Hydrobiologia 328: 85–116, 1996.

Species richness, endemism and ecology of crustacean assemblages in northern California vernal pools

Jamie L. King[1], Marie A. Simovich[2] & Richard C. Brusca[3]
[1]*Section of Evolution & Ecology, University of California, Davis, California 95616, USA*
[2]*Department of Biology, University of San Diego, Alcalá Park, San Diego, California 92110, USA*
[3]*Grice Marine Biological Laboratory, University of Charleston, 205 Ft. Johnson, Charleston, South Carolina 29412, USA*

Received 20 June 1995; in revised form 23 November 1995; accepted 29 November 1995

Key words: Temporary pools, vernal pools, crustaceans, wetlands, diversity

Abstract

Ephemeral pools occur worldwide, provide habitat for organisms with a variety of life history strategies, and may have served as evolutionary refugia for some taxa since Mesozoic times. Yet, our understanding of the ecology and evolutionary history of ephemeral pool communities is hampered by a paucity of such basic data as the species composition of pool assemblages. We surveyed 58 vernal (ephemeral spring-time) pools from 14 sites in northern California for crustaceans, and found diverse assemblages composed largely of endemic and rare species. Sixty-seven species of crustaceans were found, and as many as 30 of these may be new, undescribed species. Differences in species composition among pools correspond with physical and chemical aspects of the habitat (depth, solutes concentration, elevation, biogeographic region), and with existing geologic/floristic-based habitat descriptions. Species richness is positively correlated with both depth and surface area. This relationship can be explained in terms of hydroperiod (accommodation of species with slower developmental rates in long-lived pools, greater time for temporal resource partitioning) and size (spatial habitat heterogeneity). High species richness and numerous co-occurrences of congeneric species in temporary pools may be due to super-abundant resources, low levels of predation, and annual truncation of the community which prevents ecological interactions from going to completion. The results of this survey underscore the need for conservation of the vernal pool habitat and endemic vernal pool species in California. The best preservation strategy will include many pools at each site, multiple sites of each habitat type, and all identified habitat types.

Introduction

Ephemeral pools are an ecological feature of virtually every continent on the globe (Thorne, 1984; Williams, 1985; Zedler, 1987 and references therein). These ephemeral wetlands, which are also referred to in the U.S.A. as temporary pools, vernal or autumnal pools, hogwallows, pans, and playas, occur wherever seasonal precipitation and impervious substrates combine to create surface pools during the wet season (Holland & Jain, 1981). Ephemeral pool communities include both opportunistic (vagrant) species (e.g. flying insects, birds, amphibians) which are present during the aquatic phase and leave as the pool dries, and less-vagile (resident) species (e.g. plants, crustaceans, gastropods, many beetle species), which survive the drought phase as dormant adults, juveniles, or propagules such as seeds or cysts (see Wiggins et al., 1980 for a more exhaustive synthesis of life history strategies in temporary pools). The ecology of these unique communities thus reflects the interplay of a temporally variable habitat and the activities of many organisms with different life history strategies. Evolutionarily, ephemeral pools may be important both as refuges for certain taxa and as sites of allopatric speciation. At least one group, the large branchiopod crustaceans, became restricted to temporary pools concurrent with the rise of predatory, suction-feeding bony fishes in Mesozoic seas and lakes

(Hutchinson, 1967; Kerfoot & Lynch, 1987; Wagele, 1992; Wiggins et al., 1980). Rates of speciation and local extinction for some ephemeral pool taxa may be relatively high, reflecting the geographically fragmented nature of the habitat and the isolation of small populations (Fugate, 1992; Holland & Jain, 1988; Hoover, 1937).

Despite their worldwide distribution, ecological interest, and evolutionary importance, ephemeral pools are usually overlooked in limnological and ecological textbooks (Williams, 1985). Also, in contrast with the large body of knowledge dealing with zooplankton communities of permanent waters such as lakes, the aquatic literature contains very few surveys of ephemeral pool fauna. Consequently, the literature of temporary waters is largely scattered among species- and taxon-specific papers, and rarely addresses community-level patterns and processes (with the exception of reviews dealing with life history strategies of ephemeral pool inhabitants, e.g., Wiggins et al., 1981; Williams, 1985).

The often uncertain future of ephemeral pool habitats and their endemic species presents an additional imperative for basic research and conservation of these systems. Losses of vernal pool habitats in California's Central Valley, which began in the late 1800's with the agricultural settlement of the state and continue today due to urbanization, are estimated at between 60 and 85% of pre-settlement acreage (Federal Register, 1994b). In highly-urbanized coastal areas habitat losses have been even greater: approximately 97% of the vernal pools in San Diego County have been destroyed (Weir & Bauder, 1990). This massive loss of habitat portends extinction for many species which are uniquely adapted and endemic to California vernal pool communities. Fifteen species of vernal pool plants (Federal Register, 1991; 1992; 1993a; 1993b) and seven species of vernal pool invertebrates (Federal Register, 1980; 1993a; 1994a; 1994b) are now federally listed or proposed for listing as threatened or endangered. Inhabitants of ephemeral pools in other parts of the world are also disappearing because of habitat losses. For example, one species of ephemeral pool anostracan from France is believed to be locally extinct, and another is considered endangered (Belk, 1994); of the three eubranchiopod species known from Great Britain, one is locally extinct, and the other two are greatly reduced in range and are now protected by the British Wildlife and Countryside Act 1981 (Grainger, 1994).

This paper reports the results of a survey of the crustacean fauna inhabiting vernal pools in northern California. Our study focuses on crustaceans because of their numerical dominance and ecological importance in the pool community. We present data on the physical habitat, species assemblages, patterns of species richness, and co-occurrence of congeneric species, and we evaluate several ecological hypotheses for their potential to explain the observed patterns. Specifically, we report the discovery of 30 potentially new crustacean species, assess the correspondence of physical habitat characteristics with species assemblage similarity, and examine the extent to which ecological principles such as species-area relationships, competition, predation, productivity, and the effects of temporal variability may determine patterns and levels of species richness in these vernal pools.

This survey, although limited to crustaceans, is the first of its kind for northern California vernal pools and represents an important step toward understanding these largely unknown communities. This first step is crucial, because without a basic understanding of patterns and scales of variation in a system it is exceedingly difficult to design informative ecological field experiments. Thus, while the data we present are necessarily descriptive and exploratory, our main goal is to stimulate more ecological and evolutionary study of California's vernal pools in particular, and ephemeral freshwater pools in general. The data from our survey provide a significant foundation upon which hypothesis-oriented field experiments can be built.

Description of sites studied

We surveyed 58 vernal pools from 14 study sites situated along a 300 km north-south transect through the Sacramento Valley, from Fall River in Shasta County to Jepson Prairie in Solano County during the spring of 1992 (Figure 1). The transect route followed a Pacific Gas & Electric natural gas pipeline corridor that extends approximately 1360 kilometers from Kingsgate, British Columbia, Canada to Panoche, California, U.S.A. The subterranean pipeline was originally constructed in 1960. We consider the pipeline route to be a random (with respect to the distribution and types of vernal pool habitats encountered) transect through the Central Valley. Our survey included undisturbed pools adjacent to the pipeline corridor, as well as pools on the pipeline right-of-way which have re-established or which lie outside the trench zone and appear to have been only moderately disturbed by the 1960 construction. All pools were visited three times during the 1992

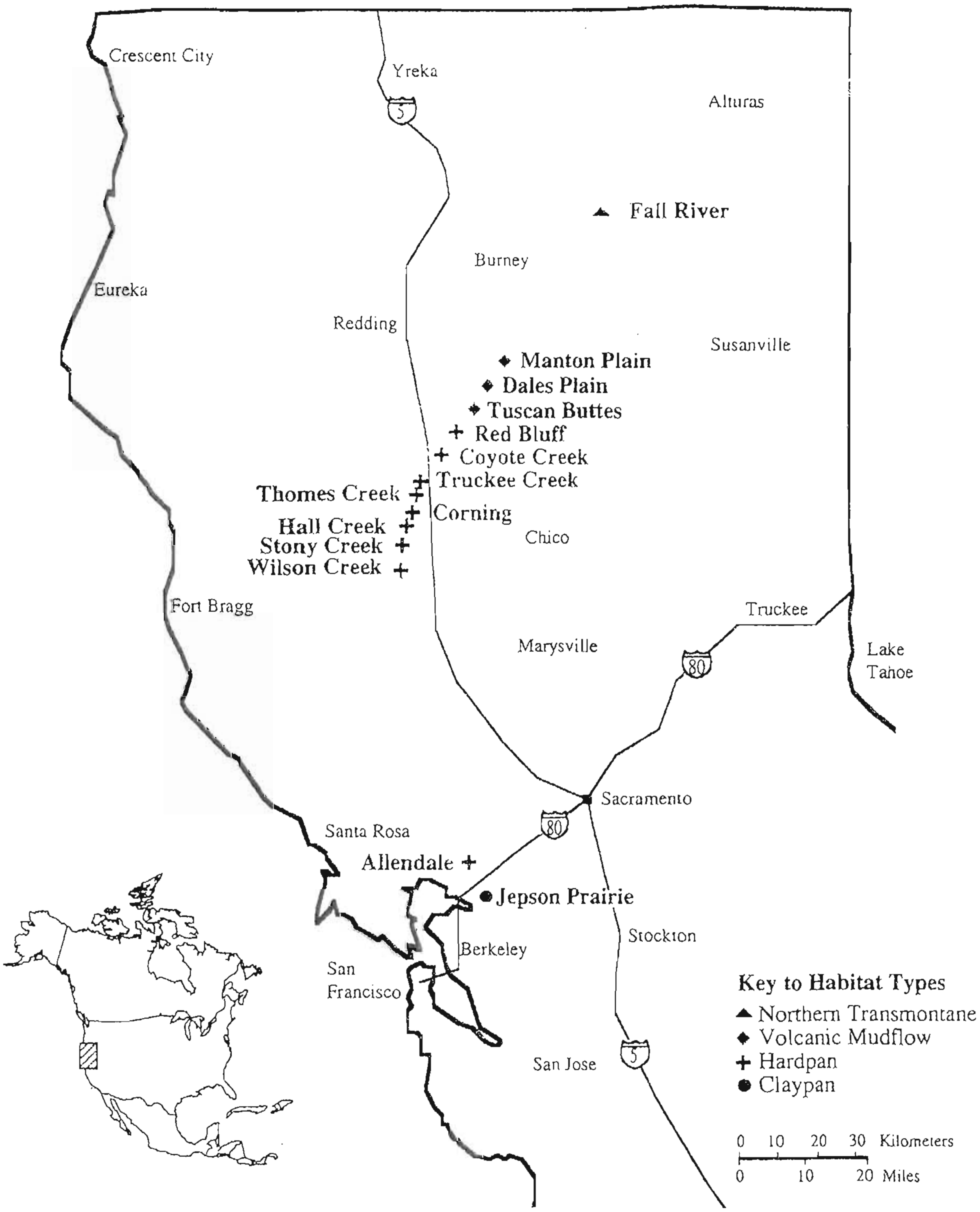

Figure 1. Map of study sites in northern California. Transect extends approximately 300 km from Fall River in the north to Jepson Prairie in the south.

wet season between February and May, although some pools were dry before the third sampling.

The transect study sites fall into four vernal pool habitat types according to the geological and floristic classification established by Cheatham & Haller (1975, as cited in Holland, 1986), described by Holland (1986), and modified by Taylor et al. (1992). Fall River (FR) is the single representative of northern transmontane vernal pools and contains very small pools (refer to Appendices A and B for pool sizes) within a mountain meadow at 1100 m elevation. All the other sites are below 100 m elevation and are situated in the Sacramento River Valley. Three sites, Manton Plain (MP), Dales Plain (DP), and Tuscan Buttes (TB), contain primarily northern Sacramento Valley volcanic mudflow vernal pools. Vernal pools at these volcanic boulder-strewn sites are few in number but medium to very large in size, despite earlier descriptions of such pools as typically small (*viz.* Holland 1986). The Jepson Prairie (JP) site is characterized by both small mima mound (hummock and swale topography, see Cox & Gakahu 1983) pools and very large, turbid, windswept playas of the Sacramento Valley claypan vernal pool type. Only the large playas are included in this survey because the small pools at this site were not sufficiently inundated during the sampling periods. The remaining nine sites, Red Bluff (RB), Coyote Creek (CC), Truckee Creek (TR), Thomes Creek (TH), Corning (CR), Hall Creek (HC), Stony Creek (SC), Wilson Creek (WC), and Allendale (AL), contain Sacramento Valley hardpan vernal pools. These sites include numerous very small to medium sized pools scattered among mima mounds in valley grasslands.

Methods

Sampling procedures. All pools were sampled three times, except for most of the hardpan pools which were sampled only twice because they were dry at the time of the third sampling. The three sampling trips (February 16–24, March 23–April 3, and April 22–May 1) spanned roughly the early, middle, and late portions of pool hydrocycles. We sampled aquatic organisms from pools by volume-standardized plankton tows using a square hand net frame (17 cm × 25 cm) fitted with 400 μm mesh plankton net. Wherever possible, we took samples separately from the surface, bottom, and edge areas of the pool. For surface tows, the net was dropped vertically into the water to a depth of 8 cm, then drawn horizontally through the water over a distance of one meter. For bottom tows, the net was dropped vertically into the water until the lower edge of the frame rested on the pool bottom. The net was drawn across the bottom for one meter, then brought vertically to the surface. This method sampled approximately the top 1 cm of bottom sediment and the overlying 16 cm of water. In pools that were not deep enough for separate surface and bottom plankton tows, we combined these as a single tow. We immediately preserved plankton samples in 70% ethyl alcohol.

Water chemistry and physical properties. We collected water chemistry data in the field, including conductivity ($\mu\Omega^{-1}$), total dissolved solids (TDS in mg l^{-1}), alkalinity (mg l^{-1}), salinity (‰), pH, dissolved oxygen (mg l^{-1}), and temperature (°C). We estimated surface area and maximum and average pool depth at the time of sampling, as well as long-term maximum surface area and depth based on observed pool characteristics such as filling, vegetation, and topography. We quantitatively defined descriptive terminology for water chemistry, pool size, and depth prior to data analysis (Appendix A).

Sample processing and curation. In the laboratory, plankton samples were screened through a 500 μm sieve because most crustaceans smaller than 500 μm are primarily larvae or juveniles and cannot be identified, although this procedure may have reduced the number of harpacticoid copepods and very small species of cypridopsine and limnocytherid ostracods in our samples. The 500 μm fraction of each sample was sorted into the following categories: Anostraca, Notostraca, Conchostraca (Laevicaudata, Spinicaudata), Cladocera, Copepoda, Ostracoda, Insecta, and 'other' (e.g. gastropods, annelids, arachnids, platyhelminths, algae, plant fragments, etc.). For a few samples, where thousands of individuals were present, aliquots were sorted. All samples were preserved in 70% ethyl alcohol, except some representative ostracod specimens which were dried and permanently curated in glass vials or on paleontology slides. All samples are permanently archived at the Los Angeles County Museum of Natural History, and are accompanied by 1:150000 scale maps showing the geographic locations of collection sites. We encourage investigators interested in accessing any specimens or the 'other' taxa to contact the appropriate LACM curator.

Species identifications. Anostracan, notostracan, and conchostracan species were identified by the authors, with some samples verified by Joel Martin (Los Angeles County Museum of Natural History), Denton Belk (Our Lady of the Lake University, San

Antonio), and Michael Fugate (University of California, Riverside). Cladocerans were identified by Brenda Hann (University of Manitoba). Copepods were identified by Janet Reid (U.S. National Museum of Natural History, Smithsonian Institution). Ostracods were identified by both Claire Carter (U.S. Geological Survey, Menlo Park) and Richard Forester (U.S. Geological Survey, Denver).

Some specimens could not be identified as a known species, and these are listed as 'sp.' Other specimens closely resembled a described species, but differed sufficiently from the current species description to be considered a 'possible' or 'probable' new species. In these cases the putative species name is given, but the uncertain taxonomic standing of the specimen is noted. Two ostracod taxa could not be assigned to a known genus and are listed as 'Unknown sp.'. Taxonomic descriptions (and redescriptions) of cladoceran and copepod species from this material are in progress and will be reported elsewhere by the specialists noted above.

Data analysis. Salinity data, although potentially biologically important, were not included in water chemistry analyses because they were always below 1‰, and our equipment was not sensitive to values in the parts per million range. Dissolved oxygen, although variable, was always above 5 mg ml^{-1} and, therefore, not biologically limiting. However, we collected these data typically between 0900 and 1700 hours; late-night or early-morning measurements may have shown periods of oxygen depletion (Scholnick, 1994). Temperature ranges are provided in Appendix B, but are not included in further data analyses. We performed a principal components analysis on the remaining water chemistry data and the pool size and elevation data using the Statview SE + Graphics software package for the Macintosh (Abacus Concepts, Inc. 1988).

We addressed patterns of community composition with a clustering analysis based upon species presence/absence among pools. For each pool we scored all species that were present as positive character states and all species found in the survey but absent from the pool as negative character states. We excluded from this analysis 24 of the 67 total species because they were present in fewer than three pools; rare species (i.e. those occurring in less than 5% of the pools) can be uninformative and often problematic in multivariate community similarity analyses (Gauch, 1982; Hill & Gauch, 1980). We used the hierarchical clustering function of the SYSTAT 5.0 software package for the Macintosh (SYSTAT, Inc. 1989) and specified the average linkage (UPGMA) method of dendrogram construction to generate a phenogram of pools.

We examined the relationship between species assemblage and geographic proximity by regressing Jaccard's Coefficient of community similarity against linear distance between pools for all pairwise comparisons among pools of the hardpan type. Jaccard's Coefficient is defined as

$$S_j = a/(a + b + c),$$

where a = the number of species in both pools, b = the number of species in pool B but not in pool A, and c = the number of species in pool A but not in pool B. Linear distances were measured among pools within sites using 1:1200 scale maps, and among pools at different sites using 1:150 000 scale maps. Although these measurements vary in accuracy across the two different scales, we use them as rough estimates.

Results

Water chemistry and physical properties. (see Appendix B for raw data) The six water chemistry and physical variables can be reduced to a representative set of four (solutes, depth, pH, and elevation). Over all samples from all pools, strong correlations exist for TDS versus conductivity (r^2 = 0.921; Figure 2a), TDS versus alkalinity (r^2 = 0.675; Figure 2b), conductivity versus alkalinity (r^2 = 0.680; Figure 2c), and maximum depth versus log surface area (r^2 = 0.394; Figure 2d). Principal components analysis revealed three factors which account for 78% of the variance in physical and water chemistry data (Table 1). A cutoff at three factors is suggested by the cumulative variance explained, the factor eigenvalue magnitudes, and a scree (eigenvalue versus factor) plot (as recommended by Cattell, 1966; Everitt & Dunn, 1992; and Joliffe 1972).

The correlations and the common factor-loading of alkalinity, conductivity, and TDS support the collapse of these variables to a single solutes variable, hereafter represented by TDS. Similarly, depth and surface area, both of which determine other biologically important properties such as pool volume and hydroperiod (duration of pool inundation), can be represented using depth as a single surrogate variable. Although elevation does not covary with any other physical or chemical variables in these analyses, it indicates an important difference between Fall River (located in the Sierra Nevada Mountains) and all the other sites (located in the valley proper), because it corresponds to major differences

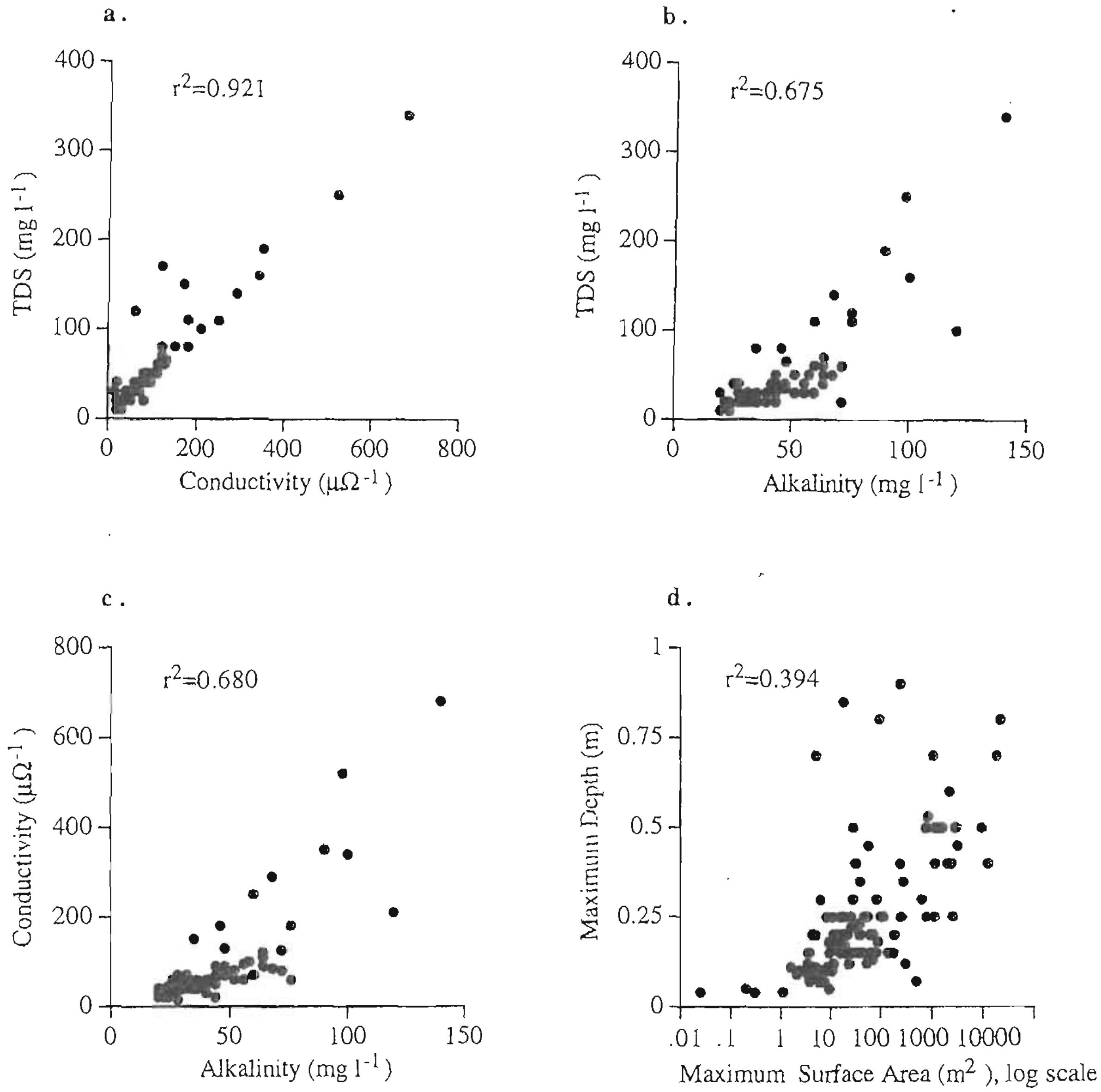

Figure 2. Water chemistry and pool size correlations. a. TDS vs conductivity ($y=0.503x+1.872$), b. TDS vs alkalinity ($y=1.839x-36.988$), c. Conductivity vs alkalinity ($y=3.719x-76.032$), d. Maximum depth vs maximum surface area, log scale ($y=0.1091\log x-0.023$).

in climatic regimes and biogeographic provinces (see Durrenberger & Johnson, 1976).

Habitat characteristics. The reduced array of pool physical and water chemistry variables (solutes, depth, pH, and elevation) specifies four groups which correspond to the four geologic/floristic habitat types previously identified. Claypan pools have significantly higher solute levels, claypan and volcanic mudflow pools are significantly deeper, and transmontane pools are significantly higher in elevation than all others. None of the pool types show any clear pattern for pH. Based on these analyses and field observations the following generalizations emerge for the areas included in this study (Figure 3): Northern transmontane vernal pools are low in solutes, shallow, fairly turbid, and high in elevation; northern Sacramento Valley volcanic mudflow vernal pools are low in solutes, deep, long-lived (4–6 mo.), very clear, and low in elevation; Sacramento Valley hardpan vernal pools are low in solutes, usually shallow, often very short-lived (1–3 mo.), clear, and

Table 1. Principal components factor analysis matrix (unrotated). Alkalinity, TDS, and conductivity load heavily on factor 1; depth and surface area load heavily on factor 2; pH and elevation both load heavily on factor 3, but the latter has a negative loading. Cumulative percent variance explained by these three factors is approximately 78%.

	Factor 1	Factor 2	Factor 3	
Depth	0.611	0.614	− 0.061	
Surface area	0.493	0.606	− 0.119	
pH	− 0.273	− 0.194	0.740	
Alkalinity	0.844	− 0.332	− 0.021	
TDS	0.926	− 0.303	0.093	
Elevation	− 0.188	− 0.453	− 0.671	
Conductivity	0.926	− 0.0270	0.111	
% variance	45.070	18.03	14.820	= 77.92

low in elevation; Sacramento Valley claypan vernal pools are high in solutes, often very deep, long-lived, highly turbid, and low in elevation.

Similarity of species assemblages. Species assemblages of vernal pool crustaceans appear to be strongly related to habitat type. Major nodes of the species assemblage phenogram coincide with physical and chemical differences among pools, and with the geologic/floristic habitat classifications presented earlier (Figure 4). With only a single exception, pools from the same habitat type cluster together on the basis of species assemblages. The Jepson Prairie (claypan) pools differ most from all others, and the separation of this cluster from all other pools at node 1 corresponds to the large difference in solutes between Jepson Prairie and all other sites. The Manton Plain, Dales Plain, and Tuscan Buttes (volcanic mudflow) pools cluster together and separate at node 2 from all the hardpan and transmontane pools, with the exception of one Manton Plain pool (MP2) which falls into the latter cluster. This second node coincides with the maximum pool depths at these sites, because the former group contains medium to deep pools and the latter contains primarily very shallow to shallow pools. The Fall River (transmontane) pools break away from the hardpan cluster at node 3, corresponding to their location at a higher elevation and in a different biogeographic province. The topology of this phenogram is highly robust; changes in both the similarity coefficient algorithm and the linkage method of dendrogram construction do not alter pool membership in the major clusters.

Two lines of evidence indicate that, for pools of the same habitat type, geographic proximity is not correlated with species assemblage similarity. The 9 hardpan sites, which include 44 pools and span the greatest distance along the transect of all habitat types, are the most exhaustive portion of our dataset. The phenogram for this subset of data shows that pools at the same site do not tend to cluster together (Figure 4). Also, a plot of all pairwise comparisons among hardpan pools shows no clear relationship between community similarity (Jaccard's Coefficient) and distance ($r^2 = 0.00007$; Figure 5).

Crustacean species, endemism, and rarity. Sixty-seven species of Crustacea occurred in the pools in this survey, including 4 species of Anostraca, 2 Notostraca, 1 Spinicaudata, 1 Laevicaudata, 18 Cladocera, 17 Copepoda (7 Cyclopoida, 6 Calanoida, 4 Harpacticoida), and 24 Ostracoda (Table 2). Taxonomic specialists identified 17 of the 67 species (25%) as probably undescribed and another 13 (19%) as possibly undescribed, based on deviations of these specimens from existing taxonomic descriptions and examinations of comparative material. These numbers indicate that up to 44% of the crustacean species inhabiting northern California vernal pools could be new species. Thirty-five of the 67 species (52%) found in this survey had not previously been reported from California.

Some of the species encountered, such as *Branchinecta conservatio, Branchinecta lynchi, Linderiella occidentalis*, and *Lepidurus packardi*, are restricted to California vernal pools (Eng et al., 1990), while many other species are widespread and also occur in permanent freshwater habitats such as lakes, ponds, or streams. The 30 potentially new species found in this survey are not known to occur elsewhere and may be endemic to vernal pools and to the region. Thus, the level of endemism for crustaceans in northern California vernal pools may be as high as 51% (potentially 34 endemics out of 67 total species). Also, a large proportion of the species in this survey are relatively rare. Over 25% (17) of the 67 total species had only a single pool occurrence (Figure 6a), and 40% (27) had only a single site occurrence (Figure 6b).

Species richness and patterns of diversity. The total species richness found in this survey is partitioned hierarchically among pools, sites, and habitat types. For example, species assemblages varied, even among pools within the same site, so that all species occurring at a site were not found within a single pool. Consequently, the species richness of any particular site was always greater than that of the most diverse pool at that site. The number of species per pool ranged from 1 (TR17, TR24, TROFF) to 27 (Dales Potholes) and averaged 9.6 species per pool (s.d = 6.1, $N = 58$). The

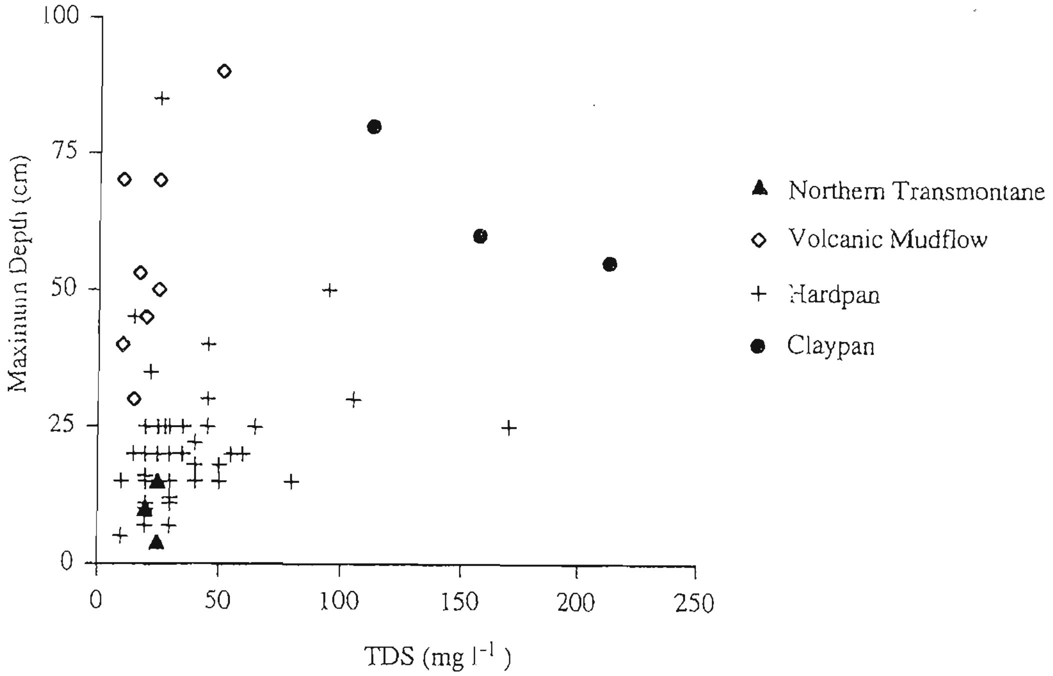

Figure 3. Bivariate plot of water chemistry and pool size: maximum depth vs TDS.

total number of species at a site ranged from 4 (Hall Creek) to 39 (Dales Plain), with an average of 18.6 species per site (s.d. = 8.7, N = 14). Species richness by habitat type ranged from 14 (northern transmontane) to 46 (volcanic mudflow) with an average of 31.8 species per habitat type (s.d. = 13.9, N = 4). Thus, on average, a given pool, site, or habitat type holds roughly 14%, 28%, and 47%, respectively, of the total diversity in the system.

The number of crustacean species occurring in a pool was positively correlated with maximum pool depth ($r^2 = 0.584$; Figure 7a) and with the logarithm$_{10}$ of observed maximum pool surface area ($r^2 = 0.300$; Figure 7b). However, some species, such as *Branchinecta dissimilis, Branchinecta lynchi, Lepidurus sp. A, Acanthocyclops vernalis, Canthocamptus sp. A, Hesperodiaptomus hirsutus, Skistodiaptomus pallidus, Heterocypris aff. H. rotundatus*, and unknown ostracod sp. G, were only found in small, shallow pools which had short hydroperiods (i.e. 1–3 months). Therefore, although deeper, larger pools (temporary 'lakes') with longer hydroperiods (i.e. 4–6 months) generally contained more species, the total diversity encountered in this survey is distributed between both highly ephemeral pools and pools of longer duration.

Co-occurrence of congeneric species. Congeneric species co-occurred in 55% (32 out of 58) of the pools. Three cladoceran genera (*Alona, Daphnia*, and *Simocephalus*), two copepod genera (*Diacyclops* and *Hesperodiaptomus*), and four ostracod genera (*Candona, Eucypris, Heterocypris*, and *Limnocythere*) include co-occurring congeners (Table 3). Some small, short-lived pools in this study had co-occurring congeneric species, but sites with the largest, most long-lived pools (Jepson Prairie and Dales Plain) were particularly rich in sympatric congeners. For example, the Jepson Prairie site contained a total of five congeneric associations, and a single pool at this site (JP5/Olcott Lake) held four congeneric species pairs. Nine sets of congeneric species were found at the Dales Plain site. Three of these combinations occurred in a single pool (Dales Lake); five others occurred in another single pool (Potholes) and included a congeneric ostracod trio. In most cases, populations of co-occurring congeners overlapped both temporally (within the same sampling period) and spatially (within the same subsample).

Discussion

Our survey of northern California vernal pools reveals a highly diverse crustacean fauna, a large proportion of which consists of endemic, relatively rare,

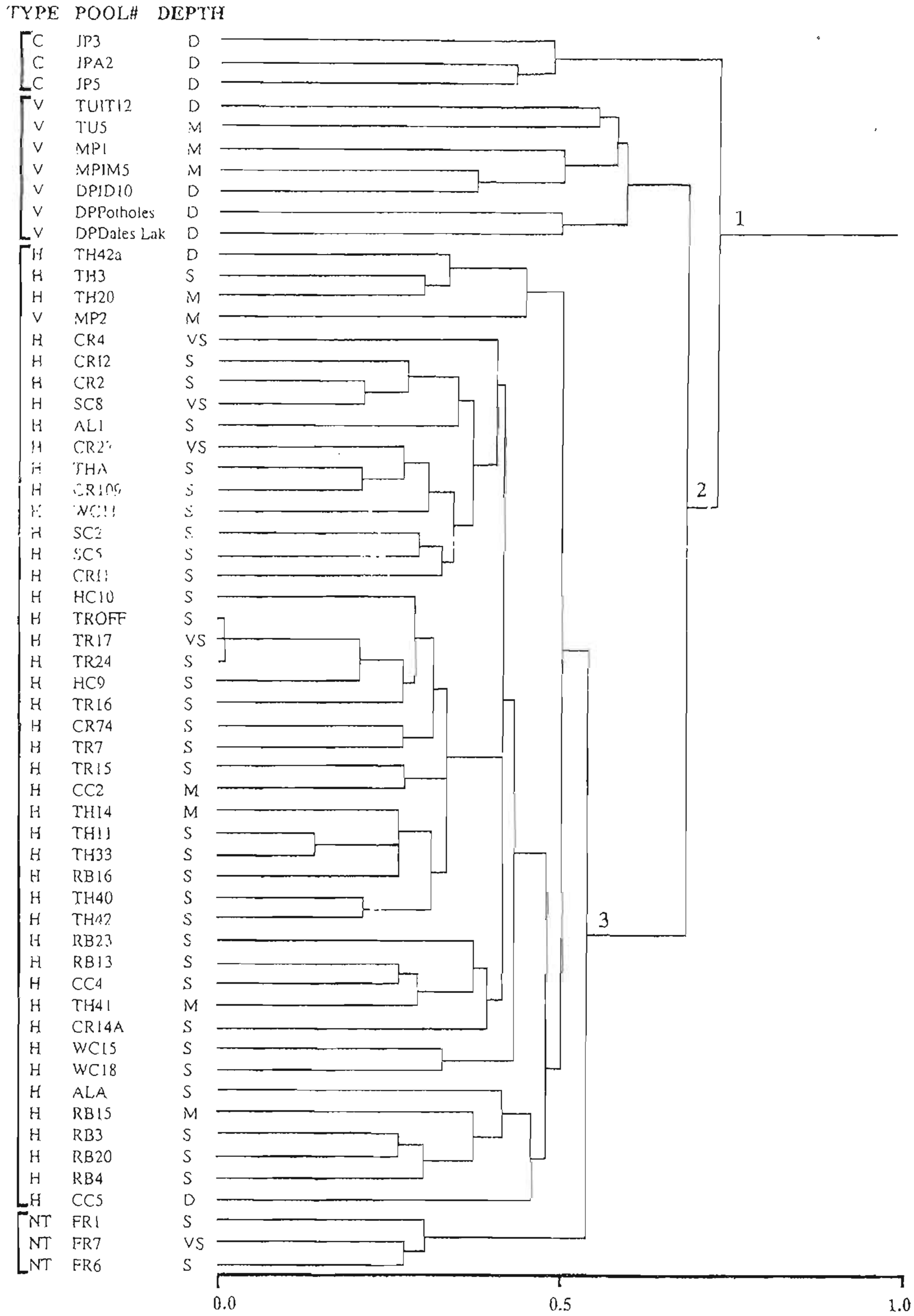

Figure 4. Similarity dendrogram of pool species assemblages. Euclidean distance, average linkage method. C = claypan, V = volcanic mudflow, H = hardpan, NT = northern transmontane, D = deep, M = medium, S = shallow, VS = very shallow. The first two letters of each pool code represent the site name. Nodes 1, 2, and 3 correspond to solutes, depth, and elevation/biogeographic province, respectively. *MP2 appears to be an artifact of pipeline construction rather than a naturally occurring pool. Because of the more recent origin of this pool relative to the other volcanic mudflow pools, MP2 may not yet be fully colonized. Alternatively, this artificial pool may not provide the same habitat quality found in the natural pools of the region.

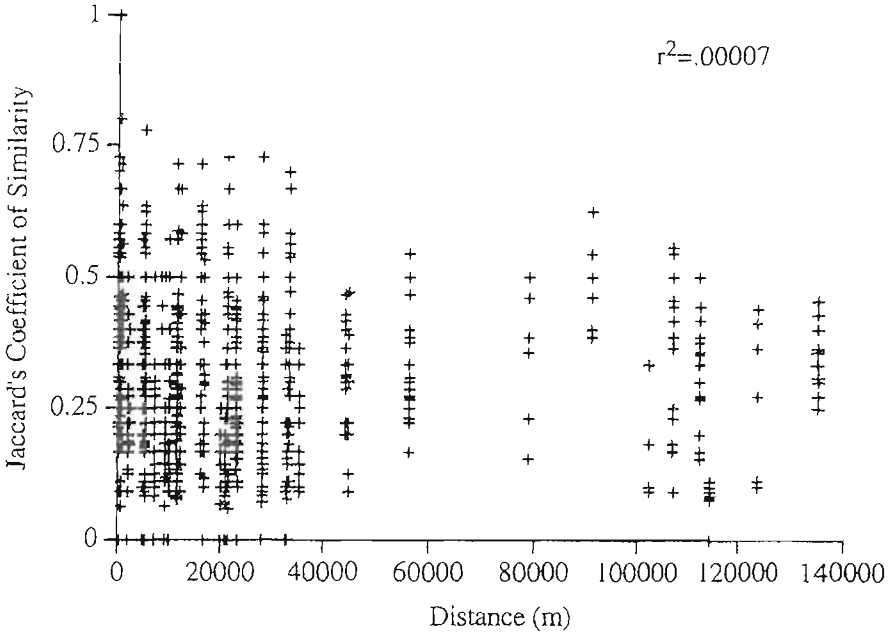

Figure 5. Species assemblage similarity (Jaccard's Coefficient) vs distance for all pairwise comparisons of hardpan pools. N=44 pools, 946 comparisons ($y=-4.937E-8x+0.287$).

and previously unknown species. Similarly high levels of endemism for California vernal pool plants have been recognized for decades (Holland & Jain, 1981; 1988). Taken together, this high level of endemism and the major loss of habitat in California's Central Valley (see introduction) suggest that many undescribed vernal pool species may have already gone extinct. Furthermore, without conservation measures designed to protect the remaining vernal pool habitats, many additional species will most likely become extinct. High endemism in vernal pools is probably facilitated by the spatially fragmented nature of the habitat which, in conjunction with restricted dispersal, promotes allopatric speciation and isolated local extinctions (Fugate, 1992; Holland & Jain, 1981). The possibility that high endemism is a general characteristic of the temporary pool habitat warrants investigation in other parts of the world as well.

The correspondence of major nodes (Figure 4 nodes 1, 2, 3) in the species assemblage phenogram with physical and chemical variables (depth, solute concentrations, elevation) and geographic location (biogeographic province) indicates that abiotic environmental factors play a role in structuring vernal pool crustacean assemblages. However, the fact that species composition varies among pools of the same habitat type and even among pools at the same site shows that, while physical and chemical characteristics may determine the physiological potential for a species to exist in a given pool, other factors must also be important in shaping these species assemblages (e.g. historical factors: past colonization, vicariance, or other chance events; ecological interactions: competition, predation).

On the mesogeographic scale of this study and among pools of the same habitat type, there is no correlation between geographic proximity and species assemblage similarity. This suggests that, for a given habitat type, geographic location may not determine whether a species will be found in a given pool. Such patchwork patterns of species occurrence at the mesogeographic scale are commonly observed for freshwater crustaceans (Anderson, 1968; 1974; Balko & Ebert, 1984; Fryer, 1993; Mahoney et al., 1990; Patalas, 1971; Reed, 1962) and can be interpreted in two ways. One possibility is that dispersal is sufficiently frequent to ensure that every species in the region colonizes all pools of the appropriate habitat type, and

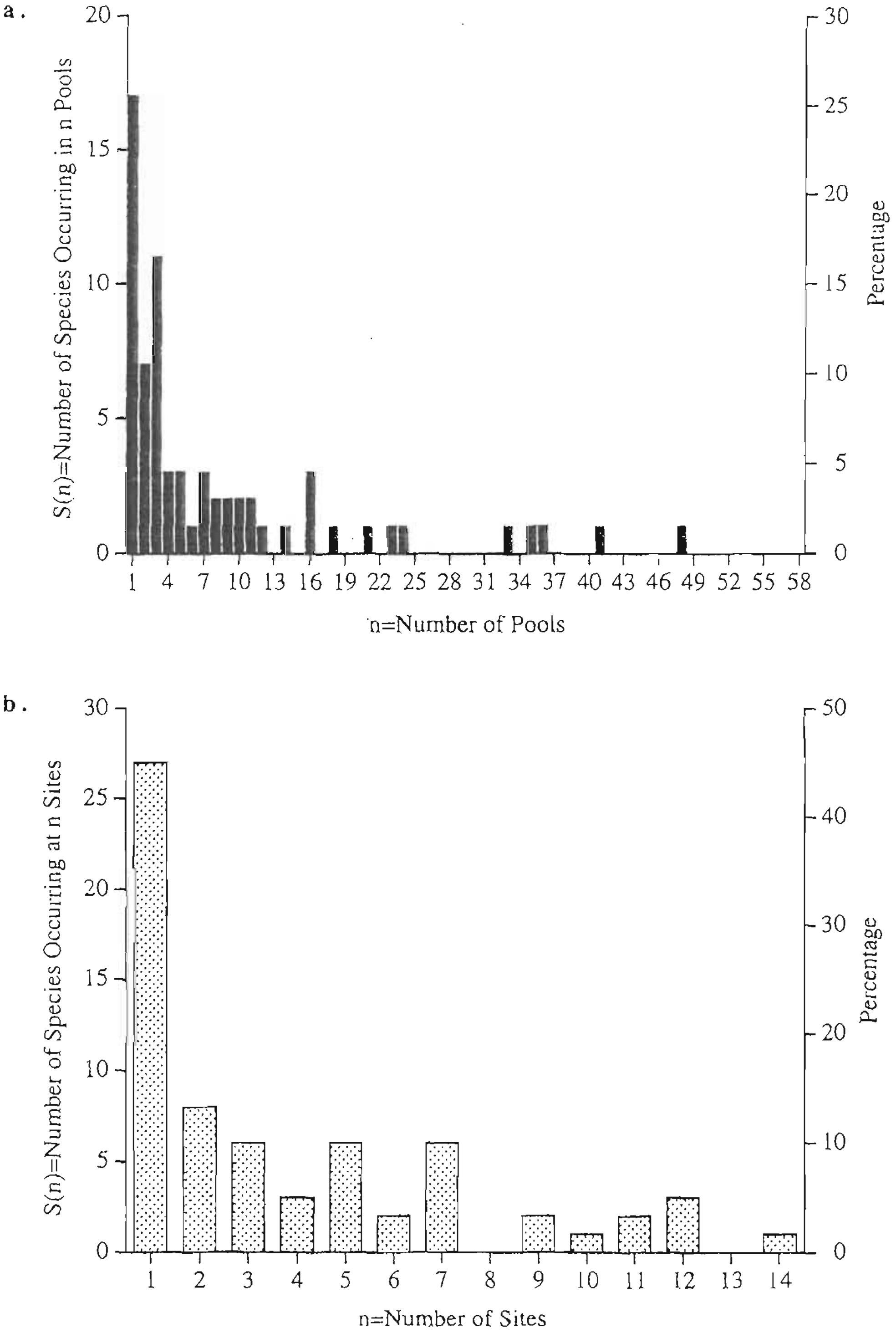

Figure 6. Histogram showing relative rarity/commonness of species found in this survey.

Table 2. Species distribution across sites. Species are listed alphabetically, sites are listed from north to south.

Species	# Sites	Prob. Undes.	Poss. Undes.	1st CA Record	NT	VM & H			H									C
					FR	MP	DP	TU	RB	CC	TR	TH	CR	HC	SC	WC	AL	JP
Anostraca (4)																		
Branchinecta conservatio	1																	+
Branchinecta dissimilis	1				+													
Branchinecta lynchi	6										+	+	+	+	+	+		
Linderiella occidentalis	3					+	+	+										
Number of anostracans per site					1	1	1	1	0	0	1	1	1	1	1	1	0	1
Notostraca (2)																		
Lepidurus packardi	4					+	+	+										+
Lepidurus sp. A	1				+													
Number of notostracans per site					1	1	1	1	0	0	0	0	0	0	0	0	0	1
Spinicaudata (1)																		
Cyzicus californicus	1																	+
Number of spinicaudatans per site					0	0	0	0	0	0	0	0	0	0	0	0	0	1
Laevicaudata (1)																		
Lynceus brachyurus	3					+	+	+										
Number of laevicaudatans per site					0	1	1	1	0	0	0	0	0	0	0	0	0	0
Cladocera (18)																		
Alona cf. davidi	1		X	X			+											
Alona cf. setulosa	2		X	X			+	+										
Alona sp. A	2	X		X			+			+								
Alona sp. B	1	X		X			+											
Camptocercus sp. A	1	X		X			+											
Ceriodaphnia reticulata	5			?			+		+	+			+		+			
Chydorus cf. sphaericus	3	X		X		+	+	+										
Daphnia cf. middendorffiana	2		X			+												+
Daphnia cf. pulex	7		X		+		+	+	+						+	+		+
Diaphanosoma cf. birgei	1		X	X			+											
Dunhevedia crassa	1			X			+											
Leydigia leydigi	2			?			+											+
Macrothrix hirsuticornis	12				+	+	+	+		+		+	+	+	+	+	+	+
Moina cf. micrura	7		X		+	+	+	+		+	+		+					
Pleuroxus aduncus	1			?			+											
Pleuroxus sp. A	1	X		X			+											
Simocephalus sp. A	12	X		X		+	+	+	+	+		+	+	+	+	+	+	+
Simocephalus vetulus	7			X			+	+	+						+	+	+	+
Number of cladocerans per site					3	5	17	7	4	5	1	2	4	2	5	4	3	6

Prob. Undes.=probably undescribed

Poss. Undes.=possibly undescribed

1st CA Record=first recorded occurrence of this species from the state of California

NT = northern transmontane vernal pools VM = northern Sacramento Valley volcanic mudflow vernal pools H = Sacramento Valley hardpan vernal pools C = Sacramento Valley claypan vernal pools

FR=Fall River MP=Manton Plain DP=Dales Plain TU=Tuscan Buttes RB=Red Bluff CC=Coyote Creek TR=Truckee Creek TH=Thomes Creek CR=Corning HC=Hall Creek SC=Stony Creek WC=Wilson Creek AL=Allendale JP=Jepson Prairie

Ca = calanoid Cy = cyclopoid Ha = harpacticoid

{ } Could be identified to genus but not to species; counted only if specimen represents sole member of that genus found at the site.

? = possibly

[1] Regarded as a synonym of *Heterocypris incongruens* by some workers.

		Prob.	Poss.	1st CA	NT	VM & II			H									C
Species	# Sites	Undes.	Undes.	Record	FR	MP	DP	TU	RB	CC	TR	TH	CR	HC	SC	WC	AL	JP
Copepoda (17)																		
Acanthocyclops carolinianus (Cy)	12			X		+	+	+	+	+	+	+	+		+	+	+	+
Acanthocyclops vernalis (Cy)	1				+													
Aglaodiaptomus forbesi (Ca)	1								+									
Attheyella sp. A (Ha)	5	X		X		+	+					+					+	+
Bryocamptus washingtonensis (Ha)	1			X								+						
Canthocamptus robertcokeri (Ha)	1		X	X														+
Canthocamptus sp. A (Ha)	1		X	X								+						
Diacyclops crassicaudis var. brachycercus (Cy)	7			X				+		+	+	+	+			+		+
Diacyclops navus (Cy)	2			X			+										+	
Diacyclops sp. A (Cy)	9	X		X		+			+	+		+	+		+	+	+	+
Eucyclops elegans (Cy)	4			X	+					+			+				+	
Hesperodiaptomus caducus (Ca)	1						+											
Hesperodiaptomus eiseni (Ca)	5					+	+	+				+						+
Hesperodiaptomus hirsutus (Ca)	1				+													
Leptodiaptomus tyrrelli (Ca)	9					+	+	+	+	+		+	+			+		+
Microcyclops rubellus (Cy)	1			X				+										
Skistodiaptomus pallidus (Ca)	1																+	
Number of copepods per site					3	5	6	5	4	5	2	8	5	0	2	4	6	7
Ostracoda (24)																		
Bradleystrandesia reticulata?	14		X	X	+	+	+	+	+	+	+	+	+	+	+	+	+	+
(Candona sp.)				X	(+)		(+)	(+)	(+)	(+)		(+)						(+)
Candona caudata	6					+	+	+	+			+						+
Candona cf. C. stagnalis	1		X	X			+											
Candona n. sp. C	4	X		X					+	+			+				+	
Candona n. sp. D	5	X		X		+	+	+								+		+
Candona sp. A	2	X		X		+	+											
Cypridopsis vidua	3			X			+			+			+					
Cypris subglobosa	1			X								+						
Eucypris sp. A	1								+					+				
Eucypris s.l. sp. A	11	X		?	+		+	+	+	+		+	+		+	+	+	+
Eucypris s.l. sp. B	5	X		?		+	+		+		+	+						
Eucypris virens media	11				+	+	+	+	+	+	+	+	+		+			+
(Heterocypris sp.)									(+)	(+)		(+)	(+)					
Heterocypris aff. H. carolinensis^2	4		X	X		+		+										+
Heterocypris aff. H. rotundatus	7		X	X	+				+	+		+	+			+	+	
Heterocypris incongruens	1							+										
(Limnocythere sp.)						(+)	(+)	(+)	(+)									(+)
Limnocythere aff. paraornata	1											+						
Limnocythere posterolimba	7			X	+	+	+	+	+	+								+
Limnocythere c.f. sanctipatricii	1								+									
Limnocythere sp. B	10	X		?		+	+	+	+	+	+	+	+			+		+
? Megalocypris sp.	3			X			+	+										+
Pelocypris aff. P. albomaculata	2		X	X				+										+
Potamocypris sp. A	5	X		X			+	+				+					+	+
Unknown sp. D	3	X		?														+
Unknown sp. G	1	X		?							+							
Number of ostracods per site					5	9	13	12	11	8	5	10	7	2	3	5	5	12
Total number of species		17	13	35	14	22	39	27	19	18	9	21	17	5	11	14	14	28

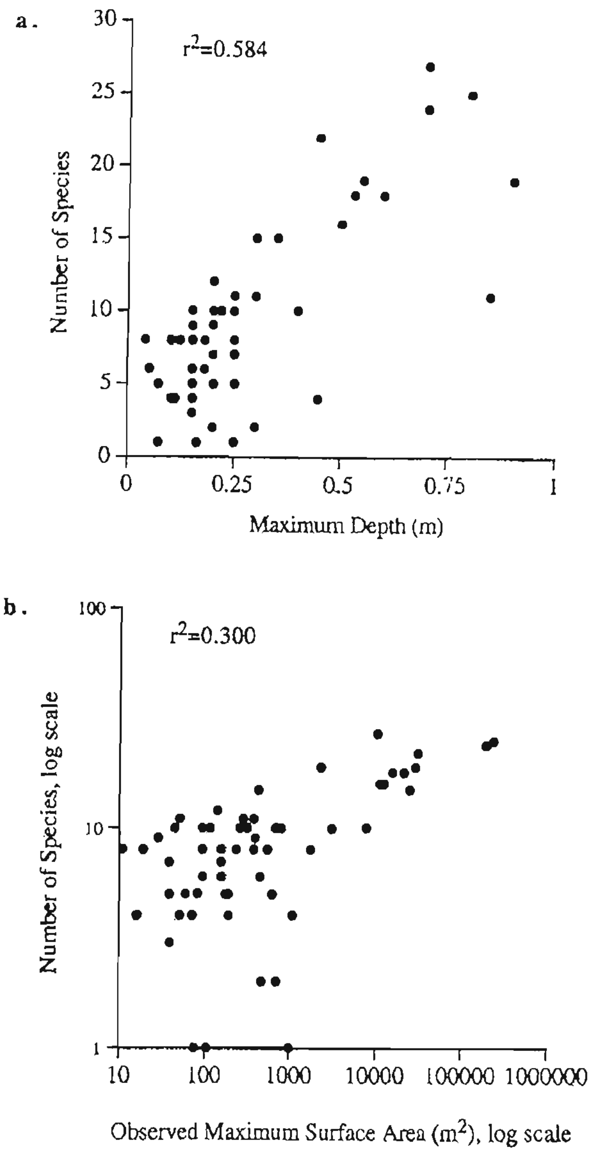

Figure 7. Species richness and pool size correlations. a. Number of species vs maximum depth ($y = 22.667x + 3.204$), b. Number of species vs observed maximum surface area, log scales ($y = 2.575x^{0.175}$).

some species are subsequently excluded from a given pool community by biotic interactions. Alternatively, dispersal may be infrequent and community composition may be largely determined by historical patterns of habitat distribution and fragmentation, and chance dispersal events (i.e. which species get there, and possibly which get there first). In the second scenario, biotic interactions may have less to do with observed species distributions than do historical events and chance. No studies have definitively answered this question for ephemeral pool crustaceans, but the available evidence indicates that dispersal rates are generally low (see below).

The results concerning levels and patterns of species richness in the pools of this survey raise two questions: (1) Why do some pools have many more species than others?, and (2) How can these relatively small, unstratified, ephemeral bodies of water contain so many species?

Why do some pools have many more species than others? This question may be answered partly by examining the positive correlation we found between crustacean species richness and both surface area and depth (i.e. hydroperiod). Other studies show the same pattern for southern California coastal mesa vernal pools (Ebert & Balko, 1987), Moroccan dayas (Thiery, 1991), temporary pools in South Carolina (Mahoney et al., 1990 for Cladocera only), freshwater bodies in Yorkshire, England (Fryer, 1985), and European lakes (Dodson, 1991). At least four alternative hypotheses can be proposed to explain this ubiquitous pattern.

First, short-lived pools may lack some species because they dry up before species with a long period of development can complete their life cycles, while pools of longer duration provide habitat for both rapidly and slowly developing species (Hamer & Appleton, 1991; Hammer & Sawchyn, 1968; Retallack & Clifford, 1980; Simovich & Fugate, 1992; Thiery, 1991; Wiggins et al., 1980). Studies of developmental rates under natural temperature and food regimes for the numerous species that are found only in large, deep pools would help to test the hypothesis that these species are unable to inhabit short-lived pools due to developmental time constraints. However, this hypothesis alone cannot fully explain the observed pattern of species richness because some fast-developing species occur only in shallow pools and the absence of these species from deeper pools cannot be due to hydroperiod. There is evidence that some species are specifically adapted to shallow, shortlived pools. For example, certain anostracan life history strategies are associated with pools of different levels of ephemerality; small, highly ephemeral pools contain species that have large clutches of small eggs, whereas the reverse is true for species inhabiting more long-lived, less ephemeral pools (Belk, 1977; Belk et al., 1990; Maynard, 1977).

Second, pools with a long hydroperiod may also allow more species to coexist if timing differences in hatching or development reduce the overlap of ecologically similar species as adults (Hammer & Saw-

Table 3. Congeneric species associations across sites.

	NT	VM&H			H									C
Species	**FR**	**MP**	**DP**	**TU**	**RB**	**CC**	**TR**	**TH**	**CR**	**HC**	**SC**	**WC**	**AL**	**JP**
Cladocera														
Alona cf. davidi			X											
Alona cf. setulosa			X											
Alona sp. A			X											
Alona sp. B			X											
Daphnia cf. middendorffiana														X
Daphnia cf. pulex														X
Pleuroxus aduncus			(X)											
Pleuroxus sp. A			(X)											
Simocephalus sp. A			X	X	(X)						X	X	X	X
Simocephalus vetulus			X	X	(X)						X	X	X	X
Copepoda														
Diacyclops crassicaudis var. brachycercus						X		X	X			X		(X)
Diacyclops navus													X	
Diacyclops sp. A						X		X	X			X	X	(X)
Hesperodiaptomus caducus			X											
Hesperodiaptomus eiseni			X											
*Hesperodiaptomus hirsutus**														
Ostracoda														
Candona caudata		(X)	X X	X	X									X
Candona cf. C. stagnalis			X											
Candona n. sp. C					X									
Candona n. sp. D		X	X X	X										X
Candona sp. A		X	X X											
Eucypris sp. A					X									
Eucypris s.l. sp. A	X		X	X	X X	(X)		X	X		X			X
Eucypris s.l. sp. B		(X)	X X		X		(X)	X						
Eucypris virens media	X	(X)	X	X	X	(X)	(X)	X	X		X			X
Heterocypris aff. H. carolinensis[1]				X										
*Heterocypris aff. H. rotundatus**														
Heterocypris incongruens				X										
Limnocythere paraornata								(X)						
Limnocythere posterolimba		(X)	(X)	X	X	X								X
Limnocythere sanctipatricii					(X)									
Limnocythere sp. B		(X)	(X)	X	X	X		(X)						X

NT = northern transmontane vernal pools VM = northern Sacramento Valley volcanic mudflow vernal pools H = Sacramento Valley hardpan vernal pools

C = Sacramento Valley claypan vernal pools

FR=Fall River MP=Manton Plain DP=Dales Plain TU=Tuscan Buttes RB=Red Bluff CC=Coyote Creek TR=Truckee Creek TH=Thomes Creek CR=Corning HC=Hall Creek SC=Stony Creek WC=Wilson Creek AL=Allendale JP=Jepson Prairie

X=same pool

(X)=same site, not same pool

* This species did not co-occur with any of its congeners.

[1] Regarded as a synonym of *Heterocypris incongruens* by some workers.

Table 4.

Table 4. Species richness of crustaceans in temporary aquatic habitats. Studies are listed in order of highest to lowest total species richness. The average and maximum numbers of crustacean species per pool are given.

					Maximum number of species per pool						
Location	Habitat	# pools	Avg	[redacted]	Clad	Cope	Ostr	Anos	Noto	Conc	Source
Alberta, Canada	ephemeral saline stream	1	58	[redacted]	26	13	9	6	1	3	Retallack & Clifford 1980
Northern California, U.S.A.	vernal pools	58	9.6	[redacted]	11	6	12	1	1	1	This study
South Carolina, U.S.A.	temporary pools	23	-	[redacted]	26	-	-	-	0	-	Mahoney et al. 1990
Michigan, U.S.A.	temporary ponds	2	22.5	[redacted]	8	8	9	1	0	1	Kenk 1949
Southwestern Canada	temporary ponds	39	7.3	[redacted]	13	8	-	4	1	0	Anderson 1974
Texas, U.S.A.	intermittent stream	1	18	[redacted]	9	9	0	0	0	0	Sollberger & Meador 1990
Manitoba, Canada	temporary marshes and ponds	13	6.8	[redacted]	2	3	14	0	0	0	McKillop et al. 1992
Ontario, Canada	temporary rock basin ponds	16	8.2	[redacted]	8	8	-	0	0	-	Carter 1971
Southern California, U.S.A.	coastal mesa vernal pools	54	6.7	[redacted]	6	2	7	1	0	0	Balko & Ebert 1984
Australia	ephemeral saline lakes	23	10.4	[redacted]	1	5	8	1	0	0	DeDeckker & Geddes 1980
Alaska, U.S.A.	arctic depression ponds	6	12*	[redacted]	2*	8*	0*	2*	0*	0*	Dodson 1975
New Zealand	temporary ponds	3	9.7	[redacted]	3	2	6	0	0	0	Barclay 1966
Mexico	temporary pools	183	-	[redacted]	-	-	-	+	+	+	Maeda-Martinez 1991
Morrocco	temporary pools (dayas)	20	-	[redacted]	-	-	+	6	2	2	Thiery 1991
Alberta, Canada	argillotrophic lake	1	10	[redacted]	5	2	0	2	1	0	Daborn 1975
Alaska, U.S.A.	tundra ponds	1	8	[redacted]	1	4	0	2	1	0	Stross et al. 1980
Canadian arctic	arctic tundra ponds	535	7*	[redacted]	2*	3*	0*	1*	1*	0*	Hebert & Hann 1986
British Columbia, Canada	temporary puddles	1	6	[redacted]	0	2	4	0	0	0	McLay 1978
Nevada, U.S.A.	ephemeral lakes	3	3	[redacted]	2	2	1	0	0	0	Hutchinson 1937
Colorado, U.S.A.	sub-alpine pools	1	4	[redacted]	1	2	0	1	0	0	Sprules 1972

Clad=Cladocera Cope=Copepoda Ostr=Ostracoda Anos=Anostraca Noto=Notostraca Conc=Conchostraca (Laevicaudata, Spinicaudata)

- incomplete data

0 none found

+ this taxon was found, but species were not identified or enumerated

* typical number of species per pool (specific values were not given in source paper)

chyn, 1968; Mura, 1991; Retallack & Clifford, 1980; Simovich & Fugate, 1992; Thiery, 1991). For example, in just a few weeks *Branchinecta lynchi* can hatch, develop to maturity, and reproduce, but in the same amount of time *Branchinecta conservatio* and *Lepidurus packardi* do not even reach reproductive maturity (pers. obs.; Ahl, 1991). *Branchinecta conservatio* and *L. packardi* are found exclusively in the deepest pools of this survey (see Appendix B), and rarely occur in small, shallow pools outside of our study area (pers. obs.; Eng et al., 1990). Although the fast developing *B. lynchi* occurred only in shallow pools in our survey, it co-occurs with both *B. conservatio* and *L. packardi* in deeper pools elsewhere (pers. obs.). In these latter cases *B. lynchi* hatches earlier, develops more quickly, and becomes dormant earlier than the other two species. Similar cases of temporal separation of species in the same pool are known for other anostracan species (Eng et al., 1990; Simovich & Fugate, 1992; Simovich & Hathaway, unpublished data).

Third, large, deep pools may hold more species because they have greater habitat heterogeneity (*sensu* Williams, 1964) which allows for more niches and greater resource partitioning (Daborn, 1978; Hamer & Appleton, 1991; Thiery, 1991). Some evidence for greater habitat heterogeneity in large pools is provided by the zonation of vernal pool plants: in large, deep pools vernal pool plants form concentric rings from the edge to the pool center, each ring being dominated by the species that is best suited for that microhabitat; in contrast, small, shallow pools are carpeted by only 'edge-adapted' species (Zedler, 1987). Also, deep pools contain open water columns, whereas the proximity of bottom and surface in shallow pools which are only a few centimeters deep precludes this type of microhabitat. Support for such a habitat heterogeneity hypothesis comes from many aquatic and terrestrial systems (Huston, 1979), including birds (MacArthur & MacArthur, 1961), cladocerans (Armitage & Davis, 1967; Quade, 1969; Whiteside & Harmsworth, 1967), eubranchiopods (Hamer & Appleton, 1991; Thiery, 1991), and crustacean assemblages (Anderson, 1974). An hypothesis of increasing species richness with increasing habitat complexity does not completely account for patterns of species richness in all systems, however (Fryer, 1985). A comparison of the claypan and volcanic mudflow habitat types from our survey demonstrates this point. Pools at these sites are of comparable size, depth, hydroperiod, and species richness (see Table 2 and Appendix B), but they differ greatly in apparent microhabitat structure. The volcanic mudflow pools have clear water, are strewn with volcanic cobbles and boulders, and support a diverse flora of unicellular, fenestrate, and filamentous algae and rooted vascular plants, whereas the claypan pools are highly turbid, have no bottom relief, and are practically devoid of vegetation (Taylor et al., 1992). If these physical and floristic variables indicate the true amount of habitat heterogeneity in these pools, then high habitat heterogeneity may explain the high species richness at Manton Plain, Dales Plain, and Tuscan Buttes (volcanic mudflow sites), but it does not account for the similarly high diversity at Jepson Prairie (claypan site). So, although crustacean species richness may be related to habitat microstructure in some vernal pools, this hypothesis cannot be accepted as a general mechanism for all pools.

Despite the temporal and spatial sampling regime used in this study, our data show either fairly complex or nonexistent patterns of within-pool species distributions and species co-occurrences over time. Subsampling randomly from edge, bottom, and surface regions is probably not sufficient to resolve microhabitat effects. For future studies we suggest finerscale sampling with greater attention to microhabitat conditions (e.g. plant growth forms present) in order to address the role of microhabitat partitioning among species.

A fourth possible explanation for the relationship between species richness and pool size/depth/hydroperiod is provided by the 'area-per se' hypothesis (Preston, 1960; 1962; MacArthur & Wilson, 1963; 1967). This hypothesis, which emphasizes the strictly spatial aspects of a habitat's size and distance from other (source) habitats, is the basis for the dynamic equilibrium theory of island biogeography (MacArthur & Wilson, 1963; 1967). The focus of this theory upon the balance between immigration and extinction rates carries with it several inherent assumptions, at least two of which – that propagules are constantly being dispersed, and that colonization is a random event – may not be valid for all freshwater crustaceans. Limited dispersal abilities, in conjunction with restricted dispersal routes and/or recency of evolution, may be largely responsible for the restricted distributions of some crustacean species in previously glaciated portions of North America (Carter et al., 1980; Hebert & Hann, 1986). Also, population genetic work has shown that levels of gene flow over mesogeographic and microgeographic scales are low for many freshwater crustaceans (Boileau & Hebert, 1988 for copepods; Crease et al., 1990 for *Daphnia*; Fugate, 1992 for anostracans; Havel et al., 1990 for ostracods; Hebert, 1974 for *Daphnia*; King, in prep. for notostracans), indicating that dispersal is rare. On the other hand, evidence suggesting frequent or effective passive dispersal has been found for other species (e.g., Maguire, 1963; Proctor et al., 1967; Reid & Reed, 1994; Saunders et al., 1993). Although none of the available evidence directly addresses the question of the actual influence of pool size on relative rates of immigration or extinction, violation of the theory's assumptions regarding dispersal and colonization of many freshwater crustacean species casts doubt on the applicability of the dynamic equilibrium theory of island biogeography to vernal pool crustaceans.

An alternative approach to the species-area relationship for vernal pools was suggested by Ebert & Balko (1987). Temporary pools are unlike oceanic islands in that they are islands in time as well as in space; they are ephemeral, periodically disappearing and reappearing, and they are re-colonized primarily from the *in situ* 'egg bank' rather than by dispersal from other habitats. Ebert & Balko's 'islands in space and time' model builds upon the concepts developed by the dynamic equilibrium theory by incorporating a third axis to account for such temporal factors. Along this third axis, frequency (i.e. predictability based upon contingency, *sensu* Colwell, 1974) of inundation is analogous to the spatial component of distance from a source, and length of inundation is analogous to physical size. The model predicts that the equilibrium number of species will be higher for pools that inundate predictably (*via* high contingency) and remain inundated longer, than it will be for pools which are unpredictable and highly ephemeral. The observed pattern of species richness in vernal pools fits this conceptual model, probably because several important factors which were discussed above (e.g. pool size and available microhabitats, hydroperiod and the number of species with appropriate developmental rates and potential for temporal habitat partitioning) are subsumed by the model.

It appears that at least three hypotheses involving hydroperiod and pool size may partially explain the observed pattern of species richness among northern California vernal pools. However, several different mechanisms may be jointly responsible for determining species richness in some habitat types, and no single explanation is applicable to all pool communities. Several points discussed above highlight the importance of obtaining reasonably accurate estimates of hydroperiod in studies of temporary pool communities. Depth is closely correlated with duration for the pools in our study. However, in some hydrologic regimes pools are recharged by groundwater (Hanes et al., 1990) or are repeatedly refilled through the season; in these cases hydroperiod should be measured directly rather than by a surrogate variable such as depth. The most important point to be drawn from these analyses concerns conservation and resource management strategies for the vernal pool habitat: the total diversity of crustaceans in northern California vernal pools can be encompassed only by preserving many pools at a given site, many sites of the same habitat type, and all the different habitat types.

How can these small, unstratified, ephemeral bodies of water contain so many species? Given the relatively small size and lack of stratification in vernal pools, the large numbers of crustacean species they hold (up to 27 species per pool) and the frequency with which congeneric species co-occur is remarkable. Other studies have shown similarly high levels of diversity in temporary pools (Table 4). Our question regarding high species richness in temporary pools is especially intriguing when posed in relation to permanent bodies of water, because the number of crustacean species found in some temporary pools, particularly large temporary lakes, appears to be substantially higher than that typically found in permanent lakes and ponds. We suspect that crustacean species richness in freshwater habitats may exhibit a non-random pattern among waterbodies of different sizes and levels of ephemerality, and we address this question in another paper (in prep.). For the moment we confine our discussion to temporary waters only. Beyond the various mechanisms of resource partitioning which were discussed in the previous section, additional hypotheses that explain the co-occurrence of many species, particularly congeners, in temporary pools include: (1) abundant food resources, (2) low levels of predation, and (3) temporal dynamics of the habitat.

Some temporary pools do not appear to be resource-limited during the early phases of inundation when crustacean populations are hatching, developing, and reproducing (Cole, 1966; Fryer, 1957; Hartland-Rowe, 1972; McLachlan, 1981a; Nikolaeva & Vekhov, 1985; Thiery, 1991; Wiggins et al., 1980). Energy is supplied to pools by allochthonous organic detritus which is washed into pools from surrounding uplands (Barclay & Knight, 1984; Barlocher et al., 1978; Cole & Fisher, 1978; Daborn, 1975, 1978; Hartland-Rowe, 1972), by autochthonously recycled organics from organisms present at the time of pool dry-down in previous seasons (e.g. long-lived aquatic invertebrates, unmetamorphosed amphibian larvae, aquatic plants, algae) (Barlocher et al., 1978; Cole, 1966; Cole & Fisher, 1978; McLachlan, 1981b; Wiggins et al., 1980), and by the wet/dry seasonality which hastens nutrient cycling (Barlocher et al., 1978; Wiggins et al., 1980). This nutrient base can provide abundant resources, allow the relaxation of competition, and maintain high species richness in two ways: via an autotrophic-based or a heterotrophic-based food web (Moore, 1970). In clear-water pools, high nutrients resulting in an early-season bloom of algae, diatoms, and macrophytes provide diverse food resources for many herbivorous species, which, in turn, allows the occurrence of carnivorous species. We propose that the volcanic mudflow pools of our study are examples of this type of trophic system. In clay-rich pools where turbidity limits photosynthesis, energy from dissolved organic matter (DOM), bacteria, and protists becomes available to suspension feeding organisms as particulate organic matter via adsorption to clay particles, resulting in an argillotrophic system (*sensu* Hutchinson, 1937; see also Barclay, 1981; Odum & de la Cruz, 1963; Pedros-Alio & Brock, 1983; Rich & Wetzel, 1978; Saunders et al., 1980; Sepers, 1977). This detritus-based trophic structure may provide a virtually unlimited food resource for suspension feeders in some temporary pools (Cole, 1966; Hutchinson, 1937; Thiery, 1991).

Argillotrophic pools have been studied in Morocco (Thiery, 1991), the Transvaal province of South Africa (Hutchinson et al., 1929, 1932), Nevada (Hutchinson, 1937), and western Canada (Daborn, 1975; Hartland-Rowe, 1966; White & Hartland-Rowe, 1969). They are characterized by high turbidity, high alkalinity, high conductivity, and low phototrophic primary production. The claypan pools of the Jepson Prairie site fit the physical, chemical, and primary productivity profile of an argillotrophic system (Barclay & Knight, 1984). However, the high crustacean species richness found in our survey contradicts original assertions of low diversity for argillotrophic pools in general (*viz.* Hutchinson, 1937; Hutchinson et al., 1929; 1932), and for the Jepson Prairie pools in particular (*viz.* Barclay & Knight, 1984). Research on feeding biology and trophic structure in both clear-water and argillotrophic-type temporary pools is needed before we can understand how nutrients and productivity affect species richness in these different habitats.

Predation can have a major influence on population dynamics and community structure in aquatic environments (Murdoch & Oaten, 1975; Kerfoot & Sih, 1987; Sih et al., 1985; Taylor, 1984; Zaret, 1980), and in some cases can operate to maintain high species richness by moderating competitive or other predatory interactions (Boucher et al., 1982; Brooks & Dodson, 1965; Dodson, 1974; Morin, 1987; Paine 1966; 1984). Fish, which are highly effective predators and often drive prey species to extinction or to very low densities in permanent freshwater communities (Brooks & Dodson, 1965; Hurlbert & Mulla, 1981; Lynch, 1979), do not occur in vernal pools. Carnivorous insects and amphibian larvae are probably the principal predators in temporary pool ecosystems. Carnivorous amphibians occurred in our survey at only the Jepson Prairie site, where tiger salamander (*Ambystoma tigrinum*) larvae occur in high densities mid to late in the season. This salamander has been shown to facilitate the existence of some microcrustacean species by mediating competition, and to maintain high crustacean species richness through time in temporary pools (Morin, 1987). Therefore, it is likely that *Ambystoma tigrinum* is at least partially responsible for the high crustacean diversity found in the Jepson Prairie pools. However, other equally diverse pools (e.g., Dales Lake, Dales Potholes) contained herbivorous anuran tadpoles (e.g., *Hyla regilla*) rather than carnivorous salamander larvae; therefore, amphibian predation does not explain all cases of high crustacean species richness. Comparative studies of food webs in these different communities are needed to elucidate the effects of different amphibians on the richness and structure of vernal pool crustacean assemblages.

Insects from 44 families and 11 orders were found in our plankton net samples. Most specimens were identified only to family or genus level, but we estimate that these insects number approximately 62 to 100 species. Twenty to 30 of these insect species are potential predators of crustaceans. Almost all pools in our study contained predatory insects, and in some cases these predators occurred in high numbers. The role these invertebrate predators play in retarding the process of competitive exclusion among vernal pool crustaceans, and thus facilitating increased diversity of coexisting species, remains unknown and could be addressed through field manipulations such as caging experiments.

High diversity and the frequent co-occurrence of congeners in temporary pools might also be due to the stochastic nature of the habitat. Crustacean populations in temporary pools exist for the relatively short period of time that the pool is inundated, and are 're-set' each year as they annually re-establish from a dormant propagule bank. This periodic interruption of the community may prevent some ecological interactions from going to completion, such as the exclusion of an inferior competitor or the elimination of a prey species by a predator. Thiery (1982) recognized the periodic interruption of a community and the resultant truncation of competitive interactions as a mechanism for increased species diversity, and called it the 'competition-interruption hypothesis.' 'This mechanism has been used to explain diversity patterns in such different communities as forests (Taylor, 1973; Bormann & Likens, 1979; Garwood et al., 1979; Veblen et al., 1980), intertidal organisms (Liebermann et al., 1979; Sousa, 1979), corals (Loya, 1976), and coral reef fishes (Bohnsack & Talbot, 1980)' (p. 702, Thiery, 1982; full references can be found in the original text), as well as arctic ponds (Dodson, 1975), coral-associated decapod crustaceans (Abele, 1976), and larval whirligig beetles (Istock, 1966, 1967).

Additionally, year-to-year variations and within-season environmental fluctuations can operate to maintain long-term coexistence under some competitive conditions (Chesson & Huntly, 1989). Such environmental variability has been invoked to explain high species richness (i.e. higher than expected by competitive exclusion theory) in freshwater crustacean assemblages (Anderson, 1974), tundra pool eubranchiopods (Nikolaeva & Vekhov, 1985), ostracods (McLay, 1978a; 1978b), and lake phytoplankton (Richerson et al., 1970). Also, research on conspecific *Daphnia* clones, which can been viewed as extremely closely related taxa, suggests that temporal heterogeneity resulting in fluctuating selection can allow the long-term co-existence of multiple clone lineages in the same pool (Carvalho & Crisp, 1987; Hann & Hebert, 1986; Hebert & Crease, 1980; Lynch, 1983; 1987; Weider, 1985; Wilson & Hebert, 1992). Thus, the annual truncation of competitive interactions, in conjunction with both differences in life history strategies employed by different species and inter-annual environmental variability, may lead to high species richness in vernal pools. For example, an inferior competitor may persist by reproducing quickly and senescing each year before pool resources become limiting; a species which has high reproductive success in one year may do poorly in other years.

It has long been suspected that the failure of some natural systems to attain equilibrium is the reason that competitive exclusion does not operate in certain situations, for example, Hutchinson's 'paradox of the plankton' (Huston, 1979; Hutchinson, 1941; 1961; Wiens, 1977). The abundance of co-occurring congeneric species found in our survey suggests that Gause's principle of competitive exclusion (Gause, 1934) may not apply to these crustacean assemblages, perhaps as a result of generation times that are of the same order of magnitude as duration of the habitat (Hutchinson, 1953; 1961). The temporary pool habitat appears to be a clear example of a periodically disturbed (i.e. truncated), non-equilibrium (or perhaps dynamic equilibrium) system. This fact alone may prove to be a satisfactory explanation for the high species richness and numerous congeneric occurrences observed in many temporary pools. This hypothesis awaits empirical testing, and should prove to be a fertile area for future ecological research.

Conclusion

California vernal pools harbor surprisingly diverse and largely unknown crustacean assemblages. Almost half of the 67 crustacean species found in this survey may be undescribed species. Endemic and rare species comprise a major portion of the crustacean assemblages of northern California vernal pools. These findings, in conjunction with the documented endemism of vernal pool plants and the possibility for similarly high endemism among the other taxa which remain largely unstudied (platyhelminths, gastropods, annelids, arachnids, insects, rotifers, algae), indicate the importance of carefully planned conservation for the communities of California vernal pools.

The species composition of crustacean assemblages corresponds with some physical and chemical aspects of the habitat (depth, solute concentrations, elevation, biogeographic province), and with existing geologic/floristic-based habitat classifications. Among pools of the same habitat type, species composition varies and assemblage similarity is not correlated with geographic proximity. These patterns of diversity indicate that preservation strategies for the vernal pool habitat should include many pools at each site, multiple sites of each habitat type, and all identified habitat types.

The positive relationship between pool size/depth/hydroperiod and species richness may be explained by at least four hypotheses which incorporate developmental rates, temporal and spatial resource partitioning, and the species-area relationship of equilibrium island biogeography. The first three of these hypotheses seem to be of varying importance among pools of different habitat types, but recent evidence for low levels of dispersal in many freshwater crustaceans casts doubt upon the applicability of the latter hypothesis to these assemblages.

Ephemeral pool crustacean assemblages frequently have high species richness and numerous co-occurring congeners. Ecological species-packing, short-term but unlimited nutritional resources derived from allochthonous input, autochthonous recycling, photosynthesis and/or argillotrophic conditions, low levels of predation, and seasonal disturbance of the community likely contribute to the maintenance of such high diversity. The most significant of these mechanisms may be temporal truncation, because it can prevent ecological interactions from going to fixation where vulnerable prey species and inferior competitors are eliminated and species richness is decreased.

We hope that these results will serve as a catalyst and a foundation for future research on topics such as trophic structure, character displacement and resource partitioning among co-occurring congeners, patterns of species distributions across a spatial mosaic of different habitat types, and relationships among temporal habitat variability, life history strategies, ecological interactions, and species richness in ephemeral pool communities.

Acknowledgments

We thank Kevin Mazzocco, Daniel Glusenkamp, Karl Kloock, and Jason Tritt for assistance in the field; Crystal Bingham, Shana Goffredi, Amy Stevenson, Erica Seymour, and Steve Chakmatian for sample processing; Crystal Bingham and Regina Wetzer for specimen curation; Denton Belk, Claire Carter, Richard Forester, Michael Fugate, Brenda Hann, Joel Martin, and Janet Reid for taxonomic identifications; Diolinda Parsick and Thor Brickman for computer support; and Chris Esparza and Stacie Hathaway for laboratory assistance. This manuscript was improved by comments from Denton Belk, Michel Boudrias, John Fauth, Richard Grosberg, Brenda Hann, Susan Harrison, Peter Marko, Koen Martens, Janet Reid, Donald Strong, Rob Toonen, Chris Wilcox, and an anonymous reviewer. This research was funded by PG & E, by a U. C. Davis Fellowship to J. L. King, and by NSF grants to R. K. Grosberg.

References

Abele, L. G., 1976. Comparative species richness in fluctuating and constant environments: Coral-associated decapod crustaceans. Science 192: 461–463.

Ahl, J. S. B., 1991. Factors affecting contributions of the tadpole shrimp, *Lepidurus packardi*, to its oversummering egg reserves. Hydrobiologia 212 (Dev. Hydrobiol 64): 137–143.

Anderson, R. S., 1968. The zooplankton of five small mountain lakes in southwestern Alberta. National Museum of Canada Natural History Papers 39: 1–19.

Anderson, R. S., 1974. Crustacean plankton communities of 340 lakes and ponds in and near the National Parks of the Canadian Rocky Mountains. J. Fish Res. Bd Can. 31: 855–869.

Armitage, K. B. & M. Davis, 1967. Population structure of some pond microcrustacea. Hydrobiologia 29: 205–225.

Balko, M. L. & T. A. Ebert, 1984. Zooplankton distribution in vernal pools of Kearny Mesa, San Diego, Calfornia. In S. Jain & P. Moyle (eds), Vernal Pools and Intermittent Streams. U. C. Davis Institute of Ecology Publication #28: 76–89.

Barclay, W. R., Jr., 1981. The role of adsorbed organic matter as a detrital food resource for aquatic filter feeding invertebrates. PhD dissertation, U. C. Davis.

Barclay, W. R. & A. W. Knight, 1984. Physicochemical processes affecting production in a turbid vernal pond. In S. Jain & P. Moyle (eds), Vernal Pools and Intermittent Streams. U. C. Davis Institute of Ecology Publication 28: 126–142.

Barlocher, F., R. J. Mackay & G. B. Wiggins, 1978. Detritus processing in a temporary vernal pool in southern Ontario. Arch. Hydrobiol. 81: 269–295.

Belk, D., 1977. Evolution of egg size strategies in fairy shrimps. Southwest. Nat. 22: 99–105.

Belk, 1994. A report on the status of Anostraca in France from Alain Thiery. Anostracan News 2: 2.

Belk, D., G. Anderson & S. Hsu, 1990. Additional observations on variations in egg size among populations of *Streptocephalus seali* (Anostraca). J. Crust. Biol. 10: 128–133.

Boileau, M. G. & P. D. N. Hebert, 1988. Genetic differentiation of freshwater pond copepods at arctic sites. Hydrobiologia 167/168 (Dev. Hydrobiol. 47): 393–400.

Boucher, D. H., S. James & K. H. Keeler, 1982. The ecology of mutualism. Annu. Rev. Ecol. Syst. 13: 315–347.

Brooks, J. L. & S. I. Dodson, 1965. Predation, body size and composition of the plankton. Science 150: 28–35.

Carter, J. C. H., M. J. Dadswell, J. C. Roff & W. G. Sprules, 1980. Distribution and zoogeography of planktonic crustaceans and dipterans in glaciated eastern North America. Can. J. Zool. 58: 1355–1387.

Carvalho, G. R. & D. J. Crisp, 1987. The clonal ecology of *Daphnia magna* (Crustacea: Cladocera), 1. Temporal changes in the clonal structure of a natural population. J. anim. Ecol. 56: 453–468.

Cattell, R. B., 1966. The scree test for the number of factors. Multivar. Behav. Res. 1: 245.

Chesson, P. & N. Huntly, 1989. Short-term instabilities and long-term community dynamics. TREE 4: 293–298.

Cole, G. A., 1966. Contrasts among calanoid copepods from permanent and temporary ponds in Arizona. Am. Midl. Nat. 76: 351–368.

Cole, J. & S. G. Fisher, 1978. Annual metabolism of a temporary pond ecosystem. Am. Midl. Nat. 100: 15–22.

Colwell, R. K., 1974. Predictability, constancy, and contingency of periodic phenomena. Ecology 55: 1148–1153.

Cox, G. W. & C. G. Gakahu, 1983. Mima mounds in the Kenya highlands: significance for the Dalquest-Scheffer hypothesis. Oecologia 57: 170–174.

Crease, T. J., M. Lynch & K. Spitze, 1990. Hierarchical analysis of population genetic variation in mitochondrial and nuclear genes of *Daphnia pulex*. Mol. Biol. Evol. 7: 444–458.

Daborn, G. R., 1975. The argillotrophic lake system. Verh. int. Ver. Limnol. 19: 580–588.

Daborn, G. R., 1978. Distribution and biology some nearctic tundra pool phyllopods. Verh. int. Ver. Limnol. 20: 2442–2451.

Dodson, S. I., 1975. Predation rates of zooplankton in arctic ponds. Limnol. Oceanogr. 20: 426–433.

Dodson, S. I., 1991. Species richness of crustacean zooplankton in European lakes of different sizes. Verh. int. Ver. Limnol. 24: 1223–1229.

Durrenberger, R. W. & R. B. Johnson, 1976. California: Patterns on the land, 5th ed. Mayfield Publishing, Palo Alto (California).

Ebert, T. A. & M. L. Balko, 1987. Temporary pools as islands in space and in time: The biota of vernal pools in San Diego, Southern California, U.S.A. Arch. Hydrobiol. 110: 101–123.

Eng, L. L., D. Belk & C. H. Eriksen, 1990. California Anostraca: Distribution, habitat, and status. J. Crust. Biol. 10: 247–277.

Everitt, B. S. & G. Dunn, 1992. Applied Multivariate Data Analysis. Oxford University Press, New York, 304 pp.

Federal Register, 1980. Endangered and threatened wildlife and plants; listing the delta green ground beetle as a threatened species with critical habitat. Fed. Reg. 45: 52807–52810.

Federal Register, 1991. Endangered and threatened wildlife and plants; determination of endangered status for three plants, *Blennosperma bakeri* (Sonoma sunshine or Baker's stickyseed), *Lasthenia burkei* (Burke's goldfields), and *Limnanthes vinculans* (Sebastopol meadowfoam). Fed. Reg. 56: 61173–61182.

Federal Register, 1992. Endangered and threatened wildlife and plants; determination of endangered status for the plant *Limnanthes floccosa ssp. californica* (Butte County Meadowfoam). Fed. Reg. 57: 24192–24199.

Federal Register, 1993a. Endangered and threatened wildlife and plants; determination of endangered status for three vernal pool plants and the Riverside fairy shrimp. Fed. Reg. 58: 41384–41392.

Federal Register, 1993b. Endangered and threatened wildlife and plants; proposed endangered status for four plants and proposed threatened status for four plants from vernal pools in the Central Valley of California. Fed. Reg. 58: 41700–41708.

Federal Register, 1994a. Endangered and threatened wildlife and plants; proposed rule to list the San Diego fairy shrimp as endangered. Fed. Reg. 59: 39874–39878.

Federal Register, 1994b. Endangered and threatened wildlife and plants; determination of endangered status for the Conservancy fairy shrimp, longhorn fairy shrimp, and the vernal pool tadpole shrimp; and threatened status for the vernal pool fairy shrimp. Fed. Reg. 59: 48136–48153.

Fryer, G., 1957. The food of some freshwater cyclopoid copepods and its ecological significance. J. anim. Ecol. 26: 263–286.

Fryer, G., 1985. Crustacean diversity in relation to the size of water bodies: Some facts and problems. Freshwat. Biol. 15: 347–361.

Fryer, G., 1993. The Freshwater Crustacea of Yorkshire. Yorkshire Naturalists' Union & Leeds Philosophical and Literary Society, 312 pp.

Fugate, M. L., 1992. Speciation in the fairy shrimp genus *Branchinecta* (Crustacea: Anostraca) from North America. PhD dissertation, University of California, Riverside, 188 pp.

Gauch, H. G. J., 1982. Multivariate Analysis in Community Ecology. Cambridge University Press, Cambridge, 298 pp.

Gause, G. F., 1934. The Struggle for Existence. Williams and Wilkins, Baltimore, 163 pp.

Grainger, J. N. R., 1994. The status of Anostraca and Notostraca in Great Britain and Ireland. Anostracan News 2: 3.

Hamer, M. L. & C. C. Appleton, 1991. Life history adaptations of phyllopods in response to predators, vegetation, and habitat duration in north-eastern Natal. Hydrobiologia 212: 105–116.

Hammer, U. T. & W. W. Sawchyn, 1968. Seasonal succession and congeneric associations of *Diaptomus* spp. (Copepoda) in some Saskatchewan ponds. Limnol. Oceanogr. 13: 476–484.

Hanes, W. T., B. Hecht & L. P. Stromberg, 1990. Water relationships of vernal pools in the Sacramento region, California. In D. H. Ikeda & R. A. Schlising (eds), Vernal Pool Plants: Their Habitat and Biology. Studies from the Herbarium No. 8, California State University, Chico: 49–60.

Hann, B. J. & P. D. N. Hebert, 1986. Genetic variation and population differentiation in species of *Simocephalus* (Cladocera, Daphniidae). Can. J. Zool. 64: 2246–2256.

Hartland-Rowe, R., 1966. The fauna and ecology of temporary pools in western Canada. Verh. int. Ver. Limnol. 16: 577–584.

Hartland-Rowe, 1972. The limnology of temporary waters and the ecology of Euphyllopoda. In R. B. Clark & R. J. Wooton (eds), Essays in Hydrobiology. Univ. of Exeter Press, Exeter (England): 15–31.

Havel, J. E., P. D. N. Hebert & L. D. Delorme, 1990. Genetics of sexual Ostracoda from a low Arctic site. J. evol. Biol. 3: 65–84.

Hebert, P. D. N., 1974. Enzyme variability in natural populations of *Daphnia magna*, 1. Population structure in East Anglia. Evolution 28: 546–556.

Hebert, P. D. N. & T. J. Crease, 1980. Clonal coexistence in *Daphnia pulex* (Leydig): Another planktonic paradox. Science 207: 1363–1365.

Hebert, P. D. N. & B. J. Hann, 1986. Patterns in the composition of arctic tundra pond microcrustacean communities. Can. J. Fish. aquat. Sci. 43: 1416–1425.

Hill, M. O. & H. G. Gauch, Jr., 1980. Detrended correspondence analysis: An improved ordination technique. Vegetatio 42: 47–58.

Hill, M. O., 1986. Preliminary descriptions of the terrestrial natural communities of California. State of California Department of Fish and Game.

Holland, R. F. & S. K. Jain, 1981. Insular biogeography of vernal pools in the Central Valley of California. Am. Nat. 117: 24–37.

Holland, M. O., 1988. Vernal pools. In: M. Barbour & J. Major (eds), Terrestrial Vegetation of California, new expanded ed. California Native Plant Society Special Publication 9: 515–533.

Hoover, R. F., 1937. Endemism in the flora of the Great Valley of California. PhD dissertation, University of California.

Hurlbert, S. H. & M. S. Mulla, 1981. Impacts of mosquito fish (*Gambusia affinis*) predation on plankton communities. Hydrobiologia 83: 125–151.

Huston, M., 1979. A general hypothesis of species diversity. Am. Nat. 113: 81–101.

Hutchinson, G. E., 1937. A contribution to the limnology of arid regions. Trans. Conn. Acad. Arts Sci. 33: 47–132.

Hutchinson, G. E., 1941. Ecological aspects of succession in natural populations. Am. Nat. 75: 406–418.

Hutchinson, G. E., 1953. The concept of pattern in ecology. Proc. natn. Acad. Sci. Philad. 105: 1–12.

Hutchinson, G. E., 1961. Paradox of the plankton. Am. Nat. 95: 137–145.

Hutchinson, G. E., 1967. A Treatise on Limnology, 2. Wiley & Sons, New York, 1115 pp.

Hutchinson, G. E., G. E. Pickford & J. F. M. Schuurman, 1929. The inland waters of South Africa. Nature 3109: 832–833.

Hutchinson, G. E., G. E. Pickford & J. F. M. Schuurman, 1932. A contribution to the hydrobiology of pans and other inland waters of South Africa. Arch. Hydrobiol. 24: 1–136.

Istock, C., 1966. Distribution, coexistence, and competition of whirligig beetles. Evolution 20: 211–234.

Istock, C., 1967. Transient competitive displacement in natural populations of whirligig beetles. Ecology 48: 929–937.

Joliffe, I. T., 1972. Discarding variables in a principal components analysis, I. Artificial data. Applied Statistics 21: 160–173.

Kerfoot, W. C. & M. Lynch, 1987. Branchiopod communities: Associations with planktivorous fish in space and time. In W. C. Kerfoot & A. Sih (eds), Predation: Direct and Indirect Impacts on Aquatic Communities. Univ. Press of New England, Hanover (NH), 386 pp.

Kerfoot, W. C. & A. Sih, 1987. Predation. Direct and Indirect Impacts on Aquatic Communities. Univ. Press of New England, Hanover.

King, J. L. (in prep.). Population genetic structure of *Lepidurus packardi*, the vernal pool tadpole shrimp: I. Spatial patterns.

Lynch, M., 1979. Predation, competition, and zooplankton community structure: An experimental study. Limnol. Oceanogr. 24: 253–272.

Lynch, M., 1983. Ecological genetics of *Daphnia pulex*. Evolution 37: 358–374.

Lynch, M., 1987. The consequences of fluctuating selection for isozyme polymorphisms in *Daphnia*. Genetics 115: 657–669.

MacArthur, R. H. & J. W. MacArthur, 1961. On bird species diversity. Ecology 42: 594–598.

MacArthur, R. H. & E. O. Wilson, 1963. An equilibrium theory of insular zoogeography. Evolution 17: 373–387.

MacArthur, R. H., 1967. The Theory of Island Biogeography. Princeton University Press, Princeton (NJ).

Maguire, B., 1963. The passive dispersal of small aquatic organisms and their colonization of isolated bodies of water. Ecol. Monogr. 33: 161–185.

Mahoney, D. L., M. A. Mort & B. E. Taylor, 1990. Species richness of calanoid copepods, cladocerans and other branchiopods in Carolina Bay temporary ponds. Am. Midl. Nat. 123: 244–258.

Maynard, S. D. S., 1977. Life history strategies of fairy shrimps (Crustacea: Anostraca) as a function of environmental predictability. PhD dissertation, Univ. of Utah.

McKillop, W. B., R. T. Patterson, L. D. Delorme & T. Nogrady, 1992. The origin, physicochemistry and biotics of sodium chloride dominated saline waters on the western shore of Lake Winnipegosis, Manitoba. Can. Field Nat. 106: 454–473.

McLachlan, A. J., 1981a. Food sources and foraging tactics in tropical rain pools. Zool. J. linn. Soc. 71: 265–277.

McLachlan, A. J., 1981b. Interaction between insect larvae and tadpoles in tropical rain pools. Ecol. Entomol. 6: 175–182.

McLay, C. L., 1978a. Comparative observations on the ecology of four species of ostracods living in a temporary freshwater puddle. Can. J. Zool. 56: 663–675.

McLay, C. L., 1978b. Competition, coexistence, and survival: A computer simulation study of ostracods living in a temporary puddle. Can. J. Zool. 56: 1744–1758.

Moore, W. G., 1970. Limnological studies of temporary ponds in southeastern Louisiana. Southwest. Nat. 15: 83–110.

Morin, P. J., 1987. Salamander predation, prey facilitation, and seasonal succession in microcrustacean communities. In W. C. Kerfoot and A. Sih (eds), Predation. Direct and Indirect Impacts on Aquatic Communities. Univ. Press of New England, Hanover: 174–188.

Mura, G., 1991. Life history and interspecies relationships of *Chirocephalus diaphanus* Prevost and *Tanymatrix stagnalis* (L.), (Crustacea, Anostraca) inhabiting a group of mountain ponds in Latium, Italy. Hydrobiologia 212: 45–59.

Murdoch, W. W. & A. Oaten, 1975. Predation and population stability. Adv. EEC. Res. 9: 1–131.

Nikolaeva, N. V. & N. V. Vekhov, 1985. Ecology of phyllopod crustaceans (Crustacea, Anostraca) of floodplain bodies of water in southern Yamal. Sov. J. Ecol. 15: 271–276.

Odum, E. P. & A. A. de la Cruz, 1963. Detritus as a major component of ecosystems. Bull. Am. Inst. Biol. Sci. 13: 39–40.

Paine, R. T., 1966. Food web complexity and species diversity. Am. Nat. 100: 65–75.

Paine, R. T., 1984. Ecological determinism in the competition for space. Ecology 65: 1339–1348.

Patalas, K., 1971. Crustacean plankton communities in forty-five lakes in the Experimental Lakes Area, northwestern Ontario. J. Fish Res. Bd Can. 28: 231–244.

Pedros-Alio, C. & T. D. Brock, 1983. The impact of zooplankton feeding on the epilimnetic bacteria of a eutrophic lake. Freshwat. Biol. 13: 227–239.

Preston, F. W., 1960. Time and space and the variation of species. Ecology 41: 611–627.

Preston, F. W., 1962. The canonical distribution of commonness and rarity, parts 1 and 2. Ecology 43: 185–215, 410–432.

Proctor, V. W., C. R. Malone & V. L. DeVlaming, 1967. Dispersal of aquatic organisms: Viability of disseminules recovered from the intestinal tract of captive killdeer. Ecology 48: 672–676.

Quade, H. W., 1969. Cladoceran faunas associated with aquatic macrophytes in some lakes in northwestern Minnesota. Ecology 50: 170–179.

Reid, J. W. & E. B. Reed, 1994. First records of two neotropical species of *Mesocyclops* (Copepoda) from Yukon Territory: Cases of passive dispersal? Arctic 47: 80–87.

Reed, E. B., 1962. Freshwater plankton Crustacea of the Colville River area, northern Alaska. J. Arctic Inst. N. Am. 15: 27–50.

Retallack, J. T. & H. F. Clifford, 1980. Periodicity of crustaceans in a saline prairie stream of Alberta, Canada. Am. Midl. Nat. 103: 123–132.

Rich, P. H. & R. G. Wetzel, 1978. Detritus in the lake ecosystem. Am. Nat. 112: 57–71.

Richerson, P., R. Armstrong & C. R. Goldman, 1970. Contemporaneous disequilibrium, a new hypothesis to explain the 'Paradox of the plankton'. Proc. natn. Acad. Sci. U.S.A. 67: 1710–1714.

Saunders, G. W., K. W. Cummins, D. Z. Gak, E. Pieczynska, V. Straskrabova & R. G. Wetzel, 1980. Organic matter and decomposers. In E. D. Le Cren & R. H. Lowe-McConnell (eds), The Functioning of Freshwater Ecosystems. Cambridge University Press: 341–392.

Saunders, J. F., D. Belk & R. Dufford, 1993. Persistence of *Branchinecta paludosa* in southern Wyoming, with notes on zoogeography. J. Crust. Biol. 13: 184–189.

Scholnick, D. A., 1994. Seasonal variation and diurnal fluctuations in ephemeral desert pools. Hydrobiologia 294: 111–116.

Sepers, A. B. J., 1977. The utilization of dissolved organic compounds in aquatic environments. Hydrobiologia 52: 39–54.

Sih, A., P. H. Crowley, M. A. McPeek, J. W. Petranka & K. Strohmeier, 1985. Predation, competition and prey communities: A review of field experiments. Ann. Rev. Ecol. Syst. 16: 269–311.

Simovich, M. A. & M. Fugate, 1992. Branchiopod diversity in San Diego, County, California, U.S.A. Trans. western sec. Wildlife Soc. 28: 6–14.

Taylor, D. W., D. Wi, G. L. Clifton, R. F. Holland & C. W. Witham, 1992. Vernal pools along the PGT-PGE pipeline expansion project, California. Unpublished report to Pacific Gas & Electric Corporation.

Taylor, R. J., 1984. Predation. Chapman and Hall, New York. Thiery, A., 1991. Multispecies coexistence of branchiopods (Anostraca, Notostraca and Spinicaudata) in temporary ponds of Chaouia plain (western Morocco): Sympatry or syntopy between usually allopatric species. Hydrobiologia 212 (Dev. Hydrobiol. 64): 117–136.

Thiery, R., 1982. Environmental instability and community diversity. Biol. Rev. 57: 671–710.

Thorne, R. F., 1984. Are California's vernal pools unique? In S. Jain & P. Moyle (eds), Vernal Pools and Intermittent Streams. U. C. Davis Institute of Ecology Publication 28: 1–8.

Wagele, J. W., 1992. Co-evolution between fishes and crustaceans. Acta Zool. 73: 355–356.

Weider, L. J., 1985. Spatial and temporal genetic heterogeneity in a natural *Daphnia* population. J. Plankton Res. 7: 101–123.

Weir, H. & E. Bauder, 1990. Vernal pool management plan Naval Air Station Mirimar. Prepared by Michael Brandman Associates, San Diego, for Mirimar Engineering Field Division.

White, G. E. & R. Hartland-Rowe, 1969. Temporal changes in physical and chemical factors in a shallow astatic saline lake. Verh. int. Ver. Limnol. 17: 440–446.

Whiteside, M. C. & R. V. Harmsworth, 1967. Species diversity in chydorid (Cladocera) communities. Ecology 48: 664–667.

Wiens, J. A., 1977. On competition and variable environments. Am. Sci. 65: 590–597.

Wiggins, G. B., R. J. Mackay & I. M. Smith, 1980. Evolutionary and ecological strategies of animals in annual temporary pools. Arch. Hydrobiol. Suppl. 58: 97–206.

Williams, C. B., 1964. Patterns in the Balance of Nature. Academic Press, New York: 93–117.

Williams, W. D., 1985. Biotic adaptations in temporary lentic waters, with special reference to those in semi-arid and arid regions. Hydrobiologia 125 (Dev. Hydrobiol. 28): 85–110.

Wilson, C. C. & P. D. N. Hebert, 1992. The maintenance of taxon diversity in an asexual assemblage: An experimental analysis. Ecology 73: 1462–1472.

Zaret, T. M., 1980. Predation and Freshwater Communities. Yale Univ. Press, New Haven.

Zedler, P. H., 1987. The ecology of southern California vernal pools: A community profile. Biological Report 85, National Wetlands Research Center, U.S. Fish and Wildlife Service.

Appendix A. Standardized terminology for pool size and water chemistry parameters.

Salinity (‰)	<1	low
	1-5	moderate
	>5	high
Secchi Disc Transparency (cm)	0–3	very turbid
	3–6	turbid
	6–13	cloudy
	clear	clear
Conductivity ($\mu\Omega^{-1}$)	<100	very low
	100–500	low
	501–700	moderate
	>700	high
pH	5.0–5.5	strong acid
	5.6–6.1	moderate acid
	6.2–6.5	mild acid
	6.6–7.4	neutral
	7.5–7.8	mild base
	7.9–8.4	moderate base
	8.5–9.0	strong base
Alkalinity (mg l^{-1})	<100	very low
	100–200	low
	201–400	moderate
	401–1000	high
	>1000	very high
Total Dissolved Solids (mg l^{-1})	<100	very low
	100–500	low
	501–1000	moderate
	1001–2000	high
	>2000	very high
Surface Area (m^2)	<300	very small
	300–1000	small
	1001–3000	medium
	3001–25000	large
	>25000	very large
Depth (m)	<0.10	very shallow
	0.10–0.25	shallow
	0.26–0.50	medium
	0.51–1.0	deep
	>1.0	very deep

King, J. L., M. A. Simovich, and R. C. Brusca. 1996. Species richness, endemism, and ecology of crustacean assemblages in northern California vernal pools. Hydrobiologia 328:85-116.

Errata

The following references were inadvertently omitted or printed incorrectly in the published paper. We apologize for any inconveniences:

Barclay, M. H. 1966. An ecological study of a temporary pond near Aukland, New Zealand. Aust. J. Mar. Freshwat. Res. 17:239-258.

Carter, J. C. H. 1971. Distribution and abundance of planktonic Crustacea in ponds near Georgian Bay (Ontario, Canada) in relation to hydrography and water chemistry. Arch. Hydrobiol. 68:204-231.

DeDeckker, P. & M. C. Geddes. 1980. Seasonal fauna of ephemeral saline lakes near the Coorong Lagoon, South Australia. Aust. J. Mar. Freshwater Res. 31:677-699.

Holland, R. F. 1986. Preliminary descriptions of the terrestrial natural communities of California. State of California Department of Fish and Game.

Holland, R. F. & S. K. Jain. 1988. Vernal pools. In: M. Barbour & J. Major (eds). Terrestrial Vegetation of California, new expanded ed. California Native Plant Society Special Publication 9:515-533.

Kenk, R. 1949. The animal life of temporary and permanent ponds in southern Michigan. Misc. Publ. Mus. Zool., University of Michigan 71:1-66.

Maeda-Martinez, A. M. 1991. Distribution of species of Anostraca, Notostraca, Spinicaudata, and Laevicaudata in Mexico. Hydrobiologia 212:209-219.

Sollberger, P. J. & M. R. Meador. 1990. Occurrence of cladocerans and copepods in an intermittent Texas stream. Texas J. Science 42:200-202.

Sprules, W. G. 1972. Effects of size-selective predation and food competition on high altitude zooplankton communities. Ecology 53:375-386.

Thiery, A. 1991. Multispecies coexistence of branchiopods (Anostraca, Notostraca, and Spinicaudata) in temporary ponds of Chaouia plain (western Morocco): Sympatry of syntopy between usually allopatric species. Hydrobiologia 212:117-136.

Appendix B. Physical, chemical, and species data for all pools. Species are listed alphabetically, pools are listed by site from north to south.

	Fall River			**Manton Plain**			**Dales Plain**			**Tuscan Buttes**		**Red Bluff**			
	FR-1	**FR-6**	**FR-7**	**IM-5**	**MP-1**	**MP-2**	**DalesLake**	**ID-10**	**Potholes**	**TT12**	**TU5**	**RB13**	**RB15**	**RB16**	**RB20**
Surface Area, observed maximum (m^2)	28	19	11	25447	11310	3142	196350	15708	10367	2356	31416	547	283	16	94
Maximum Depth (m)	0.05-0.15	0.10	0.04	0.25-0.30	0.07-0.50	0.12-0.20	0.50-.70+	0.35-0.53	0.40-0.70	0.50-0.90	0.30-0.45	0.15	0.15-0.30	0.11	0.18
TDS (mg l^{-1})	20-30	20	20-30	10-20	15-30	10	10	10-20	20-30	30-80	10-30	80	60-150	30	50
Alkalinity (mg l^{-1})	40	40	40	24-36	52	24	20-28	28-36	56-72	35-64	20-28	n.a.	60	44	n.a.
Conductivity ($\mu\Omega^{-1}$)	40-50	30	30-60	20-50	30-60	20-30	30	20-40	60-83	60-150	30-60	120	170	70	110
pH	7.4-7.6	7.8	6.6-7.6	7.4-7.6	6.8-7.2	6.1-7.6	6.5-8.0	6.6-7.8	7.4	6.8-7.4	7.3-8.0	6.5	6.6-7.6	8.6	8.2
Temperature (°C) *	19-24	16	15-24	17-18	10-18	11.5-14	10.5-21	11-24	20-28	11.6-24	11-29	13	11.6-28	26	16.8
Anostraca (4)															
Branchinecta conservatio															
Branchinecta dissimilis		+													
Branchinecta lynchi															
Linderiella occidentalis				+	+		+	+	+	+	+				
Number of anostracans per pool	0	1	0	1	1	0	1	1	1	1	1	0	0	0	0
Notostraca (2)															
Lepidurus sp. A	+	+	+												
Lepidurus packardi				+	+		+	+		+	+				
Number of notostracans per pool	0	0	0	1	1	0	1	1	0	1	1	0	0	0	0
Spinicaudata (1)															
Cyzicus californicus															
Number of spinicaudatans per pool	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Laevicaudata (1)															
Lynceus brachyurus				+	+	+	+	+	+		+				
Number of laevicaudatans per pool	0	0	0	1	1	1	1	1	1	0	1	0	0	0	0
Cladocera (18)															
Alona cf. davidi							+								
Alona cf. setulosa							+				+				
Alona sp. A									+						
Alona sp. B									+						
Camptocercus sp. A									+						
Ceriodaphnia reticulata							+		+					+	
Chydorus cf. sphaericus					+		+		+		+				
Daphnia cf. middendorffiana				+											
Daphnia cf. pulex		+					+		+	+	+		+		
Diaphanosoma cf. birgei							+	+	+						
Dunhevedia crassa							+		+						
Leydigia leydigi								+							
Macrothrix hirsuticornis	+	+	+	+	+	+	+	+	+	+	+				
Moina cf. micrura	+	+	+	+	+			+			+				
Pleuroxus aduncus							+								
Pleuroxus sp. A								+							
Simocephalus sp. A				+	+	+	+	+	+	+	+		+		+
Simocephalus vetulus							+		+	+	+				
Number of cladocerans per pool	2	3	2	4	4	2	11	6	11	4	7	0	2	1	1

*Temperature ranges represent only the temperatures recorded during daytime site visits over three sampling periods (February 16-24, March 23-April 3, April 22-May 1).

( ) Could be identified to genus but not to species; counted only if specimen represents sole member of that genus found in pool.

Ca = calanoid Cy = cyclopoid Ha = harpacticoid

[1]Regarded as a synonym of *Heterocypris incongruens* by some workers.

Appendix B. Physical, chemical, and species data for all pools. Species are listed alphabetically, pools are listed by site from north to south.

	Fall River			Manton Plain			Dales Plain			Toscan Buttes		Red Bluff			
	FR-1	FR-6	FR-7	IM-5	MP-1	MP-2	DalesLake	ID-10	Potholes	IT12	TU5	RB13	RB15	RB16	RB20
Copepoda (17)															
Acanthocyclops carolinianus (Cy)				+	+		+	+	+	+	+	+	+	+	+
Acanthocyclops vernalis (Cy)	+	+	+												
Aglaodiaptomus forbesi (Ca)													+		
Attheyella sp. A (Ha)				+			+	+	+						
Bryocamptus washingtonensis (Ha)															
Canthocamptus robertcokeri (Ha)															
Canthocamptus sp. A (Ha)															
Diacyclops crassicaudis var. brachycercus (Cy)											+				
Diacyclops navus (Cy)									+						
Diacyclops sp. A (Cy)					+	+						+	+	+	+
Eucyclops elegans (Cy)			+												
Hesperodiaptomus cadacus (Ca)									+						
Hesperodiaptomus eiseni (Ca)				+	+	+	+	+	+	+	+				
Hesperodiaptomus hirsutus (Ca)	+	+	+												
Leptodiaptomus tyrrelli (Ca)				+	+	+	+	+	+	+	+				+
Microcyclops rubellus (Cy)										+	+				
Skistodiaptomus pallidus (Ca)															
Number of copepods per pool	2	2	3	4	4	3	4	4	6	4	5	2	3	2	3
Ostracoda (24)															
Bradleystrandesia reticulata?	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
{Candona sp.}	{+}							{+}	{+}		{+}	{+}	{+}		{+}
Candona caudata						+		+	+		+		+		
Candona cf. C. stagnalis									+						
Candona n. sp. C													+		
Candona n. sp. D					+		+	+			+				
Candona sp. A					+		+		+						
Cypridopsis vidua									+						
Cypris subglobosa															
Eucypris sp. A												+			
Eucypris s.l. sp. A	+						+	+		+			+		
Eucypris s.l. sp. B				+		+		+	+				+		
Eucypris virens media	+				+				+	+		+			
{Heterocypris sp.}												{+}			
Heterocypris aff. H. carolinensis ^{1}				+						+					
Heterocypris aff. H. rotundatus		+	+									+			+
Heterocypris incongruens										+					
{Limnocythere sp.}				{+}			{+}			{+}			{+}		
Limnocythere aff. paraornata															
Limnocythere posterolimba	+		+		+			+		+	+		+		+
Limnocythere cf. sanctipatricii												+			
Limnocythere sp. B						+	+				+		+		
? Megalocypris sp.									+	+					
Pelocypris aff P. albomaculata										+	+				
Potamocypris sp. A							+			+	+				
Unknown sp. D															
Unknown sp. G															
Number of ostracods per pool	5	2	3	4	5	4	6	6	8	9	7	6	7	1	4
Total number of species per pool	9	8	8	15	16	10	24	19	27	19	22	8	12	4	8

Appendix B. Physical, chemical, and species data for all pools. Species are listed alphabetically, pools are listed by site from north to south.

	Red Bluff			**Coyote Creek**			**Truckee Creek**						**Thomes Creek**		
	RB23	RB3	RB4	COY2	COY4	COY5	TR15	TR16	TR17	TR24	TROFF	TR7	TH-A	TH11	TH14
Surface Area, observed maximum (m^2)	n.a.	1767	141	707	452	12566	628	471	75	106	1001	157	157	188	1100
Maximum Depth (m)	0.25	0.15	0.10-0.20	0.20-0.30	0.15	0.15-0.50	0.15	0.20	0.07	0.16	0.10-0.25	0.12-0.18	0.20-0.25	0.25	0.25-0.45
TDS (mg l^{-1})	170	50	60	30-60	50	40-100	50	35	30	20	40-50	40	30	20	10-20
Alkalinity (mg l^{-1})	n.a.	n.a.	76	64	n.a.	64-120	52	48	40	36	48-68	42-44	28-32	24	20-22
Conductivity ($\mu\Omega^{-1}$)	120	90	120	60-110	90	70-200	80	70	60	50	85-90	20-60	50-70	30	20-30
pH	8.8	7.2	7.8-8.6	6.7-7.4	7.2	7.2-8.1	7.0	7.2	7.2	7.4	6.8-7.4	7.2-7.5	6.6-7.4	8.4	7.8
Temperature (°C) *	18	14	27	19	19	18-27	10.8	19	27	24	12.5-28	13.7-29	11.2-29	12.5	12.5-28
Anostraca (4)															
Branchinecta conservatio															
Branchinecta dissimilis															
Branchinecta lynchi							+		+	+	+	+	+	+	
Linderiella occidentalis															
Number of anostracans per pool	0	0	0	0	0	0	1	0	1	1	1	1	1	1	0
Notostraca (2)															
Lepidurus sp. A															
Lepidurus packardi															
Number of notostracans per pool	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Spinicaudata (1)															
Cyzicus californicus															
Number of spinicaudatans per pool	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Laevicaudata (1)															
Lynceus brachyurus															
Number of laevicaudatans per pool	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cladocera (18)															
Alona cf. davidi															
Alona cf. setulosa															
Alona sp. A						+									
Alona sp. B															
Camptocercus sp. A															
Ceriodaphnia reticulata			+			+									
Chydorus cf. sphaericus															
Daphnia cf. middendorffiana															
Daphnia cf. pulex															
Diaphanosoma cf. birgei															
Dunhevedia crassa															
Leydigia leydigi															
Macrothrix hirsuticornis						+							+	+	+
Moina cf. micrura						+	+								
Pleuroxus aduncus															
Pleuroxus sp. A															
Simocephalus sp. A		+	+			+							+		
Simocephalus vetulus	+														
Number of cladocerans per pool	1	1	2	0	0	5	1	0	0	0	0	0	2	1	1

*Temperature ranges represent only the temperatures recorded during daytime site visits over three sampling periods (February 16-24, March 23-April 3, April 22-May 1).

n.a.=not available

( ) Could be identified to genus but not to species; counted only if specimen represents sole member of that genus found in pool.

Ca = calanoid Cy = cyclopoid Ha = harpacticoid

[1]Regarded as a synonym of *Heterocypris incongruens* by some workers.

Appendix B. Physical, chemical, and species data for all pools. Species are listed alphabetically, pools are listed by site from north to south.

	Red Bluff			Coyote Creek			Truckee Creek						Thomes Creek		
	RB23	**RB3**	**RB4**	**COY2**	**COY4**	**COY5**	**TR15**	**TR16**	**TR17**	**TR24**	**TROFF**	**TR7**	**TH-A**	**TH11**	**TH14**
Copepoda (17)															
Acanthocyclops carolinianus (Cy)	+	+	+	+	+	+	+						+	+	+
Acanthocyclops vernalis (Cy)															
Aglaodiaptomus forbesi (Ca)															
Attheyella sp. A (Ha)															
Bryocamptus washingtonensis (Ha)															+
Canthocamptus robertcokeri (Ha)															
Canthocamptus sp. A (Ha)													+		
Diacyclops crassicaudis var. brachycercus (Cy)				+	+		+					+	+		
Diacyclops navus (Cy)															
Diacyclops sp. A (Cy)	+	+	+		+	+							+	+	+
Eucyclops elegans (Cy)						+									
Hesperodiaptomus cadacus (Ca)															
Hesperodiaptomus eiseni (Ca)															
Hesperodiaptomus hirsutus (Ca)															
Leptodiaptomus tyrrelli (Ca)	+	+	+			+									
Microcyclops rubellus (Cy)															
Skistodiaptomus pallidus (Ca)															
Number of copepods per pool	3	3	3	2	3	4	2	0	0	0	0	1	4	2	3
Ostracoda (24)															
Bradleystrandesia reticulata?		+	+		+	+		+				+	+	+	+
(Candona sp.)	(+)		(+)			(+)									
Candona caudata		+													
Candona cf. C. stagnalis															
Candona n. sp. C						+									
Candona n. sp. D															
Candona sp. A															
Cypridopsis vidua						+									
Cypris subglobosa															
Eucypris sp. A			+												
Eucypris s.l. sp. A	+		+			+									
Eucypris s.l. sp. B												+			
Eucypris virens media	+		+		+			+							
(Heterocypris sp.)					(+)	(+)									
Heterocypris aff. H. carolinensis [1]															
Heterocypris aff. H. rotundatus	+		+		+	+									
Heterocypris incongruens															
(Limnocythere sp.)															
Limnocythere aff. paraornata															
Limnocythere posterolimba		+	+			+									
Limnocythere cf. sanctipatricii															
Limnocythere sp. B		+	+			+						+			
? Megalocypris sp.															
Pelocypris aff P. albomaculata															
Potamocypris sp. A															
Unknown sp. D															
Unknown sp. G												+			
Number of ostracods per pool	4	4	8	0	3	7	0	2	0	0	0	4	1	1	1
Total number of species per pool	8	8	13	2	6	16	4	2	1	1	1	6	8	5	5

Appendix B. Physical, chemical, and species data for all pools. Species are listed alphabetically, pools are listed by site from north to south.

	Thomas Creek							Corning							
	TH20	**TH3**	**TH33**	**TH40**	**TH41**	**TH42**	**TH42a**	**CR109**	**CR14A**	**CR2**	**CR27**	**CR4**	**CR74**	**I-1**	**I-2**
Surface Area, observed maximum (m^2)	424	377	50	82	314	177	50	393	377	157	94	38	71	94	236
Maximum Depth (m)	0.11-0.35	0.23-0.25	0.11	0.12-0.25	0.20-0.40	0.20	0.70-0.85	0.17-0.20	0.15	.05-0.25	0.05	0.07	0.10	0.04-0.15	0.12
TDS (mg l^{-1})	15-30	15-40	20	30-100	40-50	30	20-30	10-20	20	20-30	10	30	20	20-60	30
Alkalinity (mg l^{-1})	24-40	26-28	24	28-76	28-44	20	28-36	20-22	24-30	32-40	20	28	32	34-72	40
Conductivity ($\mu\Omega^{-1}$)	30-60	30-60	40	50-190	70-90	40	50-60	20	40-45	40-50	30	60	40	40-125	50
pH	7.4-9.8	8.0-9.4	7.4	6.6-6.7	6.6-7.2	7.6	6.6-7.4	7.6-8.6	7.2-9.3	7.4	7.5	7.2	8.4	6.9-7.0	7.3
Temperature (°C) *	12.3-24	12.5-24	27	12.9-30	12-28	12	12.5-24	19.5-23	20-25	17.5	25	27	21	20-24	17
Anostraca (4)															
Branchinecta conservatio															
Branchinecta dissimilis															
Branchinecta lynchi	+	+	+			+	+	+	+	+			+	+	
Linderiella occidentalis															
Number of anostracans per pool	1	1	1	0	0	1	1	1	1	1	0	0	1	1	0
Notostraca (2)															
Lepidurus sp. A															
Lepidurus packardi															
Number of notostracans per pool	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Spinicaudata (1)															
Cyzicus californicus															
Number of spinicaudatans per pool	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Laevicaudata (1)															
Lynceus brachyurus															
Number of laevicaudatans per pool	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cladocera (18)															
Alona cf. davidi															
Alona cf. setulosa															
Alona sp. A															
Alona sp. B															
Camptocercus sp. A															
Ceriodaphnia reticulata															+
Chydorus cf. sphaericus															
Daphnia cf. middendorffiana															
Daphnia cf. pulex															
Diaphanosoma cf. birgei															
Dunhevedia crassa															
Leydigia leydigi															
Macrothrix hirsuticornis	+	+			+		+	+	+	+	+	+		+	+
Moina cf. micrura														+	
Pleuroxus aduncus															
Pleuroxus sp. A															
Simocephalus sp. A	+	+			+		+	+		+	+	+		+	+
Simocephalus vetulus															
Number of cladocerans per pool	2	2	0	0	2	0	2	2	1	2	2	2	0	3	3

*Temperature ranges represent only the temperatures recorded during daytime site visits over three sampling periods (February 16-24, March 23-April 3, April 22-May 1).

{ } Could be identified to genus but not to species; counted only if specimen represents sole member of that genus found in pool.

Ca = calanoid Cy = cyclopoid Ha = harpacticoid

[1] Regarded as a synonym of *Heterocypris incongruens* by some workers.

Appendix B. Physical, chemical, and species data for all pools. Species are listed alphabetically, pools are listed by site from north to south.

	Thomes Creek							Corning							
	TH20	**TH3**	**TH33**	**TH40**	**TH41**	**TH42**	**TH42a**	**CR109**	**CR14A**	**CR2**	**CR27**	**CR4**	**CR74**	**I-1**	**I-2**
Copepoda (17)															
Acanthocyclops carolinianus (Cy)	+	+	+	+	+	+	+	+			+			+	
Acanthocyclops vernalis (Cy)															
Aglaodiaptomus forbesi (Ca)															
Attheyella sp. A (Ha)							+								
Bryocamptus washingtonensis (Ha)															
Canthocamptus robertcokeri (Ha)															
Canthocamptus sp. A (Ha)															
Diacyclops crassicaudis var. brachycercus (Cy)	+			+	+	+	+	+			+		+		
Diacyclops navus (Cy)															
Diacyclops sp. A (Cy)	+	+	+	+	+	+	+	+		+	+	+		+	+
Eucyclops elegans (Cy)												+			
Hesperodiaptomus caducus (Ca)															
Hesperodiaptomus eiseni (Ca)	+														
Hesperodiaptomus hirsutus (Ca)															
Leptodiaptomus tyrrelli (Ca)	+			+		+									+
Microcyclops rubellus (Cy)															
Skistodiaptomus pallidus (Ca)															
Number of copepods per pool	5	2	2	4	3	4	4	3	0	1	3	2	1	2	2
Ostracoda (24)															
Bradleystrandesia reticulata?	+	+	+	+	+		+	+	+	+			+	+	+
{Candona sp.}	{+}	{+}					{+}		{+}					{+}	{+}
Candona caudata	+	+				+									
Candona cf. C. stagnalis															
Candona n. sp. C										+					+
Candona n. sp. D															
Candona sp. A															
Cypridopsis vidua												+			
Cypris subglobosa					+										
Eucypris sp. A															
Eucypris s.l. sp. A	+	+						+	+	+	+				+
Eucypris s.l. sp. B	+	+					+								
Eucypris virens media	+	+			+				+					+	
{Heterocypris sp.}					{+}								{+}	{+}	
Heterocypris aff. H. carolinensis[1]															
Heterocypris aff. H. rotundatus					+			+	+				+	+	
Heterocypris incongruens															
{Limnocythere sp.}		{+}													
Limnocythere aff. paraornata		+													
Limnocythere posterolimba															
Limnocythere cf. sanctipatricii															
Limnocythere sp. B	+				+		+		+						
? Megalocypris sp.															
Pelocypris aff P. albomaculata															
Potamocypris sp. A	+														
Unknown sp. D															
Unknown sp. G															
Number of ostracods per pool	7	7	1	1	5	0	4	3	6	3	1	1	2	4	3
Total number of species per pool	15	12	4	5	10	5	11	9	8	7	6	5	4	10	8

Appendix B. Physical, chemical, and species data for all pools. Species are listed alphabetically, pools are listed by site from north to south.

	Hall Creek		**Stony Creek**			**Wilson Creek**			**Allendale**		**Jepson Prairie**		
	H10	**H9**	**S2**	**S5**	**S8**	**W11**	**W15**	**W18**	**A-1**	**A-A**	**J-3**	**J-5**	**J-A2**
Surface Area, observed maximum (m^2)	188	38	7854	44	59	687	38	259	804	118	21382	237583	29452
Maximum Depth (m)	0.09-0.15	0.15	0.18-0.25	0.09-0.20	0.07	0.13-0.25	0.08-0.20	0.11-0.22	0.12-0.15	0.10-0.20	0.40-0.60	0.50-0.80	0.40-0.55
TDS (mg l^{-1})	10	10	20-30	20	20	30-40	20-30	30-50	30	40-70	80-250	65-160	110-340
Alkalinity (mg l^{-1})	20-24	20	36-44	28-34	32	44-48	40-44	36-58	44-60	56-64	46-98	48-100	60-140
Conductivity ($\mu\Omega^{-1}$)	30	20	50	50	50	60-80	50-70	60-100	60-70	95-120	180-520	130-340	250-680
pH	8.0-8.2	6.7	7.3-9.0	8.4-9.0	8.2	6.4-7.2	8.0-8.4	8.0-8.9	6.2-7.8	6.0-7.4	7.2-7.6	6.2-8.0	7.6-7.8
Temperature (°C) *	9	9.5-18	15-25	16.9-26	26	20-23	20-24	20.5-24	13.5-32	11-33	13.2-21	17-21	18-21
Anostraca (4)													
Branchinecta conservatio											+	+	+
Branchinecta dissimilis													
Branchinecta lynchi	+	+	+	+		+	+	+					
Linderiella occidentalis													
Number of anostracans per pool	1	1	1	1	0	1	1	1	0	0	1	1	1
Notostraca (2)													
Lepidurus sp. A													
Lepidurus packardi											+	+	+
Number of notostracans per pool	0	0	0	0	0	0	0	0	0	0	1	1	1
Spinicaudata (1)													
Cyzicus californicus											+	+	+
Number of spinicaudatans per pool	0	0	0	0	0	0	0	0	0	0	1	1	1
Laevicaudata (1)													
Lynceus brachyurus													
Number of laevicaudatans per pool	0	0	0	0	0	0	0	0	0	0	0	0	0
Cladocera (18)													
Alona cf. davidi													
Alona cf. setulosa													
Alona sp. A													
Alona sp. B													
Camptocercus sp. A													
Ceriodaphnia reticulata			+										
Chydorus cf. sphaericus													
Daphnia cf. middendorffiana											+	+	+
Daphnia cf. pulex				+			+	+			+		+
Diaphanosoma cf. birgei													
Dunhevedia crassa													
Leydigia leydigi											+		
Macrothrix hirsuticornis	+		+	+	+	+		+	+			+	+
Moina cf. micrura													
Pleuroxus aduncus													
Pleuroxus sp. A													
Simocephalus sp. A	+		+	+	+	+		+	+	+		+	
Simocephalus vetulus			+			+				+	+	+	
Number of cladocerans per pool	2	0	4	3	2	3	1	3	2	2	4	4	3

*Temperature ranges represent only the temperatures recorded during daytime site visits over three sampling periods (February 16-24, March 23-April 3, April 22-May 1).

( ) Could be identified to genus but not to species; counted only if specimen represents sole member of that genus found in pool.

Ca = calanoid Cy = cyclopoid Ha = harpacticoid

[1] Regarded as a synonym of *Heterocypris incongruens* by some workers.

Appendix B. Physical, chemical, and species data for all pools. Species are listed alphabetically, pools are listed by site from north to south.

	Hall Creek		Stony Creek			Wilson Creek			Allendale		Jepson Prairie		
	H10	H9	S2	S5	S8	W11	W15	W18	A-1	A-A	J-3	J-5	J-A2
Copepods (17)													
Acanthocyclops carolinianus (Cy)			+	+		+	+	+	+	+	+	+	+
Acanthocyclops vernalis (Cy)													
Aglaodiaptomus forbesi (Ca)													
Atheyella sp. A (Ha)									+			+	+
Bryocamptus washingtonensis (Ha)													
Canthocamptus robertcokeri (Ha)												+	
Canthocamptus sp. A (Ha)													
Diacyclops crassicaudis var. brachycercus (Cy)						+					+		
Diacyclops navus (Cy)									+				
Diacyclops sp. A (Cy)			+	+	+	+		+	+	+		+	+
Eucyclops elegans (Cy)									+				
Hesperodiaptomus cadacus (Ca)													
Hesperodiaptomus eiseni (Ca)											+	+	+
Hesperodiaptomus hirsutus (Ca)													
Leptodiaptomus tyrrelli (Ca)								+			+	+	+
Microcyclops rubellus (Cy)													
Skistodiaptomus pallidus (Ca)										+			
Number of copepods per pool	0	0	2	2	1	3	1	3	5	3	4	6	5
Ostracods (24)													
Bradleystrandesia reticulata?	+	+	+	+	+	+	+	+	+	+	+	+	+
(Candona sp.)				{+}					(+)	(+)		{+}	
Candona caudata											+	+	
Candona cf. C. stagnalis													
Candona n. sp. C										+			
Candona n. sp. D							+				+	+	+
Candona sp. A													
Cypridopsis vidua													
Cypris subglobosa													
Eucypris sp. A		+											
Eucypris s.l. sp. A			+	+	+	+			+	+		+	+
Eucypris s.l. sp. B													
Eucypris virens media			+	+								+	+
(Heterocypris sp.}													
Heterocypris aff. H. carolinensis [1]											+	+	+
Heterocypris aff. H. rotundatus							+	+		+			
Heterocypris incongruens													
(Limnocythere sp.)												{+}	
Limnocythere aff. paraornata													
Limnocythere posterolimba											+	+	+
Limnocythere cf. sanctipatricii													
Limnocythere sp. B						+	+	+				+	
? Megalocypris sp.											+	+	+
Pelocypris aff P. albomaculata												+	
Potamocypris sp. A										+		+	
Unknown sp. D											+	+	+
Unknown sp. G													
Number of ostracods per pool	1	2	3	4	2	3	4	3	3	5	7	12	8
Total number of species per pool	4	3	10	10	5	10	7	10	10	10	18	25	19