

Ecological studies on *Artemia* : a review

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Introduction

Compared to other aspects of the brine shrimp's biology, ecological studies on *Artemia* are still few in number (Persoone and Sorgeloos, 1980). *Artemia* inhabit hypersaline lakes and ponds, characterized by low species diversity. Because these ecosystems are relatively simple they lend themselves particularly well to quantitative ecological analyses. At the same time the large range of habitat characteristics under which *Artemia* live provides an unusual variety of ecological responses that can be studied within a single genus. Furthermore, a better knowledge of its ecology will be of value in optimizing the production of *Artemia* for aquacultural use. This review is intended to complement a previous one by Persoone and Sorgeloos (1980). Focus will be on population dynamics, life-history strategies, productivity, and biological interactions. Each topic will be discussed first with reference to Mono Lake, California, USA, and Great Salt Lake, Utah, USA. Although not representative of all natural *Artemia* habitats, studies on these two lakes have included a greater diversity of ecological aspects than most. Next, these studies will be compared with those on other habitats. The emphasis will be on ecological responses to various biotic and

abiotic environmental factors. Discussions of habitat characteristics *per se* are treated elsewhere (e.g. Cole and Brown, 1967 ; Persoone and Sorgeloos, 1980 ; Bowen *et al.*, 1984).

Population dynamics

The population dynamics (e.g. seasonal cycles, abundance patterns and age structure) of zooplankton are affected both by the abiotic environment and by biological interactions. The latter are limited in hypersaline communities owing to low species diversity. Therefore, the abiotic factors, especially those regulating seasonal characteristics, have particularly important impact. Two critical factors determine the *Artemia* population dynamics : a) whether lake conditions are such that animals can survive throughout the year ; and b) whether the seasonality of the environment is predictable or not.

In large temperate lakes such as Great Salt Lake and Mono Lake, annual salinity changes are small and seasonality is determined primarily by the temperature cycle. The population dynamics in these two lakes have been detailed by Mason (1967), Wirick (1972), and Lenz (1980, 1982, 1984). The cold temperatures during the winter (around 2 °C) preclude the survival of the *Artemia*, and the annual cycle begins in spring with the hatching of diapause cysts. This first generation reaches maturity in May/June and a second generation is produced ovoviviparously. Two major generations have been reported per year in both lakes (Gillespie and Stephens, 1977 have estimated up to five in Great Salt Lake). In June/July reproductive mode switches and becomes primarily oviparous. During the fall the population steadily declines due to lack of recruitment, increased predation (Cooper *et al.*, 1984), and thermal death. Similar temperature regulated annual cycles can be expected in other relatively deep (mean depth greater than 2 m) temperate lakes such as Abert Lake, Oregon, USA and some of the inland Russian lakes (Spitchak, 1980). In some lakes, such as Lake Shurabil, Iran (Ahmadi, 1987), seasonal fluctuations in salinity can be substantial, but if the salinity ranges are within the tolerance limits for *Artemia*, one might expect seasonality to be primarily determined by temperature, with adults disappearing during the cold winters.

In many habitats salinity fluctuations are extreme. High salinity or desiccation kill *Artemia* and hence can be the primary factor driving seasonality. In shallow (mean depth less than 1 m) temperate ponds the annual temperature cycle is often complemented by large changes in salinity. Dana (1981, 1984) described such a physico-chemically driven cycle in Fallon Ponds, Nevada, USA. These ponds fill during winter precipitation and dry up during the summer. An *Artemia* population made up of nauplii was present in March and Dana's data suggest two or three generations during an approximate growth period of 5 months. Environmental stress increased throughout the summer as the ponds became increasingly saline, and the *Artemia* population disappeared a few weeks before complete desiccation.

Shallow tropical and sub-tropical hypersaline ponds, which may have a smaller annual temperature range, can still become uninhabitable for *Artemia* during part of the year due to salinity fluctuations. Although, as in ephemeral temperate ponds, tropical lakes may desiccate, studies on Caribbean and Indian lakes have shown that the disappearance of the *Artemia* may also be due to extreme dilution (Curaçao and Bonaire, Antilles : Kristensen and Hulscher-Erneis, 1972 ; Veppalodai and Tuticorin, South India : Ramamoorthi and Thangaraj, 1980 ; Didwana Lake, Rajasthan, India : Bhargava *et al.*, 1987). It is not clear how these ponds become resettled by *Artemia* as the salinity increases again.

The ecological situation changes markedly if there is no interruption in the growth period, so that the population is no longer dependent on a cyst hatch for the annual re-seeding of the pond. A well-documented example occurs in Lake Grassmere, New Zealand (Wear and Haslett, 1987). This lake has an insular, temperate climate with water temperatures ranging from 5 to 23 °C (Wear and Haslett, 1987). During the winter, *Artemia* abundances are lowest and females suspend reproduction, but viable individuals survive. In the spring, population numbers increase through ovoviviparous reproduction rather than cyst hatching, and ovoviviparity continues throughout the reproductive season. This results in many overlapping generations in a year (up to eight as estimated by Wear and Haslett, 1987). Oviparous reproduction is uncommon among the Lake Grassmere females. The reproductive emphasis appears to have shifted with the difference in habitat characteristics.

Similar year-round favorable conditions probably occur in several sub-tropical and tropical habitats. Solar Lake, Sinai, Egypt is characterized by a relatively constant environment and the parthenogenetic strain that inhabits this lake reproduces primarily by ovoviviparity (Por, 1969 ; Cohen *et al.*, 1977a ; Dimentman and Spira, 1982). Although complete annual population studies are lacking, uninterrupted growth seasons may also be expected at Laysan Lagoon, Hawaii, USA (Lenz and Dana, 1987), Galapagos Islands, Ecuador (Bowen, pers. commun.), and Canary Islands, Spain (Amat, 1982). Like the *Artemia* in Solar Lake and in Lake Grassmere, the females from these habitats appear to have lost or nearly lost the ability to produce cysts. Because *Artemia* are long-lived compared to their generation time, and females produce multiple broods, these tropical and sub-tropical populations, like that of Lake Grassmere, probably have a large number of overlapping generations per year with relatively small fluctuations in population densities.

Large temperate lakes like Mono Lake and Great Salt Lake have a predictable cycle, though a strongly seasonal one, with relatively little variation between years. These lakes do, of course, undergo longterm changes due to climatic fluctuations and human intervention (Mason, 1967 ; Winkler, 1977). However, the relative predictability of the environment is reflected in the reproducible dynamics of the *Artemia* population (Lenz, 1984). Permanent sub-tropical and tropical lakes are less seasonal, but may or may not be more predictable. Solar Lake, at least, has been described as a constant and predictable environment (Dimentman and Spira, 1982). By comparison the small temporary ponds, like Fallon ponds (Nevada, USA), are probably very unpredictable. Because of the small volume of these habitats, they can be expected to respond very quickly to even short periods of a particular weather condition.

Artemia life histories

Theoretical and empirical studies on life-history strategies have attempted to relate reproductive and lifespan traits to environmental characteristics (Stearns, 1977). Because of the diversity of *Artemia* habitats, it is not surprising that life-history traits vary among strains (Browne, 1980 ; Amat, 1982 ; Browne *et al.*, 1984). Although comparative life-history data have been collected for a large number of *Artemia* populations under laboratory conditions (*e.g.* Browne *et al.*, 1984), little is known about how these correlate with specific environmental conditions. *Artemia* is a good subject for the study of life-history strategy, because predictions can be tested directly through experimentation owing to ease of culture and short generation time,

and by comparing populations from the wide range of habitats available. Further investigations on life-history strategies in *Artemia* could thus contribute significantly to evolutionary theory.

PARTHENOGENETIC VERSUS BISEXUAL STRAINS

Unlike Cladocera, which are capable of both unisexual and bisexual reproduction, individual *Artemia* strains are either bisexual or parthenogenetic. The selective advantages and costs of parthenogenesis and sex are discussed extensively in the literature (e.g. Williams, 1975; Daly and Wilson, 1978; Lloyd, 1980; Browne and MacDonald, 1982). Although parthenogenetic reproduction confers an immediate advantage since it is more efficient, it also tends to promote low genetic variability (Abreu-Grobois and Beardmore, 1980). Bisexual reproduction maintains higher genetic variability among individuals, which would be advantageous in dispersal to differing habitats (Williams, 1975) and would presumably allow a more rapid evolutionary response to environmental change (Daly and Wilson, 1978).

Parthenogenesis in *Artemia* predominates among Old World strains, whereas in the New World only sexual reproduction has been reported (Abreu-Grobois and Beardmore, 1980; Bowen *et al.*, 1980; Persoone and Sorgeloos, 1980; Browne and MacDonald, 1982). Parthenogenetic *Artemia* may be absent from the New World, because it may not have arisen more than once (Abreu-Grobois and Beardmore, 1980; Browne and MacDonald, 1982) and parthenogens may not have dispersed to the New World. *A. parthenogenetica* has been introduced in Australia, where it is doing well (Geddes, 1980).

In the Old World where bisexual and parthenogenetic populations overlap in their distribution, the bisexual strains tend to occur in inland lakes, and the parthenogenetic *Artemia* are found in coastal salterns (Browne and MacDonald, 1982). Amat (1983) reported the co-occurrence of a bisexual and a parthenogenetic strain in Cadiz, Spain, and found that the bisexual strain dominated during the winter and spring at lower salinities and temperatures. The parthenogenetic strain occurred during the summer and fall at higher temperatures and salinities. Browne *et al.* (1984) found that in addition to mode of reproduction, the Old World bisexual and the parthenogenetic strains differed consistently with respect to other reproductive characteristics. The field data from Cadiz and the laboratory data suggest that in the Old World the two types of *Artemia* occupy somewhat different niches. How this correlates with dispersal characteristics or habitat unpredictability is still uncertain. It seems somewhat contradictory that the Old World bisexual strains have few offspring (see section on reproductive output), since adaptations for dispersal usually include high fecundity. Further studies on the ecology of parthenogenetic and bisexual strains are needed before the selective advantages and disadvantages of the two types of reproduction can be understood.

OVOVIVIPARITY VERSUS OVIPARITY

Artemia females of most strains can reproduce both ovoviviparously and oviparously. Nauplius production allows a rapid population growth, whereas the production of diapause cysts ensures the survival of a population through unfavorable conditions (Persoone and Sorgeloos, 1980; Lenz and Dana, 1987). Upon maturation under constant laboratory conditions, *Artemia* females tend to reproduce ovoviviparously at first and then switch to oviparity (Amat, 1982; Dana and Lenz, 1986). Switching reproductive mode in the natural environment can be expected to vary

depending on the environmental conditions. A female should continue to reproduce ovoviviparously as long as there is a good probability that her offspring will reproduce themselves. If, however, conditions are such that offspring survival is unlikely, then females should invest in oviparous reproduction, in the expectation that these cysts will hatch under more favorable conditions.

Artemia females differ in their genetic tendency to reproduce either ovoviviparously or oviparously depending on strain origin (Amat, 1982; Browne *et al.*, 1984). The preference for either reproductive mode appears to be related to the length of the inhabitable period of their environment. In both Mono Lake and Great Salt Lake, females reproduce at first ovoviviparously, and then switch to cyst production for the remaining summer and fall (Wirick, 1972; Lenz, 1984). Second generation females only reproduce oviparously. In these habitats it appears that after the initial population increase the reproductive effort is focused on providing seeds for the following year. Similarly, *Artemia* inhabiting unpredictable ponds or ponds with a short growth season would be expected to emphasize oviparity, to the near exclusion of ovoviviparity. Although most other Anostraca are only capable of oviparous reproduction, no *Artemia* strains have been reported to lack the ability to produce nauplii. Browne *et al.* (1984) found that oviparity was the preferred mode of reproduction in Old World sexual *Artemia*, and they therefore concluded these strains occur in uncertain habitats. In contrast, loss or near loss of oviparity has occurred in females inhabiting lakes with favorable conditions year-round (Lenz and Dana, 1987; Wear and Haslett, 1987). Browne *et al.* (1984) suggested that the greater preference for ovoviviparity in parthenogenetic strains indicated an adaptation to more certain habitats. This prediction awaits field verification. Thus, *Artemia* in different habitats differ markedly in this important parameter of reproductive strategy. The data are suggestive, though not conclusive, that this is mainly due to length of growth period.

REPRODUCTIVE OUTPUT AND LIFESPAN

All *Artemia* females are iteroparous, *i.e.* they produce multiple broods during their lifespan. The reproductive output, however, varies greatly among strains (Browne, 1980; Amat, 1982; Browne *et al.*, 1984). In general, a large number of offspring is advantageous in rapidly growing populations, whereas a smaller reproductive output can be expected in populations that are near carrying capacity and only maintaining population size. Females with a short reproductive period will tend to concentrate their reproductive efforts in a small number of large and closely spaced broods. Longer lived ones will distribute their reproductive effort. In theory high fecundity would also be expected in populations that have high mortality rates, which in *Artemia* would include those strains inhabiting unpredictable or temporary environments.

Under constant laboratory conditions Browne *et al.* (1984) found that lifetime production of offspring per female ranged from 100 to 1 600 offspring depending on strain. The total reproductive output reflects a combination of brood size, brood interval, and length of reproductive period. The lowest output occurred among Old World bisexual *Artemia*, which were characterized by small broods (20 to 30 offspring/brood), short reproductive periods (20 to 40 days) and relatively short brood intervals (3.5 to 4.8 days). Parthenogenetic females from Turkey and India, and *Artemia franciscana* females, both had high reproductive outputs (600 to 1 600 offspring) with brood sizes ranging from 50 to 110 offspring. These more fecund *Artemia* strains were also characterized by long reproductive periods (40 to almost 110 days), and for

the parthenogenetic females by longer brood intervals (4.6 to 6 days). Browne *et al.* (1984) ascribed the dominance of *A. parthenogenetica* in the Old World to their higher fecundity.

The laboratory data may not be representative of fecundity in the field. Genetic differences in reproductive characteristics are further modified in the natural habitat in response to environmental factors. Brood size and interval, and longevity change as a function of food level (Browne, 1982), temperature (Von Hentig, 1971; Wear and Haslett, 1987) and salinity (Dana and Lenz, 1986; Wear and Haslett, 1987). In many *Artemia* habitats at least two of these three factors undergo large seasonal fluctuations. Brood sizes determined in the field vary temporally within a habitat, as well as among habitats (Lenz and Dana, 1987). Small brood sizes in Boca Chica Salt Lake, Venezuela (mean broods of five to six offspring; Scelzo and Voglar, 1980) and Laysan Lagoon (mean broods of two to three offspring; Lenz and Dana, 1987) suggest that the populations in these habitats were near their carrying capacity. In contrast, the larger brood sizes in Mono Lake (Lenz and Dana, 1987) and Great Salt Lake (Wirick, 1972) may be necessary for a rapid population increase in the spring, and the large investment in cysts may offset high mortality rates. Brood intervals and lifespan parameters are less well studied in the field. The first generations in Mono Lake and Great Salt Lake are slow growing, taking approximately 2 months to reach sexual maturity (Wirick, 1972; Lenz, 1980, 1984). Length analyses on adults in Mono Lake suggest that some first generation animals live until September (Lenz, 1984). This would indicate a longevity of 6 to 7 months with a potential of 10 broods and over 500 offspring, which is lower than Browne *et al.* (1984)'s laboratory results for *A. franciscana*.

Further knowledge is needed before we can understand the key factors that govern life-history traits in *Artemia*. Comparative data from laboratory experiments have underscored the variation among strains. The genetic variation undoubtedly reflects adaptations to habitats with different selective pressures. Field data, however, are still limited, and it is difficult to relate the available information to present theory.

Production in *Artemia* habitats

Primary production, which is the total amount of new organic matter produced through photosynthesis, is regulated by both abiotic (*e.g.* nutrients and temperature) and biotic (*e.g.* grazing) factors. Although secondary production is also influenced by abiotic factors, it ultimately seems to be limited by the primary production. Por (1980) suggested that in saline lakes, overall production decreases with increasing salinity, in part due to the rise in physiologically stressful conditions. Although this scheme might apply to saline lakes overall, it understates the variation among *Artemia* habitats and the factors controlling productivity in these environments. Density estimates for *Artemia* are available for a number of habitats, but secondary production estimates are almost non-existent. Nutrient concentrations and primary production have been measured in a few hypersaline lakes, and these studies are reviewed below.

NUTRIENT CONCENTRATIONS

The availability of nutrients, in particular nitrogen and phosphorus, is a major factor affecting primary production in aquatic systems. Freshwater lakes are usually phosphate limited, in contrast to marine environments, where nitrogen limitation is more usual. In Great Salt Lake, nutrient concentrations are high during the summer (Table I; Stephens and Gillespie, 1976),

These authors found phosphate levels to be above $32 \mu\text{mol/l}$ in all samples. However, ammonium and nitrate concentrations did not increase until after April and enrichment experiments suggest nitrogen limitation before then (Stephens and Gillespie, 1976). Mono Lake is similar to Great Salt Lake: phosphate is abundant throughout the year, whereas ammonium and nitrate concentrations in the epilimnion are low in the spring and increase through the summer (R. Jellison, pers. commun.).

The accumulation of nutrients during the summer may be in part the result of *Artemia* excretion. Moffett and Fisher (1978) measured ammonium production by *Artemia* in laboratory experiments. From their data it can be estimated that at 20°C , and adult *Artemia* densities between 1 and 10 ind./l, ammonium production would range from 0.2 to $2.4 \mu\text{mol/l/day}$; at 25°C this estimate rises to 0.4 to $4.1 \mu\text{mol/l/day}$. These estimates for ammonium regeneration are high compared to other aquatic environments (e.g. Ganf and Blazka, 1974; Liao and Lean, 1978). Excretion rates in zooplankton change as a function of the physiological and nutritional state of the animal (e.g. Blazka *et al.*, 1982), and actual *Artemia* excretion rates in the natural environment may be different. Nutrient recycling by *Artemia* may be particularly important in Great Salt Lake and recently in Mono Lake, since both of these lakes are meromictic and lack an annual turnover, so the hypolimnion is in effect a nutrient sink.

Nutrient concentrations for other *Artemia* habitats are presented in Table I. Nutrient levels are reported high for habitats which have an inland location (e.g. Mono Lake and Great Salt Lake). Concentrations are lower in near-ocean lakes and salterns, as would be expected from the low nutrient levels of the seawater which supplies these habitats. Such differences in nutrient levels might be expected to be reflected in the primary and secondary production levels of inland *versus* near-ocean habitats.

PRIMARY PRODUCTION

Primary production in Great Salt Lake and Mono Lake is high. Mono Lake has an estimated annual production of $1\ 000 \text{ gC/m}^2/\text{year}$ (Mason, 1967). During the summer, algal biomass is low, probably as a result of grazing by the *Artemia*, and primary production is low. From July to September, 1976, mean daily primary production was about $100 \text{ mgC/m}^2/\text{day}$ (Winkler, 1977). In Great Salt Lake annual primary production was estimated at $160\text{--}220 \text{ gC/m}^2/\text{year}$, which is well below Mason's estimate for Mono Lake, but still moderately high compared to other lakes (Wetzel, 1975). Little Manitou Lake, Saskatchewan, Canada, another inland lake, seemed to be less productive and Haynes and Hammer (1978) estimated an annual primary production of only $70 \text{ gC/m}^2/\text{year}$. None of these estimates includes benthic production, which may be substantial, in particular in the shallow lakes such as Great Salt Lake and Little Manitou Lake. More primary production measurements are needed before the relationship between production and abiotic factors can be established for *Artemia* habitats.

Low primary production has been measured in coastal salterns such as Lake Grassmere (Wear and Haslett, 1987) and the ESSA salterns in Mexico (Javor, 1983). Similar to the shallow inland lakes, the contribution of the benthos to saltern production is probably important (Javor, 1983).

Meromixis, which occurs in a number of *Artemia* habitats (e.g. Solar Lake, Sinai, Egypt; Zuni Salt Lake, New Mexico, USA; Great Salt Lake, Utah, USA), has a major effect on primary production. First of all the chemical stratification serves as a barrier for nutrients between the hypolimnion and the epilimnion. Secondly, photosynthetic bacteria tend to grow in abundance

TABLE I
Nutrient concentrations in *Artemia* habitats

<i>Artemia</i> habitat	Source	Month	Nutrient concentration ($\mu\text{mol/l}$)			
			PO_4	NH_4	NO_3	NO_2
Alviso Salt Pond #6*, California, USA	Carpelan (1957)	March	0.24	—	0.89	—
		October	0.42	1.21	0.12	—
Boca Chico Salt Lake*, Venezuela	Scelzo and Voglar (1980)	June	0.14	1.7	0.08	0.007
			0.08-0.34	1.2-3.2	0.06-0.09	0.003-0.018
Didwana Lake**, India	Bhargava <i>et al.</i> (1987)	January-	0.89	—	13.6	0.13
		December	0.20-2.39	—	6.8-24.5	0.01-0.28
ESSA saltern*, Mexico	Javor (1983)	January-	<1	<5	<2	—
		December				
Lake Grassmere*, New Zealand	Wear and Haslett (1987)	January-	0-0.01	0.002-0.11	0-0.08	—
		December				
Great Salt Lake**, Utah, USA	Stephens and Gillespie (1976)	April-	≥ 32.3	37.5-50	2.1-12.9	—
		November				
Little Manitou**, Saskatchewan, Canada	Hammer (1978)	March-	10	4300	20	—
		September	2-30	1400-7100	0-110	

* Coastal
** Inland
— No data.

in the metalimnion (Cohen *et al.*, 1977ab). Algal and bacterial production has been studied in detail in Solar Lake, Sinai (Cohen *et al.*, 1977ab). It was determined that the bacteria plates in the metalimnion contribute 92 % of total water column primary productivity. In the epilimnion primary production is low, possibly because of *Artemia* grazing pressure, which is very high (Cohen *et al.*, 1977b).

SECONDARY PRODUCTION

It is difficult to estimate secondary production of a zooplankton population without a detailed understanding of its dynamics and life-history characteristics. This is further complicated by continuous changes in the abiotic environment (*e.g.* seasonal temperature fluctuations) and temporal changes and spatial patchiness in the food supply, all of which affect growth, reproduction and mortality. It is therefore not surprising that production estimates for natural *Artemia* populations are uncommon. Gillespie and Stephens (1977) estimate an annual *Artemia* production in Great Salt Lake at 100 to 200 g dry weight/m²/year. This estimate is based on preliminary data and additional information is needed before *Artemia* production in natural habitats can be judged more accurately. Under experimental, high food conditions *Artemia* production is very high (*e.g.* 208 g dry weight/m³/day, Sorgeloos and Persoone, 1975).

Biological interactions

Biological interactions can be as important as abiotic factors in affecting life-history strategies and population dynamics. The two types of interactions, which are usually studied in greatest detail, are predator-prey and competition. In hypersaline communities the *Artemia*-phytoplankton interaction is one of the major ones. However, in some *Artemia* habitats predation and competition can be important.

GRAZING

Herbivorous zooplankton have been implicated in controlling phytoplankton standing stock and influencing natural phytoplankton assemblages through selective grazing (Wetzel, 1975). *Artemia* can attain high densities in their natural habitats (*e.g.* Bradbury, 1971; Wirick, 1972; Gillespie and Stephens, 1977; Ramamoorthi and Tangaraj, 1980; Scelzo and Voglar, 1980; Lenz, 1984) and negative correlations between their densities and phytoplankton abundances have been attributed to grazing by the *Artemia* (Anderson, 1958; Mason, 1967; Wirick, 1972). As in many other zooplankton (*e.g.* Frost, 1972), grazing rates in *Artemia* are a function of algal densities (Reeve, 1963; Lenz, 1982). Peak filtering rates measured in the laboratory are between 150 and 250 ml/adult/day (Reeve, 1963; Lenz, 1982). At this feeding rate, densities of 4 to 7 adults/l would clear the water column once per day. In Mono Lake, with mean epilimnetic densities frequently above 4/l, grazing by *Artemia* exceeded phytoplankton growth during the summer (Lenz, 1982). *Artemia* may thus be food limited in this situation and might well be in many others. Although food limitation in *Artemia* has not been demonstrated, small summer brood sizes in Mono Lake (Lenz and Dana, 1987), Great Salt Lake (Wirick, 1972), Boca Chica Salt Lake (Scelzo and Voglar, 1980) and Laysan Lagoon (Lenz and Dana, 1987) support this hypothesis.

Artemia is usually described as an indiscriminate filter-feeder (Persoone and Sorgeloos, 1980) and no studies have indicated selective feeding. However, Gibor (1956) has demonstrated that *Stichococcus* cannot be digested by *Artemia* and thus passes unharmed through the gut. This may explain the high densities of this alga in the high salinity pools in the Alviso salt ponds (San Francisco Bay, California, USA), and the virtual absence of *Dunaliella salina*, which could grow readily under the existing physico-chemical conditions (Carpelan, 1957).

PREDATION

In spite of its tolerance of salinities below that of seawater, *Artemia* occurs only in hypersaline lakes. Edmondson (1966) suggested that predation and competition limited *Artemia* to the higher salinities. The absence of *Artemia* from an otherwise suitable habitat is often explained by this zooplankter's inability to withstand fish predation (Persoone and Sorgeloos, 1980). However, fish predation on *Artemia* occurs to a limited extent in certain natural habitats. Usually this area involves a salinity gradient where predation occurs in a limited area of overlap (e.g. Scelzo and Voglar, 1980). Insect predation has been observed in several Indian lakes (Rama-moorthi and Tangaraj, 1980; Bhargava *et al.*, 1987), Solar Lake (Dimentman and Spira, 1982), and Laysan Lagoon (W. Gagne, pers. commun.). Bhargava *et al.* (1987) hypothesize that invertebrate predation may contribute to the disappearance of *Artemia* during low salinity periods. Kristensen and Hulscher-Emeis (1972) report that in Curaçao and Bonaire, Antilles, *Artemia* is excluded from low salinities through predation by a cyclopoid copepod.

As discussed in the review by Persoone and Sorgeloos (1980) the primary predators on *Artemia* are waterfowl. More specifically, reported predators include gulls (Isenmann, 1975; Winkler, 1977; Wear and Haslett, 1987), flamingos (MacDonald, 1980; Bhargava *et al.*, 1987), avocets (Carpelan, 1957), stilts (Carpelan, 1957; Bradbury, 1971; Bhargava *et al.*, 1987), grebes (Bradbury, 1971; Cooper *et al.*, 1984), ducks (Bradbury, 1971) and other shorebirds (Bradbury, 1971; Carpelan, 1957).

Few studies have quantified the impact waterfowl predation has on *Artemia* populations. At Mono Lake, migrating grebes consumed between 8 000 and 70 000 *Artemia*/grebe/day, and monthly grebe predation accounted for 8 to 83% of *Artemia* mortality during the fall when predator densities were high (Cooper *et al.*, 1984). Wear and Haslett (1987) report daily consumption rates for gulls at Lake Grassmere of 50 g wet weight/gull, which is approximately equivalent to 6 000 adults/gull/day. Although waterfowl can ingest large numbers of brine shrimp per day, their densities are usually too low to severely impact the *Artemia* populations.

COMPETITION

In general, competitive ability appears to decrease with increasing salinity (Por, 1980) and *Artemia*, which is the most salt tolerant crustacean, has been described as a fugitive species (Edmondson, 1963). In Great Salt Lake, *Artemia* is reported to be the sole zooplankter (Wirick, 1972). In Mono Lake, Mason (1967) reported the occurrence of two rotifer species in addition to *Artemia*. However, recently no rotifers have been found in the lake (Lenz, 1982). Even in the 1960's, rotifers and *Artemia* were segregated temporally, rotifers predominating during the winter. Temporal or spatial separation between *Artemia* and other zooplankters has been found in other habitats (Anderson, 1958; Broch, 1969; Javor, 1983). Geddes (1980) observed

temporal separation along a salinity gradient for *Parartemia* and *Artemia* in Australia. This separation appeared to be due to competitive exclusion, since their salinity tolerances overlap.

Conclusion

The genus *Artemia* has diversified to inhabit lakes ranging from permanent to highly temporary, from seasonal to aseasonal, from predictable to unpredictable. In seasonal habitats, such as Mono Lake and Great Salt Lake, animals are adapted for a rapid repopulation of an "empty" lake at the beginning of the season, followed by a large production of cysts to assure the survival during the uninhabitable period. The life-history strategy of these *Artemia* include high fecundity with a short initial period of ovoviviparity followed by oviparity. Permanent and relatively aseasonal habitats on the other extreme, promote ovoviviparity (to the near exclusion of oviparity) and a low but steady reproductive output, resulting in a multiplicity of asynchronous generations each year.

Inland habitats may be more productive than coastal salterns and ponds, as is suggested by differences in nutrient concentrations and primary production. Thus commercial harvesting of *Artemia* from saltworks may be inefficient, unless nutrient levels are raised. Little is known about secondary production in salt lakes. However, *Artemia* population and grazing studies are suggestive that this zooplankton may be food limited in some habitats. Additional data on salt lake productivity and the factors regulating it will permit more effective management of *Artemia* production ponds.

Artemia offers an unusual opportunity for the study of the relationships between habitat characteristics and population biology within a single genus. With the marked increase in ecological data since the last Symposium, the complexities of *Artemia* ecology have become more apparent.

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