

26 Playas of the Southern High Plains

The Macroinvertebrate Fauna

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Playa lakes of the semiarid southern Great Plains are shallow, ephemeral wetlands that usually contain water from late spring to fall. They provide critical wildlife habitat in an area with a paucity of permanent water and are important foci for recharge to the Ogallala Aquifer. These lakes support a diversity of macroinvertebrates, including more than 124 taxa. Resident taxa (those with drought-resistant life stages) are dominated by phyllopod and ostracod crustaceans, as well as snails, whereas insects are the major constituents of the transient taxa (those that must immigrate after inundation). Residents are most abundant during early stages of playa succession, and consist mainly of detritivores and predators. Transients dominate later successional stages and are mostly herbivores and predators. To date, most conservation studies of playa lakes have focused on management strategies that increase habitat quality for migrating and breeding waterfowl. Much of the research has focused on moist-soil management of vegetation as food resources for waterfowl. Little has been done to explore the impact of these conservation measures on the aquatic macroinvertebrate fauna. Similarly, little research has focused on the effects of surrounding land use practices on the fauna of playa lakes. Macroinvertebrates occupy many of the intermediate trophic levels in foodwebs of playas, and consequently may directly or indirectly affect taxa at higher and lower trophic levels. Future research should focus on the effects of landscape characteristics on aquatic macroinvertebrates from the joint perspectives of conservation biology and agroecology.

SOUTHERN HIGH PLAINS

The Southern High Plains, or Llano Estacado, is an extensive, semiarid tableland (82,000 km²) lying south of the Canadian River in Texas and New Mexico (Fig. 26.1). It is devoid of permanently flowing surface water, but contains numerous ephemeral lakes or playas (Reddell 1965, Wood and Osterkamp 1984). These playas are the most important elements of surface hydrology and ecological diversity in a landscape that otherwise is dominated by agricultural activities.

The Texas High Plains is a large component of the Southern High Plains, extending from the northern Panhandle to the Trans-Pecos and Edwards Plateau. Like the rest of the Llano Estacado, it was dominated by shortgrass prairies (Stoddart and Smith 1955) until agricultural development began in the early 1900s. Irrigation from groundwater began in the area following World War II, and by 1977 more than 70,000 wells had tapped the Ogallala Aquifer in Texas (New 1979).

Agricultural development is pervasive on the Southern High Plains, producing one third of the nation's cotton. Irrigated crops are grown on about

20,000 km² (Palacios 1981), and the bulk of remaining land is used primarily for nonirrigated crop production (dry-land farming) or rangeland for grazing. Playas often are integrated into irrigation programs (e.g., pits are excavated to collect tailwater for reuse) and 65–70 percent of playas larger than 4 ha are used for grazing. The number of playas on the Southern High Plains that have been modified for agricultural use increased from 150 to 10,800 between 1965 and 1980 (Guthery et al. 1981). These practices directly alter standing biomass and species composition of floral and faunal communities, increase runoff and soil erosion, and provide fertilizer, pesticide, and nutrient inputs (Bolen et al. 1989b). Because playas are material sinks in these landscapes, accumulating both water and materials carried by water, they are affected greatly by surrounding land use practices.

The term *playa* has been used throughout the world, and even in this region, to refer to many different types of waterbodies. The playa lakes considered in this chapter conform to the description of freshwater, Type 2 playas of Reeves (1990), which are the most common lakes on the Southern High Plains. This chapter does not include those Type 2 playas that have been modified within urban stormwater management plans (see Wolf et al., this volume), municipal waste treatment facilities, or cattle feedlot operations.

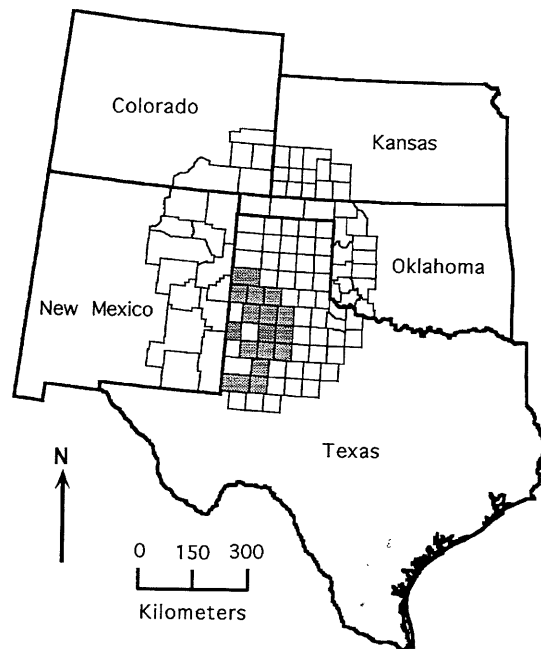


Fig. 26.1. Map of the 111 counties on the southern Great Plains that comprise the Playa Lakes Region (Playa Lake Joint Venture 1993). Playas considered in this chapter occur in the 16 shaded counties on the Southern High Plains of Texas.

PLAYA GEOMORPHOLOGY AND HYDROLOGY

Playa lakes are ephemeral wetlands (Cowardin et al. 1979) that provide critical wildlife habitat throughout the Southern Great Plains of Colorado, Kansas, Oklahoma, New Mexico, and Texas (Bolen et al. 1989b). Mechanisms for the origin of playas have been studied and debated for several decades. Reeves (1990) concludes that most playas probably formed through a combination of eolian activity at the surface and dissolution and subsidence of underlying strata. In addition, Osterkamp and Wood (1987) present evidence that playas can originate wherever water collects in a surficial depression (see also Wood and Osterkamp 1987). Moreover, Finley and Gustavson (1981) note lineament orientation of playas and attribute lake location to control exerted by underlying geologic structures. In a recent, comprehensive review, playa formation was attributed to integration of complex geomorphic, pedogenic, hydrochemical, and biological processes (Gustavson et al. 1995).

Playas have flat bottoms, resulting in a relatively uniform water depth throughout most of the basin. Generally they are less than 1 m in depth, and over 80 percent are smaller than 12 ha in surface area (Haukos and Smith 1992). The lakes occur on montmorillonitic clay lenses, which expand and seal the wetland when inundated. Typical of these soils is Randall clay, a fine, smectitic, thermic Udic Pellustert occupying the lowest elevational position in the internally drained watersheds of the Texas and New Mexico portion of the Southern High Plains (in the thermic temperature zone; Zartman and Fish 1992). The drainage basin for individual lakes ranges from less than

1 ha to more than 300 ha (Osterkamp and Wood 1987). Basin size is a primary determinant of water volume because groundwater throughout the Southern High Plains is generally quite deep and normally does not affect water levels in playa lakes. Rare exceptions may occur in urban areas and other locations where excessive recharge has created artificially elevated groundwater surfaces.

Estimates of the number of playa lakes throughout the Southern Great Plains range from 30,000 (Wood and Osterkamp 1984) to 37,000 (Reddell 1965). Recently, the Playa Lakes Joint Venture (1993), under the North American Waterfowl Management Plan, identified slightly more than 25,500 lakes in five states (Texas, 19,340; Kansas, 2,800; New Mexico, 2,640; Oklahoma, 580; Colorado, 200; see also Guthery and Bryant 1982). One hundred and eleven counties in the five-state area contain playas (Fig. 26.1), with 11,234 playas occurring in the 16 counties of Texas considered in this chapter.

In addition to their importance as wetlands, playas are primary recharge areas for the Ogallala Aquifer (Wood and Osterkamp 1984, Zartman 1987). Traditionally, most water in playas was assumed to evaporate because of low infiltration rates through the clay floor of the basin. More recent research has shown that extensive recharge occurs on the margins of clay lenses when water levels are at their highest, after storms (Zartman 1987, Zartman et al. 1994).

Playas usually contain water from late spring through fall, depending on the pattern and amount of rainfall, evaporation rates, and the extent to which the clay lining retards water loss. In Lubbock County, Texas, peak water volume usually occurs in June and playas typically are dry from December through March (Ward and Huddleston 1972). However, Curtis and Beierman (1980) found that only 33 percent of the playas in this area retained water during spring, summer, and fall, and most of these were modified for irrigation.

Several studies have examined playa water quality on the Southern High Plains (Lotspeich et al. 1969, Reeves 1970, Wells et al. 1970, U.S. Department of the Interior 1982, Wood and Osterkamp 1984). In this study we concentrate on those in which water quality was examined in conjunction with determinations of macroinvertebrate species composition (Sublette and Sublette 1967, Parks 1975, Hall 1997).

Chemical and Physical Properties of Water in Playa Lakes

Water quality differs greatly among playas. It varies temporally within playas as infiltration and evaporation occur (Table 26.1; Hall et al. 1995, Willig et al. 1995). Water quality also varies between years within the same playa, depending on the frequency and intensity of rainfall within each year (Ward 1964). Such temporal variation may compromise our ability to understand the effect of land use on spatial variability of water quality in playas.

Although extremely variable, playa water is quite turbid as estimated by either secchi depth or turbidity (Table 26.1). The organic and inorganic matter,

TABLE 26.1. Water Quality Parameters of Freshwater Playas that were Sampled for Invertebrates on the Southern High Plains of Texas

| Parameter | Number of Samples | | Maximum |
|---|-------------------|---------|---------|
| | Minimum | Maximum | |
| Physical properties | | | |
| Turbidity (NTU) | 20 | 41 | 2860 |
| Turbidity (ppm SiO ₂) | 45.0 | 17 | 1300.0 |
| Secchi depth (cm) | 2.0 | 76 | 70.0 |
| Temperature (°C) | 10.5 | 161 | 35.1 |
| Total solids (mg/L) | 195 | 41 | 2340 |
| Total suspended solids (mg/L) | 10 | 41 | 1130 |
| Total dissolved solids (mg/L) | 120 | 41 | 1570 |
| Total volatile suspended solids (mg/L) | <1 | 41 | 185 |
| Specific conductance (µmhos) | 60.7 | 80 | 1176.7 |
| Hardness (mg/L) | 6.2 | 41 | 81.5 |
| Hardness, total (mg/L CaCO ₃) | 40 | 77 | 218 |
| Hardness, calcium (mg/L CaCO ₃) | 20 | 17 | 182 |
| Alkalinity, methyl-orange (mg/L CaCO ₃) | 20 | 97 | 228 |
| Total organic carbon (mg/L) | 6.5 | 41 | 66.8 |
| Total inorganic carbon (mg/L) | <1.0 | 41 | 53.2 |
| Total carbon (mg/L) | 12.3 | 41 | 77.5 |
| Total Kjeldahl nitrogen (mg/L) | 0.36 | 41 | 3.36 |
| Ammonia-nitrogen (mg/L) | ND ^a | 132 | 4.85 |
| NO ₂ /NO ₃ -nitrogen (mg/L) | <0.02 | 41 | 1.11 |
| Nitrate nitrogen (mg/L) | ND | 91 | 0.21 |
| Total phosphorus (mg/L) | 0.13 | 41 | 2.49 |
| ortho-phosphate phosphorus (mg/L) | ND | 115 | 1.67 |
| Silica (mg/L) | 6.8 | 41 | 28.2 |
| pH | 5.0 | 111 | 9.2 |
| Calcium (mg/L) | 1.8 | 41 | 41.5 |
| Magnesium (mg/L) | 1.5 | 41 | 25.4 |
| Sodium (mg/L) | 0.8 | 41 | 22.5 |
| Nutrients | | | |
| Cations, anions and metals | | | |

| Parameter | Number of Samples | Minimum | Maximum |
|--|-------------------|---------|---------|
| Potassium (mg/L) | 41 | 0.1 | 76.8 |
| Chloride (mg/L) | 58 | 1.25 | 162.00 |
| Sulfate (mg/L) | 58 | 0.3 | 140.0 |
| Arsenic ($\mu\text{g/L}$) | 41 | <5 | 118 |
| Copper ($\mu\text{g/L}$) | 41 | 9 | 123 |
| Dissolved oxygen, surface (% Sat.) | 76 | 2.3 | 186.6 |
| Dissolved oxygen, surface (mg/L) | 137 | 0.20 | 15.34 |
| Dissolved oxygen, bottom (% Sat.) | 76 | ND | 186.6 |
| Dissolved oxygen, bottom (mg/L) | 136 | 0.02 | 15.34 |
| Biochemical oxygen demand (mg/L) | 41 | <3 | 84 |
| Chemical oxygen demand (mg/L) | 41 | 5 | 130 |
| Chlorophyll-a ($\mu\text{g/L}$) | 41 | 2 | 104 |
| Aldicarb, total ($\mu\text{g/L}$) | 41 | <1.00 | 1.68 |
| Carbofuran, total ($\mu\text{g/L}$) | 41 | <0.06 | 0.12 |
| Cyanazine, total ($\mu\text{g/L}$) | 41 | <0.04 | 5.20 |
| Triazines, total ($\mu\text{g/L}$) | 41 | <0.1 | 15.9 |
| Alachlor, total ($\mu\text{g/L}$) | 41 | <0.10 | 0.35 |
| 2,4-D, total ($\mu\text{g/L}$) | 41 | <0.7 | 15.1 |
| Captan, total ($\mu\text{g/L}$) | 41 | <0.005 | 0.100 |
| Carbaryl, total ($\mu\text{g/L}$) | 41 | <0.25 | 0.62 |
| Metolachlor, total ($\mu\text{g/L}$) | 41 | <0.1 | 16.6 |
| Chlorpyrifos, total ($\mu\text{g/L}$) | 41 | <0.10 | 0.31 |
| Pentachlorophenol, total ($\mu\text{g/L}$) | 41 | <0.05 | 0.20 |
| Benomyl/Carbendazim, total ($\mu\text{g/L}$) | 41 | <0.10 | <0.10 |

Source: Sublette and Sublette 1967, Parks 1975, Hall et al. 1995, Willig et al. 1995, Hall 1997. Pesticide levels were assessed via Ohmicron immunoassays (Hall et al. 1995, Willig et al. 1995, Hall 1997).

^aND = none detected

which contribute to turbidity, are maintained in suspension because of basin shape (i.e., shallow with a smooth, flat bottom) and high regional winds.

Because water volume is low relative to playa surface area, water temperatures reflect daily and seasonal changes in air temperature. In addition, because of high water circulation in these shallow basins, many playas are isothermal, with mean temperature differences of less than 1°C from basin sediment to water surface (Hall et al. 1995, Willig et al. 1995). Although standing vegetation within playas coupled with high turbidity can confine the effects of solar heating to the top few centimeters of water, vertical temperature differences commonly do not exceed 5°C (Hall et al. 1995, Willig et al. 1995).

Measurements of hardness and solids (total, suspended, dissolved, and volatile) yield information on erosional processes, as well as autochthonous and allochthonous inputs. The high levels of solids found in playas are to be expected, given the extensive agricultural use of playa watersheds and their attendant clay basins (Table 26.1). However, the maximum concentrations of total and suspended solids in playas are greater than those normally found in untreated sewage (Thompson 1974), although the constituents of playa and sewage solids differ.

Most playas are nutrient-rich and fulfill criteria for eutrophic status (Table 26.1, Zafar 1959, Uttormark and Wall 1975). This reflects the high concentration of nutrients available for macroinvertebrates immediately after flooding. Inorganic and organic nutrient fractions probably arise from autochthonous and allochthonous sources. Inorganic enrichment (e.g., $\text{NO}_2/\text{NO}_3\text{-N}$, orthophosphate P) probably originates from allochthonous sources (e.g., agricultural runoff). However, organic enrichment (total organic C, total Kjeldahl N, ammonia-N) chiefly may be autochthonous, given that most playa basins support rich floral communities when dry.

The profile of dissolved oxygen (DO) is probably the most important expression of the trophic state of a waterbody. In natural waterbodies DO is determined by competition between agents supplying DO (diffusion and photosynthesis) and agents requiring DO (simple chemical oxidation and biological consumption). As is true for temperature, the shallow depth of playas and near-continuous wind probably account for the similarity between DO at the water surface and bottom for both minimum and maximum values (Table 26.1).

Most playas (Hall et al. 1995, Willig et al. 1995) maintained oxygen deficits. Twenty-seven playas (66 percent) had biochemical oxygen demand (BOD) values >8.0 mg/L DO, the saturation level at this elevation. Similarly, 36 playas (78 percent) had chemical oxygen demand (COD) values >8.0 mg/L DO. This deficit suggests that anaerobic conditions may occur. However, because of the high regional winds and presence of aquatic vegetation, DO levels, at least at the surface, have never been measured at <0.20 mg/L (Table 26.1). Concomitantly, vertical mixing of the water column precludes long periods of anaerobic conditions at the playa bottom.

Variation among playas in ratios of BOD to COD ranged from 13.5 to 100 percent, but most were <50 percent. High ratios suggest the presence of highly labile resources (e.g., fertilizer) rather than more recalcitrant compounds (e.g., cellulose). Indeed, playas surrounded by agriculture have higher ratios of BOD to COD, on average, than do playas surrounded by rangeland or Conservation Reserve Program grasslands (Hall et al. 1995, Willig et al. 1995).

Although pH ranges from 5.0 to 9.2, playa water is slightly alkaline on average (Table 26.1). The dominant cations typically are calcium and potassium, followed by magnesium and sodium. These four elements usually account for 95 percent of the cations of regional playa waters. Chlorides, sulfates, bicarbonate, and carbonate account for more than 95 percent of the anions. Only chloride and sulfate concentrations are reported herein (Table 26.1). Given the above-neutral pH of most playa water, most of the inorganic carbon is in the form of bicarbonate.

Some metals commonly are found in playa lakes. Arsenic and copper occur in herbicides, defoliants, and insecticides that have been used in this region. Arsenic was recovered from more than half of 41 basins, whereas measurable copper was found in all of them (Hall et al. 1995, Willig et al. 1995). However, it is unclear if these metals naturally occur at such concentrations in this region (Irwin and Dodson 1991); their levels are probably at least partially attributable to anthropogenic sources.

In the highly agrarian environment of the Southern High Plains, pesticide use is extremely common. The pesticides most commonly found in playas were cyanazine, other triazines, alachlor, and metolachlor (Table 26.1; Hall et al. 1995, Willig et al. 1995). This is to be expected given the high regional use of products bearing these active ingredients, the results of previous water tests (Mollhagen et al. 1993), and the cross-reactivity of chemicals in these particular assays. Cross-reactivity can occur, especially for triazine and acetanilide herbicides (e.g., cyanazine, alachlor, metolachlor), resulting in uncertainty in the specific identity of the parent compounds. Because of cross-reactivity, a result above the detection limit should be interpreted to mean that one or more similar compounds (including the nominate compound, congeners, or their metabolites) were encountered.

VEGETATION

Playa lakes are dominated by annual plants with life cycles that reflect the unpredictable moisture regime during the growing season. Guthery et al. (1982) identified 14 physiognomic types of playa vegetation, based on consideration of moisture regime and physical disturbance (grazing, cultivation, and irrigation). Because quality of wintering habitat is so critical for populations of waterfowl, recent research has focused on moist-soil management of playa lakes (Haukos and Smith 1993a). Managed lakes with water supple-

mentation had higher seed biomass and greater numbers of ducks than did unmanaged lakes.

Occurrence and dominance of plant species within a particular playa is a function of moisture regimes in prior years, which developed particular seed banks, and the moisture pattern of the current year, which controls germination and subsequent growth (Haukos and Smith 1993b). In biomass studies on four playa lakes, Comer (1994) encountered two monotypic communities, one composed entirely of curly dock (*Rumex crispus*) and the other of pink smartweed (*Persicaria pensylvanica*). Mixed communities are more common (Haukos and Smith 1993b) and characterized the other two playas, one dominated by pink smartweed, barnyard grass (*Echinochloa crusgalli*), and ragweed (*Ambrosia grayi*) and the other by pink smartweed and ragweed. Other frequently occurring species (Haukos and Smith 1997) include spike rush (*Eleocharis macrostachya*), cheeseweed (*Malvella leprosa*), blue sunflower (*Helianthus ciliaris*), and evening primrose (*Oenothera canescens*).

MACROINVERTEBRATES

Playa wetlands provide essential habitat for more than 124 taxa of macroinvertebrates (Table 26.2) that spend all or part of their life cycles in water. Although intimately and inextricably associated with the aquatic system, little information is available concerning the macroinvertebrate fauna of the playas. In addition to their inherent importance as components of biodiversity in aquatic ecosystems (Pennak 1989, Merritt and Cummins 1996), macroinvertebrates represent critical links in foodwebs (Fig. 26.2) supporting many vertebrate populations (Merickel and Wangberg 1981). Macroinvertebrates are particularly crucial food sources for breeding ducks and their broods (Krapu and Swanson 1977, Bolen et al. 1989a), as well as for migrating shorebirds (Baldassarre and Fischer 1984, Davis 1996).

Diversity

Playa lakes contain a diverse macroinvertebrate fauna that can be divided into two groups, based on life history strategies for living in an ephemeral environment. Resident species have drought-resistant life stages and usually no autonomous means of movement among playas. Transient species do not have drought-resistant life stages and are capable of movement among playas some time during their life cycles, usually as adults. The transient species are mostly insects, whereas the resident fauna is composed mostly of noninsect species.

The insect community of playa lakes is actually quite rich. Of the approximately 124 taxa of macroinvertebrates in playa lakes, 84 are insects (Table 26.2). In total, 6 orders and 31 families of insects have been recorded. Families contributing the greatest number of species to the fauna are Libellulidae (ca 5 species), Corixidae (6 species), Dytiscidae (ca 12 species), Hydrophil-

TABLE 26.2. Invertebrate Taxa Collected from Freshwater Playas on the Southern High Plains of Texas^a

| Taxa | Sublette and Sublette (1967) | Parks (1975) | Merickel and Wangberg (1981) | Neck and Schramm (1992) | Horne (1996) | Hall (1997) |
|--|---------------------------------------|-----------------|---------------------------------------|----------------------------------|-----------------|----------------|
| Ectoprocta (bryozoans) | | | | | | x |
| Oligochaeta | | | | | | |
| Naididae | x | | | | | x |
| Lumbricidae | | | | | | |
| Tubificidae | | | | | | x |
| <i>Limnodrilus hoffmeisteri</i> (Claparède) | | | | | | x |
| <i>Limnodrilus</i> sp. | x | x | | | | |
| Hirudinea | | | | | | |
| Erpobdellidae | | | | | | |
| <i>Erpobdella punctata</i> (Leidy) | | | | | | x |
| Glossiphoniidae | | | | | | |
| <i>Helobdella triseriatis</i> (Blanchard) | | | | | | x |
| Gastropoda | | | | | | |
| Lymnaeidae | | | | | | |
| <i>Fossaria cockerelli</i> | | | | x | | x |
| Pilsbry & Ferriss | | | | | | |
| <i>Fossaria bulimoides</i> (Lea) | x | x | | | | |
| Physidae | | | | | | |
| <i>Physella bottimeri</i> (Clench) | | | | | | x |
| <i>Physella virgata</i> Lea | | | | x | | |
| Planorbidae | | | | | | |
| <i>Gyraulus parvus</i> Say | | | | | | |
| <i>Planorbella tenuis</i> (Dunker) | | | | | | x |
| <i>Planorbella trivolvis</i> (Say) | x | x | x | x | | |
| Pelecypoda | | | | | | |
| Sphaeriidae | | | | | | |
| <i>Sphaerium striatimum</i> (Lamarck) | | | | x | | |
| Anostraca | | | x | | | |
| Branchinectidae | | | | | | |
| <i>Branchinecta lindahli</i> Packard | | | | | | x |
| <i>Branchinecta packardii</i> Pearse | x | | | | | x |
| Streptocephalidae | | | | | | |
| <i>Streptocephalus dorothae</i> Mackin | x | x | | | | x |
| <i>Streptocephalus texanus</i> Packard | x | x | | | | x |
| Thamnocephalidae | | | | | | |
| <i>Thamnocephalus platyurus</i> Packard | x | x | | | | x |
| Notostraca | | | | | | |
| Triopsidae | | | | | | |
| <i>Triops longicaudatus</i> (LeConte) | x | x | | | | x |
| Conchostraca | | | x | | | |
| Caenestheriidae | | | | | | |
| <i>Caenestheriella setosa</i> (Pearse) | x | | | | | x |
| <i>Eocyclus concavus</i> (Mackin) | x | | | | | |
| Leptestheriidae | | | | | | |
| <i>Leptestheria compleximanus</i> (Packard) | x | x | | | | x |
| Lynceidae | | | | | | |
| <i>Lynceus brevifrons</i> (Packard) | x | x | | | | x |
| Ostracoda | | | | | | |
| | | | x | | | |

TABLE 26.2. (Continued)

| Taxa | Sublette and Sublette (1967) | Parks (1975) | Merickel and Wangberg (1981) | Neck and Schramm (1992) | Horne (1996) | Hall (1997) |
|---|---------------------------------------|-----------------|---------------------------------------|----------------------------------|-----------------|----------------|
| Candoniidae | | | | | | |
| <i>Candona patzucaro</i> Tressler | | | | | x | |
| Cyprididae | | | | | | |
| <i>Cyprinotus antillensis</i> (Broodbakker) | | | | | x | x |
| <i>Megalocypris gnathostomata</i> (Ferguson) | x | x | | | x | x |
| <i>Megalocypris pseudoingens</i> Delorme | | | | | x | |
| <i>Physocypria globula</i> (Furtos) | | | | | x | |
| Cypridopsidae | | | | | | |
| <i>Cypridopsis vidua</i> (Müller) | | | | | x | |
| <i>Potamocypris unicaudata</i> Schaefer | | | | | x | |
| Ilyocyprididae | | | | | | |
| <i>Pelocypris tuberculatum</i> (Ferguson) | | | | | | x |
| Limnocytheridae | | | | | | |
| <i>Limnocythere sanctipatricii</i> (Brady and Robertson) | | | | | x | |
| Copepoda | | | | | | |
| Cladocera | | | x | | | |
| Odonata | | | x | | | |
| Anisoptera | x | x | | | | |
| Gomphidae | | | x | | | |
| Aeshmidae | | | | | | |
| <i>Anax junius</i> (Drury) | | | x | | | x |
| Libellulidae | | | | | | |
| <i>Orthemis ferruginea</i> (Fabricius) | | | x | | | x |
| <i>Pantala flavescens</i> (Fabricius) | | | x | | | x |
| <i>Pantala</i> sp. | | | | | | |
| <i>Plathemis lydia</i> Drury | | | x | | | |
| <i>Sympetrum corruptum</i> (Hagen) | | x | x | | | x |
| <i>Sympetrum</i> sp. | | | | | | x |
| <i>Tramea</i> sp. | | | | | | x |
| Zygoptera | | | | | | |
| Coenagrionidae | | | | | | |
| <i>Enallagma civile</i> (Hagen) | | | x | | | x |
| Lestidae | | | | | | |
| <i>Lestes alcer</i> Hagen | | | | | | |
| <i>Lestes disjunctus</i> Selys | | x | | | | x |
| Ephemeroptera | | | | | | |
| Baetidae | | | | | | |
| <i>Callibaetis</i> sp. | | | x | | | x |
| <i>Cloeon</i> sp. | x | | | | | |
| Caenidae | | | x | | | |
| Heteroptera | | | | | | |
| Belostomatidae | | | | | | |
| <i>Belostoma flumineum</i> Say | x | x | x | | | x |
| Corixidae | | | | | | |
| <i>Corisella edulis</i> (Champion) | x | | x ^b | | | x |
| <i>Corisella tarsalis</i> (Fieber) | x | x | x | | | x |

TABLE 26.2. (Continued)

| Taxa | Sublette and Sublette (1967) | Parks (1975) | Merrickel and Wangberg (1981) | Neck and Schramm (1992) | Horne (1996) | Hall (1997) |
|---|------------------------------|--------------|-------------------------------|-------------------------|--------------|-------------|
| <i>Rhamphocorixa acuminata</i> (Uhler) | x | | x | | | x |
| <i>Sigara alternata</i> (Say) | x | | | | | x |
| <i>Sigara</i> sp. | x | x | | | | |
| <i>Trichocorixa reticulata</i> (Guérin-Méneville) | | | x | | | x |
| <i>Trichocorixa verticalis</i> (Fieber) | | | | | | x |
| Gerridae | | | | | | |
| <i>Gerris marginatus</i> Say | | | | | | x |
| <i>Gerris</i> sp. | | | x | | | |
| Mesoveliidae | | | | | | |
| <i>Mesoveliâ mulsanti</i> White | | | | | | x |
| Notonectidae | | | | | | |
| <i>Buena margaritacea</i> Torre-Bueno | | | x ^c | | | x |
| <i>Notonecta undulata</i> Say | | x | x | | | x |
| <i>Notonecta unifasciata</i> Guérin-Méneville | | | x | | | |
| <i>Notonecta</i> sp. | x | x | | | | |
| Saldidae | | | | | | |
| <i>Saldula interstitialis</i> (Say) | | | x | | | x |
| <i>Saldula pallipes</i> (Fabricius) | | | | | | |
| Veliidae | | | | | | |
| <i>Microvelia beameri</i> McKinstry | | | | | | |
| <i>Microvelia</i> sp. | | | x | | | x |

Coleoptera

Curculionidae

- Bagous* sp.
Lissorhoptrus simplex (Say)
Listronotus fliformis (LeConte)
Listronotus grypidoides (Dietz)
Listronotus scapularis (Casey)
Notiodes aeratus (LeConte)

Dytiscidae

- Brachyvatus* sp.
Copelatus chevrolati Aubé
Copelatus sp.
Cybister fimbriolatus (Say)
Eretes sticticus (Linnaeus)
Hygrotus nubilus (LeConte)
Laccophilus fasciatus terminalis Aubé

- Laccophilus* q. *quadrilineatis* Horn
Laccophilus sp.
Liodesus affinis (Say)
Neobidessus sp.
Thermonectus nigrofasciatus Aubé
Thermonectus nigrofasciatus ornaticollis (Aubé)
Uvarus texanus (Sharp)
Uvarus lacustris Say
Gyrinidae
Dineutus assimilis (Kirby)
Dineutus sp.

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x
x

TABLE 26.2. (Continued)

| Taxa | Sublette and Sublette (1967) | Parks (1975) | Merickel and Wangberg (1981) | Neck and Schramm (1992) | Horne (1996) | Hall (1997) |
|--|---------------------------------------|-----------------|---------------------------------------|----------------------------------|-----------------|----------------|
| <i>Gyrinus parvus</i> Say | | | x | | | |
| <i>Gyrinus</i> sp. | | | | | | x |
| Halipilidae | | | | | | |
| <i>Halipilus triopsis</i> Say | | | x | | | x |
| <i>Halipilus tumidus</i> LeConte | | | | | | x |
| Helophoridae | | | | | | |
| <i>Helophorus linearis</i> LeConte | | | x | | | x |
| <i>Helophorus</i> sp. | x | | | | | |
| Hydrophilidae | | | | | | |
| <i>Berosus exiguus</i> (Say) | | | x | | | x |
| <i>Berosus infuscatus</i> LeConte | | | | | | x |
| <i>Berosus miles</i> LeConte | x | | x | | | x |
| <i>Berosus rugulosus</i> Horn | x | | | | | |
| <i>Berosus stramineus</i> Knisch | x | | | | | |
| <i>Berosus styliferus</i> Horn | x | x | x | | | x |
| <i>Enochrus hamiltoni</i> (Horn) | | | | | | x |
| <i>Enochrus</i> sp. | | | x | | | |
| <i>Hydrophilus triangularis</i> Say | | x | x | | | x |
| <i>Othebius</i> sp. | | | | | | |
| <i>Paracymus confusus</i> Wooldridge | x | | | | | |
| <i>Tropisternus lateralis</i> (Fabricius) | x | | x | | | x |
| Trichoptera | | | | | | |
| Leptoceridae | | | | | | |
| <i>Oecetis</i> sp. | x | | | | | |
| Diptera | | | | | | |
| Ceratopogonidae | | | | | | |
| <i>Culicoides variipennis</i> (Coquillett) | x | | | | | x |
| <i>Foreipomyia</i> sp. | | | x | | | x |
| Chironomidae | | | | | | |
| <i>Ablabesmyia</i> sp. | x | | | | | x |
| <i>Apedilum</i> sp. | | | | | | x |
| <i>Chironomus stigmaterus</i> Say | | x | | | | x |
| <i>Chironomus</i> sp. | | x | x | | | x |
| <i>Clinotanypus</i> sp. | | | | | | x |
| <i>Cricotopus</i> sp. | | | | | | x |
| <i>Cryptochironomus</i> sp. | | | | | | x |
| <i>Dicrotendipes californicus</i> Johannsen | | x | | | | |
| <i>Dicrotendipes</i> sp. | | | | | | x |
| <i>Endochironomus nigricans</i> (Johannsen) | | | | | | x |
| <i>Labrundinia</i> sp. | | | | | | x |
| <i>Parachironomus</i> sp. | | | | | | x |
| <i>Polypedilum</i> sp. | | | | | | x |
| <i>Procladius bellus</i> (Loew) | | | | | | x |
| <i>Procladius</i> sp. | | | | | | x |
| <i>Tanypus</i> sp. | | | | | | x |
| <i>Tanytarsus</i> sp. | | | | | | x |
| Tanytarsini | | | | | x | |
| Tanypodinae | | | | | x | |
| Culicidae | | | | | | |
| <i>Aedes nigromaculis</i> (Ludlow) | | | | | | x |
| <i>Culex tarsalis</i> Coquillett | | | | | x | x |

TABLE 26.2. (Continued)

| Taxa | Sublette and Sublette (1967) | Parks (1975) | Merrickel and Wangberg (1981) | Neck and Schramm (1992) | Horne (1996) | Hall (1997) |
|---|------------------------------|--------------|-------------------------------|-------------------------|--------------|-------------|
| Dolichopodidae | | | | | | x |
| Ephydriidae | | | | | | x |
| <i>Notophila</i> sp. | | | | | | x |
| Psychodidae | | | | | | x |
| Stratiomyidae | | | | | | x |
| <i>Odontomyia</i> sp. | | | x | | | |
| Syrphidae | | | | | | x |
| <i>Eristalis</i> sp. | | | | | | x |
| Tabanidae | | | | | | x |
| <i>Tabanus</i> sp. | | | | | | x |
| Tipulidae | | | | | | |
| <i>Tipula</i> sp. | | x | | | | |
| Acarina | x | | | | | |
| Arrenuridae | | | | | | |
| <i>Arrenurus dentipetiolatus</i> Marshall | | | x | | | x |
| <i>Arrenurus</i> new sp. | | | | | | x |
| Eylaidae | | | | | | |
| <i>Eylais</i> sp. | | | x | | | x |
| Hydrachnidae | | | | | | |
| <i>Hydrachna</i> sp. | | | | | | x |
| Pionidae | | | | | | |
| <i>Piona floridana</i> Cook | | | | | | x |

^aSee Fig. 26.1.

^bSpecies identified by Merrickel and Wangberg (1981) as *Corisella inscripta* (Uhler) and later determined to be *C. edulis* (Champion) by RWS.

^cIndividual identified by Merrickel and Wangberg (1981) as *Buenoa scimitra* Bare and later determined to be *B. margaritacea* Torre-Bueno by RWS.

MACROINVERTEBRATE FOOD WEB OF PLAYA LAKES

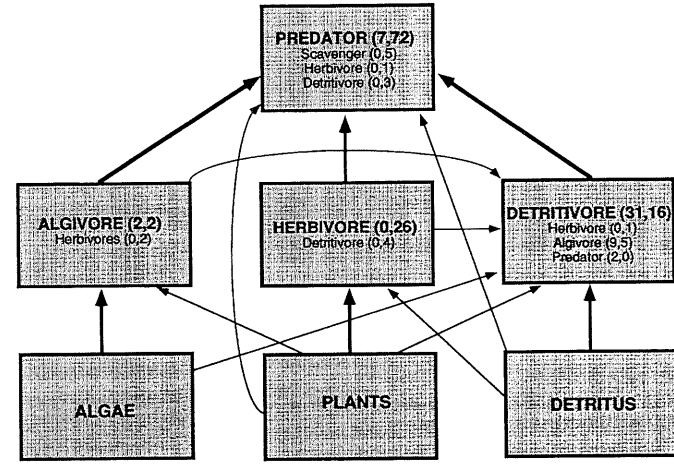


Fig. 26.2. Idealized, composite model of the foodweb of playa lakes on the Southern High Plains of Texas, illustrating the contribution of insect and noninsect macroinvertebrates. Dominant trophic classifications are indicated in capital letters (e.g., PREDATOR). In some cases a taxon may consume food from secondary sources as well, resulting in secondary trophic classifications which are indicated by upper and lower case letters (e.g., Herbivore). The number of noninsect and insect taxa, respectively, comprising a particular trophic category is represented by the numbers in parentheses adjacent to the trophic category (after Merritt and Cummins 1996, Pennak 1989, Thorp and Covich 1996). For example, 47 taxa were primarily detritivores, 9 of the 31 noninsect taxa secondarily consumed algae, and 5 of the 16 insect taxa secondarily consumed algae.

idae (11 species), and Chironomidae (ca 15 species). Because of the poor state of knowledge concerning taxonomy of chironomid larvae, assigning specific identities is especially problematic. Studies generally report chironomid presence in playas at familial, subfamilial, tribal, or generic levels (Table 26.2); thus, measures of species richness are underestimates of the true values.

In contrast to the insect fauna, the noninsect community is not especially rich (Table 26.2), being composed of only 28 families in 4 phyla (Ectoprocta [bryozoans], Annelida [oligochaetes and leeches], Mollusca [snails and clams], and Arthropoda [crustaceans and water mites]). However, the paucity of reported noninsect species may be a reflection of the historically weak taxonomic resolution of these taxa. The actual number of annelid and ectoproct species is unknown because of limited collections and improper preservation, which makes identification problematic (Sublette and Sublette 1967, Hall 1997). Similarly, the molluscan fauna has been documented poorly. Four families represented by eight species have been identified (Sublette and Sub-

lette 1967, Parks 1975, Merickel and Wangberg 1981, Neck and Schramm 1992, Hall 1997).

The most abundant noninsect taxa of playa lakes occur in the Arthropoda, numbering at least 25 species in approximately 18 families (Sublette and Sublette 1967, Parks 1975, Merickel and Wangberg 1981, Hall 1997). The most abundant arthropod taxa are crustaceans, specifically branchiopods, ostracods, and copepods. Although each subphylum is abundant during initial stages of playa succession, copepods and branchiopod cladocerans (water fleas) have been studied inadequately, with occurrences noted only at the class or ordinal level (Merickel and Wangberg 1981). Conversely, the other branchiopods (fairy, clam, and tadpole shrimp) and ostracods (seed shrimp) have been relatively well studied (Moore and Young 1964, Ferguson 1967, Belk 1975, Sissom 1976, Horne 1993, 1996) and represent 19 species in 12 families.

The final arthropod taxon represented in playa lakes is the Acari. Four families of water mites represented by five species have been collected (Sublette and Sublette 1967, Merickel and Wangberg 1981, Hall 1997). However, water mites are relatively scarce and often are recorded only at the ordinal level (Sublette and Sublette 1967).

Modes of Persistence and Immigration/Emigration

Because of the ephemeral nature of playas, their aquatic inhabitants must have life stages that are resistant to desiccation or capable of immigration to and emigration from these habitats. As mentioned previously, macroinvertebrate species of playa lakes have disparate means of coping with the dry period of their ephemeral environment. Relatively few of the aquatic insect species are year-round residents of playas. The only insects that are known to be permanent occupants are members of the dipteran families Culicidae and Chironomidae. Many species of the culicine genus *Aedes* lay eggs in the soil of low-lying areas where they may remain dormant for long periods (Merritt and Cummins 1996). *Aedes nigromaculis* has been reared successfully in the laboratory from dry playa soil (Harrell unpublished data) and occurs in the Western and Central Plains, where it is a dominant mosquito of irrigated pastures. It is well adapted for life in playas because adults can appear as early as four days after the eggs have been flooded in the spring (Harwood and James 1979).

Overall, 14 genera of chironomids have been found to possess drought-resistant larval stages (Wiggins et al. 1980). One playa-inhabiting species, *Endochironomus nigricans*, is drought-resistant (Johannsen 1905). Congeners of other playa chironomids (*Chironomus* spp., *Cricotopus* sp., *Parachironomus* sp. [Johannsen 1905], and *Polypedilum* [Hinton 1960, 1968]) have been reported to survive periods of drought, but without supporting data we can only infer that these particular species have drought-resistant stages.

Congeners of a variety of other insect species inhabiting playas have been shown to withstand periods without surface water. The haliplid beetles *Hal-*

iphus immaculicollis and *H. strigatus* were found aestivating in an inch of dried soil of prairie ponds (Wallis 1933), and Young (1960) suggests that *H. ohioensis* must be resistant to summer drought. However, it is unknown whether haliplids can survive the extended dry periods of most playas.

The damselflies *Lestes dryas* and *L. unguicaulatus*, as well as several species of the dragonfly genus *Sympetrum*, oviposit endophytically above the waterline. Eggs hatch in spring and larval development accelerates with increasing ambient temperatures, ensuring that maturation occurs before the pool is dry. *Lestes disjunctus*, which occurs in playas, does not possess physiological adaptations to increase developmental rates with temperature (Corbet 1962), and probably is a spring immigrant from permanent waterbodies.

Odontomyia (Stratiomyidae) may be able to survive eight months in dry temporary pools in southern Ontario (Wiggins et al. 1980). Because most stratiomyids are terrestrial, this is not surprising. Nonetheless, such behavior has not been reported in semiarid environments. Similarly, the horse fly, *Tabanus similis*, has been reported to overwinter as larvae in dry pool basins (Wiggins et al. 1980). However, *Tabanus subsimilis*, the most common horse fly of the Southern High Plains, has not been reported to share this behavior.

Several species of leptophlebiid and siphonurid mayflies can survive as drought-resistant eggs in vernal pools (Burks 1953, Landa 1968, Clifford 1970, Edmunds et al. 1976). However, *Callibaetis* (Baetidae), a common mayfly of playas, migrates to vernal pools from permanent bodies of water for oviposition (Ward 1992). A generation is completed in the pools, and the next generation of adults oviposits in permanent bodies of water. Generations alternate between permanent and temporary bodies of water.

Most heteropteran and coleopteran inhabitants of playas also alternate between permanent and temporary bodies of water, although a second generation in the permanent body of water is not required, because adults can overwinter and recolonize temporary bodies of water. They are considered to be true migrants because the same individual makes the return trip to the temporary body of water in the spring.

Literature regarding overwintering of Curculionidae in temporary pools is virtually nonexistent. In playas weevils apparently emigrate as soon as pools dry and the vegetation dies. In other ephemeral pools aquatic weevils move to high ground for the winter or fly to shelter in hedgerows and small woodlots or in the soil around the bases of bunch grasses (C. W. O'Brien, personal communication).

In contrast to most insect species of playa lakes, most noninsect taxa have life stages which are resistant to desiccation. Freshwater bryozoans can persist for long periods as dormant statoblasts that are resistant to freezing and drying (Brusca and Brusca 1990). Similarly, annelids can survive periods of desiccation as cocooned eggs or as adults in cysts or tests (Wiggins et al. 1980, Pennak 1989, Thorp and Covich 1991).

Several snail species burrow, as adults, into the substrate, where they endure periods of desiccation (Pennak 1989, Thorp and Covich 1991). However, it is unclear how the single clam species (Table 26.2) persists during long

periods of desiccation. Although adult members of the family Sphaeriidae burrow into mud or under damp leaves during times of drought (Wiggins et al. 1980, Pennak 1989), neither of these substrates persists for long in the semiarid environment of the Southern High Plains. Similarly, water mites of the families Arrenuridae and Pionidae persist as deutonymphs in the soil of temporary ponds (Wiggins et al. 1980). However, drought-resistant life stages of elyaid and hydrachnid water mites are not known. Consequently, sphaeriid clams, as well as elyaid and hydrachnid mites, most likely are transported from permanent waterbodies to playas after they flood.

Crustacea is the most highly drought-adapted taxon of playa lakes. All constituent species have resting eggs, cysts, or juvenile stages that are capable of withstanding extended periods of drying and freezing (Hartland-Rowe 1972, Horne 1993). The absence of fairy, clam, and tadpole shrimp from permanent water bodies suggests that they lack predator defenses or require drought or freezing to initiate development of resting eggs (Prophet 1963). However, there is some argument as to whether drying or freezing is necessary for hatching, and it appears in some cases that temperature and abrupt changes in oxygen levels may be the key signals (Belk and Cole 1975, Wiggins et al. 1980).

Colonization Patterns

The pattern of macroinvertebrate colonization of playas is reflective of the aforementioned life history strategies. Transient species immigrate in following inundation, whereas resident species emerge from the basin soil. Consequently, resident species usually are the most abundant taxa during initial stages of lake succession (first four to six weeks), with transient species dominating later.

Although insects colonize temporary waterbodies readily (Fernando 1960), few details are known regarding the mechanisms whereby they detect suitable bodies of water (Ward 1992). Most of the aquatic insect inhabitants of the playas likely colonize from nearby sources of permanent water. Deep-water pits associated with irrigation practices undoubtedly serve as a primary source of biotic recruitment in many cases.

Many aquatic insects immigrate to bodies of water via aerial dispersal (Fernando 1958, 1959). Some flying aquatic insects select colonization sites based on size and reflected color (Popham 1943, Fernando 1959). Records of flight directed into reflective surfaces that were interpreted as water have been reported for a variety of insects. For example, a dozen specimens of the corixid *Hesperocorixa laevigata* mistook a turquoise blue Datsun for water in Arizona (Shaefer and Shaefer 1979). Similar episodes of substrate confusion have been recorded for other corixids (Fattig 1932), hydrophilids (Benham 1976, Last 1976), and other taxa. Indiscriminately directed flight of dispersing aquatic insects would be ill-adaptive on the Southern High Plains because little surface water is available. These anecdotal records demonstrate

that some aquatic insects employ navigational criteria in their choice of colonization sites. Under normal circumstances these criteria facilitate an efficient and rapid colonization of appropriate habitats (i.e., playas).

Indeed, colonization of playas by insects is rapid, with many taxa appearing within the first weeks following inundation, albeit not in high abundance. Nonetheless, several studies have shown that a slight increase in diversity might occur in playas in the three to four months after vernal filling, but diversity during the first week typically is not the lowest (Parks 1975, Merickel and Wangberg 1981).

Colonization patterns of insects in playas are diverse. Species richness for some coleopterans (curculionids, gyrimids, and dytiscids) is highest in the first few weeks after filling (Hall 1997). Larvae of most dytiscid genera are present within one to two weeks of inundation. Densities of adult dytiscids can be quite high (Hall 1997), peaking approximately one month after initial arrival. Within two months most dytiscids have progressed to the adult stage, with the exception of *Cybister fimbriolatus*, which is large and requires more time to complete development.

The generation time of dytiscids in playas is much faster than that of other coleopterans, such as haliplids or hydrophilids. Both colonize playas as adults. Because haliplids feed chiefly on vegetation, which is sparse during initial stages of inundation, this taxon is not particularly common in playas immediately after flooding. Haliplid oviposition occurs soon after adult colonists arrive; after several weeks larval density increases and adult density decreases (Hall 1997).

Most heteropteran life cycles are similar to those of the haliplids. Adult density decreases through attrition, whereas nymphal density increases until late summer, when recently emergent adults emigrate. The majority of hemipteran taxa are most abundant approximately six to eight weeks following playa inundation (Hall 1997).

Dipteran taxa are abundant throughout the wet period of the playa (Hall 1997). Syrphids and some culicids, as mentioned earlier, are most abundant immediately after playa inundation. Other culicids and ephydriids are more common approximately one month after playas fill. Abundances of other dipteran taxa (chironomids, tabanids, and psychodids) increase throughout the wet period.

Unlike most insect species of playa lakes, the noninsect taxa rapidly attain high abundances once playas flood. Some species, especially phyllopodids, hatch within 48 hours and complete their life cycles in less than a month (Prophet 1963, Loring et al. 1988, Thorp and Covich 1991). They are the numerically dominant taxa during early colonization. They consist mostly of detritivores, and their abundances usually peak within the first six weeks of playa succession (Sublette and Sublette 1967, Hall 1997) when detrital resources are abundant.

Not all noninsect taxa are present within the first month of playa succession. Some species of mites only appear approximately six weeks after playa

inundation (Sublette and Sublette 1967, Hall 1997). Delayed colonization might reflect the timing of immigration of their insect hosts. Colonization by other species (e.g., physid snails and glossiphoniid leeches) may reflect dependence for transport by waterfowl and wading birds (Maguire 1959, Maguire 1963, Proctor 1964, Proctor and Malone 1965, Proctor et al. 1967).

Although most noninsect taxa can withstand periods of desiccation, they also use passive means to disperse between playas. With the exception of water mites, most noninsect taxa of playas are dispersed by birds, either adhering to feathers and other body parts (Maguire 1959, 1963; Pennak 1989) or passing unscathed as resting eggs through the digestive tract (Proctor 1964, Proctor and Malone 1965, Proctor et al. 1967). Insects are used as agents of transport by some species (Pennak 1989), especially ephemerid and hydrachnid water mites which have no drought-resistant life stages (Wiggins et al. 1980, Thorp and Covich 1991). Moreover, aerial dispersion of noninsect taxa is probably quite common among playa lakes (average density $>1/\text{mile}^2$) as a result of high winds (Wiggins et al. 1980).

SUCCESSIONAL CHANGES

Time has a pervasive effect on macroinvertebrate communities in playa lakes. Species richness and diversity increase with time (although both usually decrease immediately before drying), but the abundances of particular taxa either increase or decrease, depending on life history strategy and the rate at which the playa dries (Parks 1975, Merickel and Wangberg 1981, Neck and Schramm 1992, Moorhead et al. in press). Detritivores and omnivores dominate early stages but become less abundant in later stages, when herbivores and predators become dominant (Table 26.3). These data suggest a general

TABLE 26.3. Proportional Contributions of Particular Trophic Groups to Invertebrate Communities in Playas for each Sampling Period Based on Abundances^a

| Trophic Group | Sampling Period | | | | | |
|----------------|-----------------|-------|-------------------|-------|-------|-------|
| | 1 | | 2 | | 3 | |
| | Mean | SD | Mean | SD | Mean | SD |
| Detritivores | 41.66 | 25.67 | 45.76 | 15.84 | 25.42 | 14.51 |
| Filter Feeders | 36.14 | 27.28 | 7.82 [‡] | 13.60 | 0.48 | 0.63 |
| Herbivores | 2.30 | 4.83 | 2.64 [‡] | 2.94 | 3.25 | 2.42 |
| Omnivores | 3.96 | 6.21 | 0.07 | 0.21 | 0.00 | 0.00 |
| Predators | 14.30 | 22.05 | 42.31 | 12.87 | 69.99 | 14.28 |

Source: D. L. Moorhead, D. L. Hall, and M. R. Willig, Succession of macroinvertebrates in playas of the Southern High Plains, USA. *Journal of the North American Benthological Society*, in press.

^aSD = standard deviation; n = 10.

pattern of trophic succession beginning with early dominance of rapidly developing species (especially Crustacea) that utilize detritus and dead organic matter carried into the playa by runoff from the watershed or from the inundation of autochthonous sources. Numbers of herbivores increase as algae and aquatic vegetation grow, and predator numbers increase in later stages of succession (Table 26.3), apparently in response to an increase in available prey. This pattern is consistent with that found by Schneider and Frost (1996) for temporary ponds in Wisconsin. They suggest that the effect of predation on community structure increases with the duration of the wet period. However, the short duration of the wet phase of playas, in comparison to that of most of the Wisconsin ponds studied by Schneider and Frost (1996), may preclude any pervasive effect of predation on community structure.

Moorhead et al. (in press) also discovered temporal trends in the composition of macroinvertebrate communities in playas: (1) composition becomes more similar among playas over time and (2) differences in composition between communities within particular playas decrease over time. These results suggest that random events play a larger role in determining community structure at early stages of colonization and that more deterministic processes, such as biotic interactions, may exert greater influence on community composition during later stages of development.

CONSERVATION

As the primary wetlands in a semiarid landscape dominated by agriculture, playas represent an important source of invertebrate diversity that would otherwise be absent from the region. In addition, invertebrate production from playas represents a critical food source for vertebrate wildlife such as waterfowl (Bolen 1989a), shorebirds (Baldassarre and Fischer 1984), amphibians (Anderson 1997), and mammals (Schmidly 1991). Because playa wetlands are an important portion of the Central Flyway of the United States, they indirectly contribute to the health of wildlife populations and the diversity of avian communities in North and South America (U.S. Fish and Wildlife Service 1988).

Modifications of playa basins for conservation, recreation, and agricultural purposes have significant implications for the biodiversity of playas. For example, lands entered into the Conservation Reserve Program often are associated with playa basins. Although the seeded grasses assist in reducing erosion, they also reduce the rate at which playas fill during spring and summer convection storms, and shorten the duration of inundation. This likely has a major impact on invertebrate populations and communities and on the wildlife that rely on them for food. Similarly, modification of playas so that they are permanently filled for use in recreation or directly interconnected as part of a flood control program, as is done in a number of urban areas on the Southern High Plains (Wolf et al., this volume), changes the nature of playa

ecosystems and alters the abundance and species composition of invertebrates. Finally, agricultural practices (e.g., rowcrop cultivation of cotton and sorghum) can exacerbate sedimentary filling of playas and reduce their contribution to regional biodiversity (Luo et al. 1997).

The flora and fauna of playas are not sufficiently well studied to understand the underlying mechanisms that enhance their diversity and that of communities occupying adjacent terrestrial environments. Even fewer comparative studies have addressed the consequences of human activities on playa invertebrates or documented the consequences of altered invertebrate communities on other wildlife species. Despite the importance of playa wetlands from a conservation perspective, they are not sufficiently well represented in areas protected as part of the nation's system of nature reserves. Almost all playas are situated on privately owned land, diminishing the likelihood that they will be well studied from a long-term research perspective or sufficiently protected from development. We reiterate the concerns of Vandermeer and Perfecto (1997) as they relate to the conservation status of agroecosystems. Playas represent critical components of a biodiversity-rich agroecosystem. Understanding the abiotic and biotic factors responsible for the origin and maintenance of their biodiversity, as well as their interconnections with the surrounding agroecosystem's flora and fauna, remains an important task that should assume high priority as the foci of agroecology and conservation research merge in the coming decades.

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