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Effects of hydroperiod and predation on a Mississippi River floodplain invertebrate community

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Abstract The objective of this study was to determine if pond permanence and vertebrate predation (by fish and waterfowl) affect invertebrate community structure in the mudflat habitat of floodplain ponds. Invertebrate communities were studied for 1 year in four Mississippi River floodplain ponds with different hydroperiods. Pond 1 experienced five dry periods, pond 2 experienced four, pond 3 dried once, and standing water remained in pond 4 for the entire year. Vertebrate predator exclusion treatments (all access, no access, small-fish access and cage controls) were placed in all ponds. As pond duration increased, predatory invertebrate richness and abundance increased while overall invertebrate richness and abundance decreased. With the exception of the cladoceran *Diaphanosoma*, all commonly encountered taxa were strongly affected by pond permanence in terms of abundance, biomass and, generally, individual biomass. Taxa were nearly evenly divided between those that were more abundant in less permanent ponds and those that were more abundant in longer-duration ponds. Invertebrate taxa richness, abundance, and total biomass were lower in the all-access treatment than in the treatments that restricted predator access, and these effects were stronger in the more permanent ponds. In general, there were no significant differences in responses to the treatments with small-fish access and no access. These results support models that predict relatively weak effects of predation in frequently disturbed habitats.

Key words Disturbance frequency · Habitat duration · Macroinvertebrates · Floodplain ponds · Predation

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Introduction

The roles of abiotic and biotic factors in shaping the organization of communities has been of enduring interest to community ecologists. Physical factors are often emphasized as determining patterns in the distribution and abundance of species over broad scales, while the relative importance of biotic factors is thought to be greater over more local scales (Dayton and Tegner 1984; Menge and Olson 1990; Levin 1992). Although there has been a tendency to stress the importance of biotic factors (Dunson and Travis 1991), it is clear that abiotic and biotic factors can interact strongly over local scales to affect the structure of communities (e.g., Connell 1978; Paine and Levin 1981; McAuliffe 1984). Identifying how a complex interplay of factors affects the organization of communities and the scale dependency of various structuring mechanisms remains an important challenge to community ecologists.

In temporary ponds, the hydrologic cycle strongly influences which species can maintain populations. To complete their life cycles, organisms must be able to withstand desiccation or must complete development and emerge before the pond dries (Schneider and Frost 1996). The long larval periods of some organisms preclude the use of temporary ponds, while explosive breeders may colonize new ponds to avoid high risks of predation and competition (Wilbur 1987). The strength and relative importance of biotic interactions (e.g., competition versus predation) in affecting community structure should also depend on the hydrologic cycle of a pond. Competition and predation may be relatively unimportant in ponds that dry and refill frequently, while in more permanent ponds, predators may maintain prey densities at levels that preclude strong competitive interactions among prey (Wilbur 1987).

Floodplain systems provide a gradient in size and permanence of temporary ponds and these conditions change with the flood stage of the adjacent river (Drago 1989; Doss 1993). As river water enters the floodplain, ponds may become connected to the river depending up-

on flood magnitude and position of ponds relative to the river. River water can serve as a source of colonists for these ponds. In addition, terrestrial barriers between ponds may be eliminated during a flood, allowing organisms to move between ponds. Thus, ponds that, by chance, had lacked vertebrate predators may be colonized by them during floods. This scenario suggests that community dynamics in floodplain ponds should be more strongly influenced by colonization processes than other temporary ponds (see Schneider and Frost 1996).

Many North American large river floodplains have been altered and are now managed for the production of waterfowl. Hydroperiods are frequently managed to reduce water levels, resulting in increased germination of moist-soil plants, an important waterfowl food source. Such management has been shown to either have no effect (Batzer and Resh 1992) or a negative effect (Paterson and Fernando 1969; Kaster and Jacobi 1978; Huener and Kadlec 1992) on invertebrate communities.

As the water level declines in floodplain ponds, predation by waterfowl on benthic invertebrates increases (Reid et al. 1990). Migratory waterfowl have been shown to affect pond invertebrate communities in the spring (Krull 1976) and autumn (Peterson et al. 1989). In contrast, as water levels increase, allowing colonization and survival of fish, risk of predation to benthic invertebrates by fish increases (Batzer and Resh 1992). Fish are well known to structure invertebrate communities in littoral areas of permanent ponds and lakes (Hall et al. 1970; Gilinsky 1984; Post and Cucin 1984; Mittlebach 1988; Luecke 1990; Huener and Kadlec 1992). Similarly, invertebrate species richness has been observed to decline with increasing water depth (Banaszak and Kasprzak 1980). Therefore, water level fluctuations, waterfowl predation, and fish predation could interact in complex

ways to affect the structure of invertebrate communities in floodplain ponds.

The purpose of our study was to examine the effects of predation and pond permanence on the benthic invertebrate community of the open water habitat in floodplain ponds. We estimated the invertebrate biomass available to predators in ponds with different hydroperiods and we used predator exclusion to assess whether fish and waterfowl affect invertebrate community structure in this habitat.

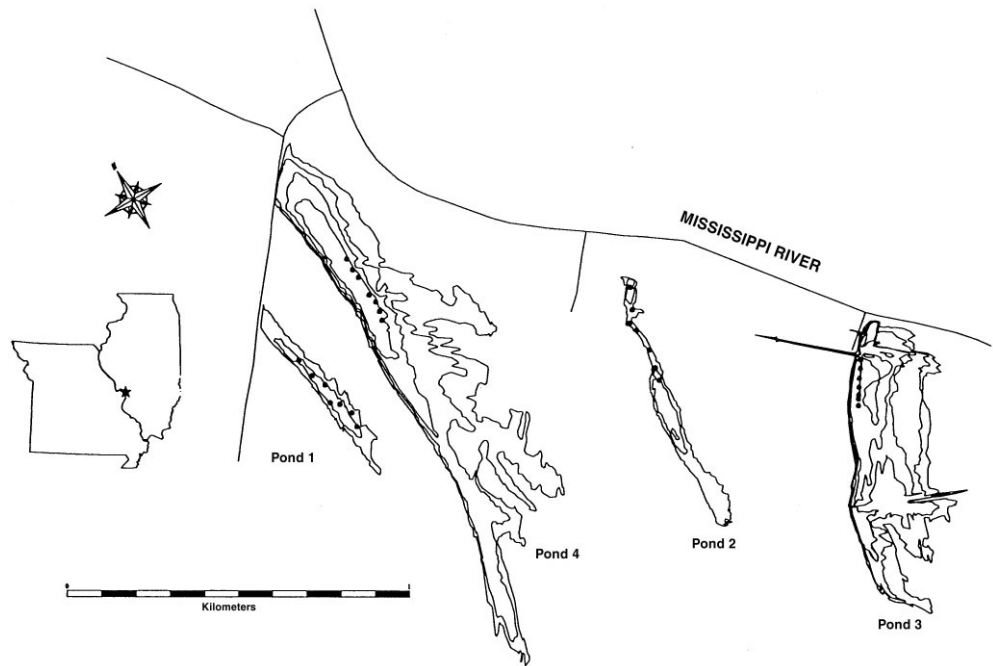
Materials and methods

Study site

This study was conducted at the US Army Corps of Engineers Riverlands Environmental Demonstration Area Wildlife Refuge (EDA; Fig. 1), located upstream of Melvin Price Lock and Dam at reach 26 of the Mississippi River in St. Charles, Missouri, 30 km (18 river miles) upstream from St. Louis. The Riverlands is a wetland complex 3.33 km in length and 0.833 km in width. The ponds are natural depressions and are connected by dredged channels extending to the Mississippi River through flood control levees. This site was restored from farmland to wetland prairie during 1989. The wetlands used were not aggressively managed by pumping. The timing and magnitude of flooding, as well as drying, were determined by water levels in the Mississippi River. The Corps operates the dam to maintain a constant water level at a gauge midway between the downstream dam and the next dam upstream. Therefore, when a large flood is anticipated, the dam gates are opened further, thereby lowering the water level at the downstream end of the reach (Sparks 1992). When the water level in reach 26 was lowered, water drained from the EDA. When the water level at the river gauge was greater than 419 ft above sea level, fish and invertebrate were able to access the area through channels. Waterbirds also used the area when it was wet.

The four ponds (Fig. 1) differed in topography and proximity to the river and therefore had different hydroperiods. Two ponds were mostly wet throughout the study, while the others were ex-

Fig. 1 A map of the Corps of Engineers Riverlands Environmental Demonstration Area, which is located next to pool 26 of the Mississippi River and Ellis Bay Waterfowl Refuge in West Alton, Missouri, 30 km upstream of St. Louis. The site has four ponds with slightly different hydrological patterns due to area topography and proximity to the river. Depth contours are for 30.5-cm intervals. Filled circles mark the location of sampling plots



pected to dry periodically. Great blue herons (*Ardea herodias*), great egrets (*Casmerodius albus*), mallards (*Anas platyrhynchos*), and other waterfowl regularly used the area. When water levels permitted, carp (*Cyprinus carpio*), green sunfish (*Lepomis cyanellus*), goldfish (*Carassius auratus*), and killifish (*Fundulus* sp.) were observed in all ponds. Fish population densities were not determined.

Methods

Seven 1×1 m sampling plots were established in the deepest point of each pond. This area was chosen to minimize the effects of daily fluctuations in water level. Three predator access treatments were applied to each pond and each was replicated twice. Two plots in each pond were open to all predators and no cage was placed on them. This treatment will be referred to as "all access". The remaining plots received exclusion cages of 1×1 m to restrict predator access. The cages were constructed using 0.4-cm plastic mesh attached to a wooden frame. Three sides and the top of each cage were covered with this mesh; the bottom was open to allow benthos immigration and emigration. The fourth side of the cage varied depending on treatment: for "no access" the final side was covered with the 0.4-cm mesh; for the "small-fish access" it was covered with 5.08 cm×7.62 cm mesh. The ponds also had one cage control plot to assess the effect of the cage structure on the invertebrate community. The fourth side of the cage controls was not covered with plastic screen. Treatments were randomly assigned to the seven plots in each pond. Except during rare high water, the cages protruded from the water and were easily sampled by lifting the top. The cages were placed in the ponds in November 1991 and secured with steel rods.

Water depth measurements were taken daily from the deepest point in each pond. If puddling was observed, but the amount of standing water was not measurable, and the benthos sampler (see below) could penetrate the soil, it was considered moist. Dry soil indicated no standing water, terrestrial plants germinated, and the sampler could not penetrate the soil. Invertebrate samples were taken at monthly intervals from January 1992–December 1992. Dissolved oxygen, temperature, pH and conductivity were measured in each pond on most sampling dates. Invertebrate samples were taken using a Plexiglass core sampler (area=0.0035 m²) to a depth of 10 cm. Two random samples were taken from each plot and preserved with 10% formalin. Samples were taken only when the ground was moist enough to allow penetration of the sampler and therefore none were taken when ponds were dry. Samples were rinsed through a 80-µm sieve, and sorted in their entirety at ×10 magnification. Samples with large numbers of individuals of certain taxa, especially Chironomidae and Oligochaeta, were subsampled prior to identification of those taxa. Only whole individuals or anterior ends of aquatic Oligochaeta were counted and identified using Brinkhurst (1986). Chironomidae (Weiderholm 1983; Merritt and Cummins 1984) and all other macroinvertebrates (Thomsen 1937; Chu 1949; Merritt and Cummins 1984; Balcer et al. 1984; Wiggins 1977; Burch 1989; Provonsha 1990) were identified to the lowest possible taxonomic level. Biomass was estimated from length-dry mass regressions on organisms from the EDA for all taxa except zooplankton (D. Corti, unpublished data). Gastropod mass was measured without shells. Zooplankton mass was estimated using published length-dry mass regressions (Dumon et al. 1975; Culver et al. 1985).

A Friedman rank analysis was used to test for differences in chemistry between ponds. A chi-square test was used to detect differences in hydroperiods of the four ponds by assessing number of days with standing water, moist soil (small puddles but no measurable depth over the deepest part of the pond), and dry soil. Taxa were separated into predator or nonpredator categories. Repeated-measure one-way ANOVAs, blocking by pond, were used to determine differences among predator treatments in taxa richness, total invertebrate abundance, and total biomass for each category. Because we were interested in whether predation effects were mediated by pond permanence, we included all possible interactions

with the blocking factor in the model. All dependent variables were transformed by $\log_{10}(X+1)$ (abundance) or $\log_{10}(X+0.001)$ (biomass) to stabilize variances. If the pond×predator interaction was insignificant, we repeated the analysis using untransformed data, because measurement scale (i.e., transformed versus untransformed) can affect interpretation of interaction effects (Winer 1971). Repeated-measure ANOVAs on abundance, mean individual biomass and total biomass were also performed for taxa that were commonly observed in the ponds.

Because the cage control treatment was unreplicated, it was not included in the model. Rather, we tested for systematic bias in the cage controls relative to the all-access treatment (open plots). For each pond and sampling date, we recorded whether the cage control value was less, greater or within one standard deviation (SD) of the no-access mean. These scores were tallied for all ponds and sampling dates. If there was no bias associated with the cage control, then an equal number of values should have occurred above and below the all-access mean±1 SD. We tested for departures from this expectation using binomial tests.

Orthogonal a priori contrasts were used to identify factors responsible for significant treatment effects. For the pond effects, orthogonal contrasts compared the two more temporary ponds (pond 1 vs pond 2), the two more permanent ponds (pond 3 vs pond 4), and the temporary ponds against the permanent ponds (1 and 2 vs 3 and 4). Orthogonal contrasts of the predator effect tested for a small-fish effect by comparing the plots with restricted predator access (small-fish access vs. no access) and for an overall effect of vertebrate predators (all access versus restricted access). Contrasts for the pond×predator interaction were the six possible combinations of orthogonal contrasts for pond and predator effects. Statistical analyses were conducted only on the eight sampling dates that all ponds had standing water.

Results

The water level in the Mississippi River at reach 26 near the dam in 1992 did not experience an unusual flood or drought. Normal river fluctuations resulted in periodic flooding of the EDA. The temporary wetland ponds in the

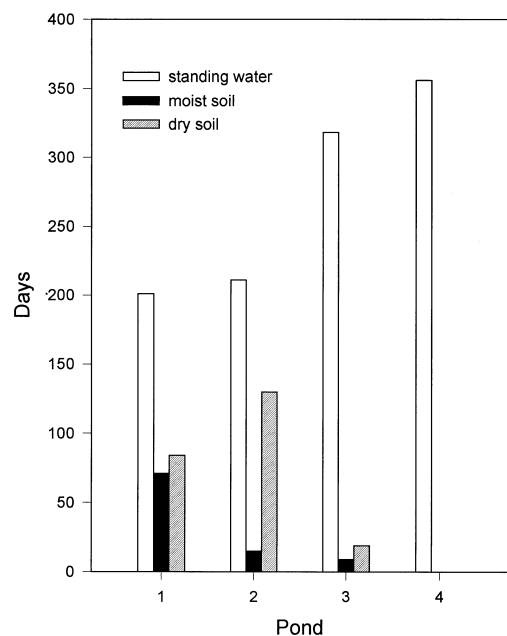


Fig. 2 The number of days during the study that each pond contained standing water, moist soil but no standing water, or dry soil

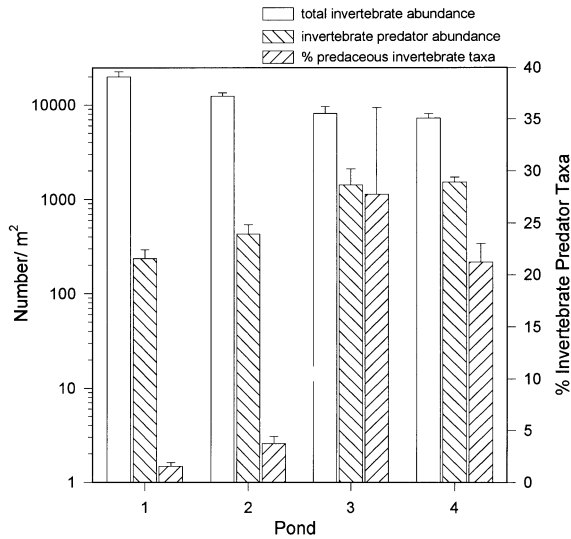


Fig. 3 Total invertebrate abundance (number/m²), the abundance of predaceous invertebrates, and the percentage of invertebrate taxa that were predaceous in each pond. Results are the mean±SE averaged over all sampling dates and treatments (n=33)

Table 1 Repeated measures ANOVA for the three summary variables of benthic invertebrate community structure

Source	SS	df	F	P	Adjusted P ^a
Taxon richness					
Pond	0.389	3	3.855	0.038	
Predator	0.409	2	3.079	0.015	
Pond×predator	0.362	6	1.794	0.183	
Error	0.404	12			
Date	0.485	7	2.453	0.024	0.058
Date×pond	2.460	21	4.146	0.000	0.000
Date×predator	0.118	14	0.299	0.993	0.964
Date×pond×predator	0.567	42	0.478	0.995	0.974
Error	2.373	84			
Abundance					
Pond	8.155	3	54.626	0.000	
Predator	1.305	2	13.108	0.001	
Pond×predator	2.016	6	6.763	0.003	
Error	0.597	12			
Date	5.497	7	9.871	0.000	0.000
Date×pond	7.9	21	4.728	0.000	0.000
Date×predator	0.538	14	0.483	0.872	0.872
Date×pond×predator	3.403	42	1.019	0.461	0.464
Error	6.683	84			
Total biomass					
Pond	5.520	3	10.697	0.001	
Predator	2.902	2	8.436	0.005	
Pond×predator	3.478	6	3.370	0.035	
Error	2.064	12			
Date	14.559	7	14.923	0.000	0.000
Date×pond	24.125	21	8.242	0.000	0.000
Date×predator	0.841	14	0.431	0.960	0.991
Date×pond×predator	0.519	42	1.284	0.165	0.217
Error	11.708	84			

^a Significance level adjusted by the Greenhouse-Geiser epsilon method

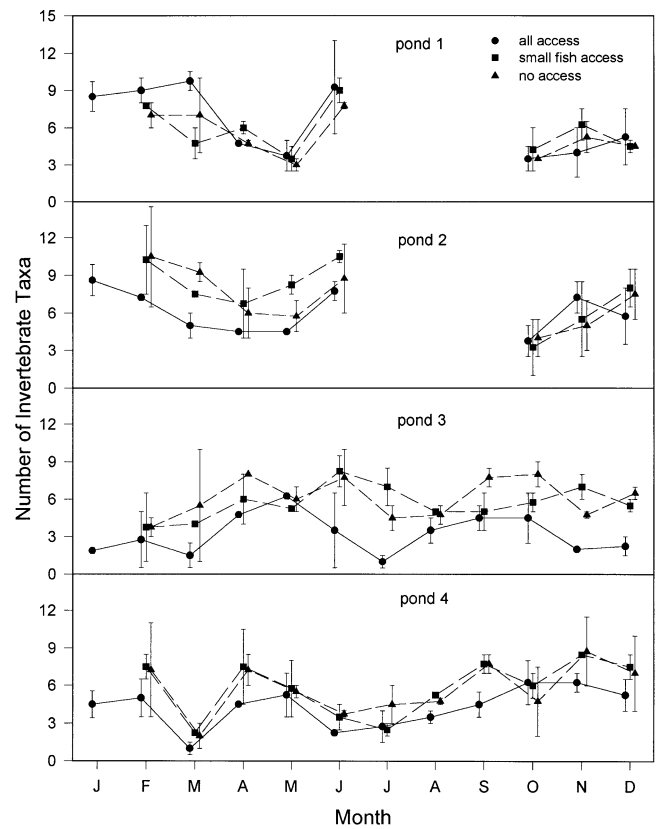


Fig. 4 Invertebrate taxa richness (mean±SE, n=2) in each pond for each predation treatment: circles indicate open plots, squares indicate small-fish access, and triangles indicate no access. Only open plots were sampled in January

EDA varied in their response to the inundation. Pond 1 dried out five times, had the least number of days with standing water, and the most days with moist soil. Pond 2 dried four times, had slightly more days with standing water, fewer moist-soil days, and the most dry-soil days. Ponds 1 and 2 lacked standing water for much of March–May and July–September. Pond 3 dried out once for a few days, and pond 4 had measurable standing water throughout the study (Fig. 2). These hydroperiod differences among ponds were highly significant ($\chi^2=364.07$, $df=6$, $P<0.001$). Pond water chemistry (dissolved oxygen, pH, conductivity, temperature) did not differ between ponds, although pond 4 tended to be slightly cooler (Friedman=6.94, $P=0.074$).

A total of 98 invertebrate taxa were observed during the study, of which 49 were found in all ponds. Thirty-one taxa were found only in the less permanent ponds (ponds 1 and 2) and 18 were found only in the longer-duration ponds (ponds 3 and 4). However, all but one of these 49 taxa with restricted distributions were encountered rarely (i.e., mean abundance/sample was ≤ 1 individual in all treatments on most sampling dates).

Total invertebrate abundance decreased as pond permanence increased. The abundance of predatory invertebrates and the proportion of invertebrate taxa composed

Table 2 Summary of *F* values and their significance levels from repeated-measures ANOVAs for responses of individual taxa to the pond treatment and, if significant, the results of orthogonal contrasts for comparisons among ponds. Months (1 January, 2 February, and so on) included in the analysis for a given taxon were those in which the mean density was >1 individual/sample, averaged over all ponds, in at least one of the predator treatments. Degrees of freedom were 3,12 for test of the pond effect and 1,12 for the orthogonal contrasts. Ponds are denoted by number, and by *LP* (=less permanent; ponds 1 and 2) and *MP* (=more permanent: ponds 3 and 4). A *dash* indicates that the test was not performed

Taxon	Month	Pond effect	1 vs. 2	3 vs. 4	LP vs. MP
Abundance					
Coleoptera					
<i>Berosus</i>	6	12.4**	1<2***	3=4	LP>MP**
Chironomidae					
Chironomini					
<i>Chironomus</i> ^a	2, 5, 6, 10–12	14.2***	1<2***	3=4	LP<MP**
<i>Dicrotendipes</i> ^a	2, 3, 5, 6, 10–12	13.6***	1<2*	3>4*	LP>MP**
<i>Endochironomus</i> ^a	2, 3, 5, 6, 11, 12	15.1***	1=2	3=4	LP>MP***
<i>Polypedilum</i> ^a	2, 3, 6	20.8***	1<2***	3>4*	LP>MP***
Other Chironomini ^a	6, 10, 11	25.8***	1<2**	3>4***	LP<MP**
Tanytarsini ^a	2–6	67.9***	1<2***	3=4	LP>MP***
Orthocladiinae	2, 11, 12	87.0***	1<2***	3=4	LP>MP***
Tanypodinae ^a	2, 6, 10	6.4**	1=2	3<4**	LP=MP
Ceratopogonidae					
<i>Palpomyia</i> ^a	3, 4, 10–12	136.4***	1=2	3<4**	LP<MP***
Crustacea					
Ostracoda ^a	10–12	4.5*	1=2	3=4	LP<MP***
Cladocera					
<i>Diaphanosoma</i>	5, 10, 11	0.2	–	–	–
Copepoda ^a	2, 4, 5, 10–12	49.9***	1=2	3>4*	LP>MP***
Nematoda	2, 6, 10–12	20.9***	1>2***	3=4	LP=MP
Oligochaeta					
<i>Branchiura</i> ^b	2, 4, 5, 10–12	–	–	–	–
Other oligochaetes	2–6, 10–12	124.7***	1>2***	3<4**	LP>MP***
Gastropoda					
<i>Physella</i>	3, 6	33.7***	1>2***	3=4	LP>MP***
Individual biomass					
Coleoptera					
<i>Berosus</i>	6	4.1*	1=2	3=4	LP=MP
Chironomidae					
Chironomini					
<i>Chironomus</i> ^a	2, 5, 6, 10–12	4.0*	1<2**	3=4	LP=MP
<i>Dicrotendipes</i> ^a	2, 3, 5, 6, 10–12	26.0***	1<2*	3=4	LP>MP***
<i>Endochironomus</i> ^a	2, 3, 5, 6, 11, 12	15.7***	1=2	3=4	LP>MP***
<i>Polypedilum</i> ^a	2, 3, 6	2.6	–	–	–
Other Chironomini ^a	6, 10, 11	10.7**	1<2***	3>4***	LP<MP*
Tanytarsini ^a	2–6	18.6***	1<2***	3=4	LP>MP***
Orthocladiinae	2, 11, 12	53.3***	1<2*	3=4	LP>MP***
Tanypodinae ^a	2, 6, 10	5.5*	1=2	3<4**	LP=MP
Ceratopogonidae					
<i>Palpomyia</i> ^a	3, 4, 10–12	33.1***	1<2**	3=4	LP<MP***
Crustacea					
Ostracoda ^a	10–12	6.2**	1=2	3=4	LP<MP***
Cladocera					
<i>Diaphanosoma</i>	5, 10, 11	0.0	–	–	–
Copepoda ^a	2, 4, 5, 10–12	9.4***	1=2	3=4	LP>MP***
Nematoda	2, 6, 10–12	4.3*	1>2*	3=4	LP=MP
Oligochaeta					
<i>Branchiura</i> ^b	2, 4, 5, 10–12	–	–	–	–
Other oligochaetes	2–6, 10–12	3.9*	1=2	3=4	LP>MP**
Gastropoda					
<i>Physella</i>	3, 6	57.3***	1>2***	3=4	LP>MP***
Total biomass					
Coleoptera					
<i>Berosus</i>	6	4.9*	1<2*	3=4	LP=MP

Table 2 (continued)

Taxon	Month	Pond effect	1 vs. 2	3 vs. 4	LP vs. MP
Chironomidae					
Chironomini					
<i>Chironomus</i> ^a	2, 5, 6, 10–12	5.3*	1<2**	3=4	LP=MP
<i>Dicortendipes</i> ^a	2, 3, 5, 6, 10–12	20.1***	1<2**	3>4*	LP>MP***
<i>Endochironomus</i> ^a	2, 3, 5, 6, 11, 12	24.1***	1=2	3=4	LP>MP***
<i>Polypedilum</i> ^a	2, 3, 6	5.5*	1<2*	3>4*	LP=MP
Other Chironomini ^a	6, 10, 11	19.1***	1<2**	3>4***	LP<MP*
Tanytarsini ^a	2–6	28.2***	1<2***	3=4	LP>MP***
Orthocladiinae	2, 11, 12	95.7***	1<2***	3=4	LP>MP***
Tanypodinae ^a	2, 6, 10	6.4**	1=2	3<4**	LP<MP*
Ceratopogonidae					
<i>Palpomyia</i> ^a	3, 4, 10–12	64.7***	1<2*	3=4	LP<MP***
Crustacea					
Ostracoda ^a	10–12	5.2*	1=2	3=4	LP>MP***
Cladocera					
<i>Diaphanosoma</i>	5, 10, 11	0.2	–	–	–
Copepoda ^a	2, 4, 5, 10–12	25.5***	1=2	3=4	LP>MP***
Nematoda					
	2, 6, 10–12	7.6**	1>2***	3=4	LP=MP
Oligochaeta					
<i>Branchiura</i> ^b	2, 4, 5, 10–12	–	–	–	–
Other oligochaetes	2–6, 10–12	39.5***	1>2***	3<4*	LP>MP***
Gastropoda					
<i>Physella</i>	3, 6	59.3***	1>2***	3=4	LP>MP***

* $P<0.05$; ** $P<0.01$;

*** $P<0.001$

^a The pond×date interaction was significant (see text)

^b Taxon found only in pond 4

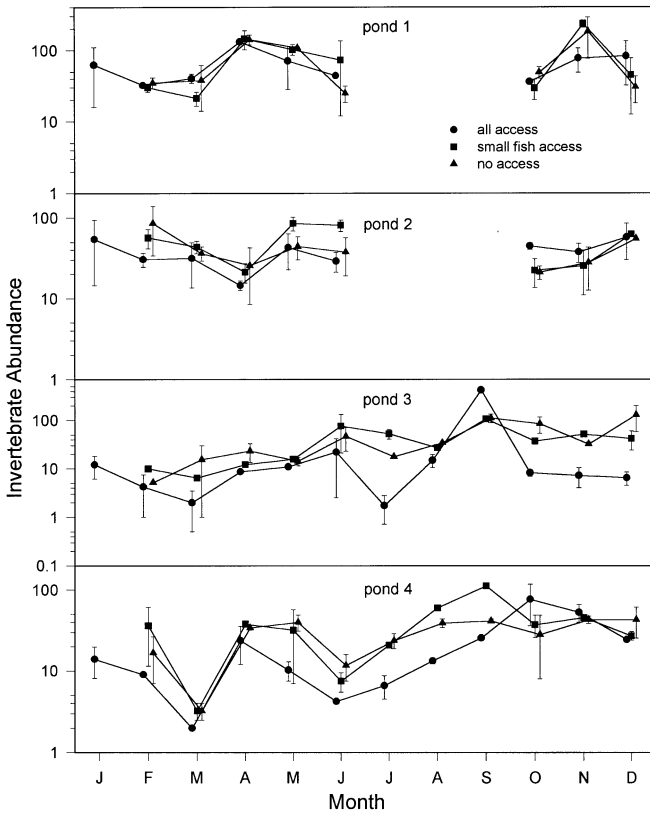


Fig. 5 Invertebrate abundance (number per core sample; mean±SE, n=2) in each pond and predation treatment. Symbols as in Fig. 4

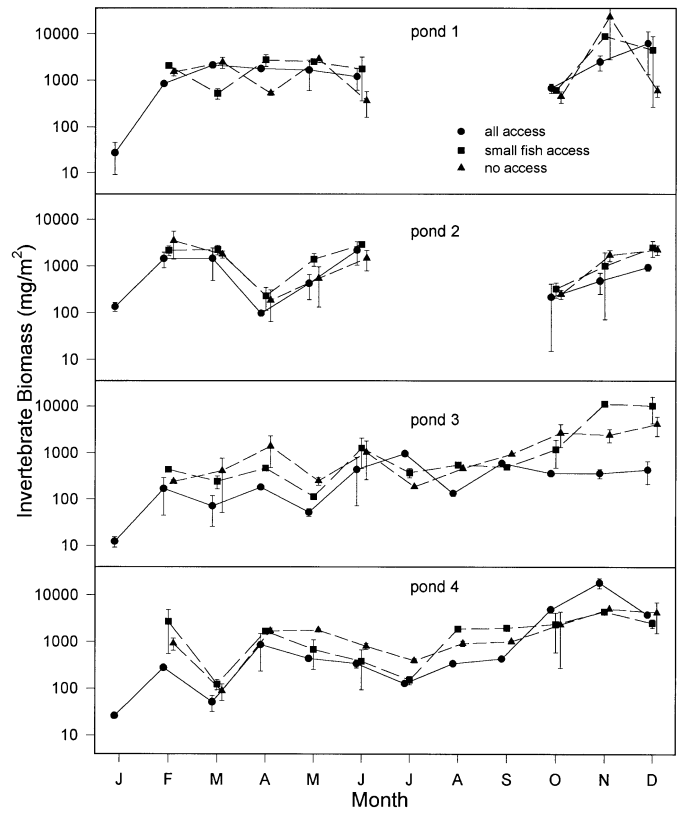


Fig. 6 Total invertebrate biomass (mg/m²; mean±SE, n=2) in each pond and predation treatment. Symbols as in Fig. 4

Table 3 Summary of *F* values and their significance levels from repeated-measures ANOVAs for responses of individual taxa to the predator treatments. Results of orthogonal contrasts of the all-access (*AA*) and restricted-access (*RA*=no access+small-fish access) treatments are presented if the predator effect or the pond×predator interaction was significant. Dates included in the analysis for a given taxon are as given in Table 2. Degrees of freedom were 2,12 for test of the predator effect and 1,12 for the orthogonal contrasts. Ponds are denoted as in Table 2. A *dash* indicates that the test was not performed. Unless noted otherwise, a significant contrast resulted when $AA < RA$

Taxon	Source of variation				
	Predator		Pond×predator		
	Overall	AA vs. RA	(1 vs. 2)* (AA vs. RA)	(3 vs 4)* (AA vs. RA)	(LP vs. MP)* (AA vs. RA)
Abundance					
Coleoptera					
<i>Berosus</i>	1.3	–	–	–	–
Chironomidae					
Chironomini					
<i>Chironomus</i>	12.9***	15.0**	17.7*	36.0***	0.3
<i>Dicrotendipes</i>	5.3**	10.0**	–	–	–
<i>Endochironomus</i>	4.6*	9.2*	–	–	–
<i>Polypedilum</i> ^a	18.3***	33.3***	9.1*	1.6	6.3*
Other Chironomini	4.9**	9.2*	1.0	11.3**	5.2*
Tanytarsini	1.2	–	–	–	–
Orthocladiinae	0.6	–	–	–	–
Tanypodinae	0.8	–	–	–	–
Ceratopogoniidae					
<i>Palpomyia</i>	6.4*	12.5**	1.0	18.2*	26.4***
Crustacea					
Ostracoda	1.4	–	–	–	–
Cladocera					
<i>Diaphanosoma</i>	0.1	–	–	–	–
Copepoda	0.5	–	–	–	–
Nematoda	45.4***	89.4***	10.5**	1.4	31.2***
Oligochaeta					
<i>Branchiura</i> ^b	7.1	–	–	–	–
Other oligochaetes	0.5	–	0.4	13.1**	19.8***
Gastropoda					
<i>Physella</i>	0.3	–	–	–	–
Individual biomass					
Coleoptera					
<i>Berosus</i>	0.7	–	–	–	–
Chironomidae					
Chironomini					
<i>Chironomus</i>	5.2*	9.1**	0.4	15.0***	5.8**
<i>Dicrotendipes</i> ^c	1.0	–	0.0	0.2	2.3
<i>Endochironomus</i>	4.0*	7.7*	–	–	–
<i>Polypedilum</i>	5.7**	7.1**	–	–	–
Other Chironomini	2.7	3.5	1.2	10.6**	5.6*
Tanytarsini ^c	1.2	–	5.1*	2.4	1.1
Orthocladiinae	1.0	–	–	–	–
Tanypodinae	1.5	–	–	–	–
Ceratopogonidae					
<i>Palpomyia</i>	1.9	–	0.8	12.7**	1.5
Crustacea					
Ostracoda	1.1	–	–	–	–
Cladocera					
<i>Diaphanosoma</i>	0.8	–	–	–	–
Copepoda	0.9	–	–	–	–
Nematoda	22.0***	34.4***	–	–	–
Oligochaeta					
<i>Branchiura</i> ^b	5.4	–	–	–	–
Other oligochaetes	0.0	–	–	–	–
Gastropoda					
<i>Physella</i>	0.6	–	–	–	–
Total biomass					
Coleoptera					
<i>Berosus</i>	0.8	–	–	–	–

Table 3 (continued)

Taxon	Source of variation				
	Predator		Pond×predator		
	Overall	AA vs. RA	(1 vs. 2)* (AA vs. RA)	(3 vs 4)* (AA vs. RA)	(LP vs. MP)* (AA vs. RA)
Chironomidae					
Chironomini					
<i>Chironomus</i>	6.4*	10.6**	2.5	17.7**	3.0
<i>Dicrotendipes</i>	4.4*	8.6*	—	—	—
<i>Endochironomus</i>	7.0**	13.8**	—	—	—
<i>Polypedilum</i> ^a	9.3***	13.3**	—	—	—
Other Chironomini	4.6*	8.3*	1.2	14.2**	7.1*
Tanytarsini	1.3	—	—	—	—
Orthoclaadiinae	1.2	—	—	—	—
Tanypodinae	1.6	—	—	—	—
Ceratopogonidae					
<i>Palpomyia</i>	2.4	—	1.1	22.6***	7.5*
Crustacea					
Ostracoda	1.2	—	—	—	—
Cladocera					
<i>Diaphanosoma</i>	0.2	—	—	—	—
Copepoda	0.5	—	—	—	—
Nematoda	34.3***	57.9***	12.4**	0.24	13.8**
Oligochaeta					
<i>Branchiura</i> ^b	12.8**	21.8*	—	—	—
Other oligochaetes	0.1	—	0.4	5.4*	11.5***
Gastropoda					
<i>Physella</i>	0.2	—	—	—	—

* $P < 0.05$; ** $P < 0.01$;

*** $P < 0.001$

^a The predator×date interaction was significant

^b Taxon only found in pond 4: df for ANOVA=2,3; df for contrast=1,3

^c The pond×cage interaction was not significant using log-transformed data. Results using untransformed data are reported here

of predators increased with water duration (Fig. 3). Because of this pattern, separate analyses were performed for nonpredaceous and predaceous invertebrates. Both groups responded similarly to the treatments, but due to the low numbers of predatory invertebrates found in the less permanent ponds, the results presented here are pooled over all invertebrate taxa.

There was no evidence that the results for the cage control were systematically biased relative to results for the all-access treatment (open plots). For all dependent variables combined, the percentage of cage control values that fell above, below, and within 1 SD of the all-access mean was 36%, 29%, and 35%, respectively ($n=128$). There was no significant difference in the number of cage control values less than or greater than the all-access mean±1 SD (binomial tests: abundance, $P=0.38$; taxa richness, $P=0.30$; total biomass, $P=0.36$). Therefore, patterns associated with the predator treatments should not be attributable to cage structure effects.

For the eight sampling dates on which all ponds contained standing water, invertebrate taxa richness was significantly affected by the predator treatments, and the magnitude of the response was consistent across ponds (Table 1). Invertebrate richness was lower in all-access plots than in plots that restricted access by predators (Fig. 4; $F_{1,12}=11.94$, $P < 0.005$). This pattern was consistent over time (the date×pond×predator and date×predator interactions were not significant; Table 2). Richness did not differ between treatments with small-fish access and no access ($F_{1,12}=0.11$, $P > 0.05$). Significantly fewer

taxa were present in the more permanent ponds (Fig. 4; $F_{1,12}=8.48$, $P < 0.025$). Although richness was greater in the less permanent ponds, annual diversity and equitability as measured by the Shannon diversity index (H' and J) was higher in the more permanent ponds (all-access plots: less permanent $H'=1.58$, $J=0.44$; more permanent $H'=2.26$, $J=0.63$). The all-access plots had a lower diversity index than the restricted-access plots in both pond types (restricted-access plots: less permanent $H'=1.85$, $J=0.40$; more permanent $H'=2.41$, $J=0.64$).

Total invertebrate abundance was significantly affected by the predator treatments, but the magnitude of the response varied among ponds (Table 1). Fewer individuals were present in the more permanent ponds (Fig. 5; $F_{1,12}=125.1$, $P < 0.001$). The total number of individuals was lower in all-access plots than in plots that restricted access by predators, but this effect was much stronger in the more permanent ponds (ponds 3 and 4; Fig. 5; $F_{1,12}=9.82$, $P < 0.01$). Over all dates, total abundance was 41.4% lower in the plots open to predators than in the restricted-access plots in ponds 3 and 4, but only 6.7% lower in ponds 1 and 2. Invertebrate density did not differ between small-fish and no-access treatments ($F_{1,12}=0.34$, $P > 0.05$). This pattern was relatively consistent over time (i.e., the date×pond×predator and date×predator interactions were not significant; Table 1).

Total biomass was significantly affected by the predator treatments, and the magnitude of response varied across ponds (Table 1). Total invertebrate biomass was lower in all-access plots than in plots has restricted ac-

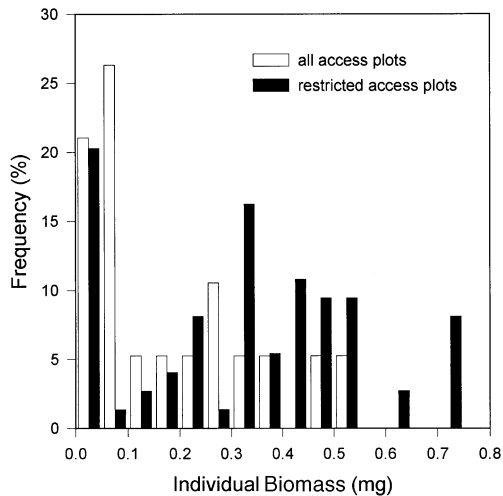


Fig. 7 Size-frequency distributions of *Polypedilum* spp. in the restricted-access and all-access plots of pond 4. Data are pooled over all sampling dates

cess by predators (Fig. 6; $F_{1,12}=16.47$, $P<0.01$), and this effect was strong in all ponds except pond 1 ($F_{1,12}=9.62$, $P<0.001$). Over all dates, total biomass was 45.6% lower in the all-access plots than in the restricted-access plots in ponds 2, 3, and 4. Total biomass was greatest in pond 1, largely due to the presence of the snail *Physella* (see below), which was not affected by the predator treatments. Strong effects of predation on biomass were consistently observed during the study (the date \times pond \times predator and date \times predator interactions were not significant; Table 2). Total invertebrate biomass did not differ between small-fish and no-access treatments ($F_{1,12}=0.39$, $P>0.05$). Significantly less biomass was present in the more permanent ponds (Fig. 6; $F_{1,12}=7.75$, $P<0.025$).

With the exception of the cladoceran *Diaphanosoma*, all commonly encountered taxa were strongly affected by pond permanence in terms of abundance, biomass and, generally, individual biomass (Table 2). The pond \times date interaction was significant for several taxa (Table 2), but these appeared to result largely from substantial variation in response variables among months rather than inconsistent responses to pond permanence. Effects of pond permanence were most pronounced for the oligochaete *Branchiura sowerbyi*, which was only found in the most permanent pond, and the snail *Physella*, which was abundant in the least permanent pond and rarely encountered elsewhere. Taxa were nearly equally divided between those that were more abundant and had greater biomass in less permanent (ponds 1 and 2) and those that were more abundant and had greater biomass in more permanent ponds (ponds 3 and 4).

Over 50% of the taxa were significantly affected by the predator treatments with respect to at least one response variable, or exhibited significant pond \times predator interactions (Table 3). For taxa in which the pond \times predator interaction was insignificant [e.g., abundance of *Dicrotendipes* and *Endochironomus*; individual biomass of

Polypedilum (Fig. 7)], response variable values were lower in the all-access treatment than in the restricted-access treatments. Significant pond \times predator interactions generally occurred when responses to the predator treatments (i.e., lower response variable values in the all-access treatment than in restricted-access treatments) were strong in two or three ponds and weak in ponds where taxon density was low in all plots. This general pattern was observed for *Polypedilum*, other Chironomini, *Palpomyia*, and nematodes. Exceptions to this pattern occurred in *Chironomus* and other oligochaetes. For these taxa, responses to the predator treatment were inconsistent among ponds. Response variable values were lowest in all-access treatment in two ponds, but greatest in the same treatment in the other two ponds. There were no significant pond \times predator \times date interactions.

In general, there were no differences in the response variables between the treatments with small-fish access and no access, so these contrasts are not presented in Table 3. The major exception to this pattern was observed for *Chironomus*, in which abundance in the treatment with small-fish access was consistently greater than in the no-access treatment.

Discussion

Our results suggest that the effects of vertebrate predation on the structure of benthic invertebrate communities in floodplain ponds are mediated by pond permanence. Although the abundance of vertebrate predators in the ponds was not quantified, it is likely that ponds that dried frequently supported lower densities of vertebrate predators, especially fish (Batzer and Wissinger 1996). As a consequence, strong effects of vertebrate predation on invertebrate community structure were largely restricted to the more permanent ponds. Invertebrate taxa richness, abundance, and total biomass were lower in the all-access treatment than in the treatments that restricted predator access, and these effects were stronger in the more permanent ponds. Because there was no systematic bias associated with the cage control results relative to the open plots, it is unlikely that the treatment effects were an artifact of the cage structure. The reduction in invertebrate abundance and biomass in open plots is consistent with other studies, which have shown decreased invertebrate biomass when fish and waterfowl are present (Peterson et al. 1989; Riera et al. 1991; Batzer and Wissinger 1996).

The strong effect of vertebrate predation detected in this study could have been due to fish, waterfowl, or both. Most waterfowl studies have been done over short periods of time and seasonally, when waterfowl consume extra protein (e.g., during spring and fall migrations) (Peterson et al. 1989; Reid et al. 1990). We recorded waterfowl use (presence/absence) of ponds on all sampling dates. Few waterfowl were observed in the ponds even during migratory periods, and none were seen foraging in any of the ponds. Because it has been shown that low

densities of waterfowl do not affect invertebrate communities significantly (Peterson et al. 1989), it is unlikely that waterfowl had a significant effect in this study. Similarly, we did not detect strong effects of predation by small fish (i.e., the treatment with small-fish access and that preventing access by all vertebrate predators generally did not differ significantly for any response variable). Therefore, in this experiment, predator effects on benthic invertebrate community structure appear to be attributable primarily to the activities of large fish.

Waterfowl and fish have been shown to exhibit prey and size selectivity (Power 1987; Peterson et al. 1989; Luecke 1990; Macchiusi and Baker 1991; Batzer et al. 1991). In this study, total invertebrate biomass and, for many taxa, mean individual biomass were lower in the all-access treatment than in the treatments that restricted predator access. Predators selected larger individuals of certain taxa (i.e., the chironomids *Chironomus*, *Endochironomus*, and *Polypedilum* and nematodes) from all access treatments. The selection of large individuals by the predators in this study supports the numerous studies in which bluegill and other fish preferred large prey items (Werner and Hall 1974; Vinyard and O'Brien 1975; Luecke 1990). However, our results contrast with those of Macchiusi and Baker (1991), who found that fish selected large *Chironomus* spp. if both large and small organisms were equally accessible, but in the field as well as in laboratory experiments using a mud substrate, they primarily selected small organisms because these were more active.

For individual taxa, significant interactions between pond permanence and predation generally occurred when effects of vertebrate predators were strong in ponds in which taxa were relatively abundant and weak in ponds where population densities were low. It should be difficult to detect strong effects of predation in habitats where population densities are already low. However, because the abundance of invertebrate (Fig. 2) and probably vertebrate predators were low in less permanent ponds, it seems likely that effects of predators were, in fact, weaker in those habitats. The abundance of only two taxa, *Polypedilum* and Nematoda, was significantly affected by the predator treatments in pond 1, while several taxa that were relatively abundant in the less permanent ponds (e.g., *Berosus*, Orthoclaadiinae, Tanytarsini, *Diaphanosoma*, Copepoda, other oligochaetes, *Physella*) showed no effects of predation there.

Although 50% of the taxa encountered had distributions restricted to either the shorter- (ponds 1 and 2) or longer-duration ponds (3 and 4), most of these were too rare to draw conclusions about effects of habitat duration on their distributions. Nonetheless, striking effects of pond duration on the distributions of taxa were observed. In particular, the abundance of predaceous invertebrates and the proportion of taxa comprised of predators increased with increasing pond permanence. For example, two predaceous invertebrate taxa, the ceratopogonid *Palpomyia* and the tanyptodine chironomids, were abundant in ponds 3 and 4 and rare in the less permanent

ponds. Schneider and Frost (1996) examined mechanisms affecting invertebrate community structure in vernal ponds and found that effects of biotic interactions, especially predation, on population abundance increased with increasing pond duration. Predators were less diverse and less abundant in ponds that held water for relatively short periods than in longer-duration ponds. Our results are in agreement with this general pattern, which has been observed in several other studies (Bradshaw and Holzayefel 1983, 1988; Smith 1983; Woodward 1983; Dodson 1987; Wilbur 1987).

In contrast with the distribution and abundance of predaceous taxa, several taxa were rare in the longer-duration ponds, especially pond 4 which always contained water, and common in the other ponds. These taxa included several chironomids (*Polypedilum*, *Dicrotendipes*, *Endochironomus*, other Chironomini, Orthoclaadiinae), *Berosus*, copepods, and *Physella*. The absence of at least two of these taxa, *Physella* and *Berosus*, from the more permanent ponds may have resulted from lower vegetation density in those ponds. Vegetation germinated during the spring and summer when water levels were low in ponds 1 and 2, and it remained after inundation. *Physella* and *Berosus* larvae commonly use the vegetation as habitat. Reduced abundance of the other taxa in the longer-duration ponds may have resulted from increased vertebrate and invertebrate predation, but additional experiments would be necessary to evaluate this and other potentially important mechanisms (see Schneider and Frost 1996).

Total invertebrate abundance declined significantly with increasing pond duration. This largely resulted from the responses of four taxa: other oligochaetes, copepods, *Physella*, and *Endochironomus*. The interplay of at least two factors may be important in producing this pattern. First, periodic flooding and drying of ponds may enhance food quality and quantity for some consumers (e.g., detritivores) by allowing increased decomposition of organic material and development of terrestrial vegetation during dry stages (Wiggins et al. 1980; Junk et al. 1989). Second, as observed in this study, the abundance and diversity of invertebrate and vertebrate predators should increase with increasing pond duration (Batzer and Wissinger 1996; Schneider and Frost 1996).

Schneider and Frost (1996) proposed that a hierarchy of mechanisms determined the structure of vernal pond communities, with the presence/absence of species in a habitat largely determined by colonization/extinction processes and life history requirements, and species abundance strongly influenced by biotic interactions. They observed a particularly strong match between life history requirements (e.g., the time needed to complete the aquatic life stage) and the presence/absence of taxa in ponds of differing duration. Because of the intimate connection between floodplain ponds and the main river, we expect colonization processes, rather than life histories, to more strongly influence taxon presence/absence in floodplain ponds. Therefore, we expect that stochastic process should play a major role in affecting the compo-

sition of floodplain pond communities. We observed a large number of taxa in the less permanent ponds, which were probably unable to complete the aquatic life stage before the ponds dried or to survive dry periods in desiccation-resistant stages. The importance of the main river and associated colonization processes in affecting community structure should increase with decreasing pond permanence, but this has not been tested.

In summary, an interplay of abiotic and biotic processes strongly affected the structure of the benthic invertebrate community in floodplain ponds. Effects of vertebrate predation on the abundance, biomass, and size structure of invertebrate populations was greatest in longer-duration ponds. The abundance and diversity of invertebrate predators was also greatest in those habitats. Virtually no effects of vertebrate predation were detected in shorter-duration ponds, presumably because fish populations were maintained at low levels by frequent pond drying. Therefore, our results are in agreement with models that predict relatively weak effects of predators on community structure in frequently disturbed habitats (e.g., Connell 1975; Menge 1976; Menge and Sutherland 1987). In contrast with vernal ponds (e.g., Schneider and Frost 1996), it is less clear how habitat duration affects the composition of invertebrate communities in floodplain ponds, and more attention to colonization dynamics in floodplain ponds is needed.

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References

- Balcer MD, Korda NL, Dodson SI (1984) Zooplankton of the Great Lakes: a guide to the identification of ecology of the common crustacean species. University of Wisconsin Press, Madison, Wis
- Banaszak J, Kasprzak K (1980) Evaluation of occurrence and density of Oligochaeta, Mollusca, Chironomidae in bottom deposits of Lake Zbechy and in melioration channel within agricultural landscape. *Po Ecol Stud* 6:221–245
- Batzer DP, Resh VH (1992) Macroinvertebrates of a California seasonal wetland and responses to experimental habitat manipulation. *Wetlands* 12:1–7
- Batzer DP, Wissinger SA (1996) Ecology of insect communities in nontidal wetlands. *Annu Rev Entomol* 41:75–100
- Batzer DP, McGee M, Resh VH, Smith RR (1993) Characteristics of invertebrates consumed by mallards and prey responses to wetland flooding schedules. *Wetlands* 13:41–49
- Bradshaw WE, Holzapfel CM (1983) Predator-mediated, non-equilibrium coexistence of tree-hole mosquitoes in southeastern North America. *Oecologia* 57:239–256
- Bradshaw WE, Holzapfel CM (1988) Drought and the organization of tree-hole mosquito communities. *Oecologia* 74:507–514
- Brinkhurst RO (1986) Guide to the freshwater aquatic microdrile oligochaetes of North America. *Can Spec Publ Fish Aquat Sci* 84
- Burch JB (1989) North American freshwater snails. Malacological Publications, Hamburg, Mich
- Chu HF (1949) How to know the immature insects. Brown, Dubuque, Iowa
- Connell JH (1975) Some mechanisms producing structure in natural communities: a model and evidence from field experiments. In: Cody ML, Diamond JM (eds) *Ecology and evolution of communities*. Belknap, Cambridge, Mass, pp 460–490
- Connell JH (1978) Diversity in tropical rainforests and coral reefs. *Science* 199:1302–1310
- Culver DA, Boucherle MM, Bean DJ, Fletcher JW (1985) Biomass of freshwater crustacean zooplankton from length-weight regressions. *Can J Fish Aquat Sci* 42:1380–1390
- Dayton P, Tegner MJ (1984) The importance of scale in community ecology: a kelp forest example with terrestrial analogs. In: Price PW, Slobodkinoff CN, Gaud WS (eds) *A new ecology: novel approaches to interactive systems*. Wiley, New York, pp 457–481
- Dodson SI (1987) Animal assemblages in temporary desert rock pools: aspects of the ecology of *Daslyhelea sublettei* (Diptera: Ceratopogonidae). *J N Am Benthol Soc* 6:61–71
- Doss PK (1993) The nature of a dynamic water table in a system of non-tidal, freshwater coastal wetlands. *J Hydrol* 141:107–126
- Drago EC (1989) Morphological and hydrological characteristics of the floodplain ponds of the middle Parana River (Argentina). *Rev Hydrobiol Trop* 22:183–190
- Dumont HJ, Vander Velde I, Dumont S (1975) The dry weight estimate of biomass in a selection of Cladocera, Copepoda and Rotifera from the plankton, periphyton and benthos of continental waters. *Oecologia* 19:75–97
- Dunson WA, Travis J (1991) The role of abiotic factors in community organization. *Am Nat* 138:1067–1091
- Gilinsky E (1984) The role of fish predation and spatial heterogeneity in determining benthic community structure. *Ecology* 65:455–468
- Hall DJ, Cooper WE, Werner EE (1970) An experimental approach to the production dynamics and structure of freshwater animal communities. *Limnol Oceanogr* 15:839–928
- Huener JD, Kadlec JA (1992) Macroinvertebrate response to marsh management strategies in Utah. *Wetlands* 12:72–78
- Junk WJ, Bayley PB, Sparks RE (1989) The flood pulse concept in river-floodplain systems. *Can Spec Publ Fish Aquat Sci* 106:110–127
- Kaster JL, Jacobi GZ (1978) Benthic macroinvertebrates of a fluctuating reservoir. *Freshwater Biol* 8:283–290
- Krull JN (1976) Abundance and diversity of benthos during the spring waterfowl migration. *Am Midl Nat* 95:459–462
- Levin SA (1992) The problem of pattern and scale in ecology. *Ecology* 73:1943–1967
- Luecke C (1990) Changes in abundance and distribution of benthic macroinvertebrates after introduction of cutthroat trout into a previously fishless lake. *Trans Am Fish Soc* 119:1010–1021
- Machiuti F, Baker RL (1991) Prey behavior and size-selective predation by fish. *Freshwater Biol* 25:533–538
- McAuliffe JR (1984) Competition for space, disturbance, and the structure of a benthic stream community. *Ecology* 65:894–908
- Menge BA (1976) Organization of the New England rocky intertidal community: role of predation, competition, and environmental heterogeneity. *Ecol Monogr* 46:355–393
- Menge BA, Olson AM (1990) Role of scale and environmental factors in regulation of community structure. *Trends Ecol Evol* 5:52–57
- Menge BA, Sutherland JP (1987) Community regulation: variation in disturbance competition, and predation in relation to environmental stress and recruitment. *Am Nat* 130:730–757
- Merritt R, Cummins K (eds) *An introduction to the aquatic insects of North America*, 2nd edn. Kendall/Hunt, Dubuque, Iowa

- Mittlebach GG (1988) Competition among refuging sunfishes and effects of fish density on littoral zone invertebrates. *Ecology* 69:614–623
- Paine RT, Levin SA (1981) Intertidal landscapes: disturbance and the dynamics of pattern. *Ecol Monogr* 51:145–178
- Paterson CG, Fernando CH (1969) The effect of winter drainage on reservoir benthic fauna. *Can J Zool* 47:589–595
- Peterson LP, Murkin HR, Wrubleski DA (1989) Waterfowl predation on benthic macroinvertebrates during fall drawdown of a northern prairie marsh. In: Sharitz RR, Gibbons JW (eds) *Freshwater wetlands and wildlife*. US Department of Energy, Charleston, SC
- Post JR, Cucin D (1984) Changes in the benthic community of a small Precambrian lake following the introduction of yellow perch *Perca flavescens*. *Can J Fish Aquat* 41:1496–1501
- Power ME (1987) Predator avoidance by grazing fishes in temperate and tropical streams: importance of stream depth and prey size. In: Kerfoot WC, Sih A (eds) *Predation: direct and indirect impacts on aquatic communities*. University Press of New England, Hanover, Pa
- Provonsha AR (1990) A revision of the genus *Caenis* in North America (Ephemeroptera: Caenidae). *Trans Am Entomol Soc* 116:801–884
- Reid FA, Kelley JR, Taylor TS, Fredrickson LH (1990) Upper Mississippi valley wetlands-refuges and moist-soil impoundments. In: Smith LM, Peterson RL, Kaminski RM (eds) *Habitat management for migrating and winter waterfowl in North America*. Texas Tech University Press, Lubbock, Tex, pp 181–202
- Riera P, Juget J, Martinet F (1991) Predator-prey interactions: effects of carp predation on tubificid dynamics and carp production in experimental fishpond. *Hydrobiologia* 226:129–136
- Schneider DW, Frost TM (1996) Habitat duration and community ecology of temporary ponds. *J N Am Benthol Soc* 15:64–86
- Smith DC (1983) Factors controlling tadpole populations of the chorus frog (*Pseudacris triseriata*) on Isle Royal, Michigan. *Ecology* 64:501–510
- Sparks RE (1992) Risks of altering the hydrologic regime of large rivers. In: Cairns JR Jr, Niederlehner BR, Orvos DR (eds) *Predicting ecosystem risk*, vol 20. Princeton Scientific, Princeton, NJ, pp 119–152
- Thomsen LC (1937) Aquatic diptera, part V Ceratopogonidae. In: Johansen OA (1969) *Aquatic diptera: eggs, larvae and pupae of aquatic flies*. Entomological Reprint Specialists, Los Angeles, pp 57–98
- Vinyard GL, O'Brien WJ (1975) Dorsal light responses as an index of prey preference in bluegill sunfish (*Lepomis macrochirus*). *J Fish Res Board Can* 33:2845–2849
- Werner EE, Hall DJ (1974) Optimal foraging and the size selection of prey by the bluegill sunfish (*Lepomis macrochirus*). *Ecology* 55:1042–1052
- Wiederholm T (1983) Chironomidae of the Holarctic region: keys and diagnoses. 1. Larvae. *Entomol Scand Suppl* 19
- Wiggins GB (1977) Larvae of the North American caddisfly genera (Trichoptera). University of Toronto Press, Toronto
- Wiggins GB, Mackay RJ, Smith IM (1980) Evolutionary and ecologies of animals in annual temporary pools. *Arch Hydrobiol Suppl* 58:97–206
- Wilbur HM (1987) Regulation of structure in complex systems: experimental temporary pond communities. *Ecology* 68:1437–1452
- Winer BJ (1971) *Statistical principles in experimental design*, 2nd edn. McGraw-Hill, New York
- Woodward BD (1983) Predator-prey interactions and breeding-pond use of temporary pond species in a desert anuran community. *Ecology* 64:1549–1555