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Primary Research Paper

Tadpole shrimp structure macroinvertebrate communities in playa lake microcosms

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Abstract

Laboratory microcosms were used to assess whether tadpole shrimp, *Triop*s *sp*., affect community structure of other native macroinvertebrates in playa lakes of the Southern High Plains of Texas. Removal of tadpole shrimp shortly after hatching reduced abundances of many taxa, and decreased subsequent taxonomic richness and diversity. For many invertebrates, the presence of tadpole shrimp in low numbers had a positive effect on mean abundance. Direct effects of tadpole shrimp include the reduction of prey species abundance, which in turn may alter biotic interactions among other taxa. Indirect effects include physical modification of the environment during foraging through surface sediments. Results suggest that tadpole shrimp may be a key species controlling structure of macroinvertebrate communities in playa lakes.

Introduction

Biotic interactions, such as competition, predation, and mutualism (Paine, 1980; Abrams et al., 1996), as well as environmental factors such as habitat structure or light availability (Jones et al., 1994) can have profound effects on community structure. If regulatory effects are linked strongly to a particular taxon, the loss of such a species may greatly alter the characteristics of the community (Paine, 1980; Power et al., 1996).

A species may simultaneously occupy a variety of functional roles that affect a community (Chapin et al., 1997; Tilman et al., 1997). For example, predators may determine community composition through preferential feeding on particular prey species (Sih et al., 1985; Thorp, 1986), or may enhance diversity by preventing competitive exclusion by dominant prey species (Paine, 1969, 1992). Indeed, predation is an important determinant of community structure in freshwater systems (Brooks & Dodson, 1965; Dodson, 1974; Hebert & Loaring, 1980; Zaret, 1980; Morin et al., 1983; Black & Hairston, 1988). Alternatively, a species may affect community structure by modifying the environment. Such disturbances create different habitat patches which have an effect on many population and community characteristics (Jones et al., 1994; Lawton & Jones, 1995; Willig & McGinley, 1999).

The common tadpole shrimp, nominal species *Triops longicaudatus* (see Murugan et al., 2002), may exert such effects on macroinvertebrate community structure in ephemeral playa lakes, important centers of biodiversity on the Southern High Plains of West Texas (Bolen et al., 1989; Haukos & Smith, 1994; Hall et al., 1999, 2004). Playa lakes are shallow basins with essentially impermeable floors that usually collect water during early spring rains and desiccate in late summer or fall (Haukos & Smith, 1994; Anderson & Smith, 2004). Because playas are ephemeral, many resident invertebrates lacking autonomous means for emigration have evolved specialized life cycles and physical adaptations for surviving drought (Belk & Cole, 1975; Wiggins et al., 1980; Pennak, 1989; Anderson & Smith, 2004). For example, the resting cysts of branchiopods and diapausing eggs of ostracods require environmental stimulus to eclose, such as changes in oxygen concentration, light, or temperature, which occur when playas fill with spring rains. More than 60 species of macroinvertebrates reside in playas, or use them as breeding or foraging sites (Sublette & Sublette, 1967; Merickel & Wangberg, 1981; Haukos & Smith, 1994; Hall et al., 1999; Anderson & Smith, 2004). However, diversity of invertebrates differs greatly among playas, depending partly on the persistence of water and surrounding landuse practices (Sublette & Sublette, 1967; Rhodes & Garcia, 1981; Hall et al., 1999; Hall et al., 2004).

In playa lakes, tadpole shrimp are primarily benthic detrital feeders that are abundant during the first few weeks of playa development (Sublette & Sublette, 1967; Moorhead et al., 1998). They forage mainly by plowing through the sediment (Dodson & Frey, 1991), but opportunistically consume other invertebrates (Ardo, 1948; Dodson, 1987; Pennak, 1989; Christoffersen, 2001). Tadpole shrimp have strong effects on abundance of dipteran prey species in ponds (Dodson, 1987; Walton, 2001) and may even be useful biological-control agents for mosquitoes (Tietze & Mulla, 1991; Fry et al., 1994). We hypothesize that tadpole shrimp substantially affect the abundance and diversity of invertebrates in playa lakes. Consequently, their removal should alter community composition and diversity of macroinvertebrate communities.

Materials and methods

Experimental procedures

Macroinvertebrate communities can be established in laboratory microcosms by simply adding water to playa soil containing drought-resistant stages (Anderson & Smith, 2004). These microcosms can be replicated, controlled, and manipulated in ways that are difficult or impossible to achieve *in situ*, such as the selective removal of tadpole shrimp. Additionally, non-resident migrants, especially predaceous insects, can be excluded so that effects of tadpole shrimp on the resident community may be examined without complications introduced by idiosyncratic presence of other predators.

To examine the effects of tadpole shrimp on macroinvertebrate community structure of playa microcosms, we established microcosms of 41 playa lakes and compared their macroinvertebrate communities in trials with and without tadpole shrimp. Treatment consisted of removing tadpole shrimp from microcosms; tadpole shrimp were retained in controls. Because lab space was limited to 41 aquaria, we conducted 4 separate trials from April to August in a fixed sequence of treatment, control, treatment, control. For each trial we established a microcosm for each of the 41 playas, subjected all 41 microcosms to either treatment or control, and maintained them for approximately one month. Microcosms were torn down at the end of each trial and re-established with fresh soil for the next trial.

Microcosms were established for each playa in each trial from soil samples collected from 41 playas in a 4-county area (Crosby, Floyd, Hale, and Lubbock) surrounding Lubbock, TX (see Hall et al., 2004 for details on playa lakes used in this study). Samples were obtained during the previous dry season, from November to January, after soils had been dry for 1–3 months. In each of the 41 playas, 40 random cores (5 cm deep, 6.4 cm diameter) were collected and combined to form a single, well-mixed soil sample. At the beginning of each trial, laboratory microcosms were established for each playa by adding 4 gal of distilled water to 800 g soil in a 18.9 l (5 gal) aquarium. Aquaria were maintained in a climate-controlled greenhouse (humidity: 60–70%, temperature: 29–35 °C). To reduce evaporative water loss and prevent invasion of aquaria by greenhouse pests, each aquarium was covered with a clear acrylic or glass plate.

For all trials, we sampled each microcosm one week after establishment by non-destructively siphoning water through an aquatic D-net, leaving the bottom layer of soil undisturbed. For treatment trials, tadpole shrimp were removed at this time, approximately 3–5 days after their emergence. The original water and all other invertebrates were returned to each aquarium. Control trials were treated in the same manner, but all invertebrates, including tadpole shrimp, were returned to each aquarium. Because smaller tadpole shrimp may be inconspicuous and new individuals may enclose during the second week, the treatment for many microcosms was a reduction in tadpole shrimp densities rather than their elimination, *per se*. After two weeks, all microcosms were sampled destructively by siphoning water through a D-net and collecting all invertebrates. Most invertebrates were classified to familial level.

Statistical analyses

Taxonomic richness, evenness, diversity, dominance, and total invertebrate abundance were calculated for each playa microcosm in each of the four trials, and compared to determine the effects of tadpole shrimp on invertebrate communities. Tadpole shrimp were excluded from calculations. Evenness or equitability (E) was estimated as $E = H'/\log S$, where H' is taxonomic diversity and S is taxonomic richness (Peilou, 1969). We calculated diversity (H′) by the Shannon–Weiner index as $H' = -\sum p_i (\log p_i)$, where p_i is the ratio of individuals in taxonomic group i to the total number of individuals in all taxonomic groups (Magurran, 1988). Dominance (D) was calculated as the Berger–Parker index: $D = N_{\max}/N$, where $N_{\max}$ is the density of the most abundant taxonomic group, and N is total invertebrate abundance (Magurran, 1988).

The effects of tadpole shrimp reduction on taxonomic richness, evenness, diversity, dominance, and total invertebrate abundance were tested with partly nested multivariate analysis of variance (MANOVA-PROC GLM, SAS Institute, 1990) to assess differences between treatments (reduced tadpole shrimp vs. controls), between trials within each treatment, and among playas, treated as a random effect. To determine if treatment effects were consistent among playas, we also examined the interaction between playa and treatment. Significant MANOVA effects were interpreted by examining univariate tests (ANOVA) for each of the five community characteristics, which have individual biological interest (Quinn & Keough, 2002). In order to homogenize variances and adhere to assumptions of normality, total abundance was square-root transformed (Sokal & Rohlf, 1995). We treated the total number of tadpole shrimp present in each microcosm during the first week of the experiment, i.e., prior to experimental reduction, as a covariate. Covariate effects were not significant, however, and subsequently dropped from analyses. In both treatment and control trials, some microcosms by chance had no tadpole shrimp. These microcosms were not excluded from analyses because we feel they contribute information about natural variability in tadpole shrimp density among playas.

We also examined the effects of tadpole shrimp on community composition by examining the abundances of each taxonomic group, excluding tadpole shrimp. We used Principal Components Analysis (PCA-PROC FACTOR, SAS Institute, 1990) to extract independent principal components representing major taxonomic compositions. In addition to PCA on non-transformed taxon abundances, two additional PCAs were run to address potential distortion due to rare taxa (Clarke & Warwick, 1994). First, taxon abundances were double square-root transformed to downweight abundances of abundant taxa. Second, because rare taxa can have a strong effect on PCA, analyses were run with only the seven most abundant (>100 individuals) taxa. In each analysis, principal components with eigenvalues greater than 1.00 were used (Hatcher & Stepanski, 1994) in subsequent analyses. The effect of tadpole shrimp on community composition was then tested using partly nested multivariate analysis of variance (MANOVA-PROC GLM, SAS Institute, 1990) to examine responses of retained principal components to treatments (reduced tadpole shrimp vs. controls), between trials within each treatment, and among playas, treated as a random effect. We also examined the interaction between playa and treatment. Significant MANOVA effects were interpreted using standardized canonical coefficients (Quinn & Keough, 2002) which account for the simultaneous responses of taxa within the community by quantifying the magnitude of the contributions of individual principal components in producing significant multivariate differences. Again tadpole shrimp density during the first week was treated as a covariate. Covariate effects were not significant, however, and subsequently dropped from analyses.

For control trials, we calculated Spearman rank correlation coefficients to quantify the association between tadpole shrimp density and abundance of each taxon, taxonomic richness, evenness, diversity, dominance, or total invertebrate abundance (SAS Institute, 1990). Results from the two control trials were combined using Fisher's test for combining probabilities (Sokal & Rohlf, 1995). Partial correlation coefficients also were calculated to assess direct effects of tadpole shrimp on each taxon after removing indirect effects via other taxonomic groups.

Results

Aside from tadpole shrimp, approximately 16000 aquatic invertebrates representing 17 taxonomic groups were collected from playa microcosms (Table 1). The most abundant groups, in descending order of abundance, were Moinidae (Cladocera), Cyprididae (Ostracoda), Diaptomidae (Copepoda), Sminthuridae (Collembola), Streptocephalidae (Anostraca), and Ilyocyprididae (Ostracoda).

Tadpole shrimp significantly affected community characteristics (richness, evenness, diversity, dominance, and total invertebrate abundance), despite considerable variability among playas (Tables 2 and 3). Multivariate analysis of variance indicated community characteristics were significantly different between treatments and among playas, but differences between trials only approached significance (Table 3). There was no significant playa x treatment interaction, indicating effects of tadpole shrimp removal were consistent among playas (Table 3). Subsequent

Table 1. Taxonomic composition of microcosms in which abundances of tadpole shrimp were reduced compared to controls in which no density reductions were in effect

		Tadpole shrimp reduction				Control			
		Trial 1		Trial 3		Trial 2		Trial 4	
Taxonomic group		Num.	Freq.	Num.	Freq.	Num.	Freq.	Num.	Freq.
Turbellaria		0	0	2	2	2	1	16	9
Acarina		1	1	0	0	0	0	0	0
Crustacea									
Anostraca	*Streptocephalidae*	118	16	61	12	28	11	173	21
	Thamnocephalidae	12	1	0	0	2	2	3	2
Notostraca	*Triopsidae*	44	22	23	13	114	34	84	26
Conchostraca	*Caenestheriidae*	2	2	0	0	8	3	1	1
Cladocera	*Daphnidae*	47	16	4	1	77	5	19	6
	Moinidae	2655	40	2364	28	3494	41	2662	34
	Unknown family	0	0	4	3	1	1	3	3
Ostracoda	*Cyprididae*	789	39	929	40	439	37	567	38
	Ilyocyprididae	45	13	126	21	46	15	76	24
Copepoda	*Diaptomidae*	172	25	304	33	364	34	364	31
Insecta									
Collembola	*Sminthuridae*	26	6	23	7	176	21	237	20
Coleoptera	*Curculionidae*	2	1	0	0	0	0	1	1
Diptera	*Chironomidae*	0	0	0	0	18	1	0	0
	Culicidae	1	1	0	0	0	0	0	0
	Ephydridae	0	0	1	1	10	4	19	3
	Psychodidae	0	0	5	3	0	0	0	0

Number (Num.) refers to the total abundance of individuals obtained from 41 replicate microcosms. Frequency of occurrence (Freq.) represents the number of microcosms that contained particular taxa.

Table 2. Mean and standard error (SE) of diversity, evenness, richness, dominance and total invertebrate abundance of microcosms in trials in which abundances of tadpole shrimp were reduced compared to control trials in which no density reductions were in effect

	Tadpole shrimp reduction				Control			
	Trial 1		Trial 3		Trial 2		Trial 4	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Abundance	94.39	11.53	93.24	13.69	113.78	15.6	101.0	15.15
Diversity	0.341	0.024	0.337	0.023	0.345	0.021	0.430	0.022
Evenness	0.585	0.035	0.612	0.039	0.563	0.035	0.672	0.033
Richness	3.930	0.220	3.680	0.160	4.290	0.210	4.710	0.210
Dominance	0.683	0.028	0.670	0.029	0.708	0.024	0.587	0.027

univariate analysis of total invertebrate abundance showed no significant differences among treatments (Table 3), although total abundance was negatively correlated with tadpole shrimp density in control trials (Fisher's test, $\chi^2 = 11.11$, $p = 0.025$). In contrast, taxonomic richness and diversity were significantly lower when tadpole shrimp were removed (Tables 2 and 3). In one control trial, richness (Spearman correlation: $r = 0.462$, $p = 0.002$) and diversity ($r = 0.308$, $p = 0.050$) in each microcosm were positively correlated with tadpole shrimp density.

The presence of tadpole shrimp affected community composition of playa microcosms. Here we present multivariate analyses for double square-root transformed taxon abundances, which balanced the contributions of rare and abundant taxa. Results from multivariate analyses on only the most abundant taxa or on non-transformed abundances were similar, except rare taxa had either no contribution or a stronger contribution to differences among factors. PCA of transformed abundances reduced the 17 taxonomic groups to 8 principal components which accounted for 63% of the variation in the taxon abundances. Taxonomic groups highly associated with each PCA factor are given in Table 4. Multivariate analysis of variance indicated community composition was significantly different between treatments, between trials within each treatment, and among playas (Table 4). There

Table 3. Multivariate analysis of variance (MANOVA) of the effect of treatment (control vs. reduced tadpole shrimp), trial within treatment, playa, and playa x treatment on total invertebrate abundance, diversity, evenness, richness, and dominance

	Treatment	Trial (Treatment)	Playa	Playa × Treatment
Multivariate				
Df	5, 36	10, 154	200, 200	200, 400
Pillai's trace	0.378	0.211	2.910	1.801
P	0.003	0.063	0.010	0.161
Univariate				
Df	1, 40	2, 80	40, 40	40, 80
F-values				
Abundance	0.46^{NS}	0.94^{NS}	1.88*	1.118^{NS}
Diversity	7.62**	3.06***	4.96**	0.85^{NS}
Evenness	0.36^{NS}	$3.02^{@}$	1.91*	0.95^{NS}
Richness	17.44***	1.94^{NS}	2.80***	0.93^{NS}
Dominance	1.28^{NS}	6.10**	$1.70^{@}$	1.08^{NS}

Univariate analyses were performed on each response variable to interpret significant MANOVA results. NS, not significant; @, $0.05 < p \leq 0.10$; *, $0.01 < p \leq 0.05$; **, $0.001 < p \leq 0.01$; ***, $p \leq 0.001$.

Table 4. Multivariate analysis of variance (MANOVA) of the effect of treatment (control vs. reduced tadpole shrimp), trial within treatment, playa, and playa × treatment on factors as determined by Principle Components Analysis

			Treatment	Trial (treatment)	Playa	Playa × treatment
		Df	8, 33	16, 148	320, 320	320, 640
		Pillai's trace	0.673	0.684	5.25	2.49
		P	< 0.001	< 0.001	< 0.001	0.844
	Significant ($p < 0.001$) correlations with taxa (r)		Standardized canonical coefficients			
PCA 1	Cyprididae (0.84), Ilyocyprididae (0.62), Turbellaria (0.44)		−0.793	−0.672	0.481	0.805
PCA 2	Streptocephalidae (0.77), Thamnocephalidae (0.80)		0.403	0.177	−0.511	0.303
PCA 3	Daphnidae (0.72), Chironomidae (0.83)		0.086	0.554	−0.109	0.727
PCA 4	Moinidae (0.70), Turbellaria (0.61), Psychodidae (−0.50)		1.039	0.878	−0.718	0.807
PCA 5	Caenestheriidae (0.76), Curculionidae (0.79)		−0.341	0.306	0.092	−0.347
PCA 6	Diaptomidae (−0.53), Ephydridae (0.40), Unk. cladoceran (0.82)		−0.214	−0.157	1.515	−0.03
PCA 7	Diaptomidae (0.53), Sminthuridae (0.54), Culicidae (−0.66)		0.777	−0.715	−0.315	−0.643
PCA 8	Sminthuridae (0.47), Acarina (0.86)		0.165	0.188	−0.16	0.085

Taxon abundances significantly correlated with PCA axes are given. Standardized canonical coefficients indicate the magnitude of contribution of each PCA factor in producing significant multivariate differences.

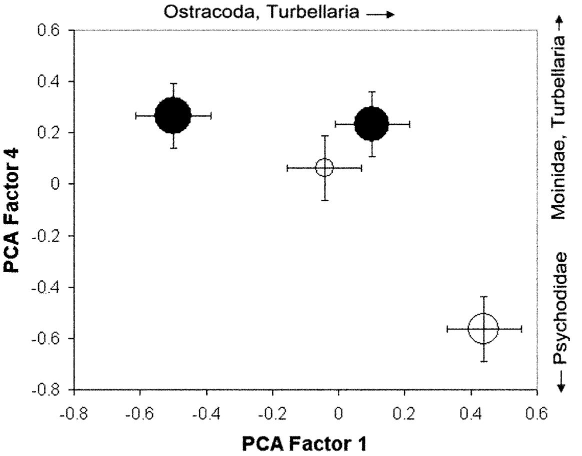

Figure 1. Means and standard errors of PCA factors contributing to significant differences among treatments for tadpole shrimp reduction trials (white circles) and control trials (black circles). Area of each circle indicates the relative size of PCA factor 7: increasing circle size reflects increasing abundances of Diaptomidae and Sminthuridae, and decreasing abundance of Culicidae.

was no significant playa *x* treatment interaction. Significant differences between treatment and control microcosms were primarily due to the responses of PCA factors 1, 4, and 7 (Table 4). This predominantly reflected higher abundances of ostracods, Psychodidae, and Culicidae, and reduced abundances of Moinidae, Diaptomidae, and Sminthuridae, when tadpole shrimp were removed (Fig. 1).

The abundance of Cyprididae was greatest when tadpole shrimp were removed (Table 1) and was correlated negatively with tadpole shrimp abundance in control microcosms (Fig. 2). Many taxa, however, evinced elevated abundances when tadpole shrimp were present compared to their abundances in reduction treatments (Table 1). Tadpole shrimp abundance was correlated positively with Streptocephalidae abundance and Sminthuridae abundance in control microcosms (Fig. 2). Partial correlation coefficients further confirmed that tadpole shrimp had direct, positive effects on abundances of Streptocephalidae and Sminthuridae (Fisher's test, $\chi^2 = 16.6$, $p < 0.001$ and $\chi^2 = 12.5$, $p = 0.017$, respectively).

For some taxa, the effects of tadpole shrimp removal contrasted patterns within control microcosms. Abundances of Moinidae and Diaptomidae tended to be higher in control microcosms than microcosms from which tadpole shrimp were

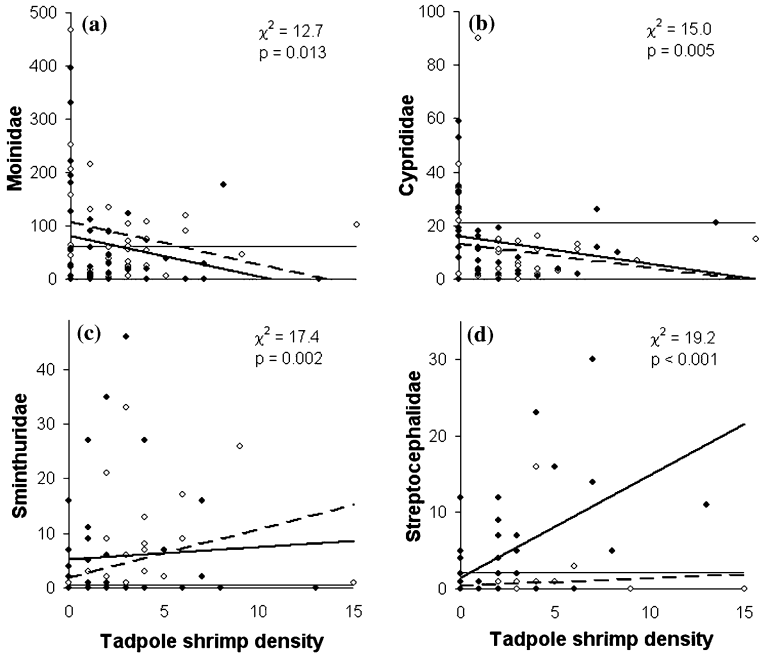

Figure 2. Relationship between tadpole shrimp density and abundance of (a) Moinidae, (b) Cyprididae, (c) Sminthuridae, and (d) Streptocephalidae in control trial 2 (open circles, dashed line) and control trial 4 (black circles, solid line). Results of Fisher's test for combining probabilities from Spearman rank correlations in each control trial are given. The thin horizontal line indicates the average abundance of each family in treatment microcosms.

removed. Hence, one might expect their abundances to be positively correlated with tadpole shrimp density across control microcosms. However within control trials, moinid density was negatively correlated with tadpole shrimp density (Fig. 2). Diaptomid abundance in microcosms was marginally correlated with tadpole shrimp density in one control trial ($r = -0.296$, $p = 0.060$). The presence of tadpole shrimp may be beneficial to these taxa, but such benefits decrease with increasing tadpole shrimp density.

Discussion

The macroinvertebrate composition of playa microcosms was highly variable within treatment groups, probably as a result of subtle differences in hatching cues among replicates, lack of perfect homogeneity in soil samples, natural variation in hatching rates for organisms, playa-specific differences in the taxonomic composition of innocula, and our ability to remove tadpole shrimp from treatment microcosms. Even within the statistical constraints imposed by such variability, it was clear that tadpole shrimp played an important role in structuring these communities.

The presence of tadpole shrimp was associated with reduced abundances of ostracods, Culicidae, and Psychodidae. Moinidae, Diaptomidae, Streptocephalidae, and Sminthuridae were positively affected by the presence of tadpole shrimp, and microcosms with tadpole shrimp had higher taxonomic richness and diversity. The importance of tadpole shrimp on playa microcosm communities is a consequence of their dual role as predators and ecosystem engineers, perhaps analogous to the effects that rodents have on desert plant communities through seed predation and burrowing activities (Moorhead et al., 1988; Brown & Heske, 1990; Willig & McGinley, 1999).

Tadpole shrimp are opportunistic predators that have been shown to decrease abundances of prey species (Dodson, 1987; Fry et al., 1994; Walton, 2001). As tadpole shrimp increase in abundance, the total number of prey consumed increases, leading to negative correlations between many taxon abundances and tadpole shrimp in control trials. Predation may be accelerated as tadpole shrimp broaden their diet as detritus becomes scarce. In addition, tadpole shrimp may have indirect positive effects on community diversity by preferentially preying on certain taxa, giving rarer competitors a better chance of survival (i.e., predator-mediated coexistence) and leading to increased taxonomic richness. Indeed, early stages of invertebrate community development in playas are dominated by detritivores (Moorhead et al., 1998), that may compete for resources.

In addition to predation, tadpole shrimp have foraging behaviors that may affect community structure. Tadpole shrimp feed by sifting through benthic debris and sediments. This may lead to direct competition with taxa, such as ostracods, which also tend to feed along the sediment surface (Delorme, 1991). Such competition could be responsible for negative correlations between many taxa and tadpole shrimp abundances in control trials. The foraging activities of tadpole shrimp may also be responsible for increased abundances of many taxa, increased richness, and increased diversity in the presence of tadpole shrimp. Tadpole shrimp scatter detritus as they feed, which floats to the water surface potentially benefiting detritivorous invertebrates, such as collembola, which feed along the surface film, and fairy shrimp, which filter the water column (Christiansen & Snider, 1984; Hilsenhoff, 1991). Moreover, the agitation of benthic sediments may increase the hatching rate of other invertebrates, such as cladocerans and clam shrimp, which rely on changes in light or oxygen concentration as hatching cues (Belk & Cole, 1975; Wiggins et al., 1980).

Microcosm communities undoubtedly differ from natural playa lakes (Anderson & Smith, 2004). Effects of tadpole shrimp on resident macroinvertebrate communities in microcosms may be representative of their effect during early succession. Overwintering residents such as phyllopod crustaceans generally dominate early successional stages of playa invertebrate communities (Sublette & Sublette, 1967; Moore, 1970; Lake et al., 1989). Consequently, tadpole shrimp may exert strong influences on invertebrate communities during the first few weeks of playa inundation when relative abundances of insect predators and other immigrants are low (Lake et al., 1989; Schneider & Frost, 1996; Moorhead et al., 1998). The composition of early resident communities may influence later stages of succession which transpire when conditions are more favorable for transient species (Lake et al., 1989). Particularly, the presence of tadpole shrimp may reduce the establishment of mosquito populations (Tietze & Mulla, 1991; Fry et al., 1994), although this is difficult to ascertain as Culicidae were rare in experimental microcosms.

Whether early successional effects of tadpole shrimp are strong enough to influence macroinvertebrate communities in playa lakes remains to be seen. Invertebrate diversity in playas of West Texas are affected by a wide range of local factors, including period of inundation, basin modification by agricultural practices, and vegetation (Sublette & Sublette, 1967; Rhodes & Garcia, 1981; Bolen et al., 1989; Haukos & Smith, 1994; Hall et al., 1999; Hall et al., 2004). Furthermore, the effects of a single species, such as tadpole shrimp, on community structure likely depends on many contextual factors such as productivity (Balciunas & Lawler, 1995; Leibold, 1996), disturbance (Menge et al., 1994), and community composition (Power et al., 1996).

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