % and 61 % of the

variation in brood size for brood 1 (Fig. 2J) and subsequent broods (Fig. 2K), respectively (Table 1).

In some treatments percent ovoviviparity differed among broods, with the first brood usually being larger in both Dana & Lenz (1986) (Fig. 5A) and Experiment 1 (Fig. 5B). A Kruskal-Wallis test yielded no significant differences (p ranged 0.06-0.8) in percent ovoviviparity among brood number for all treatments in both studies. For this reason, mean percent ovoviviparity was pooled over the first three broods. Percent ovoviviparity was consistently higher in Experiment 1 (Fig. 5B) than in Dana & Lenz (1986) (Fig. 5A) for all treatments. Percent ovoviviparity increased 3 to 43 % over the salinity range 76 to 168 g l^{-1} (Fig. 2L). An exponential regression on salinity explained 82 % of the variation in percent ovoviviparity (Table 1).

Discussion

Physiological and life history responses to salinity

Salinity affected all ten life history characteristics of *A. monica*, and in regression analyses explained 40 to 93 percent of the variation in these traits. Our analysis indicates gradual and continuous effects of increased salinity rather than thresholds, with the exception of naupliar survival. In that case, experimental results indicated survival was constant between 76 and 133 g l^{-1} followed by a linear decrease above 133 g l^{-1} (Fig. 2C). Reductions in hatching success, survival, length, weight, ovigery, and brood size were observed as salinity increased from 76 to 168 g l^{-1}. Mean day of hatch, mean day of first brood production, and inter-brood duration, were protracted as salinity was elevated. For most of the *Artemia* characteristics evaluated the response to salinity was similar in the different studies, despite the different approaches. Absolute values of the response to salinity sometimes differed among studies, most likely reflecting differences in the environmental conditions under which the experiments were conducted. For example,

both Dana & Lenz (1986) and Experiment 1 demonstrated decreased brood size with increased salinity (Figs. 4A & B), although brood size was larger in Experiment 1.

The directional change in *A. monica* life history characteristics that occurred as a function of salinity in the present study is consistent with the hypothesis that *Artemia* partitions limited energy resources between osmoregulation and other physiological processes. Partitioning of energy has to occur if the total energy stores remain constant as osmoregulatory costs increase (Conte *et al.*, 1973). This supposition is supported by *Artemia*'s respiratory response, which is an integrative measure of all metabolic processes, to salinity changes. Adult female *A. monica* maintain similar rates of oxygen consumption up to salinities of 160 g l^{-1}, and adult males maintain a relatively constant oxygen consumption up to even higher salinities of 200 g l^{-1}, presumably by virtue of the large, flattened, prehensile antennae of males, which provides a greater relative surface area over which respiratory gas exchange can occur (Herbst & Dana, 1980). There is also evidence oxygen consumption in *Artemia* nauplii is independent of salinity (Kratovich, 1964; Conte *et al.*, 1980), although reported values of naupliar respiratory rates are not in good agreement (Kuenen, 1939; Eliassen, 1952; Engel & Angelovic 1968). These data indicate shrimp distribute available oxygen according to competing processes, rather than increasing respiratory rates to compensate for growing osmoregulatory costs in elevated salinities.

The decline in adult survival observed as salinity increased (Fig. 2D) may be related to changes in important biochemical and osmoregulatory processes. Solute concentration within the haemolymph of adult *A. monica*, although it is maintained at levels substantially lower than the external medium, gradually rises as salinity is elevated (Herbst & Dana, 1980). Protein and nucleic acid biosynthesis, and ATP levels in naupliar shrimp decrease as a function of salinity, although this has not been demonstrated for adult shrimp (Conte *et al.*, 1973; 1980; Ewing *et al.*, 1979). The difference in adult *A. monica* survival observed in short-term salinity bioassays, in which survival is high and constant up

to 200 g l^{-1}, and the linear decrease in survival demonstrated in the longer term salinity bioassays presented here may be associated with cumulative effects of salinity incurred over the life time of the shrimp in the longer-term studies.

Hypoxia accompanying hypersaline conditions can be an additional stress contributing to mortality. Although shrimp increase hemoglobin synthesis as external salinity rises (Fox, 1949) oxygen concentrations below 2 mg l^{-1} have resulted in reduced respiratory rate and accompanying mortality (Vos *et al.*, 1979). Low oxygen concentrations present in high salinity water may contribute to the complete loss of respiratory ability and substantial increases in haemolymph solutes observed in *A. monica* above 200 g l^{-1} (Herbst & Dana, 1980). Survivorship may be improved by acclimating shrimp to higher salinities (Kinne, 1964). *Artemia sp.* raised in concentrated media developed a more extensive mitochondrial system in the gills than those reared in dilute media (Copeland, 1967). Acclimation effects may be illustrated by the higher survival of salinity-acclimated shrimp in Experiment 1 versus the lower survival of non-acclimated animals in Dana & Lenz (1986) (Fig. 2D). Long-term genetic adaptation of *Artemia* from Lake Grassmere, New Zealand, to higher salinities over a thirty year period is hypothesized to have conferred better survival abilities of this strain to water in which salinity rarely falls below 100 ppt sea water (Wear & Haslett, 1986).

A decline in hatching success and longer hatching times was observed as salinity increased (Figs. 2A & B). This hatching behavior can be explained in terms of salinity-mediated shifts in the carbohydrate metabolism within the cyst. The dormant embryo in encysted eggs synthesize large amounts of trehalose, most likely from glycogen, then reconverts most of the trehalose back to glycogen, which is probably the major carbohydrate used in development of the encysted embryo, and to glycerol, which is integral to the hatching process by increasing the internal osmotic pressure to the point of rupturing the cyst wall (Clegg, 1965). Converted trehalose is partitioned between these two carbohydrate pools with the relative amounts of glycerol and glycogen produced

determined by the external osmotic pressure. With rising salinity, glycerol concentrations increase while glycogen levels decrease within the cyst (Clegg, 1964). Because the embryo must synthesize more glycerol to hatch in higher salinities, fewer carbohydrates in the form of glycogen will be available for other developmental processes. It is thought this decrease in glycogen is in part responsible for the decrease in hatching success at higher salinities (Drinkwater & Crowe, 1991) and may contribute to lower naupliar survival. Indeed, nauplii raised in lower salinities have a higher energy content (cf. Sorgeloos, 1980). Higher osmotic pressures present in the cyst at elevated salinities causes a reduction in water availability which results in lower rates of trehalose oxidation (Clegg, 1964). Lower rates of development in the embryo would result from this change in trehalose utilization and may account for the longer hatch times observed at higher salinities. Conventional carbohydrate metabolism, present in all *Artemia* species, shuts down in *A. monica* between 140 and 160 g l^{-1} due to inadequate cellular water in these high salinities (Drinkwater & Crowe, 1991).

Energy constraints on growth were indicated by the inverse relationship of *A. monica* size with salinity observed in our study and the reduced growth rates reported in high salinities by other authors (e.g. Bond, 1933; Gilchrist 1960; Dana & Lenz, 1986; Wear & Haslett, 1986). There is evidence growth rates and efficiency may be optimal at salinities lower than evaluated here (Reeve, 1963), although the *Artemia* strain and acclimation history may also play a large role in growth response to salinity (Collins, 1980; Wear & Haslett, 1986). Organisms may compensate for salinity-induced growth impairment by extending the development time so that optimal size might still be attained. Prolonged growth of *A. monica* does occur in higher salinities (Dana & Lenz, 1986), and size benefits in younger instars (one through six) were realized because in these stages length did not decrease as a function of salinity (Figs. 3A & B). Size of older stages, including reproductive adults, was reduced in elevated salinities, gaining little if any benefit from prolonged development (Fig. 2E). Independent of salinity, size at maturity affects

other life history characteristics such as survival and reproduction. Larger-sized *Artemia sp.* nauplii have better survival and may mature earlier than smaller animals (Collins, 1978). Larger brood sizes have been significantly correlated with bigger *A. monica* females (G. Dana, pers. observation).

Direct effects of salinity on reproduction, in addition to the indirect effects of reduced size, also have significant bearing on the reproductive patterns observed in our study. Delay in reproduction, smaller brood size, reduced ovigery, and longer intervals between broods that occurred with each increase in salinity level (Figs. 2G-K) most likely reflect a reduction in the amount of energy available for reproduction, to compensate for the increased osmotic work required at higher salinities. Reproductive potential, a measure calculated by Dana & Lenz (1986) which integrated survival, reproduction, and hatching of some of the data presented here, decreased linearly as salinity was elevated. The increased percentage of ovoviviparous broods produced in higher salinities is further evidence of salinity stress (Fig. 2L). As energy requirements for osmoregulation rise in higher salinities, females shift from oviparous, probably a more costly mode of reproduction, to ovoviviparous reproduction. Two lines of evidence indicate the oviparous mode is more energetically costly. First is 20 % of the dry mass of the cyst is utilized for encapsulation (Clegg, 1974) and second, ovoviviparous embryos do not undergo any of the energy requiring carbohydrate interconversions described previously for encysted embryos (Clegg, 1965).

Ecological Considerations

Response to changing salinity at the population level depends, in part, on the extent to which an individual's bioenergetic budget can accommodate osmoregulatory costs without affecting survival, growth, and reproduction. Clearly, individual development in *Artemia* is reduced as salinity is increased between 76 and 168 g l^{-1}. However, numerous authors conclude salinity may not the most important factor governing species abundance, regardless of the salinity range (for a review see Williams *et*

al., 1990). Other abiotic and biotic factors are important to *Artemia* production, including interactions between physical and chemical factors (including salinity), predation, competition, and food availability.

Artemia abundance may be reduced by predators such as fish at lower salinities (Edmondson, 1966; Persoone & Sorgeloos, 1980; Bhargava *et al.*, 1987; Nimura, 1987). In Mono Lake avian predators influence *A. monica* abundance; fish do not occur in the lake. The shrimp population declines each autumn shortly after hundreds of thousands of Eared Grebes congregate to molt and feed before continuing their migration. In a two year study, Cooper *et al.* (1984) demonstrated the grebes accounted for 55 to 83 % of the decline in *Artemia* densities in 1980, and 8 to 27 % in 1981. The higher proportion in 1980 was thought to be due to higher grebe and lower shrimp densities that year compared with 1981. Although they concluded grebe predation probably has little long-term impact on the size of the *Artemia* population, its relative importance in regulating shrimp densities may change as a function of *Artemia* population size. Tens of thousands of nesting California Gulls and migrating Wilson's and Red-necked Phalaropes also feed on brine shrimp in Mono Lake, although their impact on population densities has not been quantified.

Predation and competition on *Artemia* by other zooplankton are not factors at higher salinities (>100 g l^{-1}) in Mono Lake due to salinity intolerance of these species. At lower salinities, however, predation and competition by other species may exert a significant influence on the *Artemia* population. Herbst (1988) proposed in his "intermediate salinity hypothesis" that individual species productivity reaches a maximum at salinities intermediate between physiologically limiting high salinities, and low salinities where a more diverse community of predators and competitors imposes increasing limitations on individual species.

In the Great Salt Lake, Utah a significant decline in *Artemia* abundance and subsequent restructuring of the entire ecosystem occurred during a recent invasion of an

invertebrate predator following a reduction in salinity (Wurtsbaugh & Berry, 1990). Salinity in the south arm of the Great Salt Lake decreased from 250 to 50 g l^{-1} between 1963 and 1987 as the lake level rose due to increasing freshwater inflows. Many floral and faunal changes occurred during this time. Numbers of algal species increased 20-fold and macrozooplankton species increased from one, *Artemia franciscana* Kellogg, to an assemblage of one rotifer (*Brachionus*, sp. probably *B. plicatilis*), two predatory copepods (*Cletocampus alburerquensis* Herrick and *Diaptomus connexus* Light), and a predatory corixid beetle (*Trichocorixa verticalis* Fieber). Rotifers were observed at peaks of up to 750,000 individuals m^{-3}, and corixids as high as 100 individuals m^{-3} in 1985 and 1986. The *Artemia* population declined from peaks of 18,000 individuals m^{-3} prior to 1982, to peaks of only 37 individuals m^{-3} in 1985 and 1986.

Wurtsbaugh & Berry (1990) hypothesized the *Artemia* population declined due to invasion of the predatory corixid beetle at lower salinities in the Great Salt Lake. Wurtsbaugh & Berry (1990) cite other examples of inverse correlations between corixids and *Artemia* along salinity gradients in the Great Salt Lake (Hayes, 1971) and the Alviso Salt Ponds, California (Carpelan, 1957). Microcosm experiments with corixid beetles, *Artemia*, and algae further support this hypothesis (Wurtsbaugh, 1992). The two predatory copepods mentioned earlier, *C. alburerquensis* and *D. connexus*, also probably contributed to the decline in *Artemia* (Wurtsbaugh, 1992) because they are reported to control brine shrimp numbers (Hammer & Hurlbert, 1990).

Changing structure of the Mono Lake ecosystem could offset the demonstrated physiological and life history advantages gained by *A. monica* at lower salinities, resulting in reductions in *Artemia* abundance similar to that observed in the Great Salt Lake. Species diversity of the plankton will most likely increase in a less saline Mono Lake. Mason (1967) noted the presence of two other zooplankton species, the rotifers *Brachiomus plicatilis* Müller and *Hexartha jenkinae* de Beauchamp, between 1959 and 1963 when the salinity was more dilute than present, ca. 62 to 70 g l^{-1}. Although Mason's

data are sparse, during one winter sampling date in 1959, rotifer abundance was 40,000-170,000 individuals m^{-3}, and 90 % of the population was composed of *B. plicatilis*. Competition of the rotifers with *Artemia* could influence *Artemia* productivity, and would depend partly on the degree of seasonal overlap between the two species. Although Mason observed rotifers mostly in the winter when *Artemia* are sparse, accounts of *B. plicatilis* from other lakes indicate substantial spring and summer populations (Walker, 1981; Wurtsbaugh & Berry, 1990).

Predators are likely to invade Mono Lake at lower salinities. Although the corixid beetle of Wurtsbaugh & Berry's (1990) study, *T. verticalis*, would not tolerate Mono's highly alkaline water, there are other candidates. The dyticid beetle, *Hygrotus masculinus* Crotch, is found in less saline ponds around Mono Lake, and in other alkaline Great Basin lakes of lower salinity, including Walker, Abert, and Black Lake (D. Herbst, personal communication). It has been observed to prey on copepods and is likely to be predatory on *Artemia*. Recent microcosm experiments indicate *H. masculinus* can survive in 50 g l^{-1} Mono Lake water (Herbst, personal communication). Another predator, *Notonecta spinosa* Hungerford, is also a possible candidate but has only been observed in low numbers and in salinities no greater than 30 g l^{-1} (Herbst, 1988).

Tight coupling of nutrient pools and the algal and *Artemia* populations in Mono Lake is likely to lessen the predicted response to changes in salinity based on physiological responses measured in salinity bioassays. Algal biomass limits *Artemia* productivity during much of the year through its effects on fecundity and mortality and development rates (Dana *et al.* 1990; Jellison & Dana, unpublished data). Algal biomass in turn is limited by different factors through the season, including *Artemia* grazing, light, and nitrogen.

In summary, *Artemia* are able to maintain osmotic homeostasis over a wide range of salinities. Such osmoregulatory abilities have energetic costs that uniformly affect *Artemia* survival, growth, and reproduction. However, other factors such as predation,

competition, and food availability must be considered along with physiological responses when assessing the effects of changing salinity on the productivity of natural populations of *Artemia*. Predation and competition are likely to be significant factors in influencing shrimp productivity at lower salinities, while individual physiological constraints and *Artemia* interactions with nutrients and algae attain prominence at higher salinities.

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Table 1. Regressions of *Artemia* life history characteristics on salinity.

Life history Character	Salinity Range ($g\ l^{-1}$) (y)	Equation (x)	Intercept (b)	Slope (m)	p value	r^2	Study Code	Figure Number
% Non-hatching Cysts	50-159	$y = e^{(mx + b)}$	1.21	0.021	<0.001	0.68	1,2,3,4	2A
Day of Hatch, 10°C	50-159	$y = e^{(mx + b)}$	0.865	0.0116	<0.001	0.77	2,3,5,6	2B
% Naupliar Survival	118-168	y = mx + b	186	-0.861	0.036	0.70	1,2	2C
% Adult Survival	76-168	y = mx + b	99	-0.411	0.051	0.40	1,2	2D
Adult Length (mm)	76-168	y = mx + b	12.9	-0.034	<0.001	0.89	1,2	2E
Juvenile Length (mm)	76-168	y = mx + b	8.9	-0.024	0.004	0.66	1,2	NS
Instar 7 Length (mm)	76-168	y = mx + b	6.3	-0.018	0.008	0.61	1,2	NS
Instar 6 Length (mm)	76-168	y = mx + b	5.3	-0.015	0.033	0.45	1,2	NS
Adult Weight (mg)	76-168	y = mx + b	1.743	-0.0073	<0.001	0.91	1,2	2F
Juvenile Weight (mg)	76-168	y = mx + b	0.757	-0.0033	0.004	0.66	1,2	NS
Instar 7 Weight (mg)	76-168	y = mx + b	0.328	-0.0015	0.007	0.62	1,2	NS
Instar 6 Weight (mg)	76-168	y = mx + b	0.224	-0.001	0.025	0.48	1,2	NS
Day 1st Brood Production, 20°C	76-168	$y = e^{(mx + b)}$	3.21	0.006	<0.001	0.84	1,2	2G
% Ovigery	76-159	y = mx + b	135	-0.429	<0.001	0.92	1,2	2H
Inter-brood Duration 20°C (days)	76-168	$y = e^{(mx + b)}$	1.809	0.0036	0.008	0.61	1,2	2I
Brood Size, #1 ($eggs\ brood^{-1}$)	76-168	y = mx + b	65.8	-0.28	<0.001	0.85	1,2	2J
Brood Size, #2-4 ($eggs\ brood^{-1}$)	76-168	y = mx + b	107	-0.446	<0.001	0.61	1,2	2K
% Ovoviviparity	76-168	$y = e^{(mx + b)}$	-1.32	0.031	<0.001	0.82	1,2	2L

Study Codes: 1=Experiment 1, 2=Dana & Lenz (1986), 3=Thun & Starrett (1987), 4=Drinkwater & Crowe (1991), 5=Dana (1981), 6=Experiment 3.

NS Denotes regression not shown graphically.

Figure Captions

Figure 1. Regression of mean day of hatch on temperature at salinities 94-97 g l^{-1}. Vertical lines are the standard error of the mean. See equation (1) in text for regression coefficients. Codes for studies: (●) Dana & Lenz (1986), (Δ) Thun & Starrett (1987), (□) Experiment 2, (Δ) Dana (1981).

Figure 2. Regression of *Artemia monica* life history characteristics on salinity: (A) percent non-hatching cysts, (B) mean day of hatch at 10°C, (C) percent naupliar survival, (D) percent adult survival, (E) adult length, (F) adult weight, (G) mean day of first brood production at 20°C, (H) percent ovigerous females, (I) inter-brood duration at 20°C, (J) number eggs per brood for brood one, (K) number eggs per brood for broods two through four, (L) percent ovoviviparity. Each plot contains means (individual data points), standard error of the mean (vertical lines) and best-fit regression line. Regression coefficients are presented in Table 1. Codes for studies: (●) Dana & Lenz (1986), (Δ) Thun & Starrett (1987), (■) Drinkwater & Crowe (1991), (O) Experiment 1, (□) Experiment 3, (Δ) Dana (1981). Asterisks denote points not included in the regression (see text for explanation).

Figure 3. Length of instars 1 through adults versus salinity for (A) Dana & Lenz (1986) and (B) Experiment 1. Note in (B) no data available for instar 1 and only greater than 120 g l^{-1} for instar 3. Note also salinity levels are different for (A) and (B).

Figure 4. Brood size of the first three to four broods versus salinity for (A) Dana & Lenz (1986) and (B) Experiment 1. Vertical lines are the standard error of the mean. Note salinity levels are different for (A) and (B).

Figure 5. Percent ovoviviparity of the first three broods versus salinity for (A) Dana & Lenz (1986) and (B) Experiment 1. Vertical lines are the standard error of the mean. Note salinity levels are different for (A) and (B).

Figure 1

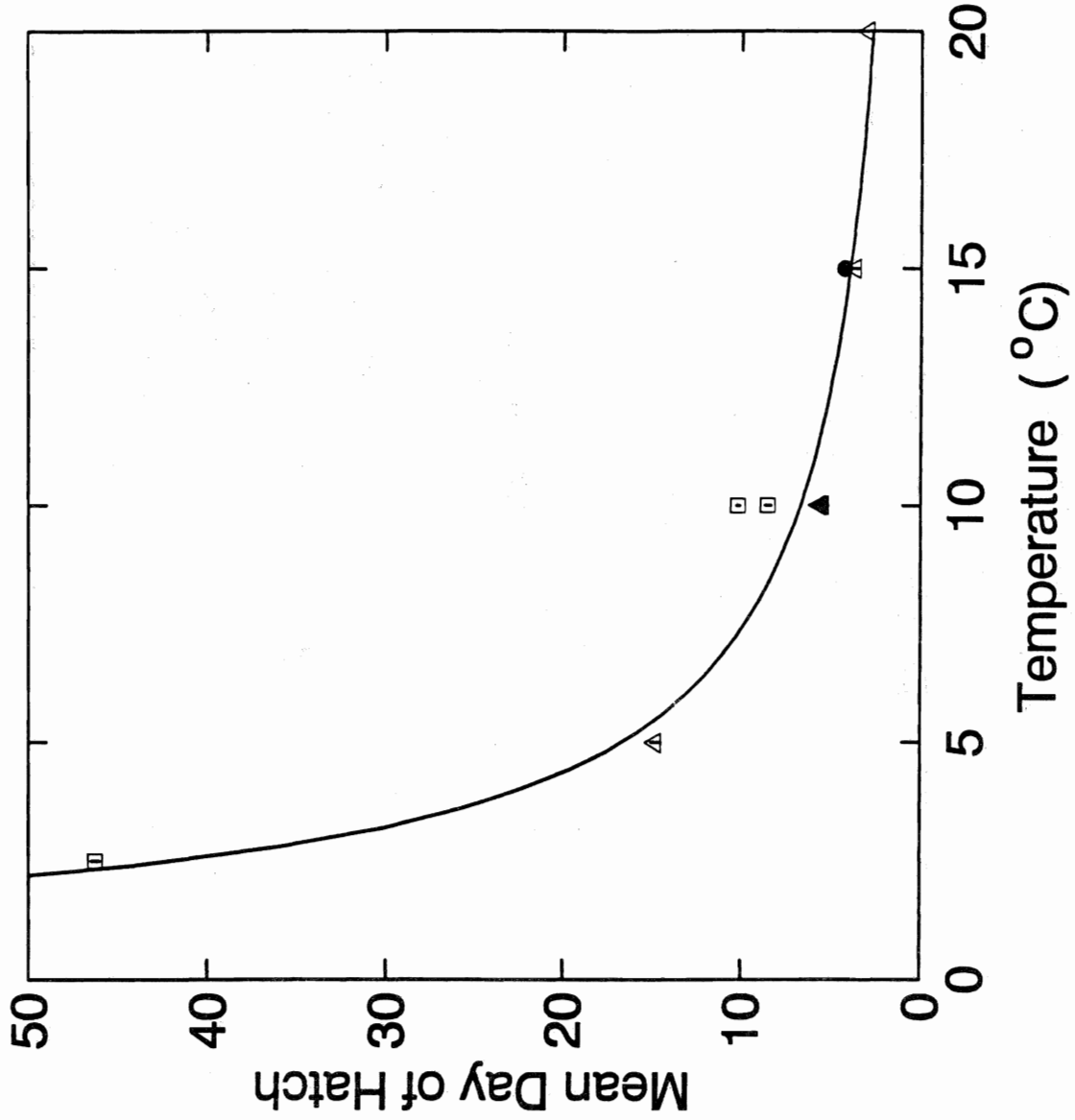


Figure 2

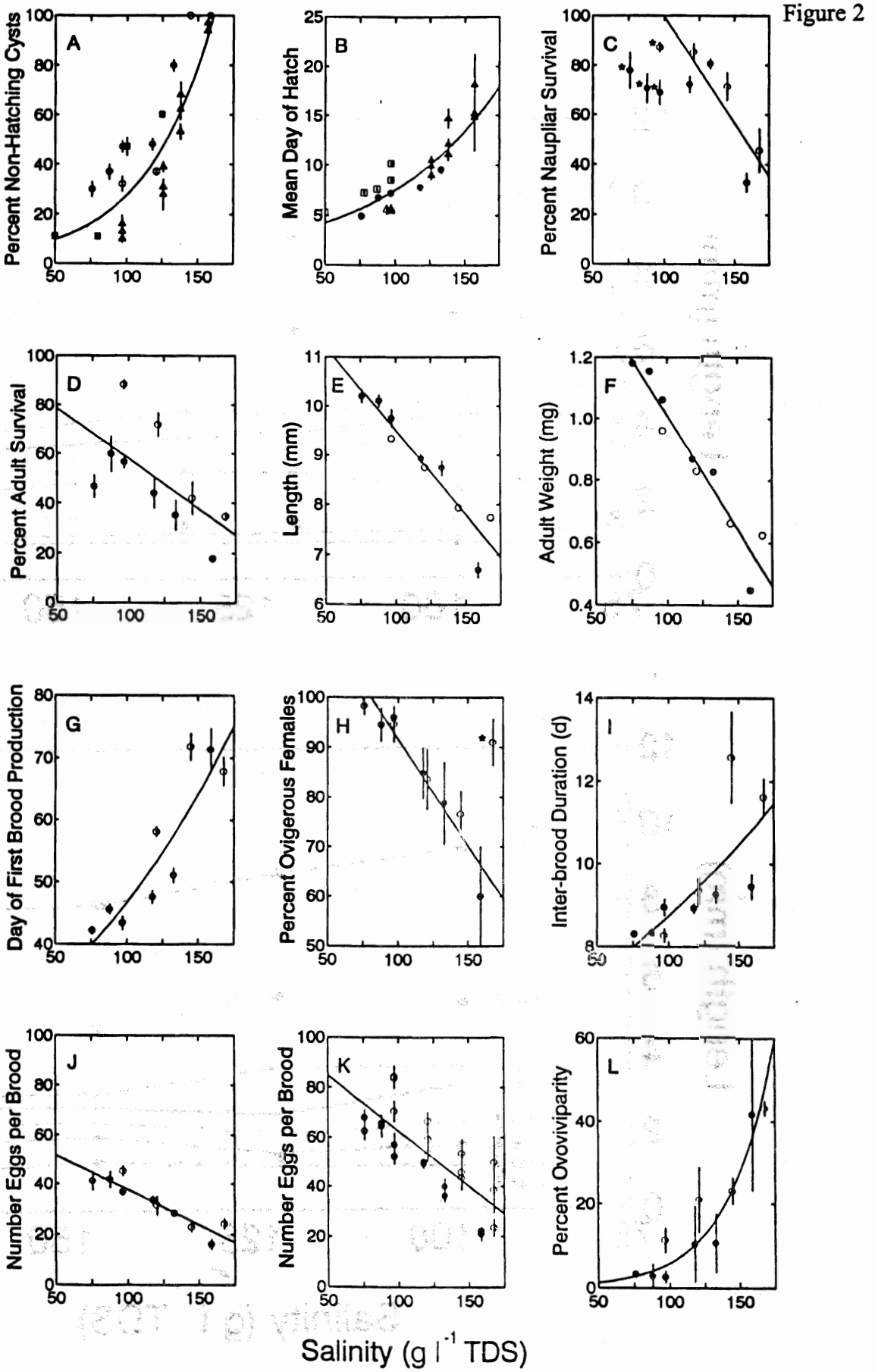

A
Percent Non-Hatching Cysts
B
Mean Day of Hatch
C
Percent Naupliar Survival
D
Percent Adult Survival
E
Length (mm)
F
Adult Weight (mg)
G
Day of First Brood Production
H
Percent Ovigerous Females
I
Inter-brood Duration (d)
J
Number Eggs per Brood
K
Number Eggs per Brood
L
Percent Ovoviviparity
Salinity (g l-1 TDS)

Figure 3

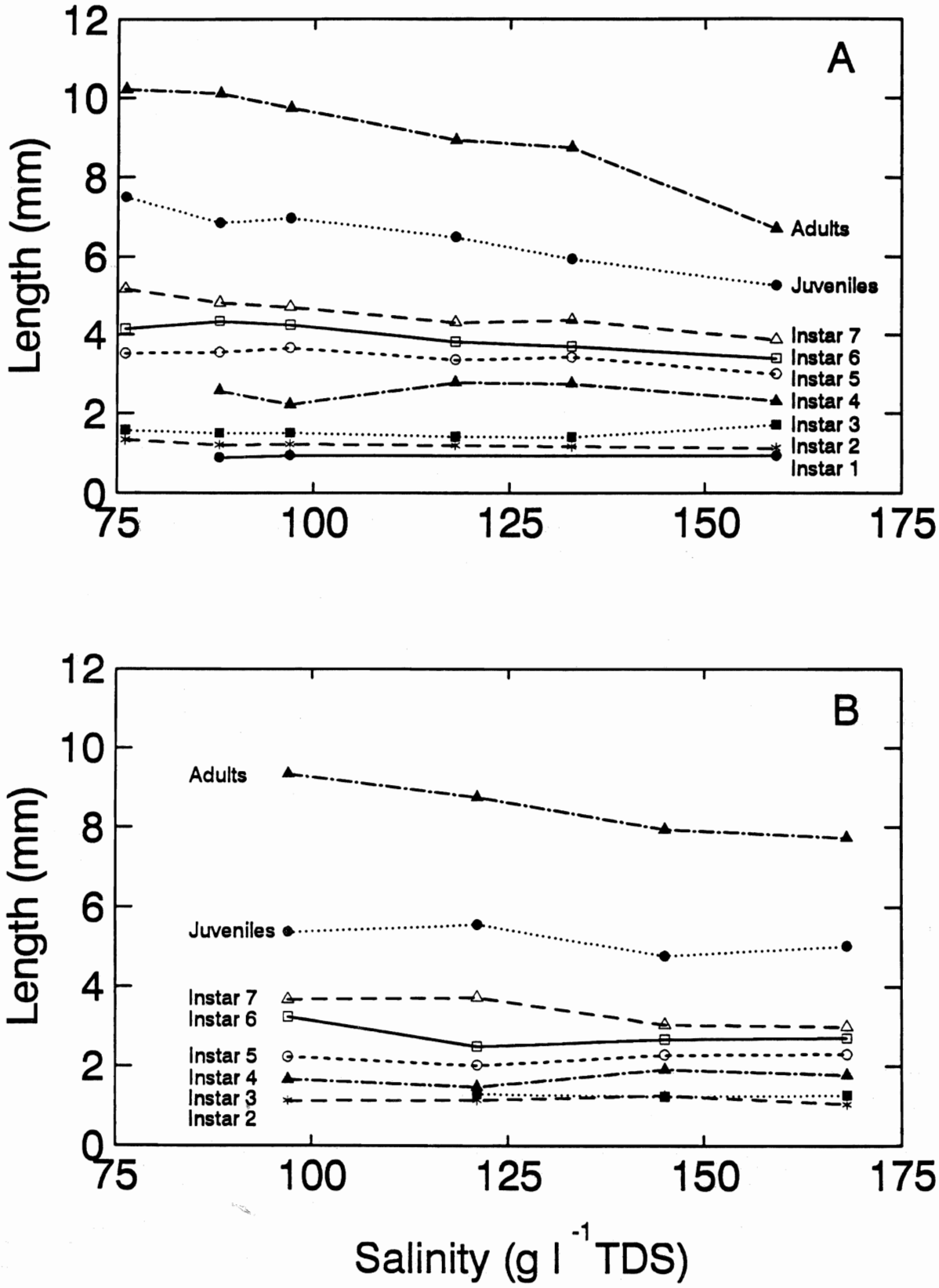

A
B
Length (mm)
Salinity (g l -1 TDS)
Adults
Juveniles
Instar 7
Instar 6
Instar 5
Instar 4
Instar 3
Instar 2
Instar 1
0
2
4
6
8
10
12
75
100
125
150
175

Figure 4

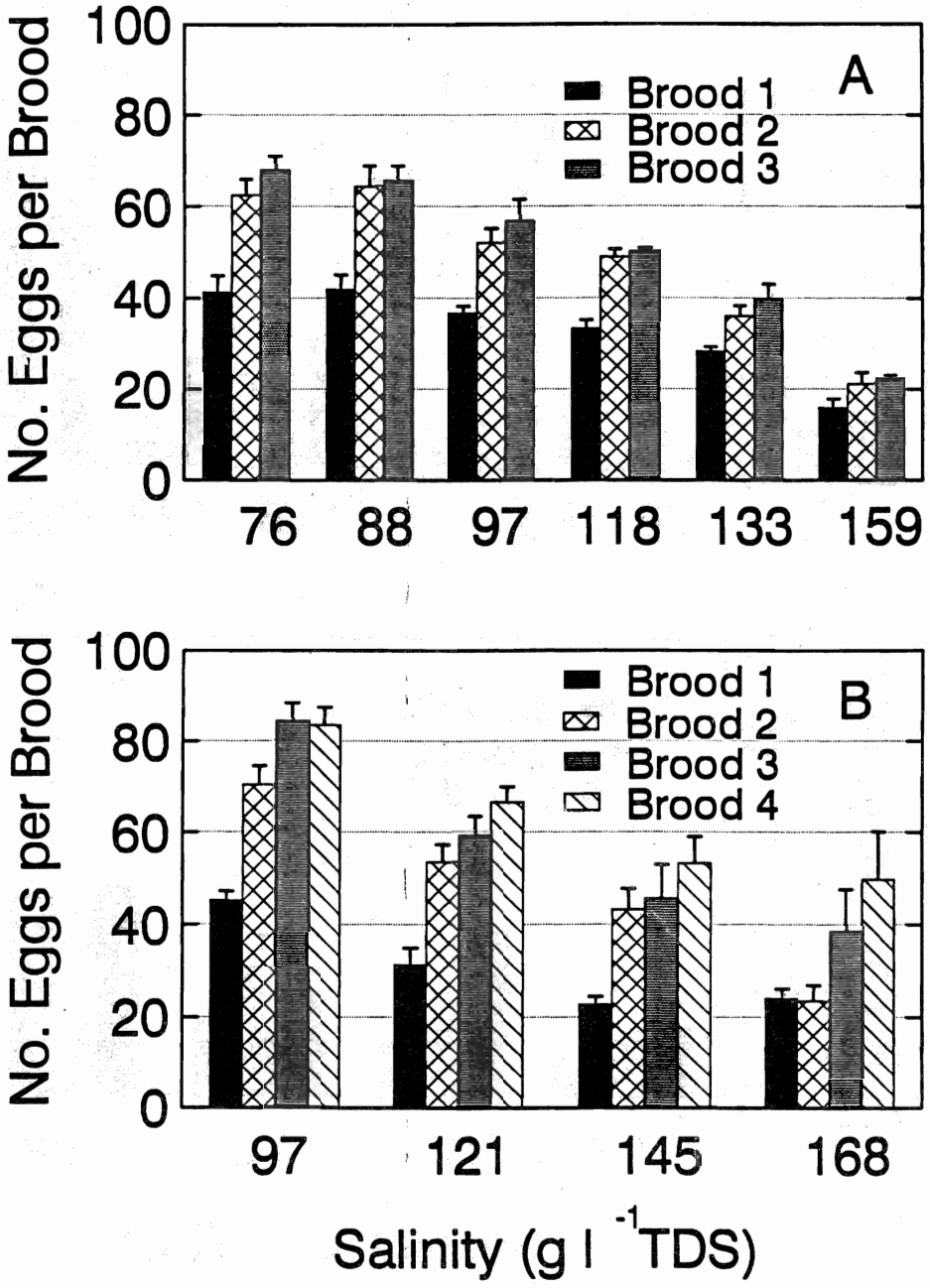
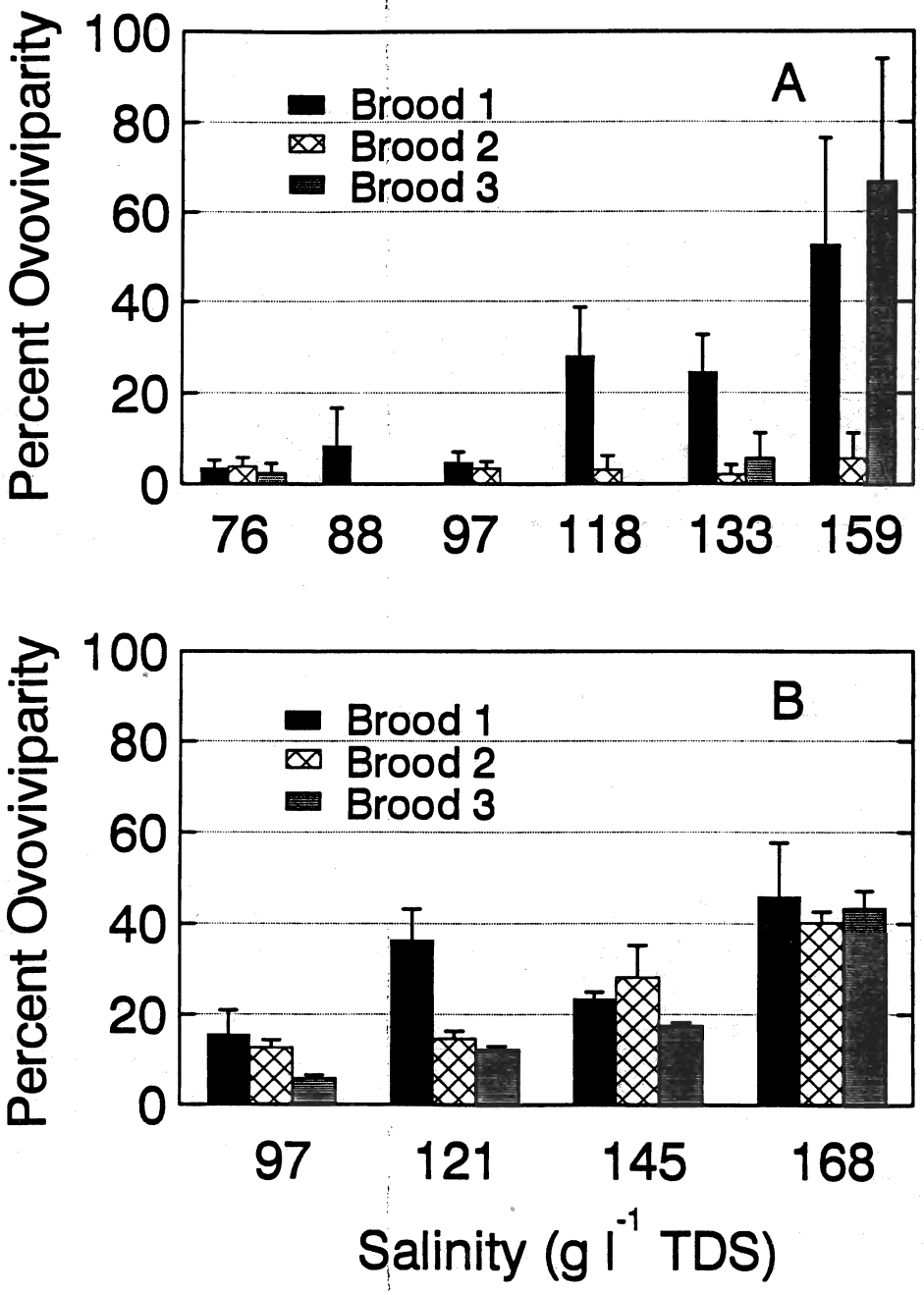

No. Eggs per Brood
100
80
60
40
20
0
Brood 1
Brood 2
Brood 3
A
76
88
97
118
133
159
No. Eggs per Brood
100
80
60
40
20
0
Brood 1
Brood 2
Brood 3
Brood 4
B
97
121
145
168
Salinity (g l -1 TDS)

Figure 5


Percent Ovoviviparity
100
80
60
40
20
0
Brood 1
Brood 2
Brood 3
A
76
88
97
118
133
159
Percent Ovoviviparity
100
80
60
40
20
0
Brood 1
Brood 2
Brood 3
B
97
121
145
168
Salinity (g l-1 TDS)