

Appendix J. Natural History of the Mono Lake Brine Shrimp

This appendix presents a discussion of the life history of the Mono Lake brine shrimp and the physical and biological constraints that affect the shrimp's abundance and distribution in Mono Lake.

CLASSIFICATION AND TAXONOMY

The genus, *Artemia*, has a worldwide distribution. All *Artemia* were formerly considered to belong to a single species, *Artemia salina* (Barigozzi 1974, 1980), but the genus has recently been divided into several closely related species, including the Mono Lake brine shrimp, *Artemia monica* Verrill (Bowen et al. 1980).

Artemia are crustaceans of the order Anostraca, which includes fairy shrimp and brine shrimp. Most anostracans are filter-feeding herbivores inhabiting environments such as temporary pools and saline lakes in which few other animals can survive. The group's success in such environments may be due in part to a flexible reproductive physiology (Browne 1992). Many anostracans, *Artemia monica* included, produce live young when growth conditions are good and produce dormant cysts when conditions are unfavorable (Barnes 1963, Lenz 1982). Anostracans generally tolerate predation and competition poorly and, perhaps for this reason, are rarely found in marine habitats or in freshwater lakes and streams (Zaret 1980).

Though *A. monica* is similar to other *Artemia* species in many respects, Mono Lake differs from habitats of other *Artemia* species. Conditions in Mono Lake are relatively constant, whereas most *Artemia* are found in lakes and pools exhibiting large daily or seasonal variations of temperature, salinity, and dissolved oxygen (Lenz 1984). Mono Lake is deep and contains water perennially, whereas many *Artemia* species inhabit shallow, temporary lakes. Consistent with this difference, cysts produced by *A. monica* are less resistant to dehydration than those of other *Artemia* species. Also, *A. monica* cysts sink, while those of other species are buoyant (Lenz 1980). Mono Lake has a unique water chemistry and other *Artemia* species do not survive well in Mono Lake water (Bowen et al. 1980).

LIFE HISTORY

The life cycle of the Mono Lake brine shrimp, like that of other anostracans, is complex. Development proceeds through seven instars of nauplii larvae, four juvenile instars, and one or more adult instars. Generally, two generations are produced per year: a spring generation originating from overwintering cysts (diapause eggs) produced during the previous summer and fall, and a summer generation originating ovoviviparously (live birth) from adults of the spring generation. In some years, a small third generation of unknown origin (cysts or live birth) appears in autumn (Jellison et al. 1989a, 1991).

Hatching of the spring generation occurs from January to May and the first adults usually appear in May (Lenz 1984). The females reproduce ovoviviparously for about a month, giving rise to the summer generation. In June, adult females of the spring generation switch from ovoviviparous to oviparous (cyst) reproduction, producing cysts that settle to the lake bottom until the following year (Jellison et al. 1989b). The summer generation matures in July and August and primarily reproduces oviparously (Lenz 1984).

Cyst production rates were measured *in situ* in 1986 and 1987 by means of sediment traps and were estimated for 1983 to 1987 from data on the abundance of oviparous adult females and their average fecundity (cyst brood size and frequency of brood production) (Dana et al. 1990). The sediment trap data indicated that annual cyst production was 3.4 million cysts per square meter (cysts/m²) in 1986 and 7.3 million cysts/m² in 1987 (Figure J-1). The data on adult female abundance and fecundity indicated that from 1983 to 1987 annual cyst production ranged between 2.4 million cysts/m² (in 1986) and 5.1 million cysts/m² (in 1987) (Figure J-1).

The estimates of annual cyst production greatly exceeded estimates of abundance of first instar nauplii produced in the following spring. This difference was partly due to the absence of oxygen in sediments as a result of chemical stratification. Cysts in anoxic sediments generally do not hatch (see below), and from 1984 through 1988 sediment oxygen concentrations were less than 1 milligram per liter (mg/l) in 51-58%, by area, of sediments (Dana et al. 1990). However, even when annual cyst production for 1983 to 1987 was estimated for oxygenated sediments only, numbers of first instars produced in the following spring ranged from 2.00% to 2.82% of cyst production (Jellison et al. 1990). In 1983, first instar production was estimated as only 0.33% of cyst production (Jellison et al. 1990). These results indicate that mortality is very high for cysts or recently hatched first instars.

Time of development, which is strongly affected by temperature (see below), is about 2 days at 20°C for each of the 12 preadult instars, for a total development time of 24 days from hatching to adult (Jellison et al. 1989a). In development experiments designed to mimic Mono Lake conditions, total development time (time from hatch to sexual maturity) for the spring generation averaged 57 days under conditions of high food supply (i.e., ambient algal density during spring) and 62 days under conditions of low food supply, and total development time for the summer generation with low food supply (i.e., ambient algal density during summer) averaged 24 days (Figure J-2) (Jellison et al. 1989a). The shorter development time of the summer generation was due to the higher summer water temperatures.

Survivorship to adulthood in the development experiments was 46% for the spring/ high food treatment, 30% for the spring/low food treatment, and 51% for the summer treatment (Figure J-3) (Jellison et al. 1989a). The average daily mortality rates for the three treatments were calculated to be 1.2%, 1.8%, and 2.2%.

EFFECTS OF ENVIRONMENTAL FACTORS ON DEVELOPMENT, SURVIVAL, AND REPRODUCTION

Temperature

Ambient temperature greatly affects rates of development of Mono Lake brine shrimp and is a major determinant of seasonal variations in shrimp production. Regression of development time on temperature explained 80% of the variation in development times in the brine shrimp development experiments and yielded the equation $DT = 285.7T^{-1.658}$, where DT is development time per instar (days), and T is temperature (°C) (Jellison et al. 1989a). As noted above, the summer generation of shrimp develops much more quickly than the spring generation because of the higher summer water temperatures. Water temperatures in the upper mixed layer in Mono Lake are generally about 5°C-15°C in spring and about 15°C-20°C in summer (Jellison et al. 1990).

Effect of temperature on reproductive output of the brine shrimp was difficult to assess, in part because effects of temperature were confounded with those of food supply. Brood size was a function of adult body size, with larger females producing larger broods (Jellison et al. 1989b), and body size of the summer generation of shrimp was less than that of the spring shrimp. However, the smaller body size of the summer shrimp could be due to the low level of food available during summer as well as to the higher temperatures (Jellison et al. 1989a). In any case, multiple regression analysis using field data indicated that food density alone explained most of the variation in brood size (see below).

Multiple regression on field data also indicated that the proportion of ovigerous (egg-bearing) females increased with female body length and with temperature (measured 15 days earlier). The regression equation is $P = -132.2709 + 4.4697T_{15} + 12.0176L$, where P is the arcsine transform of proportion of ovigerous females, T_{15} is temperature (°C) 15 days earlier, and L is female body length (millimeters). The arcsine transformation was applied to the proportions data to normalize them. Multiple regression indicated that the proportion of females reproducing ovoviviparously decreased with temperature and female body length. Temperature accounted for 78% of the variation (Jellison et al. 1989b). The regression equation is $P = 231.8900 - 7.9920T - 8.3994L$, where P is the arcsine transform of proportion of ovoviviparous females, T is temperature (°C).

Data from various sources indicated that interbrood duration is negatively related to temperature (Jellison et al. 1989b). Thus, shrimp in the summer generation produce broods more frequently than shrimp in the spring generation.

Data from the development experiments and field data indicated that the nauplii survived very poorly at water temperatures below 6°C. Brine shrimp from the Great Salt Lake also perish at temperatures below 6°C (Relyea 1937). Water temperatures fall below 6°C during winter in Mono Lake, so survival of the population from year to year depends primarily on the cysts.

Cysts of Mono Lake brine shrimp require 3 months of dormancy in cold (<5°C) water to hatch (Dana 1981, Thun and Starrett 1986). Following this obligate period of dormancy, time required for hatching of the cysts in the development experiments was negatively related to temperature (Figure J-4) (Dana et al. 1992). Regression of mean number of days to hatching (D) on temperature (T, °C) explained 93% of the variation in mean number of days to hatching and yielded the equation, $D = 139T^{-1.317}$. At a salinity of about 100 g/L of total dissolved solids, which is close to the present salinity of Mono Lake, mean number of days to hatching fell from 42 days to 3 days as temperature rose from 2.5°C to 20°C.

Salinity

High salinities osmotically desiccate aquatic organisms because body fluids are less saline than the surrounding saltwater. Even at sublethal salinities, metabolic costs of osmoregulation reduce the energy available for growth and development. Brine shrimp species accommodate high salinities by active transport of ions and water through the gut and excretion of ions across the branchiae (gills) into the water (Dana et al. 1992). The nauplii have a special neck organ that secretes salts.

Two different bioassay experiments in which Mono Lake brine shrimp were raised at salinities ranging from 76 to 192 g/L total dissolved solids indicated that salinity affects survival, growth, reproduction, and cyst hatching of the shrimp (Starrett and Perry 1985, Dana and Lenz 1986). Present salinity of Mono Lake is about 100 g/L. Regression analyses combining data from these studies and others were used to derive salinity response curves of a number of life history characteristics (Table J-1) (Figures J-6 to J-14) (Dana et al. 1992).

The effect of salinity on cyst hatching may have important effects for the survival of the Mono Lake population. Percent of cysts that failed to hatch rose steadily over the range of salinities tested in the bioassays (Table J-1) (Figure J-5) (Dana et al. 1992). No cysts hatched at a salinity of 160 g/l. Drinkwater and Crowe (1991) showed that cysts do not hatch at a salinity of 140 g/l, which suggests that survival of the brine shrimp population would be jeopardized if Mono Lake salinity was increased to this level. The time required for hatching also increased with salinity (Table J-1) (Figure J-6) (Dana et al. 1992).

Effect of salinity on survival of Mono Lake brine shrimp instars was determined for naupliar instars and for adults, but not for juveniles. Percent survival of nauplii was constant at salinities below about 130 g/l and decreased with salinity at higher values (Table J-1) (Figure J-7) (Dana et al. 1992). Survivorship of adults may have been negatively related to salinity over the full range of salinities tested, but the results at lower salinities showed a good deal of scatter (Table J-1) (Figure J-8) (Dana et al. 1992).

Salinity affected mean length and weight of the shrimp (Dana et al. 1992). Mean lengths and dry weights of adults, juveniles, and naupliar instars 6 and 7 decreased with increasing salinity (Table J-1) (Figure J-9). Mean length of instars 1-5 did not vary significantly with salinity. Dry weight (DW) in milligrams of the shrimp were estimated from lengths (L) in millimeters using the regression equation, $DW = 0.0057L^{2.296}$.

Total development time, measured as days from hatch to production of first brood of eggs was strongly related to salinity. Total development time at 20°C increased from about 40 days to about 70 days as salinity increased from 76 to 159 g/l (Table J-1) (Figure J-10). The percent of ovigerous females, the frequency of brood production, size of the first and size of subsequent broods, and percent of females reproducing oviparously all decreased with increasing salinity (Table J-1) (Figures J-11 to J-14).

Results of the salinity bioassays demonstrated that increasing salinity has several direct negative effects on Mono Lake brine shrimp production. Furthermore, except for survival of nauplii, the effects were continuous over the entire range of salinities tested (i.e., there were no salinity ranges with no effect on the shrimp). It must be noted, however, that the bioassay experiments do not mimic all potential effects of salinity changes under natural conditions. In particular, lower salinity in Mono Lake could lead to invasions by predators or competitors of the brine shrimp, which could reduce productivity of the brine shrimp population.

Dissolved Oxygen

Dissolved oxygen (DO) concentrations in Mono Lake vary with salinity, water temperature, mixing, primary production, and depth. Oxygen is less soluble in saltwater than in freshwater, and saturated oxygen concentrations in the epilimnion of Mono Lake are low to moderate. DO values are 2-6 mg/l in summer when the water is warm, and 4-7 mg/l in winter when the water is cold. Anoxic conditions develop below the thermocline or chemocline in summer due to restricted circulation between the epilimnion and the hypolimnion (NAS 1987).

Brine shrimp cannot live long in anoxic water, so they are largely restricted to the epilimnion during summer stratification. The entire water column is reoxygenated during complete mixing in winter. This reoxygenation is important for the shrimp population because the diapausing cysts, many of which settle on sediments in the hypolimnion, require dissolved oxygen for hatching (Lenz 1984). Under meromictic conditions, nearly 50% of the sediments in Mono Lake are permanently anoxic (Dana et al. 1990), so a

large percentage of the cysts produced during meromictic years fail to hatch. The cysts, however, may remain viable for a number of years and may therefore hatch if sediments are reoxygenated in a later year (Jellison et al. 1989b).

The effect of DO on hatching of cysts in Mono Lake was tested *in situ* in 1985 (Dana et al. 1988). Emergence traps were set on the lake bottom at shallow (7-m depth) and deep (21-m depth) stations to capture brine shrimp nauplii hatching from cysts in the lake sediments. Mono Lake was meromictic in 1985, so the deep station was in anoxic water while the shallow water station was in oxygenated water. In April and May, the mean hatching rates from sediments at the shallow station ranged from 720 to 25,340 nauplii per square meter per day (nauplii/m²-day) while the mean hatching rates from sediments at the deep station ranged from 3 to 138 nauplii/m²-day. In June and July, the mean hatching rates ranged from 140 to 3,200 nauplii/m²-day at the shallow station and from 6 to 13 nauplii/m²-day at the deep station.

Food Supply

The Mono Lake brine shrimp feeds primarily on planktonic algae, though protozoans and bacteria also may be important food sources (NAS 1987). Each year during summer, the shrimp population becomes food limited and the abundance of algae probably affects year-to-year changes in shrimp abundance (Jellison and Melack 1992). The algae-shrimp relationship is complex because, whereas abundance of algae limits the shrimp population during summer, grazing by the shrimp also limits abundance of the algae during summer and excretion of ammonium-nitrogen by the shrimp keeps the algae from being nutrient limited during summer.

Food supply, measured as chlorophyll *a*, affects development, growth, survival, and reproductive output of the brine shrimp population. The development experiments comparing shrimp of the spring generation raised at ambient (high) food densities with those raised at low food densities showed that the shrimp grow and develop more quickly at higher food densities and begin reproducing earlier (Jellison et al. 1989a). However, the effects of food on growth are not significant for early instars (<instar 5 or 6). Survivorship also was higher for shrimp raised at the ambient food densities (Figure J-3).

Multiple regression of field data indicated that oviparous brood size (OBS) is positively related to chlorophyll *a* concentration (Chl.*a*), as milligrams per liter chlorophyll *a*, and female body length in millimeters. The regression equation is $OBS = 1.2514 + 0.0340Chl.a + 0.2235L$ concentration (Jellison et al. 1989b).

CITATIONS

Barnes, R. D. 1963. Invertebrate zoology. W. B. Saunders Company, Philadelphia, PA.

- Barigozzi, C. 1974. *Artemia*: a survey of its significance in genetic problems. *Evolutionary Biology* 7:221-252.
- Barigozzi, C. 1980. Genus *Artemia*: problems of systematics. Pages 147-153 in G. Persoone, P. Sorgeloos, O. Roels, and E. Jaspers (eds.), *The brine shrimp Artemia*, Volume 1, Morphology, genetics, radiobiology, toxicology. Universa Press, Wetteren, Belgium.
- Bowen, S. T., M. L. Davis, S. R. Fenster, and G. A. Lindwall. 1980. Sibling species of *Artemia*. Pages 155-167 in G. Persoone, P. Sorgeloos, O. Roels, and E. Jaspers (eds.), *The brine shrimp Artemia*, Volume 1, Morphology, genetics, radiobiology, toxicology. Universa Press, Wetteren, Belgium.
- Browne, R. A. 1992. Population genetics and ecology of *Artemia*: insights into parthenogenetic reproduction. *Trends in Ecology and Evolution* 7:232-237.
- Dana, G. L. 1981. Comparative population ecology of the brine shrimp *Artemia*. Master's thesis. San Francisco State University. San Francisco, CA.
- Dana, G. L., C. J. Foley, G. L. Starrett, W. M. Perry, and J. M. Melack. 1988. *In situ* hatching of *Artemia monica* cysts in hypersaline Mono Lake, California. *Hydrobiologia* 158:183-190.
- Dana, G. L., R. Jellison, and J. M. Melack. 1990. *Artemia monica* cyst production and recruitment in Mono Lake, California, USA. *Hydrobiologia* 197:233-243.
- _____. 1992. Functional relationships between *Artemia* life history characteristics and salinity. Report to California State Water Resources Control Board and Jones & Stokes Associates, Inc.
- Dana, G. L., and P. H. Lenz. 1986. Effects of increasing salinity on *Artemia* population from Mono Lake, California. *Oecologia* 68:428-436.
- Drinkwater, L. E. and J. H. Crowe. 1991. Hydration state, metabolism, and hatching of Mono Lake *Artemia* cysts. *Biological Bulletin* 180:432-439.
- Jellison, R., and J. M. Melack. 1992. Algal photosynthetic activity and its response to meromixis in hypersaline Mono Lake. Draft manuscript. University of California, Department of Biological Sciences and Marine Science Institute. Santa Barbara, CA.
- Jellison, R., G. L. Dana, and J. M. Melack. 1989a. Phytoplankton and brine shrimp dynamics in Mono lake, California. 1988 Annual Report to the Los Angeles Department of Water and Power.
- _____. 1989b. Phytoplankton and brine shrimp dynamics in Mono lake, California. 1987 Annual Report to the Los Angeles Department of Water and Power.
- _____. 1990. Phytoplankton and brine shrimp dynamics in Mono lake, California. 1989 Draft Annual Report to the Los Angeles Department of Water and Power.
- Jellison, R., G. L. Dana, J. Romero, and J. M. Melack. 1991. Phytoplankton and brine shrimp dynamics in Mono Lake, California. 1990 Draft Annual Report to the Los Angeles Department of Water and Power.
- Lenz, P. H. 1982. Population studies on *Artemia* in Mono Lake, California. Ph.D. thesis, University of California, Santa Barbara. 230 pp.
- _____. 1984. Life-history of an *Artemia* population in a changing environment. *Journal of Plankton Research* 6(6):967-983.

NAS. 1987. See National Academy of Sciences Report.

National Academy of Sciences Report. 1987. The Mono basin ecosystem: effects of changing lake level. National Academy Press.

Pelagos Corporation. Executive summary, a bathymetric and geologic survey of Mono Lake, California.

Relyea, G. M. 1937. The brine shrimp of the Great Salt Lake. *American Naturalist* 71:612-616.

Starrett, G. L., and W. M. Perry. 1985. Multiple generation salinity acclimation experiment. Report to the Los Angeles Department of Water and Power.

Thun, M. A., and G. L. Starrett. 1986. The effect of cold, hydrated dormancy and salinity on the hatching of *Artemia* cysts from Mono Lake, California, U.S.A. Water Quality Division, Department of Water and Power, City of Los Angeles, Los Angeles, California.

Zaret, T. M. 1980. Predation and freshwater communities. Yale University Press. New Haven, Connecticut.