Anostracan Adaptations to Harsh Environments

by

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INTRODUCTION

Phylum Arthropoda is the largest and most diverse phylum of animals alive today (Pechenik 2000). This group is generally characterized by having a hardened chitinous exoskeleton that is segmented and jointed (Pechenik 2000). Within the phylum, the class Crustacea consists primarily of marine organisms, with a few freshwater and terrestrial groups. Crustacean distinguishing characteristics include a nauplius larva at some stage of their life cycle (Pechenik 2000), and the presence of five appendages in the head region: two pairs of antennae, a pair of mandibles, and two pairs of maxillas (Pearse et al. 1987). Crustaceans also have an open circulatory system with a heart that pumps hemolymph through several sinuses in body (Pechenik 2000). Although most crustaceans are dioecious and reproduce sexually, some species are parthenogenic, meaning that their offspring are produced from unfertilized eggs (Pechenik 2000).

The class Crustacea contains approximately 45,000 species divided into several subclasses including Cephalocarida, Malacostraca, Copepoda, and Branchiopoda just to name a few (Pechenik 2000). This paper focuses on the Branchiopoda, a diverse group of organisms that occurs primarily in temporary freshwater ponds and saline lakes. Most branchiopods are less than 2 cm long with modified flattened or leaf-like paddles on each of thoracic appendages used for locomotion and gas exchange (Pechenik 2000). The majority of branchiopods are filter feeders, although carnivorous and scavenger species do occur in some groups (Pearse et al. 1987). The approximately 800 species of branchiopods are separated into four orders: Notostraca contains the tadpole shrimp, Cladocera contains the water fleas, Conchostraca contains the clam shrimp, and Anostraca contains the fairy shrimp and brine shrimp (Pechenik 2000).

The order Anostraca contains approximately 266 species of brine shrimp and fairy shrimp classified into in nine different families and 27 genera (Brtek and Mura 2000). Anostracans can be found throughout the world, with approximately 28 species in North America (Prophet 1963). Anostracans can be distinguished by their lack of a carapace and the presence of swimming appendages on as many as 19 of their body segments (Pechenik 2000). Members of the order Anostraca have evolved several different characteristics to survive in the hostile environments they inhabit. The remainder of this paper will discuss the extreme habitats in which the brine shrimp (*Artemia*) and the fairy shrimp (Branchinecta, Eubranchipus, and Streptocephalus) live, the adaptations they have evolved to survive in harsh environments, and the ecological and economic significance of these organisms.

THE BRINE SHRIMP

General Characteristics

In the genus *Artemia*, sexes are separate, with males having an enlarged second antenna used for clasping the female during reproduction and females having a ventral brood chamber to hold developing eggs (Figure 1, Pearse et al. 1987). Brine shrimp are filter feeders, feeding primarily on small organisms and organic particles from the water in which they live (Pearse et al. 1987). *Artemia* use their flattened, leaf-like appendages to create a feeding current that brings the tiny particles to their mouth for consumption (Pearse et al. 1987).

Figure 1. Female brine shrimp (top), male brine shrimp (bottom). (www.seamonkeypicture.com 2002).

Distribution and Habitats

Brine shrimp are distributed throughout the world, occurring on every continent except Antarctica (Browne and MacDonald 1982). These tiny shrimp inhabit hypersaline lakes and ponds of varying ionic composition, temperature, and altitude (Triantaphyllidis et al. 1998). Found in terminal inland salt lakes and commercial salterns, *Artemia* can tolerate salinity up to five times higher than seawater (Browne and Macdonald 1982). In addition, brine shrimp have been found in waters high in carbonate with pH values as high as 10 (Cole and Brown 1967). *Artemia* populations have been observed at altitudes from below sea level to approximately 4500 meters above sea level in both humid and arid climates (Triantaphyllidis et al. 1998). Because *Artemia* are susceptible to predators such as fish, birds, and other invertebrates, they typically will inhabit waters with ionic compositions too high for their major predators to tolerate (Browne and MacDonald 1982). It is probable that *Artemia*'s ability to tolerate conditions few other organisms can withstand may also effectively eliminate interspecific competition, a topic in need of further study.

Adaptations to Harsh Environments

How is it possible that *Artemia* can thrive in water that most other organisms cannot even tolerate? A study conducted by Broch (1969) showed that *Artemia salina* has evolved an osmoregulatory mechanism that involves a change in hemolymph concentration that coincides with changes in water salinity. In addition to discovering *Artemia*'s ability to osmoregulate, the study reported that there is an increase in blood hemoglobin in A. salina. The change in hemoglobin was in direct response to a decrease in oxygen content caused by an increase in salinity. These physiological adaptations to salinity allow for the survival of brine shrimp in their environments, but the evolution of modifications to certain stages of their life cycle may be what has made the brine shrimp highly successful throughout the world.

Artemia have evolved two different modes of reproduction to ensure survival in harsh environments: sexual reproduction and parthenogenesis (Pearse et al. 1987). Browne and MacDonald (1982) discovered that reproduction of *Artemia franciscana* found in the western hemisphere is exclusively sexual, while reproduction of *Artemia parthenogenetica, A. tunisiana, A. uniramia*, and *A. franciscana* in the eastern hemisphere it is predominantly pathenogenic. In addition, they discovered that all known *Artemia* populations in the western hemisphere are diploid, but in the eastern hemisphere di-, tri-, tetra-, and pentaploid populations occurred commonly. Parthenogeneic brine shrimp appear to be most successful when temperatures and salinity are higher, while lower temperatures and lower salinity are more suitable for the sexual groups (Browne and MacDonald 1982). It was later concluded that the evolution of parthenogenic forms of brine shrimp occurred in the Mediterranean between 5.4 and 1.7 million years ago in response to a dramatic increase in the salinity of the basin there (Triantaphyllidis et al. 1998). Geographic isolation of the groups is a probable reason why parthenogenic species have not appeared in the Western hemisphere, despite the benefits of a parthenogenic life cycle.

Economic and Ecological Significance

Brine shrimp are important primary consumers in many habitats, though they often occur in conditions where organisms from higher trophic levels cannot survive. Brine shrimp are often seasonally preyed on by water foul such as grebes that often flock to salt lakes during their migration (Cooper et al. 1984). In 1980, a study found that grebe predation accounted for up to 83% of the decline in *Artemia* density in Mono Lake, California (Cooper et al. 1984). In addition, *Artemia* have been commonly used as food by the aquaculture industry in rearing many marine fish and shellfish species (Triantaphyllidis et al. 1998). Approximately 2000 metric tons of *Artemia* cysts are harvested primarily from the Great Salt Lake in Utah for use in aquaculture around the world annually (Triantaphyllidis et al. 1998). Although brine shrimp are much more abundant than other anostracans, their economic and ecological importance cannot be overlooked.

THE FAIRY SHRIMP

General Characteristics

The fairy shrimp are usually less than 5 cm long and have a short head containing two pairs of antennae, 11 pairs of flattened legs on the thorax for locomotion and filter feeding, a thin abdomen with no legs, and no carapace (Eriksen et al.1990). Fairy shrimp swim with their legs and antennae inverted, giving the appearance of swimming "upside down" (Figure 2). Like brine shrimp, the second pair of antennae of fairy shrimp is modified for clasping the female during copulation, and females have prominent ovisacs for brooding eggs (Figure 3, Bauder et al. 1998).

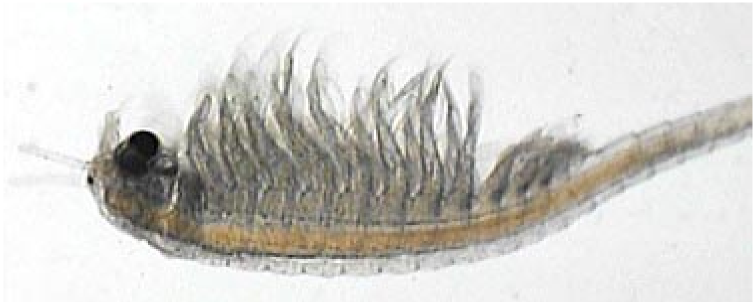

Figure 2. Adult fairy shrimp in typical swimming position (Walker 2000). (www.microscopy-uk.org.uk)

Figure 3. Male (left) and Female (right) fairy shrimp (Turner 1997). (www.meltingpot.fortunecity.com)

Distribution and Habitats

More that 200 species of fairy shrimp have been found and classified throughout the world (Brtek and Mura 2000), 23 of those documented in California (Bauder et al. 1998). There are several genera of fairy shrimp: *Branchinecta*, *Eubranchipus*, and *Streptocephalus* are the most common North American species (Pechenik 2000). Fairy shrimp typically inhabit temporary freshwater pools and ponds, though some species have been observed in roadside ditches, potholes, and even water-filled tire tracks (Prophet 1963). Broch (1969) found a species of fairy shrimp, *Branchinecta campestris*, inhabiting the same saline lakes as the brine shrimp *Artemia salina*.

The habitats in which fairy shrimp live exhibit extremely variable seasonal fluctuations in ionic composition, temperature, and water level depending on their location. Pools located in humid climates contain water during much of the year, and therefore often contain fairy shrimp that are active throughout the year (Moore 1963, Prophet 1963). In arid climates, such as that found in the Mojave desert, fairy shrimp inhabit pools that may last from as little as three days to as long as four months, with much more variable levels of dissolved salts than found in pools that found in humid climates (Brown and Carpelan 1971).

Adaptations to Harsh Environments

Several modifications within a fairy shrimp's life cycle have evolved to help ensure survival in the hostile environments where they live. Brown and Carpelan (1971) found that, in humid environments where changes in water salinity are slight throughout the year, fairy shrimp cysts hatch primarily in response to changes in oxygen composition. In contrast, most species found in arid regions will only hatch in response to salinity levels and temperature (Brown and Carpelan 1971). These conditions indicate that the pool will remain filled with water long enough for the fairy shrimp to complete their life cycle, which averages from 10 to 14 weeks for most species (Moore 1963).

Once a pond becomes filled, individuals will begin to hatch that are either encysted embryos that have been dormant in the top 5-10 millimeters of mud, eggs that were ejected from living females when the pool was filled, or eggs that were remaining in the ovisacs when females died in the previous season (Brown and Carpelan 1971). The eggs are able to withstand several months of dry conditions due to the presence of a thick "shell," and the dormant nauplii larvae, or cysts, are covered by a thin cuticle that is able to withstand desiccation (Saiah and Perrin 1990). Only approximately 10 percent of the eggs in a pond will hatch during any one hydration event (Bauder et al. 1998). Clutch sizes can range between 10 and 700 eggs and are usually produced every one to three days when conditions are suitable (Wiman 1979). In a study done by Hildrew (1985), some of the eggs from the same clutch did not hatch until their pools had been flooded eight successive times. If all eggs hatched during the same hydration and the conditions did not allow those organisms to survive, the species would likely face extinction.

Differences in hatching times allow many species of fairy shrimp to avoid predation and interspecific competition. The main predators of fairy shrimp include small fish, tadpoles, insect larva, and copepods (Moore 1963). Although some species of fairy shrimp have been found seasonally in the same ponds as permanent fish populations (McCarraher 1970), most predators are unable to survive in the temporary ponds favored by fairy shrimp species. Competition for food can occur between cladocerans and fairy shrimp, or between different species of fairy shrimp when they occur together in the same pool (Moore 1963). Prophet (1963) found that in the rare instance that two fairy shrimp species, *Eubranchipus serratus* and *Streptocephalus seali*, occurred in the same pond, *E. serratus* was active during the winter months and *S. seali* was active in the summer, thus eliminating competition for food and space between the two species.

Economic and Ecological Significance

Fairy shrimp are of extreme economic and ecological significance in San Diego County due to the existence of two endangered species in the area, the San Diego fairy shrimp (*Branchinecta* *sandiegoensis*), and the Riverside fairy shrimp (*Streptocephalus woottoni*) (Bauder et al. 1998). These two species are found in vernal pools throughout San Diego County, but their existence is being severely threatened by increased agricultural and urban development, livestock grazing, off-road vehicle use, pollution, and watershed alteration (Eriksen 1990). The San Diego fairy shrimp was listed as endangered under the Endangered Species Act (1973) on February 3, 1997, and the Riverside fairy shrimp was listed as endangered on August 3, 1993 (Bauder 1998). In addition, vernal pools are protected under the Clean Water Act and regulated by the Army Corps of Engineers, which requires permits for the filling of any vernal pools (Eriksen 1990). The fairy shrimp and vernal pool habitats have proven to be a frustrating barrier to developers in several areas such as Otay Mesa where several pools still exist.

DISCUSSION AND FURTHER RESEARCH

Although many different studies have been done on the adaptive characteristics that anostracans have evolved, there are still several areas in need of further research. First, how did brine and fairy shrimp become established in their current hostile habitats? A study conducted by Moore and Faust (1972) proposed crayfish as a possible agent of dissemination of fairy shrimp into different pools. Although viable brine shrimp and fairy shrimp were found in dried crayfish species in the laboratory, crayfish rarely occur in the same ponds as the species tested in nature and thus are not a likely source for a large scale migration of anostracans. Another study done by Proctor (1964) tested the viability of crustacean eggs in duck feces. He found that the eggs of both *Artemia salina* and *Streptocephalus* sp. could pass through the digestive tracts of Mallard ducks and successfully hatch, making ducks a possible mode of dissemination. It is also possible that an ancestor of Anostracans was left behind in inland lakes when ocean water receeded, and the organisms evolved to become what they are today. Clearly, further research on this topic is necessary to determine other ways anostracans may have become restricted to their habitats.

One possible way to determine when and how fairy shrimp and brine shrimp may have evolutionarily branched off from marine crustaceans would be to conduct a phylogenetic analysis of the groups. Using the DNA sequences of fairy shrimp and brine shrimp, and the DNA sequences of several marine crustaceans, phylogenetic trees could be made to compare the lineages of the groups (Ridley 1996). Based on the phylogenetic analyses, the relationships of anostracans to other crustaceans could be determined. This data along with fossil evidence, could help determine when the anostracans may have branched off from other groups.

Another area worth studying further is how much of an effect interspecific competition has had on the evolution of anostracan characteristics. The studies done by Broch (1969) showed that the different life cycles of *Artemia salina* and *Branchinecta campestris* kept their coexistence at a minimum when they both occurred in the same water body, reducing competition between the two species. Moore (1963) found that competition was reduced between two species of fairy shrimp that occurred in the same ponds due to their differences in environmental conditions necessary for survival. It is possible that the changes in hatching requirements evolved to reduce competition. It, however, is also possible that the differences are caused by environmental factors or to reduce predation. More studies are needed on this topic to determine the amount of impact competition has on anostracan evolution.

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