

Crustacean Biodiversity and Endemism in California's Ephemeral Wetlands

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ABSTRACT. While knowledge of the fauna of California's ephemeral wetlands has lagged behind that of the flora, recent work has revealed extraordinarily diverse and highly endemic communities. Two recent surveys of crustaceans have shown a number of important attributes of these systems. 1) Species richness and species composition differ among habitat types. 2) Not all pools in an area contain all the same species. 3) Some species are widespread while others are found rarely. 4) Many species are undescribed and little is known of their requirements. 5) Large ephemeral lakes are richer than many permanent lakes. 6) Some populations of restricted species have low genetic variability. 7) The co-occurrence of congeners is common. Several factors may be involved in producing this unexpected richness, including high primary productivity, reduced predation, and habitat heterogeneity. However, while some of these factors apply to some pools, they are not sufficient to explain the richness of all pool types. Those factors which do apply to all pools and are potentially the most interesting are produced by the effects of the ephemerality and unpredictability of the system on life history evolution. These attributes of California's ephemeral wetlands, along with their rapid loss, have numerous implications for the conservation of biodiversity in these systems.

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INTRODUCTION

The varied California landscape has endowed the state with an array of habitats rivaled by few places on earth. Among these are the ephemeral wetlands, the focus of this symposium. These wetlands encompass a variety of types and exhibit a broad range of characteristics. They range from wet mountain meadows to mima mound pools and playas. They can be alkaline, neutral, or saline, they may fill in winter or summer and they differ in size and duration. They do, however, share three attributes. They are patchy in space, discontinuous in time, and disappearing. These attributes contribute to their substantial biodiversity, but also to their loss.

Botanists have long appreciated these unique wetlands and have documented a highly diverse and largely endemic flora whose distribution patterns are in part associated with the physical/chemical nature of the different pool types (Hoover, 1937; Holland and Jain, 1981; Holland, 1986). They have subsequently been able to document losses of this diversity as the habitats have been reduced. Currently 15 plant species associated with California's ephemeral wetlands have been listed as endangered (Federal Register, 1991; 1992; 1993a; 1993b). While zoologists lagged behind for some time, recent reports are beginning to reveal a similar pattern of diversity and endemism. As information about the richness of the faunal communities grows, so

does the associated list of species at risk. Currently seven ephemeral pool invertebrates are listed (Federal Register, 1980; 1993a; 1994; 1997).

As we continue this line of inquiry, we need to enhance our understanding of the ecology and dynamics of ephemeral wetland systems. To do this, we need to explore the relationships between community structure and geological and floristic influences and to anticipate how these relationships might be disrupted by human intervention. Such inquiries may allow us not only to understand the evolution of these systems, but also to predict the effects of habitat loss and to investigate approaches for conservation and management.

In this paper, I summarize two studies involving California ephemeral pool fauna with an emphasis on crustaceans (Simovich et al., 1993; Simovich et al., 1995; King et al., 1996). While limited in geographic and taxonomic scope, these are, to my knowledge, the most extensive data sets on California ephemeral pool fauna available at this time. I also discuss some of the factors potentially responsible for shaping these communities. Finally, I relate the findings to implications for management and conservation. In the following paper, Jamie King will use one of these data sets in a model projecting extinction rates for California's vernal pool fauna (King, 1998).

TABLE 1. Habitat types, number of crustacean species, and number of pools for sites over both surveys.

Site	Habitat Type	Number of Species	Number of Pools
Northern			
Fall River	Northern Transmontane	14	3
Central			
Manton Plain	Northern Sacramento Volcanic Mud Flow	22	3
Dales Plain	Northern Sacramento Volcanic Mud Flow	39	3
Tuscan Buttes	Northern Sacramento Volcanic Mud Flow	27	2
Red Bluff	Sacramento Valley Hardpan	19	7
Coyote Creek	Sacramento Valley Hardpan	18	3
Truckee Creek	Sacramento Valley Hardpan	9	6
Thomas Creek	Sacramento Valley Hardpan	21	10
Corning	Sacramento Valley Hardpan	17	8
Hall Creek	Sacramento Valley Hardpan	5	2
Stony Creek	Sacramento Valley Hardpan	11	3
Wilson Creek	Sacramento Valley Hardpan	14	3
Allendale	Sacramento Valley Hardpan	14	2
Jepson Prairie	Sacramento Valley Claypan	28	3
Southern			
NAS Miramar	San Diego Mesa Hardpan	27	66

Species Richness

Faunal richness is amazingly high. The northern and central sites include 67 species of crustaceans (8 large branchiopods, 18 cladocerans, 17 copepods and 24 ostracods) (Table 2), 60 to 100 species of insects and various mollusks, platyhelminths, annelids and amphibians. For the crustaceans, the taxonomic experts consider 30 (43%) to be probably or possibly new, undescribed species. Due to the paucity of published references, it is hard to say exactly, but it seems that 35 species have not been previously reported for California. Some species are widespread and occur in permanent waters as well. However, many species are rare and exhibit restricted distributions along the transect. Eighteen species (27%) occur in only a single pool and 27 species (40%) at only a single site. If we include the potentially new species, 34 of the 67 species appear to be endemic to California (King et al., 1996).

Pools within a habitat type are most similar in terms of species composition, but pools within a particular site are not necessarily most similar to each other. Species richness varied between sites from a low of 4 at Hall Creek to a high of 39 at Dales Plain (Table 1). The hardpan and northern transmontane pools were less rich than the volcanic mudflow and claypan ones.

The species richness of individual pools varied from a low of 1 to a high of 27 and averaged 9.6 across all 58 pools. Within a site, not all pools contained all species found at that site. Thus,

the richness of a site is greater than the richness of any given pool. Species richness was positively correlated with pool depth ($r^2=0.584$) and with pool maximum surface area ($r^2=0.300$), both indicators of duration. The large vernal lakes were particularly rich (Dales Lake = 24, Dales Potholes = 27, Olcott Lake = 25); however, some species were only found in smaller pools. The richness of these vernal lakes is comparable to or higher than that seen for the same taxonomic groups in permanent lakes (see King et al., 1996 for review). Furthermore, the richness of pools disturbed by the installation of the pipeline was lower than that of nearby undisturbed pools, even after 32 years of recovery time (Simovich et al., 1993).

Congeneric species co-occurred at high frequency at the sites surveyed. Fifty-five percent of the pools included at least one pair of congeners. This included various combinations of species belonging to three genera of cladocerans, two genera of copepods and four genera of ostracods. The long-lived vernal lakes had the most co-occurrences with four pairs found in Olcott Lake. The Dales Plain site had nine sets of congeners including three sets in Dales Lake and five sets in Dales Potholes including a trio. In most cases our sampling regime could not determine any obvious patterns of spatial or temporal partitioning among congeners (Simovich et al., 1993).

The southern pools were rich as well (Simovich et al., 1995). A total of 27 species of crustaceans were identified, including 3 large branchiopods, 8 cladocerans, 3 copepods and 13 ostra-

TABLE 2. Species occurrence for the North/Central survey.

Species	# Pools All Sites	Number of Sites	Species (continued)	# Pools All Sites	Number of Sites
Large Branchiopods (8)			Copepoda (continued)		
<i>Branchinecta conservatio</i>	3	1	<i>Diacyclops crassicaudis</i> var. <i>brachycercus</i>	16	7
<i>Branchinecta dissimilis</i>	1	1	<i>Diacyclops navus</i> (Cy)	2	2
<i>Branchinecta lynchi</i>	24	6	<i>Diacyclops</i> sp. A (Cy)	36	9
<i>Linderiella occidentalis</i>	7	3	<i>Eucyclops elegans</i> (Cy)	4	4
<i>Lepidurus packardii</i>	9	4	<i>Hesperodiaptomus caducus</i> (Ca)	1	1
<i>Lepidurus</i> sp. A	3	1	<i>Hesperodiaptomus eiseni</i> (Ca)	12	5
<i>Cyzicus californicus</i>	3	1	<i>Hesperodiaptomus hirsutus</i> (Ca)	3	1
<i>Lynceus brachyurus</i>	7	3	<i>Leptodiaptomus tyrreli</i> (Ca)	21	9
Cladocera (18)			<i>Microcyclops rubellus</i> (Cy)	2	1
<i>Alona</i> cf. <i>davidi</i>	1	1	<i>Skistodiaptomus pallidus</i> (Ca)	1	1
<i>Alona</i> cf. <i>setulosa</i>	2	2	Ostracoda (24)		
<i>Alona</i> sp. A	2	2	<i>Bradleystrandesia reticulata</i>	49	14
<i>Alona</i> sp. B	1	1	<i>Candona caudata</i>	11	6
<i>Camptocercus</i> sp. A	1	1	<i>Candona</i> cf. <i>C. stagnalis</i>	1	1
<i>Ceriodaphnia reticulata</i>	7	5	<i>Candona</i> n. sp. C	5	4
<i>Chydorus</i> cf. <i>sphaericus</i>	4	3	<i>Candona</i> n. sp. D	8	5
<i>Daphnia</i> cf. <i>middendorffiana</i>	4	2	<i>Candona</i> sp. A	3	2
<i>Daphnia</i> cf. <i>pulex</i>	11	7	<i>Cypridopsis vidua</i>	3	3
<i>Diaphanosoma</i> cf. <i>birgei</i>	3	1	<i>Cypris subglobosa</i>	1	1
<i>Dunhevedia crassa</i>	2	1	<i>Eucypris</i> sp. A	3	2
<i>Leydigia leydigi</i>	2	2	<i>Eucypris</i> s.l. sp. A	23	11
<i>Macrothrix hirsuticornis</i>	26	12	<i>Eucypris</i> s.l. sp. B	9	5
<i>Moina</i> cf. <i>micrura</i>	10	7	<i>Eucypris virens media</i>	18	11
<i>Pleuroxus aduncus</i>	1	1	<i>Heterocypris</i> aff. <i>H. carolinensis</i>	5	4
<i>Pleuroxus</i> sp. A	1	1	<i>Heterocypris</i> aff. <i>H. rotundatus</i>	16	7
<i>Simocephalus</i> sp. A	33	12	<i>Heterocypris incongruens</i>	1	1
<i>Simocephalus vetulus</i>	9	7	<i>Limnocythere</i> aff. <i>paraornata</i>	1	1
Copepoda (17)			<i>Limnocythere posterolimba</i>	14	7
<i>Acanthocyclops caroliniaus</i> (Cy)	41	12	<i>Limnocythere</i> c.f. <i>sanctipatricii</i>	1	1
<i>Acanthocyclops vernalis</i> (Cy)	3	1	<i>Limnocythere</i> sp. B	16	10
<i>Agladiatomus forbesi</i> (Ca)	1	1	<i>Megalocypris</i> sp.	5	3
<i>Attheyella</i> sp. A (Ha)	8	5	<i>Pelocypris</i> aff. <i>P. albomaculata</i>	3	2
<i>Bryocamptus washingtonensis</i> (Ha)	1	1	<i>Potamocypris</i> sp. A	6	5
<i>Canthocamptus robertcokeri</i> (Ha)	1	1	Unknown species D	3	1
<i>Canthocamptus</i> sp. A (Ha)	1	1	Unknown species G	1	1

Cy = Cyclopoid, Ca = Calanoid, Ha = Harpacticoid

cods (Table 3). Species richness for individual pools ranged from 2 to 22 .

Within the southern pools, some species were wide-spread while others were not. The rarest species occurred in only one pool, while the most common was found in 94% of the pools. While such an extensive survey would be less likely to find species in only one pool, 18% of the species occurred in less than 25% of

the pools. Again, nearby pools are not necessarily most similar and pools next to one another did not always contain all of the same species. There was no clear relationship between pool size and diversity; however, it must be noted that the larger pools have been artificially enhanced (by berms or run-off from free-ways). Species diversity peaked about four weeks after filling. In longer-lived pools, many species present early in the season were missing later.

Congeneric associations were again common; for example, 65% of the pools contained two species of the copepod genus *Acanthocyclops*. For the ostracod genus *Cypris*, 92% of the pools had more than one species and 55% had four species of this genus (Simovich et al., 1995).

Comparison of Studies

As the scope of the two studies was quite different, direct comparisons are difficult to make. However, some trends are evident. A comparison of the north/central and southern surveys reveals almost no similarity in species composition. No large branchiopods, only 2 to 3 cladocerans, and a single copepod species are shared. We have not compared ostracods because different taxonomists did the identifications.

Across both studies, habitats differ in species richness and composition. The volcanic mudflow and claypan pools were the most diverse. The San Diego hardpan sites had more species than any of the Sacramento Valley hardpan sites (and more species than were found in a previous study of a portion of the same area [Balko and Ebert, 1984]). The between-habitat differences can be most easily seen for the large branchiopods (Table 4). Each habitat type has a different array of species. Only one species (*Lepidurus packardii*) was found in more than one of the four habitats sampled along the north/central transect (although it is also found elsewhere). Also, each habitat had a different anostracan. In the shallow hardpan pools for example, the quickly developing branchinectids dominate. *Branchinecta lynchi* was found in the Central Valley while its sister species, *B. sandiegonensis*, was found in the south. Alternatively, the longer-lived claypans and volcanic mudflow pools had three species in three different orders including a more slowly developing tadpole shrimp (*L. packardii*), a clam shrimp, and a fairy shrimp. Most of the large branchiopods are California endemics and several are federally listed as threatened or endangered.

A closer look at the Southern California anostracans is informative as well. One of the three species in the southern survey, *Branchinecta lindahli*, is considered a weedy species found in a variety of habitats through the western states (Eng et al., 1990). In this area, it is found in only two highly disturbed pools. The second species, *Streptocephalus woottoni*, was found in only a single pool. This is a local endemic and an endangered species (Eng et al., 1990; Simovich and Fugate, 1992; Federal Register, 1993a) found in only a few pools in southern California and in Baja California, Mexico (Brown et al., 1993). It is relatively slow to mature (> 30 days), a feature which may be involved in its restriction to deeper, more long lived pools (Hathaway and Simovich, 1996). The third species, *Branchinecta sandiegonensis*, is found in most pools. It is seemingly a very narrow endemic and is found only in San Diego County and just over the border in northern Baja California, Mexico, on the extension of the same mesa system (Fugate, 1992;

TABLE 3. Species occurrence for the southern California (NASM) survey.

Species	Number of Pools	Percent of Pools
Large Branchiopods		
<i>Branchinecta sandiegonensis</i>	53	80%
<i>Branchinecta lindahli</i>	2	3%
<i>Streptocephalus woottoni</i>	1	2%
Cladocerans		
<i>Macrothrix hirsuticornis</i>	55	83%
<i>Ceriodaphnia dubia</i>	42	64%
<i>Moina micrura</i>	43	65%
<i>Alona cf. diaphana</i>	32	48%
<i>Daphnia rosia</i>	10	15%
<i>Daphnia magna</i>	2	3%
<i>Simocephalus sp.</i>	25	38%
<i>Scapholebris cf. rammneri</i>	7	11%
Copepods		
<i>Hesperodiptomus franciscanus</i> (Ca)	10	15%
<i>Acanthocyclops vernalis</i> (Cy)	62	94%
<i>Acanthocyclops robustus</i> (Cy)	44	67%
Ostracods		
<i>Cypris sp. 1</i>	45	68%
<i>Cypris sp. 2</i>	48	73%
<i>Cypris sp. 3</i>	55	83%
<i>Cypris pubera</i>	61	92%
<i>Cypridopsis vidua</i>	13	20%
<i>Cypria pustulosa</i>	11	17%
<i>Prionocypris sp.</i>	22	33%
<i>Herpetocypris sp.</i>	6	9%
<i>Cypriconcha sp.</i>	13	20%
<i>Limnocythere glypta</i>	24	36%
<i>Cypris virens</i>	15	23%
<i>Potamocypris sp.</i>	22	33%
<i>Ostracod N</i>	2	3%
Cy = Cyclopid, Ca = Calanoid		

Simovich and Fugate, 1992). This more rapidly developing species is found in very shallow (<0.10m) as well as deeper pools. Where it is found with *S. woottoni*, the two do not overlap as adults (Hathaway and Simovich, 1996). Neither of the two endemics is tolerant of high solutes (Gonzalez et al., 1996), and both hatch best at low temperatures and poorly or not at all above 25°C (Hathaway and Simovich, 1996). These conditions may be involved in their absence from the desert pools and playas to the east where other more widely distributed anostracans are found, e.g. *Branchinecta mackini*, *Branchinecta gigas*, *Streptocephalus dorothae* and *Thamnocephalus platyurus*, (Eng et al., 1990; Simovich and Fugate, 1992; pers.

TABLE 4. Large branchiopod associations over habitat types in both surveys. * = California endemics and + = federally listed as threatened or endangered.

Habitat Type	Species	Order
Northern Transmontane	<i>Lepidurus</i> sp.	Notostraca
	<i>Branchinecta dissimilis</i>	Anostraca
Northern Sacramento Volcanic Mud Flow	<i>Lepidurus packardi</i> *+	Notostraca
	<i>Linderiella occidentalis</i> *	Anostraca
	<i>Lynceus brachyurus</i>	Laevicaudata
Sacramento Valley Hardpan	<i>Branchinecta lynchi</i> *+	Anostraca
Sacramento Valley Claypan	<i>Lepidurus packardi</i> *+	Notostraca
	<i>Branchinecta conservatio</i> *+	Anostraca
	<i>Cyzicus californicus</i> *	Spinicaudata
San Diego Mesa Hardpan	<i>Branchinecta sandiegonensis</i> *+	Anostraca
	<i>Branchinecta lindahli</i>	Anostraca
	<i>Streptocephalus woottoni</i> *+	Anostraca

observ.). While there is a large amount of good data indicating that the distributions of anostracans are influenced by habitat characteristics (see Eng et al., 1990 for review; Gonzalez et al., 1996) this information is not available for most other ephemeral pool crustaceans, most obviously the undescribed ones.

On a genetic note, an associated study involving allozyme analysis of 10 populations of *B. sandiegonensis* across San Diego County reveals very low genetic variability ($P_{95} = 0$ to 45.5%) and a high degree of structuring ($F_{st} =$ up to 0.889 over 36 km) in this very restricted species (Davies, 1996; Davies et al., 1997). Importantly, larger pools and pools with larger populations do not necessarily have higher levels of genetic variability. The largest pool sampled had very little variability ($P = 9.1\%$) and a medium size pool with very high density of individuals had none. Furthermore, 35% percent of the polymorphic loci over all populations are not in Hardy-Weinberg equilibrium, and allele frequencies and alleles present varied between years within the same pool (Davies, 1996). The low level of variability may be attributable to founders effects enhanced by the incomplete hatching of dormant cysts (Moorad and Simovich, unpublished data). In another paper in this volume, Michael Fugate addresses in detail, gene flow and speciation in this genus and its implications for conservation (Fugate, 1998).

DISCUSSION

The data from these surveys only begin to unfold a picture of the faunal communities of California's ephemeral wetlands. This picture is one of high diversity and endemism which, in large part, parallels that of the geological/floristic habitat types. This high diversity over a large scale is doubtless the product of two major factors. The first factor is the spatially patchy nature of the distribution of pools that restricts gene flow, and is thought

to facilitate speciation (Holland and Jain, 1981; Fugate, 1992; King, 1996; Fugate, 1977; 1998). The second factor is the extensive variety of physical and chemical conditions presented by the various pool types (e.g. duration, solutes, temperature), as these would be expected to promote specialization and thereby differentiation. The influence of these physical factors can be seen in the anostracan physiology and life history studies which are associated with these surveys, as well as those which have been done for other California species (see Eng et al., 1990; Gonzalez et al., 1996; Hathaway and Simovich, 1996; Simovich and Hathaway, 1997).

It is informative to contrast the situation in California with that in the prairie states. Sublette and Sublette (1967) sampled invertebrates from 23 playas across a large portion of Texas and New Mexico. They found 14 species of crustaceans but a different balance of taxa; 13 large branchiopods and 1 ostracod. All of these are wide-spread species found across the prairie states, and congeners frequently co-occurred. In an ephemeral stream system in Alberta, Canada, Retallack and Clifford (1980) found 58 species over the range of taxa in our studies, (10 large branchiopods, 26 cladocerans, 13 copepods and 9 ostracods). These species were not ones with restricted distributions, and several congeners co-occurred. Thus, while these other ephemeral systems have high diversity and co-occurrence of species in the same genus, they are not characterized by the endemism seen in California. This difference may be due, in part, to the spatial distribution of pools and to the availability of vectors for dispersal. In California, pools often occur in complexes or clusters. Dispersal between complexes is probably accomplished, in large part, by the movements of birds which have eaten gravid invertebrates. Thus, the distribution of vernal pool animals is patchy and restricted. The prairies by contrast form a large, vegetatively fairly homogeneous area that is more con-

ductive to dispersal via large herds of grazers and avian migratory routes, and more recently via agriculture.

On a smaller scale, we are left with further patterns to decipher. For example: why are some pools more diverse than others (e.g. large vs. small), and why are these ephemeral and often unpredictable habitats exhibiting richness which parallels or surpasses that of permanent wetlands? There are several, non-mutually exclusive hypotheses to explore relative to these questions.

Q. Why are some pools more diverse than others?

Duration/Developmental Time: It is conceivable that short-duration pools have fewer species because they lack the more slowly developing species which the longer-lived pools can accommodate. This does in fact seem to be the case for some taxa in some habitats (Hammer and Sawchyn, 1968; Retallack and Clifford, 1980; Hamer and Appleton, 1991; Simovich and Fugate, 1992; Hathaway and Simovich, 1996) and may help to explain the restriction of more slowly developing large branchiopod species to larger or longer-lived pools. It is not however, sufficient to explain things from the opposite perspective; for example, why are some species found only in small, shallow pools?

Duration/Niche Overlap: Long-lived pools might allow similar species to co-exist if differences in developmental time reduced temporal overlap of similar/competing life cycle stages. This offset development has been seen in some groups (Hammer and Sawchyn, 1968; Retallack and Clifford, 1980; Mura, 1991) and in this case may help to explain why the rapidly developing *Branchinecta lynchi* can coexist with the more slowly developing *B. conservatio* (pools in the northern area but not on the transect, pers. observ.; Eng et al., 1990) or, why the anostracans *B. sandiegonensis* and *S. woottoni* can coexist in the southern pools (Hathaway and Simovich, 1996). Again, however, this is not a sufficient explanation in itself for all species or all pools. First, at least at the level of our sampling, adults of most congeneric pairs (except some anostracans) were found to coexist and were often found together in more than one sampling period. Second, this hypothesis requires competition to be involved and as yet, we have no direct evidence for competition in these pools.

Pool Size/Habitat Heterogeneity: Large pools may provide more niches for more species if they also provide a more heterogeneous habitat (Williams, 1964; Daborn, 1975; Hamer and Appleton, 1991; Thiery, 1991). However, when large pools are compared to one another this hypothesis becomes less applicable. For example, the volcanic mudflow pools offer a very heterogeneous habitat of boulders, diverse floating and emergent plants etc., yet they exhibit species diversity roughly equivalent to the claypans, which are largely devoid of physical structure or macroflora. Furthermore, at the generic level, there was

little evidence of spatial partitioning between congeners within the sampling regime used. It is possible that structure within the faunal community exists, however, a more fine-scale sampling regime may be needed in order to discern it.

Size/"Area Per Se": In an analogy to oceanic islands, larger pools may simply be a larger target for dispersing propagules and have a higher extinction/colonization equilibrium (Preston, 1960; 1962; MacArthur and Wilson, 1963; 1967). Although tempting, this hypothesis also has a major shortcoming in this case due to its requirement of constant and random colonization by propagules. There is good evidence for the passive dispersal of cysts via birds and grazing animals (Maguire, 1963; Proctor et al., 1967; Krapu, 1974; Saunders et al., 1993; Reid and Reed, 1994) and this must surely happen as the crustaceans have no active means of dispersal. The frequency of successful long distance colonizations however, may be a fairly rare occurrence as recent population genetic studies indicate levels of gene flow to be quite low (Hebert, 1974; Boileau and Hebert, 1988; Crease et al., 1990; Havel et al., 1990; Fugate, 1992; Davies, 1996; Davies et al., 1997; King, 1996). Also, larger pools tend to be more widely spread than small pools which occur in complexes, possibly allowing for more frequent local colonization. Again, of itself, this explanation is not sufficient.

Thus, it seems plausible from the information available to date that we need to invoke a pluralistic explanation for some of the patterns of species richness and genetic diversity in ephemeral pool faunal communities. There may well be multiple reasons why some pools are more diverse than others. Different factors or combinations of factors may be the dominant forces in different types of pools, in different geographical or climatic regions, or in different years. While such pluralistic, "it all depends" explanations are not satisfying to many, a more precise understanding awaits the availability of more data.

Q. How do some ephemeral lakes support richer faunal communities than permanent lakes, despite their lack of stratification and the periodic complete loss of all non-dormant aquatic life cycle stages? (See King et al., 1996 for a review of crustacean diversity of ephemeral and permanent lakes.)

Predation: While predators have been shown to allow the coexistence of competing species in other systems by reducing densities (Brooks and Dodson, 1965; Paine, 1966; Dodson, 1975; Boucher et al., 1982; Paine, 1984; Morin, 1987), the potential role of predation in ephemeral wetlands may be quite complex. Some groups, such as the anostracans, are thought to be restricted to ephemeral (or hypersaline) wetlands because their lack of fish provides them with an "enemy-free space" (sensu Fryer, 1986). However, ephemeral wetlands are not always completely devoid of predators. At least in the later stages of the pools, insect predators abound and in some pools salamander and spadefoot toad larvae are present. Along the northern

transect, there is evidence that the California Tiger Salamander (*Ambystoma tigrinum*) is facilitating crustacean species coexistence at the Jepson Prairie (Morin, 1987). However, this hypothesis is not globally applicable to ephemeral pools. First, predation can conceivably both increase and decrease diversity. In order to increase it, competition must be present (which we have yet to show for these systems). Second, some pools have high predation and some do not. In the north, only a small portion of the pools have salamander larvae. While Spadefoot Toad tadpoles do eat anostracans (Simovich et al. 1991), in these studies they occurred only in a few pools in the southern area. Third, relative to the quickly developing species, reproduction may be largely complete before predation pressure is significant. The predators, amphibian or insect, must be laid as eggs in the pools by adults finding them after they form. They only then begin their development. The crustaceans, in the pools as cysts, get a head start. In arctic pools, while insect predation has an effect, early cohorts of *Daphnia* are considered likely to escape (Wilson and Hebert, 1993). In temperate pools which are frequently quite short lived, the net effect of predation may be very weak and its role in determining species richness uncertain.

Non-Limited Resources: It is generally thought that ephemeral pools are highly productive and may not be resource-limited during the relatively short life cycle of most crustacean inhabitants (Hutchinson, 1937; Fryer, 1957; Cole, 1966; Hartland-Rowe, 1972; Belk, 1977; Wiggins et al., 1980; McLachlan, 1981; Nikolaeva and Vekhov, 1985; Thiery, 1991; Brendonck and Persoone, 1993). Active populations may always be below the carrying capacity of the pools (Belk, 1977; Wiggins et al., 1980). If so, then the relaxation of competition may allow more extensive niche overlap than is possible in permanent lakes by reducing or negating competitive exclusion. This may well apply to all ephemeral pools.

Ephemerality/"Intermediate Disturbance": Because of the ephemerality of these systems, it is tempting to invoke a version of the intermediate disturbance hypothesis. However, disturbance is not really applicable here. The habitat is not disturbed, but temporally truncated. Thus, a version of the "competition interruption hypothesis" (Thiery, 1982) may be more applicable. In this case, habitat ephemerality and unpredictability of duration has selected for species with rapid development and reproduction. In many years, pools may not persist long enough for competition to be a problem. Even in high rainfall years when pools persist for some time, and are still very productive, we frequently see many crustacean taxa reproduce and disappear before the pool dries. The selective pressure for fast development and a compact life history may make competition for resources in these systems moot. Again, more data are needed.

Storage Effect/Variable Environment: Numerous recent papers have advanced the notion that diversity (at the community or

population genetic level) can be maintained in a variable environment (e.g. Herbet and Crease, 1980; Chesson and Warner, 1981; Chesson, 1983; Lynch, 1983; Weider, 1985; Hann and Herbet, 1986; Carvalho and Crisp, 1987; Lynch, 1987; Chesson and Huntly, 1989; Ellner and Hairston, 1994; Hairston et al., 1996; Wilson and Herbet, 1992). Some, but not all, of the requirements of these models are met in ephemeral pool systems. The first is a variable environment. Pool longevity is affected by precipitation. Some smaller pools may last for a few months one season and only a few days the next, or may fill and dry within a season. The second is that generations overlap, providing storage of individuals in some life cycle stage. Many ephemeral pool organisms produce desiccation resistant eggs or cysts which survive the dry portion of the cycle. Furthermore, not all cysts hatch when first hydrated, producing a hedge against years when the pools dry before maturity is reached (Brendonck, 1996; Simovich and Hathaway, 1997). The third is that recruitment of types varies relative to environmental variation. In low rainfall years, rapidly developing forms would be expected to experience higher recruitment than those slower to mature while both would survive longer wet cycles. The lack of reproduction in a year would not eliminate a species from a pool, as cysts would still be available to hatch in the next filling. The fourth requirement however, competition, is one for which we have little evidence in ephemeral pools other than those in the arctic (Wilson and Hebert, 1993).

Thus, the high faunal diversity of California pools may conceivably be due to a combination of rich resources and compacted life histories which may negate the need to invoke competition- or equilibrium-based hypotheses (Wiens, 1977; Huston, 1979; sensu "the paradox of the plankton," Hutchinson, 1941; 1961) and to a patchy, variable habitat in which propagules are stored. Obviously, more studies targeting the role of competition, predation, and other factors are needed. However, while we are only beginning to put together a picture of the structure and dynamics of California's ephemeral wetland communities, a few things are certain. These communities are rich, largely endemic, and their habitats are rapidly disappearing.

California's ephemeral wetlands are unique and complex systems, and they are vanishing. We should look not only to the vanishing biodiversity of the rainforests but to our own backyard, where we are losing species we never knew we had.

IMPLICATIONS FOR CONSERVATION AND MANAGEMENT

Several implications for conservation can be gleaned from these studies. Most point to the need for a more detailed understanding of these systems.

1) The physical/chemical properties of the ephemeral habitat are involved in species distributions by merit of their influence on physiological tolerance and life history evolution. These

habitat dimensions are many and at this time, poorly understood for most species. The result is that it will be very difficult to "create" habitat once lost, or recreate habitat after a disturbance. While created/recreated pools hold water, they may not contain all or any of the original species. This is an important consideration when making decisions about potential mitigation. Data on the tolerance limits and requirements of more species are needed.

2) Pools of different habitat types differ in species richness and composition. To preserve biodiversity it is necessary to preserve many pool types, not just the most aesthetically pleasing ones or those in areas not conducive to development or agriculture. It is also not appropriate to use the preservation of pools of one type as mitigation for another type, or to say pools in one place may be destroyed because there are more elsewhere. This can result in a net species loss.

3) Pools of the same type, and pools adjacent to one another can differ in species composition. Therefore, preserving a few pools at a site while destroying others can result in net species loss.

4) Some species are rare. The loss of just a few pools may result in the loss of some of these species. Focusing on preserving only pools of "highest quality," if that is defined as highest richness, while admirable, will not preserve all species. More data are needed on the distributions of previously unknown species.

5) The fact that some pools may have large numbers of crustaceans, does not imply high genetic diversity in those populations. If all individuals in a large population are genetically similar, evolutionarily, the situation is like having only a few individuals. We cannot always presuppose large effective population sizes from numbers of individuals. This is particularly evident in the southern pools, where very low genetic variability in anostracan populations indicates substantial drift effects. Thus, a dense pool is not necessarily a healthy pool in the long run. This is particularly a problem if habitat fragmentation cuts off previously existing sources of gene flow and results in further reductions of genetic variability and evolutionary potential.

6) Pools differ not only in species composition, but also in terms of intraspecific genetic variability. This makes the choice of inoculum for creation, recreation, or restoration efforts a delicate and complex issue, and one which will necessitate individual solutions based on analysis of local genetic structure and community composition.

7) Some species develop quickly, reproduce and are gone before pools dry (at least in wet years). Sampling a pool once a

year, or only in one year, may not produce an accurate species list for a pool or area.

8) Many species are undescribed. This makes the use of taxonomic specialists a must, and the comparison of vouchers between projects highly advisable.

9) Our knowledge of the distributions, life histories and requirements of most ephemeral pool species is sorely lacking. Much more work is needed if we are to distinguish between the various potential forces affecting and shaping the communities of different habitat types.

10) We currently have no understanding of what a viable population is relative to vernal fauna. This makes the establishment of "criteria for success" for mitigation, especially in the few years of monitoring usually required by agencies, extremely chancy.

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