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Population Dynamics of a Playa Community in the Chihuahuan Desert

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POPULATION DYNAMICS OF A PLAYA  
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**ABSTRACT**—Population responses of desert playa organisms were examined following two separate rain storms (spring and late summer–fall) that flooded a playa and stock tank located in southern New Mexico. Invertebrate species that appeared following both floods included the crustaceans *Streptocephalus texanus*, *Thamnocephalus platyurus*, *Eulimnadia texana*, *Triops longicaudatus*, *Moina wierzejskii* and the rotifers *Brachionus* sp., *Polyarthra* sp., and *Pedalia* sp. *Moina wierzejskii* produced three generations during the single spring flood while other species produced a single generation. Initial population levels for all species were very high. Fairy shrimp levels decreased quickly, and population levels of *Moina wierzejskii* were depressed until levels of all other species were low. Arthropod species did not produce large numbers of drought-resistant eggs in response to the lowering of the water level. Tadpoles of two species of anurans, the spadefoot toad (*Scaphiopus multiplacatus*) and the true toad (*Bufo cognatus*) occurred in the playa following spring flooding. Tadpoles of *Bufo cognatus* were not collected after the late summer rain. Tadpoles, particularly spadefoot toads, preyed on other tadpoles and fairy shrimp (Anostraca). Apparently, both biotic and abiotic factors were important in the population dynamics of playa organisms. Biotic interactions appeared more important during the second flood when the population densities of most species were higher.

A playa is an undrained basin which can become an ephemeral pond or small lake depending on the duration and intensity of rain and the size of the drainage area. Playas are extremely common in the southwestern United States (Reeves, 1972). There are at least 20 thousand playas in the Llano Estacado of eastern New Mexico and western Texas (Sublette and Sublette, 1967). Although considerable work has been done on the geomorphology and physiogamy of playas (Neal, 1975; Merickel and Wangberg, 1981), the fauna of flooded playas has been incompletely studied. Most data on temporary pond faunas are from studies in grasslands and forests (Prophet, 1963; Horne, 1967, 1974; Donald, 1983). Playas are characterized by intense biological activity after flooding and often have high species diversity (Cole, 1968; Crawford, 1981). Life histories of invertebrates from temporary grassland ponds (e.g., Weaver, 1943; Mattox, 1950) and detailed physiology have been presented for some species (Banta and Brown, 1929; Banta and Stuart, 1932;

Horne, 1971; Eriksen and Brown, 1980a, 1980b, 1980c). More complete ecological studies of playa fauna include those of Sublette and Sublette (1967), McCarraher (1970), Goulden (1971), Creusere and Whitford (1976), Merickel and Wangberg (1981), and Woodward (1982, 1983). Feeding and resource use by macroinvertebrates have been reported by Holm et al. (1983), Pace et al. (1983), and Richman and Dodson (1983).

The objectives of this investigation were to study the population dynamics, predator-prey interactions, and community structure of larger animals in a flooded playa in the northern Chihuahuan Desert. We present responses of consumer organisms to two floods and examine the trophic interactions of these organisms.

**MATERIALS AND METHODS**—*Study Site*—The study area was a 12-ha playa basin on the northern edge of the Dona Ana mountains located on the Long Term Ecological Research Site, 40 km NNE of Las Cruces, New Mexico (Creusere and Whitford, 1976). The long-

term average annual precipitation at the Jornada site was 210 mm, 55% of which occurs from July through September as convectonal storms. The playa was subjected to little human alteration, with the exception of an excavation serving as an open-end stock tank (approximately 10 by 30 m, or <5% of the playa surface area). Cattle have been excluded from the playa since 1972. Soils varied from coarse gravels on the bajada to sandy loams on the playa fringe and heavy clay silts on the playa bottom. The basin was characterized by many "potholes," primarily resulting from collapsed mammal burrows. Clay silt soils of the playa bottom swelled after rain and accumulated run-off water. Compared with most desert playas, this was a relatively small, non-saline playa (C. Bowser, pers. comm.) with heavy vegetation cover. Dominant plant genera included *Prosopis*, *Panicum*, *Amaranthus*, *Hymenoxis*, and *Helianthus*.

Flooding normally occurs during July and August once every 3 to 10 years. The floods of 1984 were unusual. Flooding in May 1984 happened after the watershed received 49 mm of rain in approximately 2.5 h. The August flood occurred after 48 mm of rain fell in 6 h. On 3 October 1984, approximately 25 mm of rain fell; on 12 October, 20 mm of rain fell in 40 min; the watershed received 25 to 33 mm of rain in 5 days (22 to 26 October). After each of these rains, the playa basin flooded. The basin retained water for a few weeks; the tank for a few months. The maximum depth of the tank was 140 cm (Loring et al., 1988).

*Sampling Procedure*—Samples of arthropods and tadpoles were taken at approximately 3-day intervals when the playa or tank contained water. All samples were taken between 0600 and 0800 h, except for the 24 August sample, which was taken at 1600 h. Samples were not taken in May 1984 until 7 days after flooding of the playa. In August 1984, samples were first taken within 17 h of the rainfall. We used a 20-cm-diameter, circular, aquatic net (1-mm mesh) to sample macroinvertebrates and tadpoles. Each sample consisted of 10 pooled sweeps, 1.5 m length/sweep. Samples were taken in areas with water deep enough to allow the net to be completely submerged or from the middle of the water column in deeper water. We sampled macroinvertebrates by passing 10 l of playa water through a 53- $\mu$  mesh sieve. These samples were taken from similar areas as the previous samples.

All macroinvertebrates and tadpoles were removed from samples, sorted to species, measured to the nearest millimeter, and stored in 10% formalin. *Moina wierzejskii* (Richards) (Cladocera) were counted in 1 ml subsamples of samples collected in the field. Rotifers were counted in five samples of 0.25 ml for each date and identified; the mean density for each genus was calculated and adjusted to numbers per liter.

During the spring flood, we used microcosms to study predator-prey relationships. We removed the tops and bottoms of white plastic buckets (15 l), replaced one

end with 1-mm mesh heavy cloth, and floated them in the tank water. We assumed that the mesh allowed water, microinvertebrates, and algae to pass in and out of the buckets to simulate a natural condition. A 7-cm strip of plastic "bubble-pak" was used to float the buckets in an upright position. Twenty buckets were used containing combinations of the following species: *Thamnocephalus platyurus* Packard (broad-tailed fairy shrimp), *Streptocephalus texanus* Packard (fork-tailed fairy shrimp), *Triops longicaudatus* (LeConte) (tadpole shrimp), two morphs (predator and herbivore, see Altig, 1970, for details) of *Scaphiopus* tadpoles. Three buckets per combination were used, and the results were pooled for statistical tests.

After 4 days, Chi-square  $2 \times 2$  contingency tables were used to test for differences in survivorship of potential prey between controls (only prey species present) and treatments (prey and potential predator present). These experiments were supplemented with laboratory observations to ensure that predators were actually capturing live prey and not scavenging.

**RESULTS**—The playa contained water for 16 days following rain in May 1984 and 14 days following the flooding in August. The playa flooded again on 3 and 22 October 1984. Water remained on the playa for 3 days following the flood on 3 October and 11 days following the flood on 22 October. The stock tank contained water for 65 days after the flood in May and >100 days after the flood in August.

Several species of insects occurred in the playa (Richardson, 1971). Following the flood in August 1984, mosquito larvae (*Aedes* sp.) quickly attained very high levels, pupated, and were gone from the playa within 8 days. Within 17 h after the rain event in August, there were 12.9 mosquito larvae/l; on day 4, there were 2.5 larvae and pupae/l; by day 6, there were 0.66 larvae and pupae/l. In addition, we collected a few dytiscids and hydrophyllids (see Richardson, 1971, for an extensive list).

The clam shrimp, *Eulimnadia texana* Packard, reached highest densities within 6 days of flooding (Fig. 1A) and was gone after 17 days in May 1984. In August, *E. texana* disappeared after 6 days. Nauplii larvae of the notostracan *T. longicaudatus*, the anostracans *S. texanus* and *T. platyurus*, and the conchostracan *E. texana* were collected within 17 h of the flood on 23 August. The tadpole shrimp population peaked 15 days after the flood in May 1984 (Fig. 1B); by day 16, the playa was almost dry, and no individuals were found. The population in the stock tank

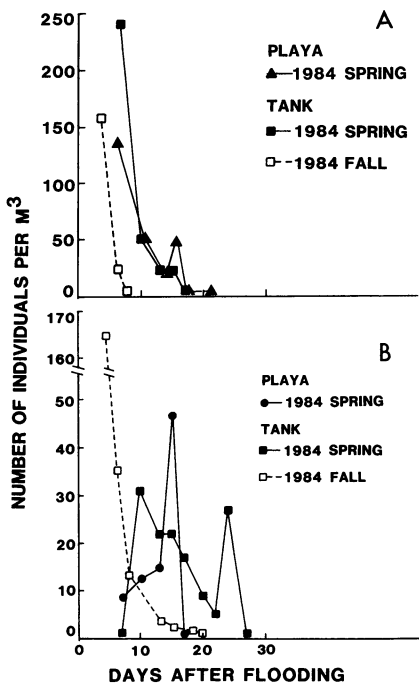


FIG. 1—Population fluctuations in a stock tank in 1984 and in a playa during 1970 and 1984. A) *Eulimnadia texana*. B) *Triops longicaudatus*.

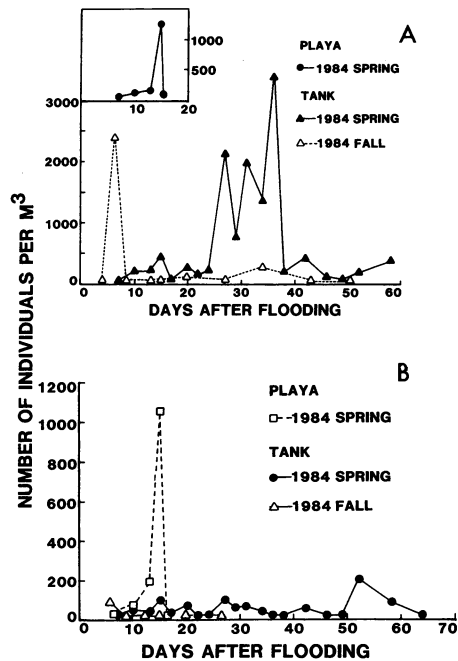


FIG. 2—Population fluctuations (A) of *Streptocephalus texanus* in a playa in 1970 and 1984 and in a stock tank during 1984 and (B) of *Thamnocephalus platyurus* in 1984.

peaked 10 days after the flooding in May 1984 and gradually dropped. Another peak appeared 24 days after flooding. Tadpole shrimp were no longer present after 27 days, even though water was present for 65 days. Population levels of *T. longicaudatus* in the tank following the fall flooding were initially much higher than during the May-June flood; however, the population density decreased exponentially (Fig. 1B).

The population of *S. texanus* peaked in the playa 15 days after the flood in May 1984 (Fig. 2A). Its density in the tank was very high 27 to 36 days after flooding. The numerous peaks in the data may be due to the contagious distribution of the shrimp or sampling error, rather than changes in the population. The population became concentrated as the stock tank dried. Populations of *S. texanus* were extremely high 6 days after the flood in August but dropped rapidly to low levels until they disappeared about 50 days following the flood (Fig. 2A). By day 34 after flooding, 94.3% of female *S. texanus* carried eggs.

*Thamnocephalus platyurus* occurred at lower population densities (Fig. 2B) than *S. texanus* (Fig. 2A). The spring playa population peaked

on day 15 and crashed on day 16. The population in the stock tank remained relatively constant after day 10 until it peaked on day 52. The population levels in the tank during the fall flood were never high (averaging 1 or 2 individuals/m<sup>3</sup>) and were short-lived compared with their levels in the spring flood (Fig. 2B). Female *T. platyurus* were never seen with eggs following the August flood. Both species of fairy shrimp were seen “schooling” on many occasions.

There was only one generation of fairy shrimps (*S. texanus* and *T. platyurus*), although populations did peak (Fig. 2A,B). Total lengths of five randomly chosen individuals of each sex after each sample of the spring flood show no size fluctuation (Fig. 3A,B), indicating that all individuals are members of the same cohort. In the May flood, adult size was reached within 10 days of flooding. At that time, 60% of the *S. texanus* females were gravid, while no *T. platyurus* females were gravid. After day 13 of the May flood, all females of both species were gravid. Female *S. texanus* increased in size over time; the regression slope was significantly greater than zero (Table 1). Males showed no significant change

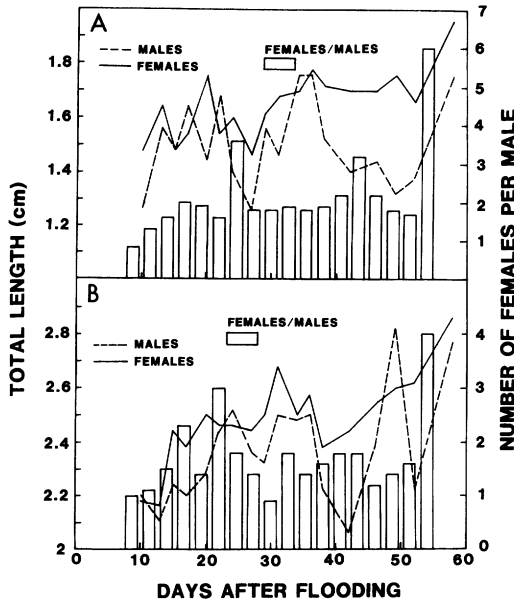


FIG. 3—Total lengths and sex ratios during a flood in spring 1984. A) *Streptocephalus texanus*. B) *Thamnocephalus platyurus*.

in size. Both sexes of *T. platyurus* increased in length significantly over time. In the relatively “long-lived” body of water provided by the stock tank, these species did not produce a second generation but continued to grow. Eggs may require drying before they will hatch.

The sex ratios of both species of fairy shrimp remained unchanged (regression slope not significantly different from zero) throughout most

of the time the tank was flooded following the May event (Table 1). Approximately two females/male were present for each species during most of the spring flood (Fig. 3A,B). On day 58, we observed a large shift of the sex ratio of both species to females that we attribute to differential mortality. Following the August flood, the sex ratio of *S. texanus* remained skewed toward males for nearly the entire time the playa and tank contained water. Population densities of *T. platyurus* were so low that no meaningful determination of sex ratio could be made.

The cladoceran *M. wierzejskii* occurred in the playa during 1984. The adult population density in the playa was already high when sampling began on day 7 of the flood in May 1984. The immature population density was low and may have been part of the same cohort as the adult population. There appeared to be three generations of *M. wierzejskii* in the tank after the flood in May 1984 (Fig. 4A,B; see also Loring et al., 1988). The first generation peaked at 15 days, the second around 30 days, and the third about 40 days after flooding.

Population densities were somewhat different in late summer of 1984 (Fig. 4C,D). An early surge was followed by a rapid decrease. The population levels remained low, increasing gradually in the latter part of September (days 60 to 80) and peaking on 2 November 1984 (day 71). Male *M. wierzejskii* were first observed on 2 November and are included in both the 0.5 to 0.6 mm (Fig. 4C) and 0.7 to 0.9 mm (Fig. 4D) size classes.

Female cladocerans produce resting eggs, or

TABLE 1—Linear regression analysis of the changes in total body length (mm) of individuals and changes in sex ratio of populations of *Streptocephalus texanus* and *Thamnocephalus platyurus* over time. In the analysis of sex ratios, the final data points (Fig. 3) were excluded from the analysis. Sample size is from five replicates from each of six sample times; Student's *t*-test was with slope = 0 as the null hypothesis (Snedecor and Cochran, 1967).

Species	Sex	<i>n</i>	<i>r</i>	Slope	Intercept	<i>t</i>
Total length						
<i>S. texanus</i>	Female	18	0.725**	0.0065	1.45	4.23**
<i>S. texanus</i>	Male	18	0.110	0.0012	1.46	0.42
<i>T. platyurus</i>	Female	18	0.765**	0.0088	2.21	4.75***
<i>T. platyurus</i>	Male	18	0.497*	0.0073	2.13	2.28*
Sex ratio						
<i>S. texanus</i>		17	0.336	0.0167	1.45	1.38
<i>T. platyurus</i>		17	0.030	-0.0012	1.62	-0.12

\*  $P < 0.05$ .

\*\*  $P < 0.01$ .

\*\*\*  $P < 0.001$ .

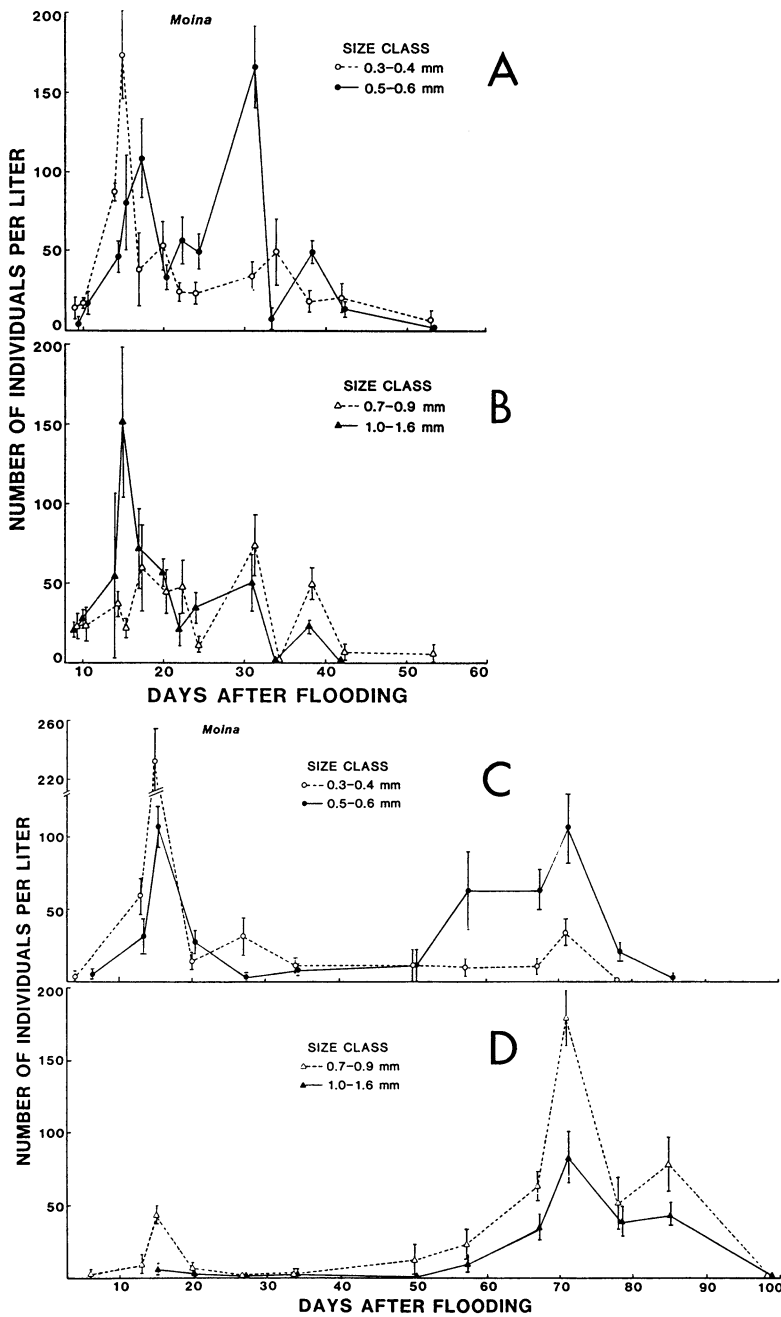


FIG. 4—Population fluctuations of *Moina wierzejskii* in a stock tank during the flood in May 1984. A) May 1984 small size classes. B) May 1984 large size classes. C) August 1984 small size classes. D) August 1984 large size classes. Standard error bars are indicated.

ephippia (Pennak, 1978). Ehippia are able to withstand drying and freezing; thus, their production is an adaptation to adverse environmental conditions. When a playa floods again, ehippiat

eggs hatch into parthenogenetic females. We expected the numbers of females carrying ehippia to increase immediately before the playa dried, but this did not happen (Fig. 5A). Only a small

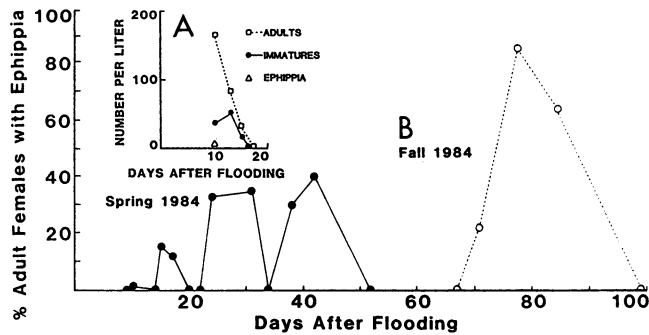


FIG. 5—A) Population fluctuations of *Moina wierzejskii* in a playa after a flood in spring 1984. The numbers of immatures (<0.6 mm total length), adults (>0.7 m total length), and females carrying ephippia (resistant egg-bearing structures) are indicated. B) The percent of adult females carrying ephippia in a stock tank during both floods in 1984.

proportion of the population was carrying ephippia 10 days before the playa was almost dry. The data from the tank support the hypothesis that initiation of ephippial production was not stimulated by drying. The three peaks in ephippial production (Fig. 5B) in spring of 1984 correspond to the fluctuations in density of adults (Figs. 4A,B and 5B). Apparently, the same process occurred in the autumn of 1984. A peak in the adult population did not occur until after 70 days (Fig. 4C,D) and was followed by a peak of ephippia in the population (Fig. 5B). Drying of the playa had no apparent effect. Females produce ephippia when they are near the end of their normal lifespan.

Rotifers were represented primarily by three genera: *Polyarthra*, *Pedalia*, *Brachionus* (Fig. 6). *Brachionus* was the most abundant of the genera

present during the spring flood. The density increased after day 40 to very high levels (day 58) prior to the tank becoming dry. All three genera were present during the fall flood, and their populations were temporally isolated. *Brachionus* appeared somewhat sooner after the fall event than it did after the spring flooding. The density dropped after day 35 and remained low. The population of *Polyarthra* sp. remained low until day 58 when it increased dramatically. By day 80, the density was again low. No *Pedalia* were detected until after day 70. The population reached a peak at day 85. By day 100, the populations of all three genera were very low. *Polyarthra* and *Pedalia* may not respond to a spring flooding, or the water may not have been present long enough for them to appear. Other genera were present in very small numbers.

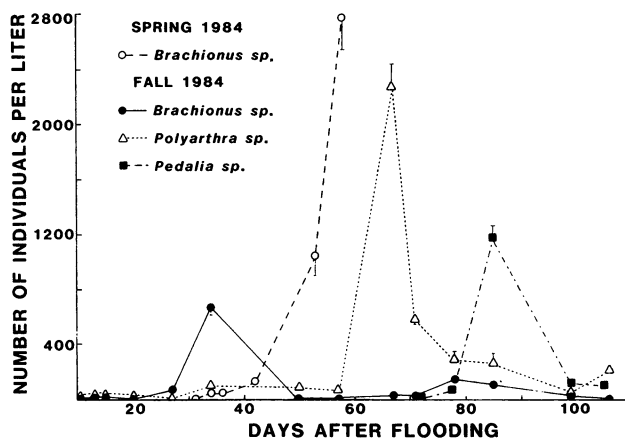


FIG. 6—Population fluctuations of three genera of rotifers in a stock tank during floods in 1984.

Two species of anurans, the spadefoot toad (*Scaphiopus multiplicatus* [Cope] [=hammondi], Pelobatidae) and the true toad (*Bufo cognatus* Say, Bufonidae), bred in the playa after the flood in spring 1984. Adult *Bufo debilis* Girard were seen near the playa, but no tadpoles were ever collected. *Scaphiopus* tadpoles were not collected in May 1984 until 10 days after flooding (Fig. 7A). The population of tadpoles of *S. multiplicatus* in the playa peaked on day 13. Because the predaceous morph did not increase during this time, we assume that the peak is real. After the playa dried, many small toads were seen in the mud cracks and moist depressions. The tadpole population in the tank remained fairly constant until about day 36; tadpoles of *S. multiplicatus* were present until day 42. The density of tadpoles of *B. cognatus* was very low until day 46, after which the population increased considerably. Before this, we saw many adult *B. cognatus* on the shore beneath mesquite bushes (*Prosopis glandulosa* [Torr.]).

Only one species of tadpole, *S. multiplicatus*, was found in the playa and tank after the August flooding event. The tadpole population density was very high just after the flood and dropped exponentially (Fig. 7C). Tadpoles did not get as large as during the first flood (pers. obser.). Gut content analysis showed that at least some *S. multiplicatus* ate fairy shrimp.

We were able to examine predator-prey relationships of the larger animals in the playa in the spring 1984 flood using a series of microcosms (Table 2). Both the predaceous and herbivorous morphs of *Scaphiopus* tadpoles were important

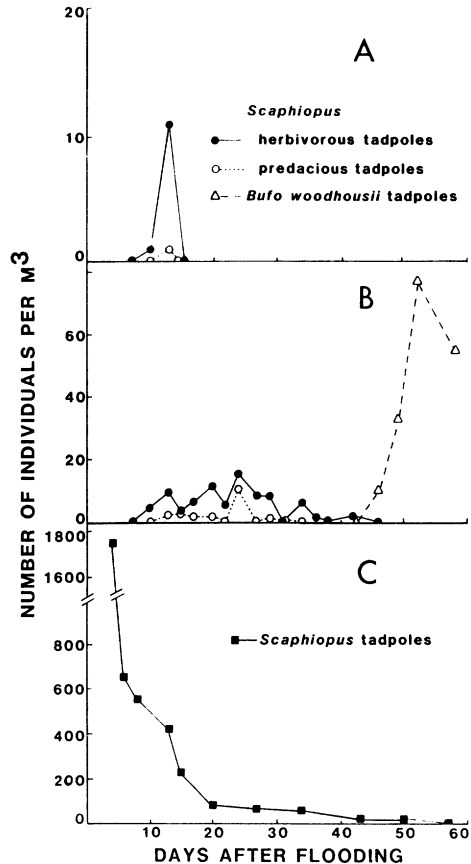


FIG. 7.—Population fluctuations of tadpoles in a playa and a stock tank during floods in 1984. A) Playa, spring. B) Tank, spring. C) Tank, fall.

TABLE 2.—Summary of the analysis of the Chi-square contingency tables involving various combinations of animals in the Jornada Playa. The tables were based on a comparison of the survivorship and mortality of possible prey in the treatments and controls.

Possible prey species <sup>1</sup>	Possible predator	$\chi^2$
<i>Triops longicaudatus</i> (10, 5, 13, 5)	<i>Scaphiopus multiplicatus</i> (predator morph)	0.12
<i>Streptocephalus texanus</i> (9, 21, 10, 20)	<i>T. longicaudatus</i>	0.08
<i>S. texanus</i> (9, 21, 0, 30)	<i>S. multiplicatus</i> (predator morph)	10.59**
<i>S. texanus</i> (9, 21, 2, 28)	<i>S. multiplicatus</i> (herbivore morph)	5.45*
<i>Thamnocephalus platyurus</i> (15, 15, 19, 11)	<i>T. longicaudatus</i>	1.09
<i>T. platyurus</i> (15, 15, 4, 26)	<i>S. multiplicatus</i> (predator morph)	9.32**
<i>T. platyurus</i> (15, 15, 0, 30)	<i>S. multiplicatus</i> (herbivore morph)	20.00**

<sup>1</sup> Numbers in parentheses are (from left to right) animals alive in control, animals dead in control, animals alive in treatment, animals dead or missing in treatment, after 4 days. Animals found dead without missing body parts presumably died of causes other than predation.

\*  $P < 0.05$ .

\*\*  $P < 0.01$ .



predators of both fairy shrimp species. Tadpoles did not actively hunt shrimp, but would capture and eat a shrimp whenever one touched the mouth or underside of a tadpole (pers. obser.). In bucket experiments involving both morphs of *Scaphiopus* tadpoles, there was no mortality of either morph (pers. obser.). Because both morphs were large at the time of the experiments (snout vent lengths of 27 to 40 mm), an individual probably was not able to eat another individual, although they did attack and remove pieces from tails of others.

*Triops longicaudatus* was also examined and was neither a predator of fairy shrimp nor prey for the tadpoles. Because tadpole shrimp are mostly gone by the time tadpoles become large enough to become predators, the potential for contact between these animals is slight. Adults are relatively large and have a sturdy carapace; therefore, they would be unlikely prey.

**DISCUSSION**—The assembly of playa organisms may result from a combination of fast-acting physical forces and subsequent biotic responses. In some communities, biotic interactions are thought to lead a relatively ordered and predictable succession of organisms (Sousa, 1979a, 1979b; Grossman, 1982); however, in some instances, such predictable patterns may not occur (Sale, 1977, 1984; Grossman et al., 1982). The relative importance of physical and biotic mechanisms and the predictability of their effects vary among ecosystems.

Two extreme alternative scenarios are possible in population responses to playa flooding. If biotic interactions are unimportant, species should exhibit relatively quick, synchronized population growth; negative correlations in growth among organisms would not occur. If biotic interactions develop, negative effects of one species on another would be detectable, and species would differ in the timing of their response to flooding. Both interpretations must consider constraints related to the life histories of playa organisms living in an ephemeral habitat.

We have evidence for both scenarios occurring in different groups of organisms. Biotic interactions with other animals are unimportant for mosquitoes (*Aedes* sp.), clam shrimp, and tadpole shrimp which have short population cycles. Apparently, these organisms avoid major competition for food sources, or predation from slower-developing organisms, by completing their life cycles before the populations of other organisms

have developed in the playa. Short life cycles in tadpole shrimp have been reported previously (Sublette and Sublette, 1967; Goulden, 1971; Pennak, 1978).

Competition and predation may be important for other species. There was obvious temporal partitioning in the three monogonate rotifer genera. *Brachionus* sp. were found primarily during the spring flood, while all three genera were found following the August flood. All the species belonging to these genera are reported to eat suspended particulate matter (Edmondson, 1959). The temporal partitioning simply may be differential timing of life cycles or possibly could be the result of intergeneric competition.

The course of the scenarios depends on conditions preceding the flood. Our data and a comparison with a flood in fall 1970 (Richardson, 1971) suggest that a flood which occurs after a period of dry years results in relatively low numbers of playa organisms compared to what occurs after a second flooding in the same year. Mortality of aestivating eggs (or adult toads) prior to flooding would lower the pool of potential organisms available to exploit the playa when water becomes available. As the length of intervening dry periods increases, fewer eggs and adults survive (Whitford and Meltzer, 1976). The flood in May was the first complete flooding since 1974. The August flood occurred only 1.5 months after the first flood. Apparently a large proportion of eggs and aestivating adults survived. Consequently, initial populations after the August flood were extremely high, after which many of the populations crashed. In some cases, the rapid reduction in numbers may be characteristic of the species. For example, the population changes of *Eulimnadia texana* were similar for both floods in 1984.

The response of *M. wierzejskii* to the flood in August showed possible effects of competition which did not occur after the May flood. The number of individuals belonging to the smallest size classes quickly fell without a concomitant rise in the numbers of the larger size classes. The population remained low until about day 50 after the August flood. At this time, populations of tadpoles and fairy shrimp were very low. If these groups compete with *M. wierzejskii* for food, the population fluctuations of *M. wierzejskii* can be explained more easily. Lower population densities also could be due to lower temperatures in fall.

For many species, the reduction in population

density may have been due to predation by tadpoles (Table 2). The rapid decline in numbers of *S. texanus* during fall occurred when the density of *Scaphiopus* tadpoles was high. Tadpoles were smaller and a predator morph never developed during the fall flood. Falling temperatures in late summer and fall probably prevented complete development of tadpoles.

The most intriguing anuran reaction was that of *B. cognatus*. During the spring flood, this species was not present until *Scaphiopus* tadpoles had left the tank. *Bufo cognatus* did not reappear during the fall flood. We do not know whether *B. cognatus* is capable of responding to floods only 1.5 months apart.

Pennak (1978) reported that male fairy shrimp usually die within a few hours after copulation, which would shift the sex ratio of a population toward a predominance of females. This was the case with at least one species of fairy shrimp in our playa.

The fauna and flora of playas have potential interest to many ecologists. Physiological adaptations that allow organisms to complete their life cycles within days and remain dormant in dry soil for years are poorly understood. The importance of biotic and abiotic factors on the population dynamics depends on the taxon being considered and time since the last flood. However, playas are relatively simple systems that should be easy to manipulate to test ecological theory.

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