Considerations for the Management of Vernal Pool Faunal Communities[1]

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Abstract

The faunal community of California's vernal pools is less obvious and has been less studied than the floral community but is similarly diverse, endemic, and endangered. Species richness and composition vary between pool types, between pools of a given type, and within individual pools between years and through the season. The physiology, life history, and ecology of the pool organisms contribute to this complexity. Management considerations must take into account a large number of factors including maintaining pool hydrology and water chemistry, avoiding crushing cysts in the soil, avoiding the input of toxins, and maintaining genetic variability. Decisions must be made at the landscape level and focus on functioning communities, not just individual species or single pools.

Key words: crustacean communities, management, restoration, vernal pools

Introduction

California's diverse climate and topography support a wide variety of ephemeral wetlands. Among these are the vernal pools of the Central Valley and southern coastal mesas. These pools are inherently biphasic. In most areas, the pools are dry for the majority of the year, but they are temporarily converted into aquatic habitats when they fill from winter rains or spring snow melt. The pools then support a diverse flora and fauna, specifically adapted to their oscillating extremes.

The floral communities of California's vernal pools are quite well known (for example, Bauder 1987, Holland 1978, Holland and Jain 1988, Hoover 1937, Stone 1990, Zedler 1987); however, the faunal communities have been less studied. Although amphibians and waterfowl are quite visible, the much smaller invertebrates are not. These include crustaceans, rotifers, insects, worms, and snails.

The crustacean contingent is the more visually apparent of the invertebrates and includes branchiopods (fairy shrimp, tadpole shrimp, clam shrimp, and water fleas), ostracods (seed shrimp), and copepods. These obligately aquatic organisms survive the terrestrial phase of the pool as desiccation resistant, diapausing propagules (cysts, embryos, or eggs) in the soil. Upon hydration, they hatch, quickly develop, mate, and produce new propagules. The life cycle is compact because the pools are ephemeral. In some areas pools may last for months; in others they may last a few weeks or sometimes just days.

Ephemeral pools only exist in areas that are relatively flat and underlain by impermeable soils. Generally, the pools occur in clusters or complexes, creating a

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spatial patchwork across the landscape. Unfortunately these are also the areas utilized for agriculture and urban development. It is currently estimated that for these reasons, 90 percent of the pools have been lost statewide (Holland 1978, Stone 1990). In rapidly growing areas such as San Diego County, the estimates are upwards of 97 percent (Bauder and Wier 1990). This loss of vernal pools and their associated populations has resulted in the listing of several species of vernal pool plants and animals as endangered (Federal Register 1980, 1991, 1992, 1993a, 1993b, 1994, 1997). Unfortunately, a lack of information regarding obligate vernal pool invertebrates complicates this problem. Many more organisms are taxonomically undescribed and may merit listing as well, but their distribution, ecology, and life history are not well known. Only a very few have had primary research targeted toward them specifically. Furthermore, symbiotic interactions within the community and roles of community members in ecosystem cycles are poorly understood. Consequently, decisions regarding management, protection, restoration, and recovery have been difficult.

Here, I briefly discuss a few key findings from the research on vernal pool organisms (focusing on crustaceans) and suggest some of the implications which are relevant to management decisions. The majority of the research to date concerns branchiopods, but most of the implications for management are expected to extend to other taxa as well.

Key Research

Diversity and Endemism

California's vernal pool invertebrate communities exhibit quite high alpha (within site) and beta (across space) diversity.

- Single pools may have as many as 27 species of crustaceans, which exceeds the diversity seen in most permanent lakes (King and others 1996).
- Pools of different types (due to location and soil chemistry) can differ significantly in the species that are present (King and others 1996, Simovich 1998) (*table 1*).
- Within a pool complex, the faunal community can vary in richness (number of species) and species composition (which species) between pools (King and others 1996, Ripley and Simovich unpublished data, Simovich 1998).
- Many species appear to be highly endemic and are limited to one or a few types of pools (Eriksen and Belk 1999, King and others 1996).
- Sampling over a six-year period has shown that the same pool can differ in richness and composition between years and over the season within a year (Ripley and Simovich unpublished data). Similar variability is seen in ephemeral pool plants (Holland 1987). Thus, richness and composition vary spatially and temporally.

Table 1—*Summary of crustacean diversity for two surveys. Only three species were found in both studies.*

	North/Central Calif. (King and others 1996)	Southern Calif. (Simovich 1998)
# sites	14	1
# pools	58	66
# species	67	27
Range of # species per sites	4-39	NA
Range of # species in single pools	1-27	2-22

Physiology and Life History

Work done with the more visible vernal pool crustaceans, the anostracans or fairy shrimp, points to differences in physiological tolerance and life history associated with the species distributions.

- Some species appear to be broadly tolerant of a variety of water chemistry conditions. Others however, are restricted in their temperature, pH, alkalinity, turbidity, and salinity tolerance (Alexander 1976, Belk and Cole 1975, Belk and Nelson 1995, Bernice 1972, Brendonck 1996, Brown and Carplan 1971, Donald 1983, Eng and others 1990, Forro 1989, Gonzalez and others 1996, Hartland-Rowe 1972, Horne 1967, 1971, Lanway 1974, Moore 1967, Prophet 1963, Sam and Krishnaswamy 1979, Thiéry 1991, or see Eriksen and Belk 1999 for a review). This restricts the elevation (temperature) and location (soil chemistry) of the pools in which they can occur (*table 2*).
- Some species take several weeks to grow, mature, and reproduce while others can do so in as little as 10 days (Eng and others 1990, Hamer and Appleton 1991, Hamer and Sawchyn 1968, Hathaway and Simovich 1996, Mura 1991, Patton 1984, Pennak 1989, Rettalack and Clifford 1980). These life history characteristics restrict species' distributions to areas where precipitation and pool size/depth result in pool longevity consistent with their needs. Although precipitation (and consequently pool duration) can vary among years, pools must last long enough, often enough for reproduction. These factors contribute to endemism, beta diversity, and the differences within pools over time and among years.
- Some vernal pool organisms do not spend their entire life in the pool. Insect pollinators and amphibians are dependent on surrounding uplands for most of their life cycle.

Table 2—*A comparison of three species of fairy shrimp with differing habitat requirements (data reviewed in Eriksen and Belk 1999).*

Hatching temp. °C	TDS ppm	Pool duration	Example species
0-15°	<300	>3 weeks	*Eubranchipus serratus*
5-20°	<600	>3 weeks	*Branchinecta conservatio*
17-30°	300-600	<3 weeks	*Thamnocephalus platyurus*

Incomplete Hatch

In areas where precipitation is extremely variable, pools fairly frequently may fill and dry before some species can reproduce. If all the propagules in the soil hatched in such a filling, the species would be extirpated.

- As an apparent adaptation to such occurrences, fairy shrimp species in unpredictable habitats exhibit incomplete hatch (al-Tikrity and Graninger 1990, Belk 1977, Belk and Nelson 1995, Brendonck 1996, Brendonck and Persoone 1993, Dexter 1973, Hildrew 1985, Mossin 1986, Philippi and others 2001, Simovich and Hathaway 1997). As a hedge against failure, only a portion of the cysts hatches in a given pool filling. As predicted by theory (Cohen 1966, 1967, 1968) and demonstrated in the lab (Philippi and others 2001, Simovich and Hathaway 1997), this portion approximates the proportion of time the pool fills sufficiently for reproduction; in other words, the probability of success. Thus, a cyst bank in the soil is crucial to the persistence of the population over time.
- There are several theoretical consequences of incomplete hatch. For example, if a number of cysts are transported to a new pool, only a small portion will hatch. When these reproduce, their offspring (cysts) will dominate the cyst bank, thus dominating the subsequent gene pool. Essentially there are fewer actual founders of the population than cysts transported. This can contribute to genetic drift and inbreeding.

Population Genetics

Vernal pools generally occur in clusters or complexes. Distances between pools within a complex are generally on the order of meters. Distances between complexes are commonly on the order of kilometers.

- As vernal pool crustaceans are obligately aquatic, they must rely on external means of dispersal. Within a complex, cysts may move between pools via overland water flow in high rainfall years. For dispersal between pools in drier years, or between complexes, the species must rely on vectors. The cysts can be transported on the legs of grazing animals or through the digestive tracts of waterfowl and amphibians (Bohonak and Whiteman 1999, Krapu 1974, Maguire 1963, Proctor and others 1967, Reid and Reed 1994). Thus, these species are distributed spatially as metapopulations, numerous subpopulations linked by varying levels of migration and gene flow.
- Genetic studies have shown evidence of low gene flow and consequently high differentiation between populations (Bohonak 1998, Boileau and Her-

bert 1988, Crease and others 1990, Davies and others 1997, Fugate 1992, 1998; Hann and Herbert 1986, Herbert 1974, King 1996). The narrowly endemic San Diego fairy shrimp (*Branchinecta sandiegonensis*) shows low genetic variability (allozymes) within subpopulatons and high differentiation between populations, even over short distances (F_{ST} > 0.50 at less than 50 km) (*fig. 1*) (Davies and others 1997). A similar result was found for a Rocky Mountain species (*Branchinecta coloradoensis*) (Bohanak 1998). A more detailed analysis shows the differentiation by distance relationships of the two species to be almost identical (Bohanak and Simovich unpublished data).

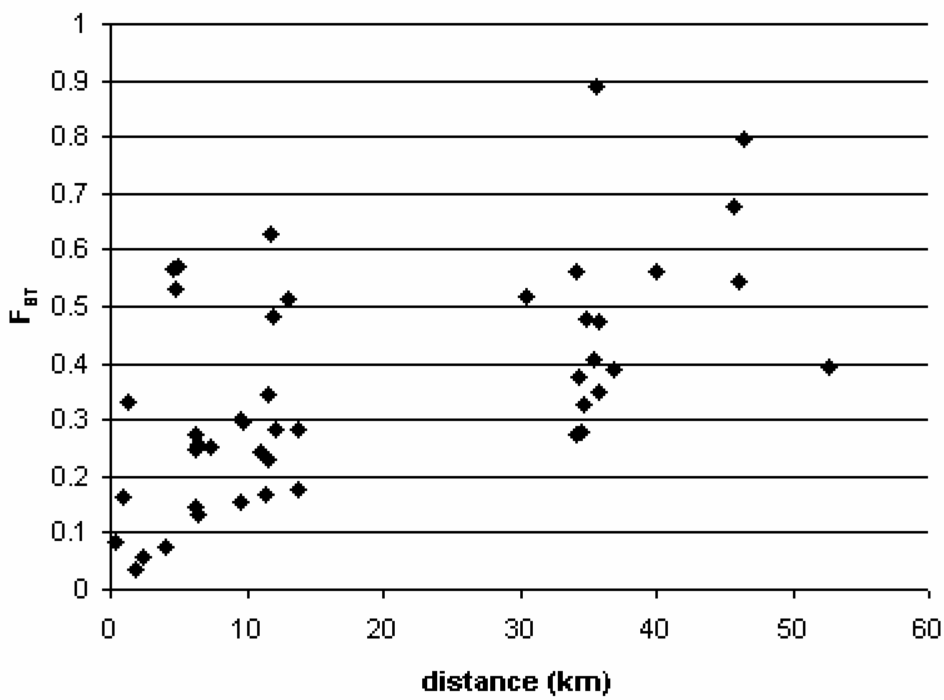

Figure 1—Isolation by distance. F_{ST} versus physical distance for populations of *Branchinecta sandiegonensis* in San Diego County, California (data from Davies and others 1997). F_{ST} can be considered an indicator of differentiation due to genetic drift. r=0.57

Missing Knowledge and Missing Species

Although some physiological and ecological information is available for some fairy shrimp species, these data are largely missing for most vernal pool crustaceans and other invertebrates.

- It appears that approximately 50 percent of California's vernal pool crustaceans are undescribed species about which essentially nothing is known (King and others 1996, Simovich 1998).
- Habitat loss models estimate that approximately 30 percent of California's vernal pool crustacean species have already been lost (King 1998).
- Very little is known about the food web, symbiotic relationships, and nutrient and energy cycles of vernal pools. The algae, plants, and invertebrates are food for birds and amphibians (Bohonak and Whiteman 1999, Krapu 1974,

Morin 1987, Proctor and others 1967, Simovich and others 1991). Some anostracans consume mostly algae while others are predators (see for review Parsick 2002). However, there are no studies available for most vernal pool invertebrates.

Additional information

- Anostracan cysts crush very easily, especially when wet (Hathaway and others 1996).
- Commonly used chemicals such as Malathion can kill vernal pool crustaceans (Davis and others 2001).
- At least some cysts (Wells and others 1997) and seeds (Cox and Austin 1990) in pools survive after fire.

Management Implications

These findings have important implications for management including habitat preservation, habitat restoration, and species relocation efforts.

Diversity and Endemism

- Pools at different sites or of different types differ in richness and composition. Therefore, preserving pools at one site as mitigation for losses at another may not preserve all of the same species.
- Pools within a site differ. Therefore, preserving a few pools at a site while losing the others may not preserve all species.
- Pools can differ between years in richness and composition. Therefore, more than one season of pre-manipulation surveying is necessary to establish base-line conditions, and several years of post-manipulation monitoring are necessary to establish success.

Physiology and Life History

- Many species, particularly the narrow endemics that are generally the species of concern, have very specific requirements for water chemistry, temperature, and pool longevity. Thus restoration or habitat creation must result in pools with appropriate chemistry and hydrology that mimic the range and variation of natural pools.
- Any manipulation involving the transport or introduction of organisms must consider the appropriate source. Organisms from different areas or pool types will probably not be appropriate and may not establish populations.
- Preservation of vernal pool communities requires preservation of the surrounding uplands for watershed and for amphibian, pollinator, and vector habitat.

Incomplete Hatch

- Although incomplete hatch provides a hedge against cycles with low reproduction, this life history strategy complicates simple management decisions. For example, after inoculation of a created or restored pool with soil, shrimp could hatch over several hydrations from the cysts in the inoculum. However, if the pool did not last long enough or hydrate often enough for sufficient reproduction, the cyst bank would not be replenished. Thus, initial monitoring would suggest a successful restoration, while in reality the cyst bank was being depleted to extirpation. Consequently, successful reproduction must be documented over several years to establish success.
- Incomplete hatch of the cysts used to inoculate pools may result in lower genetic variability of the new population due to genetic drift. This can have adverse effects on population fitness and evolutionary potential over time. Use of inocula with low cyst density may compound the problem.

Population Genetics

Particularly with narrow endemics, such as the San Diego fairy shrimp (*B. sandiegonensis*), genetic variation within populations and gene flow among populations (as indicated by allozymes) is apparently low.

- Populations should be surveyed in order to preserve those with higher genetic variability, which could, and may now, serve as source populations for gene flow and colonists for other populations.
- Increased isolation of pools will reduce visitation by vector organisms. This will further reduce gene flow and subsequently result in further reductions in genetic variation. This would be expected to put the species in jeopardy of reduced fitness due to inbreeding depression. It would also be expected to reduce evolutionary potential and the ability of the species to adapt over time and to reduce the possibility of rescue (re-colonization) if a population is extirpated or reduced. Consequently, preservation efforts must be considered at the landscape level rather than pool by pool. Sufficient buffer and corridor access must remain to encourage the usage of the area by potential distribution vector species.

Missing Knowledge and Species

- If an organism is undescribed, it is difficult to make decisions necessary to preserve and protect it. Taxonomic description, surveys, and natural history studies to establish species' distributions and resource requirements are critical.
- Any management or manipulations must focus on the entire community, not simply a single species. If a species' food is missing, or for plants, if a pollinator is missing, the species simply will not survive long.

Additional information

- Vehicles should be kept out of pools.
- Pollution run-off from surrounding areas is a potential problem.
- Fire should not be excluded from fire-type habitats, but excessive unnatural fuels in a pool (weeds) may increase fire temperatures and be a problem for cyst survival.

Summary

When trying to preserve communities about which little is known, careful decisions based on the best scientific knowledge available and a clear understanding of population ecology and genetics are necessary. Preservation decisions must be at the landscape level and consider functional communities, not just individual species or single pools. For restoration attempts, a careful, scientific approach documenting pre- and post-restoration conditions and based on well-reasoned experimental design is critical. This can best be accomplished by closely linking research and management. Finally, results must be published, to increase our knowledge, increase the probability of making good decisions, and decrease the probability of repeating poor ones.

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