

Succession of macroinvertebrates in playas of the Southern High Plains, USA

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Abstract. Playas are seasonal wetlands that constitute the principal surface-water features of the semiarid, Southern High Plains, USA. They are shallow pools that usually persist for 2–4 mo following inundation by spring rains. The development of macroinvertebrate assemblages in 10 playas located in West Texas was examined during the summer of 1994. Playas were sampled 3 times at approximately monthly intervals, beginning shortly after initial inundation in early May. All playas were dry within 90 d. Species richness and diversity (Fisher's log-series α) increased significantly over time ($p < 0.05$). Thirteen of the 16 species representing at least 1% of collected individuals, showed significant differences in abundances over time ($p < 0.05$). Some taxa increased in abundance (especially insects), whereas others decreased (most crustaceans). Trophic structure of assemblages also changed over time, with a significant reduction in the abundances of detritivores ($p < 0.05$) and filter-feeders ($p < 0.05$) occurring concurrently with an increase in the abundance of predators ($p < 0.05$). The composition of macroinvertebrate assemblages became more similar among playas over time (Ochai's index, $p < 0.05$), and changes in composition within individual playas tended to decrease with time ($p < 0.05$). These results suggest a rapid development of macroinvertebrate assemblages in playas, beginning with early dominance of crustacean detritivores and filter-feeders (e.g., phyllopo­ods and ostracods), followed by later dominance of herbivorous and predaceous insects (e.g., hydrophilids and notonectids). Increases in species richness, diversity, and similarity in assemblage composition among playas over time are consistent with a pattern of progressive colonization by a finite set of species capable of exploiting these ephemeral habitats.

Key words: macroinvertebrates, succession, playas, temporary ponds.

Temporary aquatic habitats are a common feature of many regions of the world, but they have received considerably less attention than permanent rivers and lakes. Intermittent systems are ideally suited for examining patterns of community succession, especially with regard to aquatic invertebrates. For example, Mozley (1932) reported a pattern in the appearances of particular groups of invertebrates in a temporary pond of western Canada, with early dominance of crustaceans shifting to greater dominance of insects over time. Lake et al. (1989) noted a similar pattern of succession for the invertebrate fauna of a temporary pond in western Australia, and also observed that predators became a much greater component of the community during later stages of succession. In contrast, McLachlan (1985) found that competition was a primary determinant of the distributions of 2 species of chironomids in rain-pools of tropical Africa. Recently, Schneider and Frost (1996)

found that abiotic factors were the most important determinants of community structure in temporary ponds in Wisconsin, but biotic interactions (i.e., competition and predation) were increasingly important as the period of inundation increased.

Playas are ephemeral wetlands in the Southern High Plains, USA, that usually are briefly inundated each year (<3 mo; Bolen et al. 1989). Invertebrates rapidly colonize these habitats, so that a progression of species follows initial inundation (Sublette and Sublette 1967, Parks 1975, Merickel and Wangberg 1981). However, analyses of the temporal dynamics of taxa or trophic groups for playas have been of limited scope (Sublette and Sublette 1967, Parks 1975, Merickel and Wangberg 1981). We present the results of a study of macroinvertebrate assemblage development in playas on the Southern High Plains of West Texas. Our primary objectives were: 1) to determine numerically dominant taxa, 2) to elucidate the general pattern of species succession following inundation, and 3) to examine trophic structure of playa assemblages over time, to understand the factors con-

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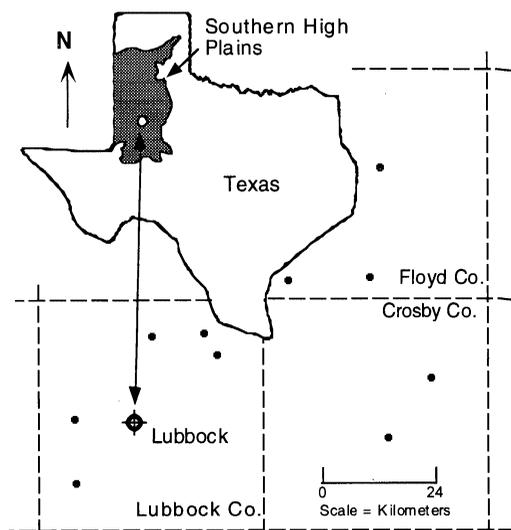


FIG. 1. Southern High Plains region of West Texas showing the 10 study playas near Lubbock, Texas.

trolling successional patterns and assemblage structure.

Study Site

The Southern High Plains, or Llano Estacado, are an extensive, semi-arid tableland (82,000

km²) lying south of the Canadian River in Texas and New Mexico (Fig. 1). The High Plains are devoid of permanently flowing rivers or streams, but contain ~22,000 ephemeral lakes or playas (Playa Lakes Joint Venture 1993). Playa watersheds are typically 50 to 800 ha in size, with a maximum elevational relief of 6–10 m. Playas store surface runoff, which subsequently is lost primarily through evaporation. Seepage is minimized by a nearly impermeable lining of montmorillonitic clay soil (i.e., Randall clay). Playas are shallow (<1 m) and range in surface area from <1 ha to >80 ha. Playas typically are dry during the late winter and early spring, and may hold water from spring through fall depending on patterns of rainfall, the volume of water received on filling, and the extent of the clay lining that retards water loss (Ward and Huddleston 1972).

Ten playas near the city of Lubbock, Texas, on the southeast border of the Southern High Plains, were selected for study (Fig. 1) based on the persistence of water—each playa was inundated throughout the study period (26 May through 14 July 1994). Physicochemical attributes of the playas and characteristics of the landscape surrounding them (Table 1) were representative of playas in the region (Mollhagen et

TABLE 1. Mean (± 1 SD) landscape characteristics and physicochemical attributes of 10 study playas. Units are in mg/L unless otherwise noted. % = playa watershed area devoted to each land use.

| Landscape characteristics | | | |
|----------------------------------|----------------------|-----------------------------------|---------------------|
| Basin size (ha) | 9.79 \pm 3.01 | Row crop (%) | 77.17 \pm 17.17 |
| Maximum water surface (ha) | 7.59 \pm 2.24 | Conservation land (%) | 11.70 \pm 18.28 |
| Watershed size (ha) | 185.54 \pm 64.86 | Rangeland (%) | 3.08 \pm 6.92 |
| | | Bare soil (%) | 2.13 \pm 3.52 |
| Water-quality attributes | | | |
| Hardness (as CaCO ₃) | 84.23 \pm 24.41 | Turbidity (NTU) | 1073.0 \pm 904.27 |
| Suspended solids | 216.10 \pm 234.53 | Calcium | 13.85 \pm 7.56 |
| Dissolved solids | 792.00 \pm 402.69 | Magnesium | 12.05 \pm 3.39 |
| Total solids | 1013.70 \pm 572.04 | Sodium | 5.89 \pm 5.79 |
| Organic carbon | 19.86 \pm 9.59 | Potassium | 31.13 \pm 20.87 |
| Inorganic carbon | 10.77 \pm 8.99 | Chlorine | 3.46 \pm 1.04 |
| Total carbon | 30.64 \pm 10.44 | Sulfate | 2.65 \pm 1.68 |
| Total Kjeldhal nitrogen | 1.24 \pm 0.66 | Silica | 14.83 \pm 1.80 |
| Ammonia | 0.40 \pm 0.54 | Arsenic (μ g/L) | 12.36 \pm 17.18 |
| Nitrate + nitrite | 0.21 \pm 0.18 | Copper (μ g/L) | 42.00 \pm 17.01 |
| Total phosphate phosphorus | 0.82 \pm 0.42 | Chlorophyll <i>a</i> (μ g/L) | 4.50 \pm 3.36 |
| Ortho-phosphate phosphorus | 0.62 \pm 0.23 | Temperature ($^{\circ}$ C) | 21.69 \pm 2.27 |
| Biological oxygen demand | 8.05 \pm 5.99 | Dissolved oxygen | 5.62 \pm 2.95 |
| Chemical oxygen demand | 28.40 \pm 15.98 | Conductivity (μ S/cm) | 139.00 \pm 40.80 |

al. 1993). The area has extensive irrigation agriculture, rangeland, and Conservation Reserve Program lands (Hall and Willig 1994, Hall et al., in press).

Methods

Physical and chemical measurements

Land-use and water-quality characteristics were determined for the study playas (see details in Hall 1997, Hall et al., in press). During the 1st sampling period, 4 L of water were collected from the center of each playa, according to the protocol described by Mollhagen et al. (1993). One L was treated with sulfuric acid and used for nutrient assays (e.g., nitrate + nitrite, soluble reactive phosphorus, total Kjeldahl nitrogen). One L was treated with nitric acid and used for metal assays (arsenic, copper, lead, etc.). Two L had no preservatives added and were assayed for pesticides (Alachlor, Aldicarb, Cyanazine, etc.) and inorganic characteristics (e.g., hardness, alkalinity, solids). All water samples were maintained on ice and delivered to the laboratory for analyses within 10 h of collection; collection and analytical methods conformed to quality control requirements of the US Environmental Protection Agency (Mollhagen et al. 1993).

Size and land-use patterns of playas were examined (Table 1). The % of total land area dedicated to agricultural row-crop production, pasture for livestock, or conservation grassland within the watershed of each playa was estimated by visual assessment during the 1st sampling period. Basin size of each playa was defined as the areal extent of the Randall clay. Basin and watershed size were obtained from a Geographical Information System developed for the region (E. B. Fish, Texas Tech University, personal communication). Areal extent of water surface was determined by measuring the distances between stakes placed at the edge of each playa, in each of the 4 cardinal directions on each sampling period. Surface area of each playa on each sampling date was calculated as the area of an ellipse given the lengths of the N-S and E-W axes.

Invertebrate sampling

Invertebrate sampling was initiated ~3 wk after the playas were inundated by spring rains in

1994. Invertebrates were collected during 3 sampling periods: 26 May–7 June, 20–28 June, and 11–14 July. Within each period, 50 sites were sampled in each playa. At each site, 2 surface, 6 subsurface, and 5 benthic samples were collected, resulting in 100 surface, 300 subsurface, and 250 benthic samples from each playa during each sampling period.

Surface and subsurface samples were taken with an aquatic D-net (opening height = 19 cm, width = 31 cm, mesh size = 500 μ m). Surface samples consisted of two 180° sweeps of the net, with the flat portion of the net not more than 2.5 cm below the surface of the water. Subsurface samples consisted of 6 sweeps, 2 taken from directly in front of the person collecting the sample and 2 taken from each side. Each subsurface sweep consisted of maximally extending the net, letting it fall to the sediment surface, and retrieving it along the top of the sediment. A single-bore corer (5-cm inner diameter) was used to collect benthic samples; 5 cores were taken within 1 m of each sampling point and sieved through a 500- μ m mesh.

Macroinvertebrates (all invertebrates retained by the 500- μ m mesh) from surface and subsurface samples were preserved in the field in 95% ethanol; benthic macroinvertebrates were preserved in a solution of 37% formaldehyde. In the laboratory, macroinvertebrates were separated from debris and sediment, and all specimens were transferred to 80% ethanol for permanent storage.

Invertebrate identification

Individuals were identified to the species level whenever possible (voucher specimens have been deposited in the Enns Entomology Museum, University of Missouri, Columbia). Early instars of libellulid dragonflies and most oligochaetes lacked many generic or specific characteristics and could not be identified reliably below the family level. These individuals were therefore pooled at the family level. Several families of insects contained immature forms that also could not be identified below family or genus, although adults could be identified to the species level. For these taxa, immature individuals were assumed to occur in the same proportion as adults, and apportioned accordingly. Similarly, female streptocephalid fairy shrimp and arrenurid water mites have no diagnostic

species-level characteristics; these females were apportioned according to the abundances of males. Distinct taxa that could not be readily identified below the family level were classified as morphospecies.

Quantitative analyses

Macroinvertebrate species richness and diversity (Fisher's log series α , Taylor et al. 1976) were calculated for each playa for each sampling date. Repeated measures (sampling period), analysis of variance (ANOVA) without replication was used to test for differences in richness and diversity across sampling periods (Data Desk 4.2, Data Description, Inc., Ithaca, New York).

Abundances of organisms (i.e., total numbers of all taxa collected at each playa from each sampling period) were examined at the species and family levels across sampling periods. Only those taxa representing $\geq 1\%$ of the total number of individuals collected were included in statistical analyses. Abundances of individuals (x) were transformed ($\log[x + 1]$) for use as dependent variables in the ANOVA. Sixteen analyses were done at the species level and 14 analyses were done at the family level.

Ochai's index of similarity (Ludwig and Reynolds 1988), based on species-level data, was used to evaluate patterns of assemblage composition among sampling dates within playas and among playas within sampling dates. To assess if assemblages differed within playas over time, Ochai's index was calculated for each playa between each pair of sampling periods. A repeated measures ANOVA (see above) was used to test for differences in index values among dates. To assess if patterns of similarity among playa assemblages differed over time, Ochai's index was calculated for each pair of playas within each sampling period. A 1-way ANOVA was used to test for differences among sampling dates (Data Desk 4.2, Data Description, Inc.). Scheffé post hoc tests were used to evaluate differences between all possible pairs of dates.

Our interests included both structural and functional features of invertebrate assemblage succession, so we assigned 1 of 6 trophic identities (herbivores, detritivores, filter-feeders, predators, parasites, and omnivores) to each collected species (Pennak 1989, Thorp and Covich 1991, Merritt and Cummins 1996). Adult hydrophilids were classified as herbivores, whereas

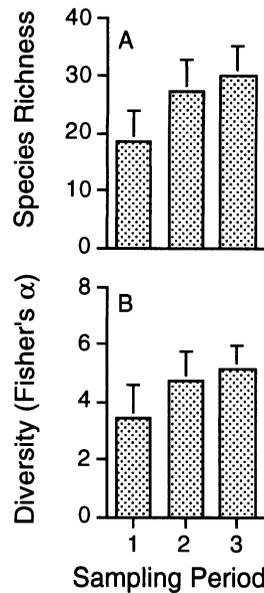


FIG. 2. Mean species richness (A) and diversity (Fisher's log-series α , B) of aquatic macroinvertebrates in the 10 West Texas playas during 3 successive sampling periods following inundation (see methods for dates of sampling intervals). Error bars show +95% CI for the mean values. (Post hoc comparisons are not appropriate for repeated measures analysis of variance.)

larvae were considered to be predators (Merritt and Cummins 1996). The relative abundance of each trophic group from each playa was calculated for each sampling period. Differences between dates in the relative abundances of each trophic group were assessed with a repeated measures ANOVA (see above). Relative abundances of trophic groups were transformed (arcsine square-root) for analyses.

Results

Over 100 species, representing nearly 50 families, were collected from the study playas (Appendix 1). The most abundant groups were insects, crustaceans, and gastropods.

The duration of inundation had a pervasive effect on the macroinvertebrate assemblages in the playas (Figs 2, 3; Tables 2, 3, 4). Significant differences among sampling periods were found for the following variables: species richness, diversity, similarities in assemblage composition, abundances of 13 of the 16 species examined, abundances of 12 of 14 families examined, and

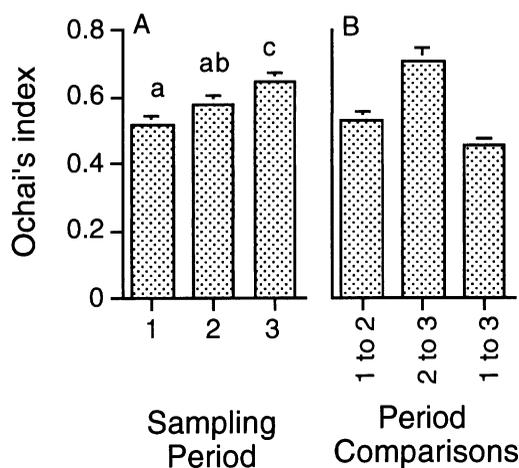


FIG. 3. Ochai's index of similarity for macroinvertebrate assemblages in the 10 playas in West Texas. A.—Mean similarity (+95% CI) among all possible pairs of playas within sampling period. Different letters above means indicate significant differences ($p \leq 0.05$) between dates estimated by Scheffé post hoc tests following 1-way ANOVA (see text). B.—Mean similarity (+95% CI) between pairs of sampling dates within playas. (Post hoc comparisons are not appropriate for repeated measures analysis of variance.)

trophic group composition. Species richness and diversity increased significantly over time ($p < 0.01$ in both cases, Fig. 2), but abundances of particular taxa either increased or decreased (Tables 2, 3). In general, taxa that lack active dispersal mechanisms, such as crustaceans, tended to have high densities early in the season (e.g., Caenestheriidae and Streptocephalidae). Of the non-dispersing taxa, gastropods (Planorbidae) and tadpole shrimp (*Triops lateralis*) increased between the 1st and 2nd sampling period. Taxa with dispersal mechanisms (flight), especially insects, tended to reach higher numbers later in the season. Trophic structure also changed over time, with a progressive shift from the numerical dominance of filter-feeders and detritivores to predators (Table 4).

Decreases in the inundated areas of playas throughout the study could have affected invertebrate densities and thus confounded estimates of invertebrate abundance and diversity. Average area of water surface for playas declined from 7.59 to 5.68 to 4.01 ha over the 3 sampling periods. However, decreasing abundances of some taxa (e.g., Dytiscidae and Caenestheriidae) contradict this hypothesis, and patterns of abun-

dance for the Hydrophilidae indicate that this concentration effect could not fully explain all increases; adult populations increased 3-fold over time, whereas larval populations increased 7-fold (Table 3). Other taxa appeared only as immatures (e.g., Chironomidae), indicating reproductive input by non-aquatic adults. The impacts of diminishing size of playas on richness, diversity, and trophic structure are uncertain.

Assemblage composition became more similar among and within playas over time (Fig. 3). Ochai's index values for all possible pairs of playas differed over time ($p < 0.001$, $n = 135$), with a significant increase in similarity between the 1st and 3rd sampling dates ($p < 0.001$), a significant increase between the 2nd and 3rd dates ($p < 0.05$), and differences between the 1st and 2nd dates approaching significance ($0.06 > p > 0.05$). These results indicate that taxonomic composition of invertebrate assemblages became more similar among playas over time (Fig. 3A). Similarities in composition of the assemblages within individual playas also showed significant differences over time ($p < 0.001$, $n = 30$); assemblages were most similar between the 2nd and 3rd sampling dates, and least similar between the 1st and 3rd dates (Fig. 3B).

Discussion

Previous studies of invertebrate assemblages in playas of West Texas found no consistent relationships between abiotic factors and species richness, diversity, or abundances of particular taxa (Sublette and Sublette 1967, Hall 1997). Thus, composition of playa assemblages may be more strongly determined by biotic factors, such as life-history characteristics, competition, and predation, which influence invertebrate assemblages in other temporary aquatic habitats (e.g., Moore 1963, 1970, Reisen 1973, McLachlan 1983, 1985).

Consistent trends in successional patterns have been observed for invertebrates inhabiting a variety of ephemeral aquatic habitats (Mozley 1932, Moore 1970, Lake et al. 1989), including playas in West Texas (Sublette and Sublette 1967, Merickel and Wangberg 1981). Early dominance by crustaceans is common, followed by increasing numbers of insects, a pattern also displayed in playas of this study (Tables 2, 3). Consistent changes in trophic structure also occur in temporary aquatic habitats, typified by

TABLE 2. Results of repeated measures analysis of variance assessing the effect of sampling period on abundance of each of 16 species of invertebrates from 10 study playas. (Numbers of adults and larvae were combined.)

| Species | <i>p</i> ≤ | Mean (±1 SD) abundance in study playas | | |
|-----------------------------------|------------|--|---------------|---------------|
| | | Sampling Period | | |
| | | 1 | 2 | 3 |
| Crustacea | | | | |
| <i>Caenetheriella setosa</i> | 0.001 | 524.3 ± 642.4 | 24.2 ± 31.7 | 25.9 ± 64.4 |
| <i>Megalocypris gnathostomata</i> | 0.116 | 153.4 ± 288.0 | 78.1 ± 103.3 | 13.6 ± 19.8 |
| <i>Streptocephalus dorotheae</i> | 0.012 | 751.2 ± 1192.2 | 133.9 ± 280.5 | 18.7 ± 44.3 |
| <i>S. texanus</i> | 0.001 | 387.7 ± 997.6 | 3.5 ± 9.1 | 0.0 ± 0.0 |
| <i>Triops longicaudatus</i> | 0.001 | 135.2 ± 325.1 | 1.4 ± 4.4 | 0.0 ± 0.0 |
| <i>Tropisternus lateralis</i> | 0.001 | 6.2 ± 8.6 | 59.1 ± 107.7 | 59.9 ± 67.7 |
| Gastropoda | | | | |
| <i>Planorbella tenuis</i> | 0.001 | 75.6 ± 74.7 | 509.6 ± 477.5 | 393.6 ± 340.1 |
| Insecta | | | | |
| <i>Berosus miles</i> | 0.099 | 12.3 ± 8.9 | 26.8 ± 17.6 | 85.7 ± 167.6 |
| <i>Berosus styliferus</i> | 0.014 | 5.4 ± 8.1 | 25.1 ± 17.5 | 53.5 ± 88.9 |
| <i>Buenoa margaritacea</i> | 0.001 | 1.5 ± 3.0 | 87.5 ± 78.8 | 506.4 ± 801.5 |
| <i>Callibaetis</i> sp. | 0.009 | 12.8 ± 18.6 | 171.7 ± 331.0 | 67.4 ± 61.6 |
| <i>Enallagma civile</i> | 0.001 | 2.4 ± 7.2 | 417.8 ± 381.8 | 623.6 ± 522.2 |
| Libellulid sp. | 0.032 | 2.1 ± 6.0 | 24.2 ± 50.5 | 76.7 ± 196.4 |
| <i>Notonecta undulata</i> | 0.001 | 0.4 ± 0.7 | 15.9 ± 18.9 | 57.0 ± 81.6 |
| <i>Procladius bellus</i> | 0.001 | 0.0 ± 0.0 | 6.7 ± 13.1 | 61.5 ± 106.9 |
| <i>Sigara alternata</i> | 0.044 | 7.4 ± 11.6 | 56.4 ± 103.0 | 66.0 ± 100.1 |

the increasing dominance of predators in later stages of succession (Lake et al. 1989, Schneider and Frost 1996). Trophic structure of the playas in this study also changed, with predators becoming more abundant over time (Table 4).

Duration of inundation is 1 of the most important factors influencing invertebrate assemblages in temporary aquatic habitats (Sublette and Sublette 1967, Parks 1975, Lake et al. 1989, Jeffries 1994). Schneider and Frost (1996) noted that the relative importances of life-history characteristics and biotic interactions varied with period of inundation. Abiotic factors exerted the greatest control on youngest communities, competition became more important at intermediate stages of development, and the effects of predation were most apparent in older communities. Our 10 study playas remained inundated for <90 d, but most measures of the structural and functional attributes of invertebrate assemblages varied over this period (Tables 2, 3, 4; Figs 2, 3). The reasons for these changes are uncertain, but Lake et al. (1989) proposed 3 phases of community development in temporary ponds

that are consistent with the model of Schneider and Frost (1996). The 1st phase is a rapid increase in species richness as a result of colonization. The 2nd phase is a period of constant species richness but continual turnover of taxa, probably as a result of increasing competition and predation. The final phase is dominated by high levels of predation.

Successional patterns of playa invertebrates were consistent with patterns reported by Lake et al. (1989) and changing controls on community structure proposed by Schneider and Frost (1996) in temporary ponds. Species richness and diversity within playas increased over time, as described by Lake et al. (1989) for the 1st phase of community development. Assemblage composition of playas also changed over time (Fig. 3), without loss of diversity (Fig. 2), as the relative abundances of predators increased (Table 4), consistent with Lake et al.'s (1989) prediction for the 2nd phase of succession. The relative abundance of predators in playas was highest on the last sampling date, as Lake et al. (1989) predicted for the final phase of succession. These data

TABLE 3. Results of repeated measures analysis of variance assessing the effect of sampling period on abundance of each of 14 families of invertebrates from 10 study playas. (Numbers of adults and larvae were combined.)

| Family | $p \leq$ | Mean (± 1 SD) abundance in study playas | | |
|----------------------------|----------|--|-------------------|-------------------|
| | | Sampling period | | |
| | | 1 | 2 | 3 |
| Crustacea | | | | |
| Caenestheriidae | 0.001 | 469.3 \pm 655.8 | 24.1 \pm 31.6 | 25.9 \pm 64.4 |
| Cyprididae | 0.128 | 123.2 \pm 285.1 | 91.7 \pm 122.6 | 13.6 \pm 19.8 |
| Lynceidae | 0.001 | 17.4 \pm 24.8 | 0.1 \pm 0.3 | 0.0 \pm 0.0 |
| Streptocephalidae | 0.001 | 797.7 \pm 1200.8 | 137.4 \pm 289.4 | 18.5 \pm 44.3 |
| Tripsidae | 0.001 | 135.2 \pm 325.1 | 1.4 \pm 4.4 | 0.0 \pm 0.0 |
| Gastropoda | | | | |
| Planorbidae | 0.001 | 75.6 \pm 74.7 | 509.6 \pm 477.5 | 455.9 \pm 411.5 |
| Insecta | | | | |
| Baetidae | 0.009 | 12.8 \pm 18.6 | 171.7 \pm 331.0 | 67.4 \pm 61.6 |
| Chironomidae | 0.002 | 1.6 \pm 1.9 | 19.7 \pm 30.0 | 93.9 \pm 150.9 |
| Coenagrionidae | 0.001 | 2.2 \pm 7.0 | 417.3 \pm 382.1 | 628.9 \pm 528.8 |
| Corixidae | 0.004 | 9.2 \pm 15.8 | 67.1 \pm 102.0 | 179.7 \pm 332.1 |
| Dytiscidae | 0.950 | 24.0 \pm 24.9 | 20.2 \pm 34.1 | 12.3 \pm 15.4 |
| Hydrophilidae ^a | 0.044 | 16.4 \pm 14.0 | 29.5 \pm 22.7 | 52.1 \pm 50.8 |
| Hydrophilidae ^b | 0.001 | 23.0 \pm 25.3 | 96.1 \pm 119.0 | 163.8 \pm 231.3 |
| Notonectidae | 0.001 | 1.9 \pm 3.1 | 103.4 \pm 73.4 | 563.4 \pm 871.1 |

^a Adults only

^b Larvae only

suggest a general pattern of trophic succession beginning with early dominance of rapidly emerging or colonizing taxa (especially crustaceans) that use detritus and dead organic matter. Numbers of herbivores then increased, perhaps as algae and aquatic vegetation increased in abundance and biomass. Densities of predators likely increased because of high densities of prey (i.e., early successional species). In turn, in-

creasing densities of predators could contribute to the decline in earlier successional species (Lake et al. 1989, Schneider and Frost 1996).

Concurrent increases in species richness, diversity, and compositional similarity of invertebrate assemblages over time suggest that chance colonization may be an important factor affecting structure of playa invertebrate assemblages early in succession. The convergence in

TABLE 4. Results of repeated measures analysis of variance assessing the effect of sampling period on % contributions of trophic groups to invertebrate assemblages in 10 study playas.

| Trophic group | $p \leq$ | Mean (± 1 SD) abundance in study playas | | |
|---------------|----------|--|-------------------|-------------------|
| | | Sampling period | | |
| | | 1 | 2 | 3 |
| Unknown | 0.585 | 1.65 \pm 3.22 | 0.93 \pm 1.22 | 0.40 \pm 0.76 |
| Detritivore | 0.036 | 41.66 \pm 25.67 | 45.76 \pm 15.84 | 25.42 \pm 14.51 |
| Filter-feeder | 0.001 | 36.14 \pm 27.28 | 7.82 \pm 13.60 | 0.48 \pm 0.63 |
| Herbivore | 0.030 | 2.30 \pm 4.83 | 2.64 \pm 2.94 | 3.25 \pm 2.42 |
| Omnivore | 0.002 | 3.96 \pm 6.21 | 0.07 \pm 0.21 | 0 |
| Predator | 0.001 | 14.30 \pm 22.05 | 42.31 \pm 12.87 | 69.99 \pm 14.28 |
| Parasite | 0.001 | 0 | 0.47 \pm 0.40 | 0.45 \pm 0.27 |

composition of playa assemblages over time is most readily explained by assuming that the pool of potential colonizers is limited, so that taxonomic structure necessarily becomes more similar as colonization proceeds. This assumption does not exclude the possible importance of biotic interactions in structuring playa assemblages, as suggested by changes in trophic structure, but it does corroborate the proposition of Schneider and Frost (1996) that controls on invertebrate assemblages probably change over time. The trophic and taxonomic characteristics of playa assemblages were not independent because most of the crustaceans were detritivores or filter-feeders, whereas most of the predators were insects. In general, these 2 taxonomic groups differ with respect to key life-history attributes that are related to patterns of abundance (Wiggins et al. 1980). The crustaceans have no active dispersal mechanism and persist as eggs in playa sediments between periods of inundation. They are most abundant shortly after playas fill with water, and forage on available detritus. In contrast, most insects do not persist in dry playa soils, and many species reside in inundated playas only as developing immature stages. Adults fly between playas and other bodies of water, so that colonization is from external sources and apparently takes longer than the hatching of resident crustacean eggs. The successful establishment of some predatory insect populations also may require substantial numbers of prey and, thus, be limited to later stages of succession.

Much of the classical work on processes of community succession has focused on plants (e.g., Connell and Slatyer 1977), although some comparisons to macroinvertebrate assemblages of ephemeral wetlands may be valid. For example, early succession of macroinvertebrates in temporary ponds is dominated by colonization processes in which random events play a larger role in structuring the community than in later phases; interspecific competition becomes more important as succession progresses (Lake et al. 1989, Schneider and Frost 1996). However, ephemeral habitats differ from more permanent ones usually occupied by plants. In this regard, macroinvertebrate assemblages in playas may be comparable to decomposer communities that are based on dead organic matter, with a series of species replacements occurring as the nature of the environment changes (Frankland 1982).

The role of predation in succession varies among communities, but may affect macroinvertebrate assemblages of playas. In addition to the invertebrates, many vertebrate species use these playas, especially amphibians and birds (Bolen et al. 1989, Newman 1989), but their roles in structuring macroinvertebrate assemblages have not been examined.

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APPENDIX 1. Taxa collected from playas, their life-history classification as *residents* (possessing drought-resistant life stages) or *transients* (no drought-resistant life stages), and their trophic designations (Pennak 1989, Thorp and Covich 1991, Merritt and Cummins 1996). Hydrophilids are listed as *predator* and *herbivore*, reflecting the disparate trophic levels of larvae and adults, respectively.

| Phylum | Class | Order | Family | Genus | Species and authority | Life history | | |
|------------|--------------|--------------------------|-----------------------------|---|--|--------------------------------------|------------------------|---------------------|
| Annelida | Oligochaeta | Haplotaxida | Lumbricidae | unknown | unknown | resident, detritivore | | |
| | | | Tubificidae | <i>Limnodrilus</i> | <i>hoffmeisteri</i> Claparède | resident, detritivore | | |
| | | | | <i>Limnodrilus</i> | sp. | resident, detritivore | | |
| | | | | unknown | unknown | resident, detritivore | | |
| Mollusca | Gastropoda | Basommatophora | Glossiphonidae | <i>Helobdella</i> | <i>triserialis</i> (Blanchard) | resident, predator | | |
| | | | Erpobdellidae | <i>Erpobdella</i> | <i>punctata</i> (Leidy) | resident, predator | | |
| | | | Lymnaeidae | <i>Fossaria</i> | <i>cockerelli</i> (<i>bakerilymnaea</i>) Pilsbry and Ferriss | resident, filter-feeder | | |
| | | | Physidae | <i>Physella</i> (<i>Costatella</i>) | <i>bottimeri</i> (Clench) | resident, detritivore | | |
| Arthropoda | Chelicerata | Acari | Planorbidae | <i>Planorbella</i> (<i>Pierosoma</i>) | <i>tenuis</i> (Dunker) | resident, detritivore | | |
| | | | Arrenuridae | <i>Arrenurus</i> | <i>dentipetiolatus</i> Marshall | resident, parasite | | |
| | | | | <i>Arrenurus</i> | n. sp. | resident, parasite | | |
| | | | Eylaidae | <i>Eylais</i> | sp. | transient, parasite | | |
| | | | Hydrachnidae | <i>Hydrachna</i> | sp. | transient, parasite | | |
| | | | Pionidae | <i>Piona</i> | <i>floridana</i> Cook | resident, parasite | | |
| | | | Baetidae | <i>Callibaetis</i> | sp. | transient, detritivore | | |
| | | | Aeshnidae | <i>Anax</i> | <i>junius</i> Drury | transient, predator | | |
| | | | Lestidae | <i>Lestes</i> | <i>disjunctus</i> Selys | transient, predator | | |
| | | | Coenagrionidae | <i>Enallagma</i> | <i>civile</i> (Hagen) | transient, predator | | |
| | Insecta | Ephemeroptera Odonata | Libellulidae | <i>Tramea</i> , <i>Pantala</i> , and <i>Sympetrum</i> ^a | | transient, predator | | |
| | | | Hemiptera | Belostomatidae | <i>Belostoma</i> | <i>flumineum</i> Say | transient, predator | |
| | | | | Corixidae | <i>Corisella</i> | <i>edulis</i> (Champion) | transient, predator | |
| | | | | | <i>Corisella</i> | <i>tarsalis</i> (Fieber) | transient, predator | |
| | | | | | <i>Rhamphocorixa</i> | <i>acuminata</i> (Uhler) | transient, predator | |
| | | | | | <i>Sigara</i> | <i>alternata</i> (Say) | transient, herbivore | |
| | | | | | <i>Trichocorixa</i> | <i>reticulata</i> (Guérin-Méneville) | transient, predator | |
| | | | | | <i>Trichocorixa</i> | <i>verticalis</i> (Fieber) | transient, predator | |
| | | | | | Gerridae | <i>Gerris</i> | <i>marginatus</i> Say | transient, predator |
| | | | | | Mesoveliidae | <i>Mesovelia</i> | <i>mulstanti</i> White | transient, predator |
| | Notonectidae | <i>Buenoa</i> | | <i>margaritacea</i> Torre-Bueno | transient, predator | | | |
| | | <i>Notonecta</i> | <i>undulata</i> Say | transient, predator | | | | |
| | Saldidae | <i>Saldula</i> | <i>pallipes</i> (Fabricius) | transient, predator | | | | |
| | Veliidae | <i>Microvelia</i> | sp. | transient, predator | | | | |

| Phylum | Class | Order | Family | Genus | Species and authority | Life history | |
|--------|-------|-----------------|-----------------|---------------------|--------------------------------------|---|------------------------|
| | | Coleoptera | Halipidae | <i>Halipus</i> | <i>triopsis</i> Say | transient, herbivore | |
| | | | | <i>Halipus</i> | <i>tumidus</i> LeConte | transient, herbivore | |
| | | | Dytiscidae | <i>Brachyvatus</i> | sp. | transient, predator | |
| | | | | <i>Copelatus</i> | sp. | transient, predator | |
| | | | | <i>Cybister</i> | <i>fimbriolatus</i> (Say) | transient, predator | |
| | | | | <i>Eretes</i> | <i>sticticus</i> (Linnaeus) | transient, unknown | |
| | | | | <i>Hygrotus</i> | <i>nubilus</i> (LeConte) | transient, predator | |
| | | | | <i>Laccophilus</i> | <i>fasciatus erminalis</i> Aubé | transient, predator | |
| | | | | <i>Laccophilus</i> | <i>quadrilineatus quadrilineatus</i> | transient, unknown | |
| | | | | | Horn | | |
| | | | | | <i>Neobidessus</i> | sp. | transient, predator |
| | | | | | <i>Thermonectus</i> | <i>nigrofasciatus ornatcollis</i> (Aubé) | transient, predator |
| | | | | | Gyrinidae | <i>Uovarus</i> | <i>lacustris</i> Say |
| | | <i>Dineutus</i> | sp. | | | transient, predator | |
| | | <i>Gyrinus</i> | sp. | | | transient, predator | |
| | | Helophoridae | | <i>Helophorus</i> | <i>linearis</i> LeConte | transient, herbivore | |
| | | Hydrophilidae | | <i>Berosus</i> | <i>exiguus</i> (Say) | transient, pred./herb. | |
| | | | | <i>Berosus</i> | <i>infuscatus</i> LeConte | transient, pred./herb. | |
| | | | | <i>Berosus</i> | <i>miles</i> LeConte | transient, pred./herb. | |
| | | | | <i>Berosus</i> | <i>styliferus</i> Horn | transient, pred./herb. | |
| | | | | <i>Enochrus</i> | <i>hamiltoni</i> (Horn) | transient, pred./herb. | |
| | | | | <i>Hydrophilus</i> | <i>triangularis</i> Say | transient, pred./herb. | |
| | | | | <i>Paracymus</i> | <i>confusus</i> Wooldridge | transient, pred./herb. | |
| | | | | <i>Tropisternus</i> | <i>lateralis</i> (Fabricius) | transient, pred./herb. | |
| | | | Curculionidae | | <i>Bagous</i> | sp. | transient, herbivore |
| | | | | | <i>Lissorhoptrus</i> | <i>simplex</i> (Say) | transient, herbivore |
| | | | | <i>Listronotus</i> | <i>grypidioides</i> (Dietz) | transient, herbivore | |
| | | | | <i>Listronotus</i> | <i>filiformis</i> (LeConte) | transient, herbivore | |
| | | | | <i>Listronotus</i> | <i>scapularis</i> (Casey) | transient, herbivore | |
| | | Diptera | Ceratopogonidae | <i>Notiodes</i> | <i>aeratus</i> (LeConte) | transient, herbivore | |
| | | | | | <i>Forcipomyia</i> | sp. 1 Coquillett | transient, detritivore |
| | | | | | | sp. 2 | transient, detritivore |
| | | | | | | sp. 3 | transient, detritivore |
| | | | | | | sp. 4 | transient, detritivore |

APPENDIX 1. Continued.

| Phylum | Class | Order | Family | Genus | Species and authority | Life history |
|--------------|-----------|-------|-------------------|--|------------------------------------|--------------------------|
| | | | Chironomidae | <i>Ablabesmyia</i> | sp. | transient, predator |
| | | | | <i>Apedilum</i> | sp. | transient, unknown |
| | | | | <i>Chironomus</i> | sp. 1 | resident, detritivore |
| | | | | <i>Chironomus</i> | sp. 2 | resident, detritivore |
| | | | | <i>Clinotanypus</i> | sp. | resident, predator |
| | | | | <i>Cricotopus</i> | sp. | resident, unknown |
| | | | | <i>Cryptochironomus</i> | sp. | transient, predator |
| | | | | <i>Dicrotendipes</i> | sp. | resident, detritivore |
| | | | | <i>Endochironomus</i> | <i>nigricans</i> (Johannsen) | resident, herbivore |
| | | | | <i>Labrundinia</i> | sp. | transient, predator |
| | | | | <i>Parachironomus</i> | sp. | resident, predator |
| | | | | <i>Polypedilum</i> | sp. | resident, herbivore |
| | | | | <i>Procladius</i> | <i>bellus</i> (Loew) | transient, predator |
| | | | | <i>Procladius</i> (<i>Holotanypus</i>) | sp. | transient, predator |
| | | | | <i>Tanypus</i> | sp. | resident, predator |
| | | | | <i>Tanytarsus</i> | sp. | resident, filter-feeder |
| | | | Culicidae | <i>Culex</i> | <i>tarsalis</i> Coquillet | transient, detritivore |
| | | | Dolichopodidae | | sp. 1 | transient, predator |
| | | | Ephydriidae | <i>Notophila</i> | sp. 1 | transient, detritivore |
| | | | | | sp. 2 | transient, detritivore |
| | | | | | sp. 3 | transient, detritivore |
| | | | | | sp. 4 | transient, detritivore |
| | | | | | sp. 5 | transient, detritivore |
| | | | Psychodidae | | sp. 1 | transient, filter-feeder |
| | | | | | sp. 2 | transient, filter-feeder |
| | | | Stratiomyidae | <i>Odontomyia</i> | sp. | transient, herbivore |
| | | | Syrphidae | <i>Eristalis</i> | sp. | transient, filter-feeder |
| | | | Tabanidae | <i>Tabanus</i> | prob. <i>subs similis</i> Bellardi | transient, predator |
| Branchiopoda | Anostraca | | Branchinectidae | <i>Branchinecta</i> | <i>lindahli</i> Packard | resident, detritivore |
| | | | | <i>Branchinecta</i> | <i>packardi</i> Pearse | resident, detritivore |
| | | | Streptocephalidae | <i>Streptocephalus</i> | <i>dorotheae</i> Mackin | resident, filter-feeder |
| | | | | <i>Streptocephalus</i> | <i>texanus</i> Packard | resident, filter-feeder |
| | | | Thamnocephalidae | <i>Thamnocephalus</i> | <i>platyurus</i> Packard | resident, filter-feeder |

APPENDIX 1. Continued.

| Phylum | Class | Order | Family | Genus | Species and authority | Life history |
|--------|-----------|--------------|-----------------|------------------------|----------------------------------|-----------------------|
| | | Conchostraca | Caenestheriidae | <i>Caenestheriella</i> | <i>setosa</i> (Pearse) | resident, detritivore |
| | | | Leptestheriidae | <i>Leptestheria</i> | <i>compleximanus</i> (Packard) | resident, detritivore |
| | | | Lynceidae | <i>Lynceus</i> | <i>brevifrons</i> (Packard) | resident, detritivore |
| | | Notostraca | Triopsidae | <i>Triops</i> | <i>longicaudatus</i> (LeConte) | resident, omnivore |
| | | Podocopida | Cyprididae | <i>Megalocypris</i> | <i>gnathostomata</i> (Ferguson) | resident, detritivore |
| | Ostracoda | | | <i>Cyprinotus</i> | <i>antillensis</i> (Broodbakker) | resident, detritivore |
| | | | Ilyocyprididae | <i>Pelocypris</i> | <i>tuberculatum</i> (Ferguson) | resident, detritivore |

^a Diagnostic characteristics have not been determined for immatures of these genera