

# ***Branchinecta* of North America: Population Structure and Its Implications for Conservation Practice**

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**ABSTRACT.** The worldwide loss of temporary waters threatens many branchiopod crustacean species. Single-locus genetic variation within and among pools is often high - temporally due to a large egg bank and spatially due to a stepping-stone pattern of pools. Quantitative-genetic variation, although less well studied, is also high. Abiotic factors are often implicated in speciation events, but the actual impact of both abiotic and biotic factors on species diversity is not well understood. Given the large within pool population sizes, the biggest threats are likely to be due to habitat degradation and loss.

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## INTRODUCTION

Wetlands, currently covering less than 6% of the earth's land surface, are being destroyed at an alarming rate worldwide: over 50% of the historic wetlands have been lost in the United States, over 70% in Portugal, over 80% in southwest France, and over 90% in New Zealand (Dugan, 1993). Urban expansion and agricultural conversion have modified or destroyed more than 95% of the historic wetlands in California (Gilmer et al., 1982), endangering migratory and wintering bird populations and many of the native vertebrate, invertebrate, and plant species dependent on aquatic habitats (e.g. Elias, 1987; Heitmeyer et al., 1989; Eng et al., 1990; Moyle and Williams, 1990). California's ephemeral waters, and vernal pools in particular, are wetland types which have suffered tremendous losses in recent years due to a variety of factors (e.g., Bauder, 1986), yet are inhabited by many rare and endemic plants and animals (e.g., Cogswell, 1976, Ebert and Balko, 1987; Elias, 1987; Eng et al., 1990; Fugate, 1993).

Much of the work on threatened and endangered species focuses on the contribution of small population sizes to extinction, yet the biggest threat for most species is habitat loss (e.g., Wilcox and Murphy, 1985; Saunders et al., 1991). Although habitat loss or degradation is often concurrent with reductions in population size for birds, mammals, trees, and other large organisms, it need not be for many invertebrates and herbaceous plants. In either case, the ultimate causes of extinction are primarily ecological and not genetic or demographic, although genetics and demography are closely tied to ecology (Boyce, 1992). Ecological factors such as niche parameters, density dependence, interspecific competition, predation, and mutualism should be a central focus of management plans, but data on genetic and demographic factors are needed in order to monitor a species' ability to respond to a changing environ-

ment (e.g., Lande and Barrowclough, 1987; Lande, 1988; Boyce, 1992).

In this paper, I discuss the implications of habitat losses on the long term viability of fairy shrimp populations; fairy shrimp and other crustacean populations inhabiting temporary waters are declining worldwide (e.g., Dimentman, 1981; Herbst, 1982; Brendonck, 1989; Bratton and Fryer, 1990; Löffler, 1993; Mura, 1993; Hödl, 1994). I concentrate on single-locus genetic data from the genus *Branchinecta* in North America, but I also comment on the need for the inclusion of quantitative genetic and ecological data.

## SINGLE-LOCUS GENETICS

Conservation biologists often use single-locus genetics to predict the long-term survival of fragmented populations (e.g., Schonewald-Cox et al., 1983; Soulé, 1986); inbreeding depression, and loss of genetic variability are probable consequences of small population size (Lande, 1988). Random genetic drift tends to reduce genetic variation if small size is sustained for several generations (Wright, 1968). The maintenance of substantial single-locus variation by mutation at neutral loci may require an effective population size of  $10^5$  individuals. The need for such large population size can be lessened if the species is either spatially or temporally subdivided; new alleles can be introduced from surrounding populations through migration (Slatkin, 1985) and from previous generations through a combination of an eggbank and fluctuating selection (Lynch, 1987; Hairston and Dillon, 1990).

Freshwater systems closely resemble stepping stones with small habitable patches surrounded by large uninhabitable areas. Darwin (1859) concluded, based on the best taxonomic evidence of his day, that most freshwater organisms had cosmo-

opolitan distributions and, in spite of their passive dispersal, migration between pools, ponds, and lakes was not uncommon. When examined using genetic or morphological analyses, so-called cosmopolitan species of many freshwater crustaceans are actually either species complexes or the result of morphological convergence (e.g., Frey, 1987; Boileau, 1991; Taylor and Hebert, 1994; Colbourne and Hebert, 1996). Given this population structure, genetic variation both within and among pools over each species' range should be analyzed in order to understand the pattern and maintenance of genetic variation within species.

Single-locus genetic variation within populations of freshwater crustaceans is often quite high (see Mort, 1991 for review). Using Nei's (1987) estimate of expected heterozygosity, species in the cladoceran genus *Daphnia* have individuals that are heterozygous at 5 - 20% of 5 - 12 protein-coding loci (Lynch and Spitze, unpubl. ms.). Individuals in the fairy shrimp genus *Branchinecta* are heterozygous at 8 - 26% of 10 loci and populations have on average 2 or more alleles per locus (Fugate, 1992). *Branchinecta* species also show modest, yet insignificant, deviations from Hardy-Weinberg expectations within pools (Fugate, 1992). Since *Branchinecta* species are sexual, the most likely explanation for deviations from Hardy-Weinberg expectations is a temporal Wahlund effect created by the multi-year egg bank (Hairston and De Stasio, 1988). Cladocerans, due to the presence of cyclical parthenogenesis, often show marked deviations from Hardy-Weinberg within populations (Lynch and Spitze, unpubl. ms.). The large amounts of single-locus genetic variation, coupled with estimates of diapausing egg densities in natural systems, suggest that population sizes within pools are often on the order of  $10^5$  or larger (Hairston, 1996).

Genetic variation among populations living in different pools is also quite high. Using variations of Wright's (1951)  $F_{ST}$  statistics, populations within 1000 km of each other have  $F_{ST}$  values (the deviation from panmixia due to population subdivision) of approximately 0.3 or greater (Innes, 1991; Fugate, 1992; Lynch and Spitze, unpubl. ms.). Assuming an island model of migration, the data suggest one individual is exchanged every other generation. Given the spatial pattern of pools and passive dispersal of cysts, isolation-by-distance is a better assumption than equal migration among all populations (Wright, 1943). Using an isolation-by-distance model developed by Slatkin (1993), species of *Branchinecta* from North America have populations appearing to exchange on the order of 3 - 100 migrants per generation (most species above 20) at 1 km separation and 0.1 - 0.2 per generation at 1000 - 2000 km (Fugate, unpubl. ms.). Based on an estimated  $Nm < 1$ , populations become well isolated from each other on a scale of 100 - 200 km separation. Populations of the brine shrimp *Artemia franciscana* from western North America, appear to exchange 12 migrants per generation at 1 km and 0.2 at 1000 - 2000 km with populations becoming well isolated at 100 km separation (Abreu-Grobois,

unpubl. ms.). Studies of the cladocerans *Daphnia pulex* near the Great Lakes (Innes, 1991), *Bosmina coregoni* in central Europe (Demelo and Hebert, 1994), and the copepod *Heterocope septentrionalis* from western Canada are more limited in scale, but suggest that populations exchange 1 - 3 migrants per generation at 1 km separation and 0.2 - 1 at 1000 - 2000 km. These populations, as well as those of other cladocerans, are often well isolated when less than 10-20 km apart (e.g., Hebert, 1974; Boileau et al., 1992; Boileau and Hebert, 1991; Boileau, 1991), but data from *D. pulex* and *B. coregoni* suggest no relationship between migration and distance (Innes, 1991; Demelo and Hebert, 1994).

Founder events and restricted gene flow, due to passive dispersal, are frequent explanations for the pattern of short-distance differentiation found in many freshwater crustaceans (Hebert, 1974; Hebert and Moran, 1980; Boileau and Hebert, 1991; Boileau et al., 1992). On the other hand, Lynch (1987) and Hairston and Dillon (1990) concluded fluctuating selection often maintains the high levels of genetic variation both within and among cladoceran and copepod populations. The sufficiency of the isolation-by-distance model to explain the relationship among *Branchinecta* populations suggests that drift and/or fluctuating selection are of lesser importance in these species. Since fairy shrimp populations (excluding *Artemia*) are restricted to temporary pools, to reproducing sexually, and to producing only diapausing eggs, opportunities for fluctuating selection are more limited; cladocerans and copepods can switch either from asexual to sexual reproduction or from nondiapausing to diapausing eggs in response to food shortages, daylength, or predation (e.g., Hebert, 1987; Ellner and Hairston, 1994). Hebert (1974) and Innes (1991) also found that permanent lake populations of cladocerans had higher levels of genetic variation than temporary pool populations over the same distances. Given that the diapaused eggs of fairy shrimp, cladocerans, and copepods are all passively dispersed with high probability by shore birds and other animals (e.g., Proctor, 1964; Proctor et al., 1967; Moore and Faust, 1972; Thiéry, 1987), but many cladoceran and copepod populations are well isolated at distances one-tenth those of *Branchinecta* populations, the assumptions of the model used by Boileau and Hebert (1991) to conclude that founder effects are the cause of short distance genetic differentiation appear unrealistic.

#### QUANTITATIVE GENETICS, DEMOGRAPHY, AND LIFE HISTORY

Life-history characters figure directly in an organism's survival and reproduction (Stearns, 1992). Individual variation in life-history traits leads to variation in fitness. Phenotypic variation is produced by the combined effects of genetics and the environment. Phenotypic differences between populations and species are often influenced by many genes of small effect (polygenic variation) rather than single-locus variation (Wright, 1968). Combining quantitative genetics, the study of polygenic

inheritance, and demography, the study of birth and death processes, to study life history variation allows for predicting short-term response to selection (e.g., Stearns, 1991); an organism's ability to respond to changing environmental conditions is important in the face of habitat loss and degradation (Kareiva *et al.*, 1993). The life cycle of most organisms can be partitioned into age, stage, or size classes in order to assess survivorship and reproduction and predict population growth (van Groenendahl *et al.*, 1988). Matrix projection models of demography can be linked to quantitative genetics given information about the genetic covariance between traits and selection gradients on traits (Lande, 1982). These methods can help discover which life-history characters are most critical to a population's fitness by perturbing each element of the projection matrix while holding the others constant (Caswell, 1989). Storfer (1996) has outlined how quantitative genetic models can often provide a better prognosis for endangered species than single-locus models.

The limited studies of life-history characters in freshwater crustaceans indicate that significant phenotypic and/or genetic variation exists both within and among populations (e.g., Belk 1977; Wyngaard, 1986a; 1986b; Lynch *et al.*, 1989; Belk *et al.*, 1990; Hairston and Dillion, 1990; Liebold and Tessier, 1991; Spitze, 1991). Liebold and Tessier (1991) provided evidence that genetic variation for life-history characters within *Daphnia* species is due to vertebrate predators. After four generations of selection in the laboratory, Spitze (1991) achieved life-history character change in response to predation by the midge *Chaoborus*. Belk (1977) and Belk *et al.* (1990) demonstrated phenotypic variation in egg size and number among *Streptocephalus sealii* populations, presumably in response to pool duration. Lynch and Spitze (unpubl. ms.) summarize work on *Daphnia* species and conclude that quantitative genetic variation among populations is equal to or greater than that of single-locus genetic variation.

These studies concentrate on the post-hatching stages of the life cycle, but as in annual plants, freshwater crustaceans have a two-stage life cycle with the majority of their life cycle spent in the egg stage (e.g., Templeton and Levin, 1979; Schaal and Leverich, 1981; Herzig, 1985; Hairston and De Stasio, 1988; Venable, 1989). The presence of a large between-year egg bank creates overlapping generations in a population that has discrete adult generations. The egg bank acts a filter by reducing the the fitness uncertainty created by random between-year environmental variation and dramatically slows the rate of allelic change (Templeton and Levin, 1979). The egg bank can also conserve and/or create evolutionary novelties especially in the face of habitat loss or degradation (Levin, 1990; Ellner and Hairston, 1994). In freshwater crustaceans, eggs appear to be capable of persisting in the soil egg bank for a decade or more (e.g., Atkinson, 1898; Moore, 1979; Herzig, 1985; Hairston; 1996; Belk, 1997). This longevity could easily double the ef-

fective population size, but the actual influence of egg bank dynamics (e.g., age structure and age-specific viability) on post-hatching stages remains unstudied (Lande and Barrowclough, 1987; Nunney and Elam, 1994).

## ECOLOGY

Boyce (1992) stresses that in light of significant habitat loss, conservation biologists should concentrate on modeling the habitat of endangered species and the various approaches to managing that habitat. Both the abiotic and biotic habitat should be studied; factors such as salinity, temperature, and pH, as well as competition, predation, and parasitism can often be correlated with long-term viability in the absence of other data. Limnologists studying temporary waters have focused on abiotic factors to help explain biogeographies of individual species (e.g., Ekman, 1914; Beadle, 1943; McCarraher, 1970; Hartland-Rowe, 1972; Geddes, 1983; Alonso, 1985; Metz and Forró, 1989; Eng *et al.*, 1990; Löffler, 1993) often with the aid of experiments on hatching and growth in relation to temperature and salinity (e.g., Kallinowsky, 1955; Horne, 1967; Belk, 1977; Bowen *et al.*, 1988; Broch, 1989; Al-Tikrity and Grainger, 1990). For longer-lived species, studies have alternatively focused on biotic factors, especially predation (e.g., Hebert and Loaring, 1984; Wyngaard, 1986b; Kerfoot and Lynch, 1987; Spitze, 1991; Wilson and Hebert, 1993; Hössler *et al.*, 1995). In the Canadian arctic, *Daphnia pulex* is replaced by *Daphnia middendorfianna* when the copepod *Hetercope septentrionalis* is present (Hebert and Loaring, 1980; Dodson, 1984). Bengtsson (1989) found that interspecific competition increased local extinction rates among three species of *Daphnia* in Swedish rock pools. Parasitism of freshwater crustaceans, including fairy shrimp, appears to make them more susceptible to predation (e.g., Daborn, 1976; Thiéry *et al.*, 1990; Threlkeld *et al.*, 1993; Xu, 1993). Baltz and Moyle (1993), however, found that native fish assemblages in California rivers were able to resist non-native species when rivers remained undisturbed and the invasion resistance was apparently due to abiotic factors. Other studies of freshwater communities have also concluded that abiotic factors are likely to be more important in determining species diversity (e.g., McLachlan, 1985; Jeffries, 1991), but very little is known about the role of competition within or between branchiopod species.

Although physical and chemical factors are thought to play an important role in the distribution and abundance of branchiopods (e.g., Hartland-Rowe, 1972; Bowen *et al.*, 1988; Eng *et al.*, 1990). Data compiled by Sugnet and Associates (1992) highlights our limited understanding of the actual ecological factors determining branchiopod distributions. *Branchinecta lynchi*, *Lindleriella occidentalis*, and *Lepidurus packardi* are found in the same pools over portions of their distributions. *Branchinecta lynchi* however is found in less than 20% of the total pools in which one of the three species is found, but for five abiotic

factors compiled by Eng et al. (1990), *B. lynchi* and *L. occidentalis* have completely overlapping ranges. Gallagher (1996), in recording distribution data on these three species in Butte County, California, found some indication that pool depth restricted the distribution of *L. occidentalis* and *L. packardii*, but did not indicate why *B. lynchi* was not found in all pools. Obviously, more detailed studies of abiotic, biotic and historical factors are needed to predict the distribution of branchiopod populations.

#### CONCLUSIONS

Given that habitat loss is the major threat to temporary-pool species and the reason for listing endemic, vernal pool *Branchinecta* species in California as threatened or endangered (U.S. Fish and Wildlife, 1992), biologists need to study the genetics, demography, and ecology of these species to develop management strategies. The single-locus genetic data inform us that the majority of individual populations are unlikely to go extinct for genetic or demographic reasons; population sizes are easily large enough to generate adequate quantitative-genetic variation through mutation in the absence of migration and are probably large enough to generate adequate single-locus genetic variation (Lande and Barrowclough, 1987). Isolation-by-distance suggests gene flow between pools is common and increases local population sizes by uniting pools within vernal pool complexes. By removing connecting steps in the stepping-stone pool pattern, pool destruction will alter historical patterns of gene flow and increase isolation between pool complexes. The consequences of pool loss will result in a reduced likelihood of recolonization events following population extinction.

Most of the *Branchinecta* species studied share similar amounts of genetic variation, life-history strategies, and ecologies. Almost all species can be grown under identical conditions in the laboratory, and many are found sympatrically in nature (Fugate, pers. obs.). In spite of the apparent similarities, different species often have distinct and non-overlapping geographic ranges suggesting that historical factors may play a dominant role in determining distributions (Fugate, 1992). Without a more detailed knowledge of each taxon's niche (the abiotic and biotic factors determining positive fitness) we can neither easily distinguish between historical and current ecological reasons for a population's presence or absence, nor predict a population's persistence in the face of habitat loss or alteration. As Baltz and Moyle (1993) found with native fish populations, vernal pools are also likely to be invaded by non-native species when disturbed or when other habitat is reduced. For instance, *Branchinecta lindahli*, a generalist and the most widespread North American species in the genus, is found sympatrically with Californian endemic species only in vernal pools altered by human activities, such as off-road driving and diking (Fugate, pers. obs.). The introduction of non-native species could

lead to species' extinction due to hybridization (common in some *Daphnia* species in the field [e.g., Wolf, 1987] and *Branchinecta* species in no-choice laboratory crosses [pers. obs.]), competition (e.g., Bengtsson, 1989), or the introduction of predators or disease.

In light of the tremendous habitat loss and our limited understanding of branchiopod ecology, I agree with Boyce's (1992) conclusion that habitat management should be a major part of our efforts to reduce species' extinctions. Branchiopods have inhabited temporary freshwater pools for hundreds of millions of years (Fryer, 1987), but as with species, temporary pools also are created and destroyed over time (Norwick, 1991). We can neither conserve present species nor allow for future speciation without conserving the potential for pool creation in the face of pool loss. Given our limited knowledge of branchiopod ecology, we cannot currently create pools that will both replace naturally created pools and insure the persistence of an endemic species for the next 100 years. We must begin to understand the natural cycle of vernal pool creation and destruction to allow for pool replacement and the continued diversity of freshwater systems.

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