

INTERACTIVE EFFECTS OF PREDATION AND DISPERSAL ON ZOOPLANKTON COMMUNITIES

JONATHAN B. SHURIN¹

Department of Ecology and Evolution, University of Chicago, 1101 E. 57th St., Chicago, Illinois 60637 USA

Abstract. Communities of coexisting organisms are formed by both dispersal among habitat patches in a region and local interactions within patches. The supply of colonists from the regional pool has the potential to alter the outcome of local interactions by providing species that fill different ecological roles. I examined the consequences of invasion by fish (juvenile *Lepomis macrochirus*) and insect (*Notonecta undulata*) predators on experimental plankton communities that were either connected to or isolated from the regional pool of zooplankton species. The effects of predators on zooplankton composition and diversity depended on dispersal by members of the regional zooplankton species pool. Fish and notonectids reduced the abundance of large zooplankton and thereby facilitated invasion by new species from the surrounding region. Both predators reduced zooplankton species richness in the absence of dispersal, while fish had positive effects and notonectids had no effects with rapid dispersal. Fish facilitated invasion by more species than they excluded, while similar numbers of species invaded with notonectids as were driven extinct. The effects of predators on planktonic trophic structure (zooplankton size structure and biomass, phytoplankton biomass) were independent of the level of dispersal. Both predators reduced zooplankton mean body size, but only fish enhanced phytoplankton density. Invasion by members of the regional species pool slightly increased zooplankton mean body size and reduced phytoplankton biomass; however, the effects were small and independent of the predator treatment. Predator-facilitated invasion of new species altered the effects of predators on zooplankton species composition and diversity, but not on plankton trophic structure. The results suggest that spatial heterogeneity in predator abundance promotes regional coexistence among zooplankton. Connection to a diverse regional species pool via dispersal may therefore be important for determining the impact of local interactions such as predation on communities.

Key words: ecosystem function; immigration; local and regional processes; phytoplankton; planktivory; species diversity; species invasions; trophic cascades; zooplankton.

INTRODUCTION

The influence of top predators on species abundance, diversity, and biomass at lower trophic levels can vary across spatial scales. Within relatively small, homogeneous areas (hereafter called local sites or patches), predators often reduce the abundance of their prey, sometimes to the point of exclusion, and may thereby indirectly facilitate other species (Brooks and Dodson 1965, Paine 1966, Lubchenco 1978, Zaret 1980, Sih et al. 1985, Kerfoot and Sih 1987, Carpenter and Kitchell 1993, Carson and Root 2000). Indirect facilitation can take place through release from either competitors (i.e., keystone predation) or intermediate predators (i.e., trophic cascades). Predators may either reduce or enhance local diversity at lower trophic levels, depending on whether more species are excluded or facilitated (Paine and Vadas 1969, Hunter and Price 1992, Pacala and Crawley 1992, Schoener and Spiller 1996, Gough and

Grace 1998, Proulx and Mazumder 1998). Community-level effects may or may not be manifested in terms of trophic structure (biomass of lower trophic levels), depending on how the impact of the predator on a species is related to its contribution to community productivity or biomass. If the species that are most susceptible to predation are also highly productive, then predators may have strong cascading effects on trophic structure (Brooks and Dodson 1965, Carpenter and Kitchell 1993, Brett and Goldman 1997). Alternatively, if species that are indirectly facilitated compensate for the production that is lost to predators, then the predator may cause shifts in species composition but have no effect on biomass at lower trophic levels (Crawley 1989, Strong 1992, Polis and Strong 1996, Persson 1999).

Because of their potential for strong local effects, spatial variability in the abundance of predators can have major impacts on community structure at the regional scale. Models of food webs typically assume that the top trophic level is limited primarily by its resources (Hairston et al. 1960, Oksanen et al. 1981, Holt et al. 1994, Leibold 1996). However, predators may also be excluded from local habitats by distur-

Manuscript received 21 September 2000; revised 15 January 2001; accepted 23 January 2001.

¹ Present address: National Center for Ecological Analysis and Synthesis, University of California, 735 State Street, Suite 300, Santa Barbara, California 93101 USA.
E-mail: shurin@nceas.ucsb.edu

bance history or stochastic extinction (Tonn and Magnuson 1982, Schoener 1989, Holt 1993, 1997, Werner and McPeck 1994, Schneider and Frost 1996, McPeck 1998). The presence of habitats with heterogeneous predator communities can promote regional coexistence among species at lower trophic levels that cannot coexist locally (Shurin 2000b). For instance, species of amphibians, insects, and zooplankton often segregate between ponds with and without fish or salamander predators as a result of chains of indirect interactions (Dodson 1970, 1974, Sprules 1972, Giguère 1979, Arnett and Vanni 1993, Werner and McPeck 1994, Wellborn et al. 1996, McPeck 1998, Zimmer et al. 2000). These patterns suggest that the effect of a predator on a particular local community may depend on the identities of species in the regional pool, and the rate at which they arrive via dispersal (Spencer and Warren 1996, Warren 1996, Shurin 2000b). The present study is an experimental test of the role of dispersal from the regional zooplankton species pool in determining the impact of predators on planktonic community composition and trophic structure. I examined the effects of planktivorous fish and insects on zooplankton communities that were either isolated from or open to dispersal by a large number of species from the surrounding region.

This experiment was designed to test two hypotheses. The first was that the effects of planktivory on local zooplankton species composition and diversity depend on dispersal by species from a diverse regional pool. Size-selective predators have been shown to facilitate small-bodied zooplankton through suppression of competitors or intermediate predators (Brooks and Dodson 1965, Dodson 1970, 1974, Hall et al. 1976, Morin 1987, Vanni 1988, Carpenter and Kitchell 1993). If predators promote invasion by small zooplankton through interactions involving either competitors or intermediate predators, then we expect to find interactive effects of dispersal and predation on zooplankton species composition. That is, the first hypothesis predicts that some species will be more abundant in the presence of predators and dispersal, but not in either treatment alone. The net effect of predators on local zooplankton diversity depends on whether more species are excluded or facilitated. In the absence of dispersal, predators may reduce local prey diversity by driving some species extinct (Sih et al. 1985, Schoener and Spiller 1996, Spiller and Schoener 1998). However, predator-facilitated invasion by members of the regional pool may compensate for or reverse the loss of species due to predation. The relationships between competitive ability, susceptibility to predation, and rate of dispersal among members of the regional species pool determine the net impact of predators on local diversity (Shurin 2000b). This experiment asked how the effects of predators on local prey diversity depend on connection of the prey community to the regional species pool.

The second hypothesis was that the effects of pred-

ators on trophic structure (zooplankton size structure and biomass, phytoplankton biomass) would be weakened by invasion of new species from the region. Size-selective predation, especially by fish, has been shown to enhance phytoplankton biomass, and have idiosyncratic effects on zooplankton community biomass in a wide variety of lakes (Brooks and Dodson 1965, Carpenter and Kitchell 1993, Mittelbach et al. 1995, Brett and Goldman 1997). In addition, zooplankton mean body size is often negatively related to increases in planktivory, and positively associated with grazing pressure on phytoplankton (Pace 1984, Soranno et al. 1993). Despite the generality of these patterns, the response of lakes to manipulations of top predators is often quite variable (Leibold et al. 1997, Elser et al. 1998, Persson 1999). One potential explanation for this variability is that the effects of predators depend on colonization by new species from the surrounding region (Leibold et al. 1997, Chase et al. 2000). For instance, introduction of a predator into a novel community can potentially have very large effects on the local biota (Fritts and Rodda 1998). This is especially likely to be the case if the traits that favor coexistence with predators are negatively correlated with traits that are ecologically important in their absence. However, if colonization by new species balances predator-induced extinction, the effect of the predator on trophic structure may be weakened by species turnover within the prey community. In this case, changes in species composition may play an important role in determining the impact of predator introductions on trophic structure (Leibold et al. 1997, Chase et al. 2000).

I tested these hypotheses by examining the effects of planktivorous fish and insects on experimental zooplankton communities under two contrasting situations. Predator-free plankton communities were established in large outdoor enclosures (plastic cattle watering tanks) by inoculating the tanks with zooplankton and phytoplankton collected from four fishless ponds. In this baseline assemblage, I imposed two cross-factored predation regimes: the presence or absence of juvenile bluegill sunfish (*Lepomis macrochirus*) and planktivorous insects (*Notonecta undulata*). Bluegills and notonectids are regionally abundant and frequently coexist in ponds and the littoral zones of lakes in North America, although notonectids are sometimes suppressed by fish (Bendell 1986, Bennett and Streams 1986). Both predators selectively consume large zooplankton and can have major impacts on planktonic community structure (Murdoch et al. 1984, Mittelbach et al. 1995, Arner et al. 1998). The predator treatments were crossed with two levels of dispersal (high or none) by a large number of zooplankton species from the surrounding region (a $2 \times 2 \times 2$ factorial design). In the no-dispersal treatment, no new zooplankton were added. In the high-dispersal treatment, diverse mixtures of species from many lakes and ponds in the area (southwestern Michigan) were repeatedly introduced at

low densities throughout the experiment. The no-dispersal treatment represented isolated communities with little or no dispersal from the regional zooplankton species pool, whereas the high-dispersal treatment simulated rapid immigration by new species.

METHODS

The experiment was performed during the summer of 1999 at the W. K. Kellogg Biological Station (hereafter KBS) Pond Lab facility in Kalamazoo County, Michigan, USA. Experimental mesocosms were cylindrical, plastic, cattle watering tanks, 1.6 m in diameter by 1 m deep. The tanks were filled to a depth of 0.5 m (volume 1000 L) with well water on 28 April and fertilized with NaNO_3 (10.4 g) and NaH_2PO_4 (0.33 g). These nutrient levels were the mean found in a survey of 29 natural ponds around KBS (J. M. Chase and A. L. Downing, unpublished data). A layer of sand was provided for substrate. The tanks were covered at all times with 1-mm mesh fiberglass screening to prevent oviposition by insects. The tanks were inoculated on 1 May with zooplankton and phytoplankton collected from four fishless experimental ponds at the KBS pond lab. Nutrients (2.46 g NaNO_3 and 0.12 g NaH_2PO_4) were added weekly until 18 July, and biweekly thereafter, to maintain roughly constant levels of productivity. There were four replicate tanks per treatment.

Twenty-two adult *Notonecta undulata* were added to each tank in the notonectid treatment on 25 June. This density was the mean found in a survey of natural ponds (J. M. Chase and A. L. Downing, unpublished data). A mean of 21.6 animals (1 SD = 4.4) were recovered from the notonectid treatment at the end of the experiment (29 September), indicating very little change in density. Three juvenile bluegill sunfish (*Lepomis macrochirus*, mean standard length = 51.1 mm, 1 SD = 5.0 mm) were added to the fish treatment on 9 July. This density (1.5 fish/m²) is slightly below the 1.6 fish/m² reported by Mittelbach (1988) for juvenile bluegill in the littoral zone of nearby Lawrence Lake. All of the fish were recovered alive at the end of the experiment and had grown by a mean of 9.6 mm (1 SD = 5.6). The growth rate of fish (0.12 mm/d) was greater than the maximum growth rate of 0.1 mm/d reported by Osenberg et al. (1988) for wild Michigan bluegills in the 45–50 mm size class. These results suggest that both predators were stocked at densities comparable to or below natural levels. No notonectids were present in the notonectid + fish treatment at the end of the experiment although they persisted through early September. The fish ate juvenile, but not adult, *N. undulata*, so that there was recruitment by notonectids only in the absence of fish (J. B. Shurin, personal observation).

Zooplankton for the high-dispersal treatment were collected from 7 to 10 (mean = 8.2) lakes and ponds around KBS on five days during the experiment. The live zooplankton were gently mixed together in a carboy and distributed into inocula that were added to the

high-dispersal tanks. Heat-killed inocula were added to the no-dispersal treatment to control for the addition of nutrients and water. Inocula were added to the tanks within 4 h of collection to minimize stress to the animals. Zooplankton were introduced on the day after sampling so that the individuals added would not appear in the samples. A mean of 43.6 species (11.6 cladocerans, 4.2 copepods, and 27.8 rotifers, not counting nauplii and unidentifiable cyclopoid copepodid stages, Appendix A) were introduced on each date with a mean of 152.2 individuals per species. Animals were added to the high-dispersal treatment in low densities; not counting nauplii or cyclopoid copepodids, the mean density of species introduced in the inoculum was 0.15/L (median = 0.02/L), while the mean total density of new animals was 6.4/L (range: 2.4–13.5/L, Appendix A). The mean total density of zooplankton found in the tanks during the experiment was 279.0 animals/L; thus, the addition of the inoculum did not greatly elevate zooplankton density. The mean volume of the zooplankton samples was 4.1 L. Samples were collected between 14 and 21 d after the inoculum was added (mean = 18.6 d). This interval is longer than the generation time of most of the organisms (2–10 d for most cladocerans and rotifers, although longer for some copepods; Lynch 1980, Stemberger and Gilbert 1985). Since animals were introduced at low densities that were below detection and the tanks were sampled 14–21 d later, is unlikely that the new species found in the high-dispersal treatment represented sink populations (sensu Pulliam 1988) being sustained by immigration.

Because little is known about zooplankton dispersal rates, it is difficult to compare the magnitude of immigration in the high-dispersal treatment with natural levels. Experimental evidence (Shurin 2000a) suggests rapid dispersal by many species as 11 natural fishless pond communities resisted invasion by most members of the regional species pool. Jenkins and Buikema (1998) found that 57 crustacean and rotifer species colonized 12 newly constructed ponds in one year. It is likely that natural ponds vary considerably in their degree of connection to the regional species pool. Because the number of colonists received by real ponds is unknown, I did not try to mimic natural levels of dispersal. Rather, the goal of the dispersal treatment was to bracket the range of potential variation (none vs. high).

Depth-integrated zooplankton and phytoplankton samples were collected six times over 100 d, including once before the treatments were established, with 2" (~5.08 cm) diameter PVC tube samplers. A different sampler was used for each tank to prevent cross contamination. Water for chlorophyll *a* analysis was collected from the center of the tank, filtered through Whatman GF filters, extracted in ethanol, and analyzed by fluorimetry (Welschmeyer 1994). Replicate zooplankton samples were taken from seven locations in the tanks, filtered through a 44- μm Nitex mesh, and

combined into a single sample for analysis. A mean of 4.1 L of water from each tank was filtered for zooplankton samples (1 SD = 0.56 L). Zooplankton samples were fixed at the time of collection with Lugol's iodine solution. Macrozooplankton (cladocerans and adult copepods) were counted by species at 30 × magnification under a dissecting microscope. Each sample was examined in its entirety and species with <500 individuals per sample were counted. Subsamples were taken with a wide-bore pipette for counting individuals of species with >500 individuals per sample. Rotifers and copepod nauplii were counted under a compound microscope at 40–100×. Mean biomass density for each species was estimated by measuring 25–50 haphazardly chosen individuals and applying length–mass regressions for crustaceans and length–volume relations for rotifers (McCauley 1984).

Data analysis

The effects of the three treatments and their interactions on zooplankton species composition were tested by redundancy analysis (RDA). RDA is a relatively new and powerful approach to the analysis of multivariate response data in factorial experiments (Legendre and Anderson 1999). RDA is a form of direct gradient analysis that assumes linear relationships between the experimental treatments and the species (Jongman et al. 1995, Legendre and Legendre 1998). Legendre and Anderson (1999) describe the use of RDA for analyzing multispecies responses in experiments, the calculation of test statistics and probability levels. RDA is computationally similar to MANOVA with two important differences. First, RDA uses a Monte Carlo permutation procedure to calculate *F* statistics and is therefore free from distributional assumptions. Second, MANOVA is limited to situations where the number of dependent variables is smaller than the number of replicates, whereas RDA is not (Legendre and Anderson 1999:9). RDA allows for assessment of the amount of total variation in species densities among replicates that can be explained by each treatment and interaction (Jongman et al. 1995, Legendre and Legendre 1998). Ordination diagrams based on RDA can also be used to interpret the relationship between species and experimental treatments (i.e., whether a species is more or less abundant in a given experimental treatment).

The algebra of RDA was performed as follows. First, the density of each taxa was averaged over the last four sampling dates for each replicate. The time-averaged density of each species in the 32 tanks was square-root transformed to reduce the influence of extreme observations and then regressed on a 7 × 32 matrix of dummy variables representing the three treatments plus four interactions. Separate multiple regressions were performed for each of the 44 taxa found in the experiment (11 cladocerans, 5 copepods, and 26 rotifers, plus nauplii and unidentifiable cyclopoid copepodids). An 8 × 44 matrix of fitted values for each species in each treat-

ment combination was constructed based on individual multiple regressions. This matrix of predicted densities was then subjected to principal components analysis (PCA) to reduce its dimensionality. The significance of each treatment and interaction was determined by sequentially entering a dummy variable representing the treatment into the matrix of predictor variables by forward selection and repeating the above procedure. On each step, the samples were permuted 999 times and the observed *F* statistic compared with the rank distribution from the Monte Carlo simulations. RDA was performed using the CANOCO v. 4.02 computer package (ter Braak and Smilauer 1999). Finally, univariate analyses (three-way full factorial ANOVAs on species densities averaged over the last four sampling dates) were performed for the 22 species that responded most strongly to the treatments, as indicated by the RDA. Species densities were $\ln(x + 1)$ transformed to normalize variance and a Bonferroni adjusted significance level of 0.0023 (0.05/22) was used. RDA measures the effects of the treatments on overall zooplankton community composition, while the univariate tests indicate the significance of the response by individual species.

The effects of the treatments and their interactions on zooplankton species richness, mean body size, total community biomass, and phytoplankton biomass (chlorophyll *a* concentration) were tested by a full factorial repeated measures ANOVA based on the five post-treatment sampling dates. Deviations from normality were tested by a Liliefore's test and dependent variables that were non-normal were \log_e transformed. I tested the a priori hypothesis that predators would reduce zooplankton richness in the no-dispersal treatment, and that the effects would be weakened or reversed in the high-dispersal treatment (i.e., there would be significant predator-by-dispersal interactions). Predators were also predicted to reduce zooplankton mean body size and enhance phytoplankton biomass, and these effects were expected to be greater in the no-dispersal than in the high-dispersal treatment. These hypotheses predict significant interactive effects of the predator and dispersal treatments on zooplankton richness, mean size, and phytoplankton biomass. Effects of the treatments on zooplankton community biomass were also tested, however other studies have found complex and often counterintuitive effects of predators on zooplankton biomass (e.g., Soranno et al. 1993). In addition, zooplankton size structure, but not biomass, has been found to influence the relationship between chlorophyll and phosphorous and may therefore be a better indication of grazing (Pace 1984). Two-tailed tests of significance were therefore used for the main effects of predators and their interactions with dispersal for zooplankton biomass, whereas one-tailed tests were used for mean body size and phytoplankton biomass. Planned orthogonal contrasts, based on the values for each dependent variable averaged over the last four

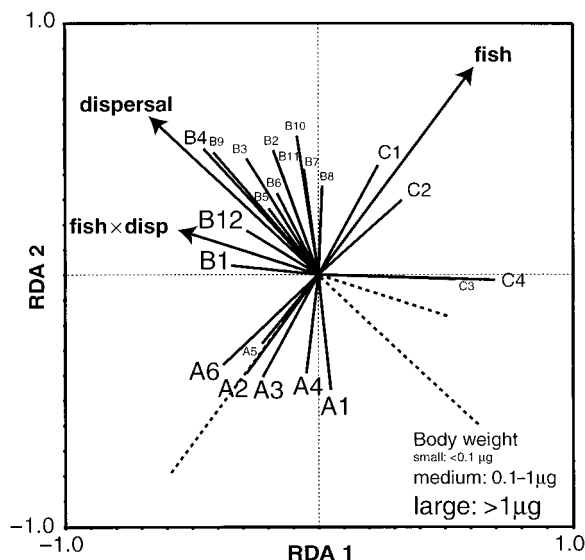


FIG. 1. Canonical ordination (redundancy analysis) of species abundances with respect to the treatments. The response variables are the mean densities (square-root transformed) of all 44 taxa found in the experiment in each replicate on the last four sampling dates. Only dispersal, fish, and their interaction contributed significantly to the fit of the model by a forward selection criterion based on 999 Monte Carlo simulations (Table 1). Only the 22 species that were most correlated with the treatment axes are shown. Species codes are shown in Table 2. Font sizes of the species symbols are proportional to mean dry body mass, as shown in the lower right. The first canonical axis (RDA axis 1) explains 75.6% of the species–treatment relationship, and the second axis (RDA axis 2) explains 10.8%.

sampling dates, were used to test the effects of predators under each of the two dispersal regimes.

RESULTS

Fish and dispersal had both independent and interactive effects on zooplankton species composition. A redundancy analysis (Fig. 1) found that variation in species abundance among replicates was associated with the fish and dispersal treatments, as well as their interaction (Table 1). These three axes accounted for 28.0% of the total variation in species composition, and 85.5% of the explained variation (that accounted for by all three treatments and four interactions). Species composition was not significantly related to the notonectid treatment, or to any interaction terms associated with it. Fig. 1 shows the relationships between species and the treatment axes and Fig. 2 shows the mean densities of the 22 species that had the highest correlations with the treatments in the RDA.

To determine a species' response to an experimental treatment, project the position of the species in the ordination space perpendicular to the treatment axis. The solid lines in Fig. 1 show the treatment axes in the positive space while the dashed lines show the negative space. The direction of the arrow indicates in-

creasing positive values along the treatment axis. Species that have positive positions on a treatment axis were more abundant in the presence of the experimental factor, while species with negative positions were less abundant. For instance, to determine the response of *Bosmina* (C1) to the fish treatment, draw a line from *Bosmina*'s position at a right angle to the fish axis. *Bosmina* falls on the positive portion of the fish axis, therefore this species was more abundant with fish than without. The lengths of the treatment axes indicate the strength of the relationship between the independent variable and the species data. Species that are farther from the origin responded more strongly to the treatment than those closer to the origin. For instance, *Macrothrix laticornis* (B4) has a larger positive position on the dispersal axis than *Monostyla bulla* (B5), therefore *M. laticornis* was more strongly affected by the dispersal treatment than *M. bulla*. The angles between the treatment axes and the ordination axes (RDA 1 and 2) indicate the correlations between the treatments and the ordination axes. That is, the fish treatment is positively correlated with both RDA 1 and 2, while the dispersal treatment and fish-by-dispersal interaction are negatively correlated with RDA 1 and positively correlated with RDA 2.

The species can be considered in three groups based on their response to the treatments. The species in the lower left of Fig. 1 (labeled "A") are large (except *Lepadella patella*, A5, Table 2) and were less abundant in the presence of fish (i.e., their positions on the fish axis are negative). These effects are reflected by significant (*Simocephalus serrulatus*, A6) or nearly significant (*Daphnia pulex* [A3] and *Ceriodaphnia reticulata* [A2]) responses to fish in the univariate ANOVAs (Fig. 2). These species generally fall close to the origin on the dispersal axis (Fig. 1), indicating that they were relatively unaffected by the dispersal treatment (Fig. 2). Species in the upper left in Fig. 1 (labeled "B") are positively associated with the dispersal and fish-by-dispersal interaction axes. These species are primarily rotifers and small cladocerans (Table 2) that

TABLE 1. Redundancy analysis of the abundance ([animals/L]^{1/2}) of the 44 zooplankton taxa found, averaged over the last four sampling dates.

Variable	λ	F	P
Fish	0.10	3.60	0.02
Notonectids (Noto)	0.01	0.30	0.85
Dispersal (Disp)	0.11	3.59	0.02
Fish \times Noto	0.01	0.40	0.72
Fish \times Disp	0.07	2.72	0.04
Noto \times Disp	0.02	0.46	0.73
Fish \times Noto \times Disp	0.01	0.69	0.52

Notes: The eigenvalue for each treatment or interaction, λ , indicates the portion of the total variance in the species data explained by each treatment. F statistics are from a forward selection criterion, and P values are based on 999 Monte Carlo simulations. Statistical significance ($P < 0.05$) is indicated by bold type.

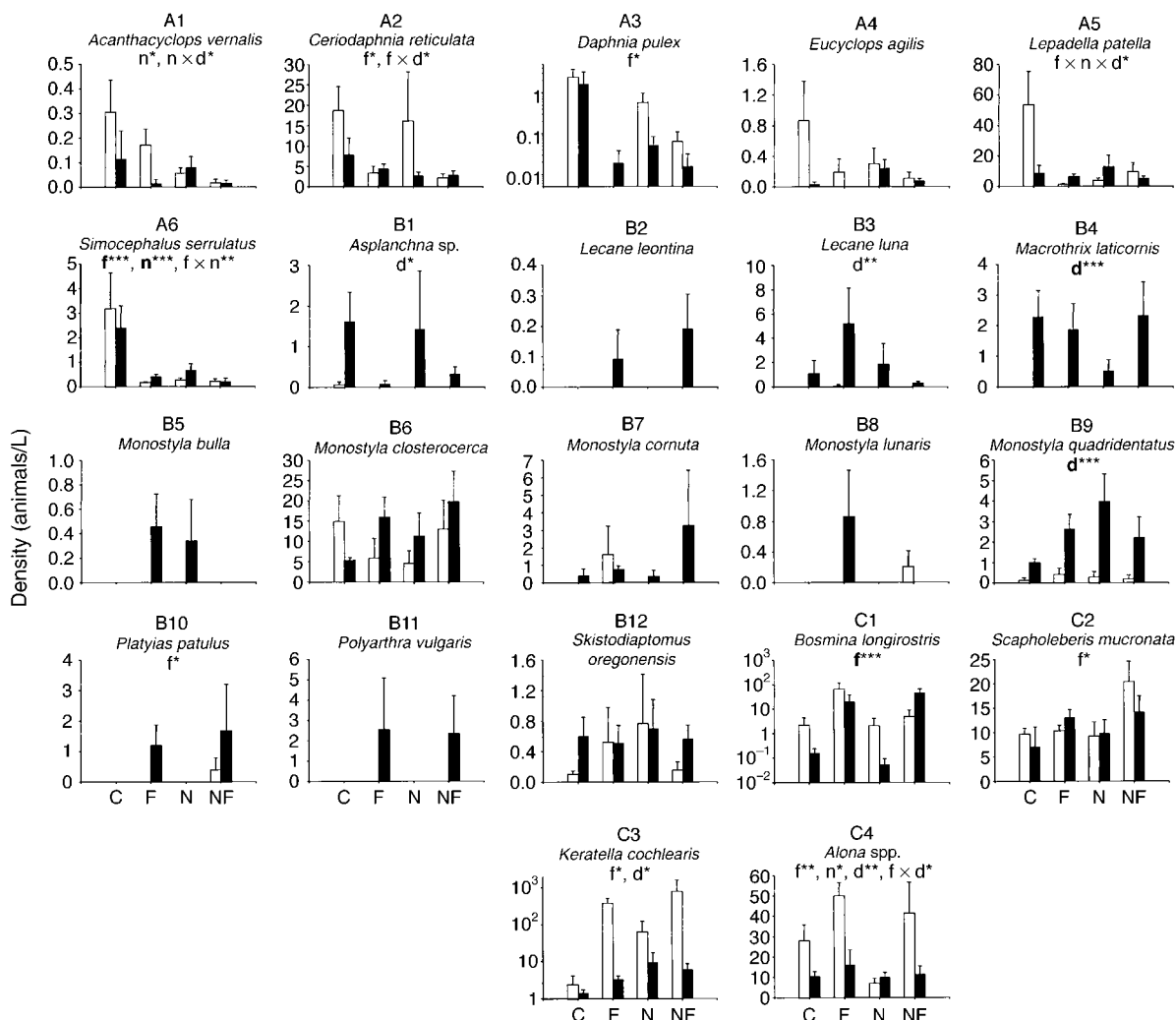


FIG. 2. Effects of the treatments on the 22 species that were most strongly correlated with the treatment axes in the RDA. Densities are means of the last four sampling dates (+ 1 SE). The x-axis treatment labels are control (C), fish (F), notonectid (N) and fish + notonectid (NF). White bars indicate the no-dispersal treatment, and black bars the high-dispersal treatment. Significant treatment effects (f = fish, n = notonectid, d = dispersal) and interactions, based on three-way ANOVAs, are shown on the panels. Significant effects at the Bonferroni adjusted level of 0.0023 are in bold. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

invaded the high-dispersal treatment. Their positive positions on the fish-by-dispersal axis indicate that their densities were greatest in the high-dispersal treatment in the presence of fish. Of these, only *Macrothrix laticornis* (B4) and *Monostyla quadridentatus* (B9) were significantly affected by the dispersal treatment in the univariate ANOVA (Fig. 2). Species on the right half of Fig. 1 (labeled "C") were most abundant with fish and either unrelated (*Bosmina longirostris* [C1] and *Scapholeberis mucronata* [C2]) or negatively related (*Keratella cochlearis* [C3] and *Alona* spp. [C4]) to the dispersal treatment (Fig. 2). Although the fish-by-dispersal interaction term contributed significantly to the fit of the RDA model, this term was not significant in any of the univariate ANOVAs at the Bonferroni corrected critical level of $P < 0.0023$ (Fig. 2).

The impact of predators on zooplankton species richness depended on the dispersal treatment (i.e., both predator-by-dispersal interaction terms were significant in the repeated measures ANOVA, Fig. 3A and B, Table 3). In the no-dispersal treatment, zooplankton richness declined in the presence of both predators, although the overall effect of fish was not significant (Fig. 3A and B, planned orthogonal contrasts for the means of the last four sampling dates; fish $F_{1,24} = 2.692$, one-tailed $P = 0.057$; and notonectids $F_{1,24} = 5.364$, $P = 0.015$). In the high-dispersal treatment, zooplankton richness was greater in the presence of fish but not notonectids (Fig. 3B; fish $F_{1,24} = 6.056$, $P = 0.011$; and notonectids $F_{1,24} = 0.189$, $P = 0.334$). Overall, predators had negative effects on zooplankton diversity in the absence of dispersal (the contrast between the

TABLE 2. Codes for the species labels in Fig. 1.

Code	Species
A1	<i>Acanthacyclops vernalis</i>
A2	<i>Ceriodaphnia reticulata</i>
A3	<i>Daphnia pulex</i>
A4	<i>Eucyclops agilis</i>
A5	<i>Lepadella patella</i>
A6	<i>Simocephalus serrulatus</i>
B1	<i>Asplanchna</i> sp.
B2	<i>Lecane leontina</i>
B3	<i>Lecane luna</i>
B4	<i>Macrothrix laticornis</i>
B5	<i>Monostyla bulla</i>
B6	<i>Monostyla closteroerca</i>
B7	<i>Monostyla cornuta</i>
B8	<i>Monostyla lunaris</i>
B9	<i>Monostyla quadridentatus</i>
B10	<i>Plyarhias patulus</i>
B11	<i>Polyarthra vulgaris</i>
B12	<i>Skistodiaptomus oregonensis</i>
C1	<i>Bosmina longirostris</i>
C2	<i>Scapholebris mucronata</i>
C3	<i>Keratella cochlearis</i>
C4	<i>Alona</i> spp.

control and tanks with predators in the no-dispersal treatment, $F_{1,24} = 8.075$, $P = 0.005$), and positive effects in the high-dispersal treatment ($F_{1,24} = 3.279$, $P = 0.042$). The results were qualitatively the same when an index of diversity (Fisher's alpha) was used instead of species richness, although the notonectid-by-dispersal interaction was not significant ($F_{1,24} = 0.345$, $P = 0.562$).

Predators had cascading effects on lower trophic levels that were independent of the dispersal treatment. Fish and notonectids reduced the mean body size of the zooplankton community (Fig. 3C and D, Table 4), although fish had a larger effect (Fig. 3D). The effect of notonectids on zooplankton body size was reduced in the presence of fish (i.e., there was a significant fish-by-notonectid interaction term in the repeated measures ANOVA, Table 4). Notonectids, but not fish, had a significant effect on zooplankton community biomass, however, the notonectids effect was only apparent in the no-dispersal treatment (Fig. 3E and F, Table 5). That is, zooplankton biomass was lower with notonectids in the no-dispersal treatment ($F_{1,24} = 11.424$, $P = 0.002$), but not with high dispersal ($F_{1,24} = 0.029$, $P = 0.866$). This effect is reflected by the nearly significant notonectid-by-dispersal interaction term in the repeated measures ANOVA (Table 5). There were nearly significant positive main effects of dispersal on mean zooplankton body size (Fig. 3D, Table 4) and negative effects on zooplankton biomass (Fig. 3F, Table 5). Fish, but not notonectids, enhanced phytoplankton biomass (Fig. 3G and H, Table 6). There was a nearly significant (Fig. 3G and H, Table 6) negative main effect of the dispersal treatment on phytoplankton biomass. The effects of the predators on plankton trophic structure (zooplankton body size, biomass, and phytoplankton

biomass) were not influenced by the dispersal treatment ($P > 0.05$ for all interactions between the dispersal and predator treatments, Tables 4–6).

DISCUSSION

This experiment suggests that local and regional processes interact to produce patterns of species composition and diversity in freshwater pond ecosystems. At the regional level, disturbances such as winter kill events or drying, coupled with colonization limitation, generate a mosaic of ponds with and without predators such as fishes or salamanders (Tonn and Magnuson 1982, Werner and McPeck 1994, Mittelbach et al. 1995, Schneider and Frost 1996, Wellborn et al. 1996, McPeck 1998). The presence of ponds with heterogeneous predator communities may create spatial refugia that promote regional coexistence by species that cannot coexist locally (Shurin 2000b). Connection to this diverse regional species pool may therefore be important for determining the impact of predation on local communities (Spencer and Warren 1996, Warren 1996). The results of the present experiment supported this contention. Predation and dispersal had interactive effects on the composition of local zooplankton communities (Table 1). A number of species were more abundant in the presence of fish and dispersal than predicted by an additive expectation based on the two treatments alone. Predators extirpated a number of large-bodied species, and thereby weakened the resistance of the zooplankton community to invasion by small species (Figs. 1 and 2). These results suggest that small zooplankton coexist regionally with larger species because of their ability to coexist locally with size-selective predators such as fish.

The effects of predators on local zooplankton diversity depended on dispersal by members of the regional pool. Both fish and notonectids reduced zooplankton species richness by precipitating extinctions when introduced into assemblages that were isolated from the regional species pool. In communities that were open to dispersal by a diverse group of species, fish promoted colonization by more species than were excluded, resulting in a net increase in local diversity (Fig. 3B). Invasion by members of the regional pool compensated for the loss of species due to notonectids, resulting in no effect on diversity in the high-dispersal treatment. Although some species invaded the high-dispersal tanks in the absence of predators (e.g., *Macrothrix laticornis*, Fig. 2), the dispersal treatment had no effect on zooplankton richness in the control (Fig. 3B). These results support predictions of a metapopulation model of predator-mediated coexistence among competitors (Shurin 2000b). The model predicts that the effects of predators on local diversity depend on the relationships among dispersal rates, competitive abilities, and susceptibility to predator-induced extinction among members of the regional species pool. Predators tend to reduce local diversity when species that

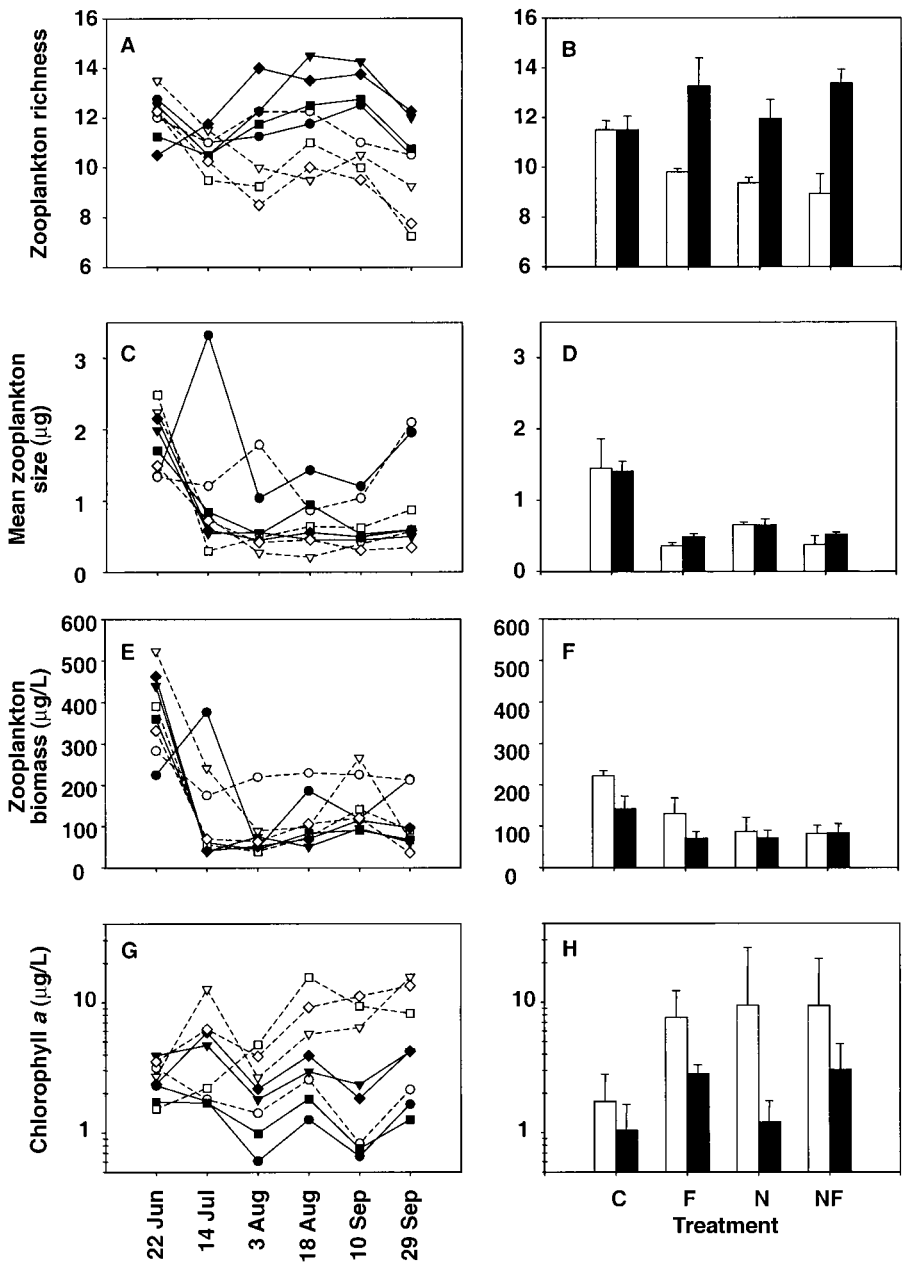


FIG. 3. Effects of the treatments on zooplankton species richness (A, B) and plankton trophic structure (C–H) through time (left panels) and averaged over the last four sampling dates (+ 1 SE; right panels). Dependent variables are zooplankton species richness (A, B), mean zooplankton body size (C, D), total zooplankton community biomass (E, F), and chlorophyll *a* (G, H). Open symbols and dashed lines indicate the no-dispersal treatment; solid symbols and solid lines are the high-dispersal treatment. Symbols refer to the treatments in the time series as follows: control (circles), fish (triangles), notonectid (squares), and fish + notonectids (diamonds). Notation for the bar graphs is as in Fig. 2. Repeated-measures ANOVAs are shown in Tables 3–6.

are facilitated by their presence have low dispersal rates and to enhance diversity in the opposite case (Shurin 2000b).

This experiment may help to resolve the apparent disparity among different studies of the impact of predation on local prey species richness. Experimental predator manipulations have found both positive (Paine

1966, Sih et al. 1985, Proulx and Mazumder 1998, Carson and Root 2000) and negative effects (Paine and Vadas 1969, Sih et al. 1985, Schoener and Spiller 1996, Spiller and Schoener 1998) of predators on local prey diversity. Two studies (Gough and Grace 1998, Proulx and Mazumder 1998) suggest that the response depends in part on productivity, with predators tending to pro-

TABLE 3. Repeated-measures ANOVA for the effects of the treatments on zooplankton species richness.

Source	ss	df	F	P
Between subjects				
Fish†	0.007	1	0.094	0.381
Notonectids†	0.136	1	1.738	0.100
Dispersal†	1.475	1	18.892	< 0.001
Noto × Fish	0.031	1	0.399	0.533
Disp × Fish†	0.337	1	4.322	0.024
Disp × Noto†	0.355	1	4.551	0.022
Noto × Disp × Fish	0.019	1	0.245	0.625
Error	1.874	24		
Within subjects				
Date	0.690	4	6.046	< 0.001
Date × Fish	0.031	4	0.274	0.894
Date × Noto	0.056	4	0.492	0.742
Date × Disp	0.302	4	2.644	0.038
Date × Noto × Fish	0.038	4	0.332	0.856
Date × Disp × Fish	0.136	4	1.192	0.319
Date × Disp × Noto	0.127	4	1.114	0.355
Date × Noto × Disp × Fish	0.041	4	0.360	0.836
Error	2.742	96		

Notes: *P* values < 0.05 are shown in bold. Values were ln-transformed.

† Treatments where one-tailed tests were used. All others are two-tailed tests.

mote diversity at high productivity more than at low productivity. The present study suggests that the effects of predators on local diversity also depend on the traits of species in the regional pool and their rates of dispersal among sites. Invasion of predators such as fish may reduce prey diversity in the short term. However, colonization by species from nearby fish ponds may compensate for the initial loss of species and result in a long term positive effect if there is sufficient dispersal

TABLE 4. Repeated-measures ANOVA for the effects of the treatments on zooplankton mean body size.

Source	ss	df	F	P
Between subjects				
Fish†	20.023	1	18.504	< 0.001
Notonectids†	7.531	1	6.960	0.007
Dispersal	4.519	1	4.176	0.052
Noto × Fish	7.457	1	6.891	0.015
Disp × Fish†	0.876	1	0.810	0.189
Disp × Noto†	0.294	1	0.271	0.304
Noto × Disp × Fish	0.003	1	0.003	0.959
Error	25.970	24		
Within subjects				
Date	3.460	4	1.748	0.146
Date × Fish	2.512	4	1.269	0.287
Date × Noto	5.606	4	2.833	0.029
Date × Disp	1.095	4	0.553	0.697
Date × Noto × Fish	3.195	4	1.614	0.177
Date × Disp × Fish	6.902	4	3.487	0.011
Date × Disp × Noto	0.565	4	0.286	0.887
Date × Noto × Disp × Fish	3.191	4	1.612	0.177
Error	47.500	96		

Notes: Values are ln-transformed. *P* values < 0.05 are shown in bold.

† Treatments where one-tailed tests were used. All others are two-tailed tests.

TABLE 5. Repeated-measures ANOVA for the effects of the treatments on zooplankton community biomass.

Source	ss	df	F	P
Between subjects				
Fish	2.686	1	2.474	0.129
Notonectids	11.272	1	10.381	0.004
Dispersal	3.913	1	3.604	0.070
Noto × Fish	4.738	1	4.363	0.048
Disp × Fish	0.175	1	0.161	0.692
Disp × Noto	3.826	1	3.523	0.073
Noto × Disp × Fish	0.079	1	0.073	0.790
Error	26.061	24		
Within subjects				
Date	9.290	4	4.565	0.002
Date × Fish	2.099	4	1.031	0.395
Date × Noto	2.594	4	1.274	0.285
Date × Disp	1.693	4	0.832	0.508
Date × Noto × Fish	0.977	4	0.480	0.750
Date × Disp × Fish	5.365	4	2.636	0.039
Date × Disp × Noto	1.438	4	0.706	0.589
Date × Noto × Disp × Fish	4.436	4	2.180	0.077
Error	48.842	96		

Notes: *P* values < 0.05 are shown in bold. Values are ln-transformed.

among local habitats. The outcome of other types of local interactions may also depend on spatial heterogeneity and movement of species at broad regional scales.

The hypothesis that invasion by members of the regional pool would compensate for the productivity that was lost to predators, and thereby weaken control of predators over trophic structure, was not supported. The effects of predators on zooplankton mean body size, community biomass, and phytoplankton biomass

TABLE 6. Repeated-measures ANOVA for the effects of the treatments on chlorophyll *a*.

Source	ss	df	F	P
Between subjects				
Fish†	44.984	1	14.841	< 0.001
Notonectids†	1.903	1	0.628	0.218
Dispersal	12.356	1	4.077	0.055
Noto × Fish	1.584	1	0.523	0.477
Disp × Fish†	0.677	1	0.223	0.320
Disp × Noto†	0.278	1	0.092	0.382
Noto × Disp × Fish	1.025	1	0.338	0.566
Error	72.743	24		
Within subjects				
Date	20.571	4	10.237	< 0.001
Date × Fish	2.050	4	1.020	0.401
Date × Noto	2.382	4	1.185	0.322
Date × Disp	2.045	4	1.018	0.402
Date × Noto × Fish	1.273	4	0.633	0.640
Date × Disp × Fish	0.888	4	0.442	0.778
Date × Disp × Noto	0.829	4	0.413	0.799
Date × Noto × Disp × Fish	0.663	4	0.330	0.857
Error	48.226	96		

Notes: *P* values < 0.05 are shown in bold. Values are ln-transformed.

† Treatments where one-tailed tests were used. All others are two-tailed tests.

were independent of the dispersal treatment. Both predators reduced zooplankton mean body size, although fish had larger effects than notonectids (Fig. 3C and D). This result is consistent with a number of studies showing that size selective predation shifts the size structure of zooplankton communities in favor of smaller species (Brooks and Dodson 1965, Hall et al. 1976, Carpenter and Kitchell 1993, Brett and Goldman 1997). There was a nearly significant ($P = 0.052$) positive main effect of the dispersal treatment on zooplankton size (Table 4). This effect arose because zooplankton in the fish treatment were, on average, 0.14 μg larger with dispersal than without (Fig. 3D). Zooplankton were very slightly (0.04 and 0.005 μg) smaller with dispersal in the control and notonectid treatments, respectively. This result suggests that the species that were facilitated by fish may have shifted the size structure of the zooplankton community toward larger bodied species to a small degree. The difference in mean size may also account for the apparent negative effect of the dispersal treatment on phytoplankton biomass (Fig. 3H, Table 6). However, the effects of dispersal were slight compared to the reduction in mean body size by fish or notonectids, or the effect of fish on phytoplankton (Fig. 3D and H). These results suggest that the species that were negatively affected by predators were functionally distinct from those that were facilitated in that they had greater impacts on zooplankton size structure and phytoplankton biomass.

Although both predators consistently reduced mean zooplankton body size, their effects and those of the dispersal treatment on community biomass were somewhat idiosyncratic. This result is similar to those found by other studies, including Soranno et al. (1993:182) who stated, "More often than not, total biomass responded oppositely to predictions." Soranno et al. propose a number of plausible explanations for the variable effects of planktivores on community biomass, and argue that mean zooplankton body size responds much more predictably to planktivory than biomass, and is a better indicator of grazing (see also Pace 1984). Similarly, in this experiment, both predators reduced zooplankton body size (Fig. 3C and D) while only notonectids affected total biomass (Fig. 3E and F). The effect of notonectids appeared to be driven by the pattern that biomass was greater in the no-dispersal treatment in both the control and fish treatments (Fig. 3F). There was a nearly significant (Table 5) negative main effect of dispersal on biomass. The reason for the apparent increase in zooplankton biomass in the absence of dispersal is unknown. However, the results of this study support the contention of Soranno et al. (1993) that zooplankton community biomass responds in complex and sometimes counterintuitive ways to changes in predation.

Although invasion by members of the regional pool did not weaken the effects of fish on trophic structure, this result depended on both the initial local assemblage

and the regional pool from which colonists were drawn. The mean initial local richness of 9.5 crustaceans species per tank was representative of natural fishless ponds in the area (a mean of 8.3 and a range of 4–16 from 11 ponds, Shurin 2000a), while the number of rotifers (2.5 per tank) was relatively low (mean = 10.9, range = 4–16). The low rotifer diversity may be due to the absence of major zooplankton predators in the initial assemblage. Drawing species for the high-dispersal treatment from a larger regional pool would have increased the number of potential invaders, and possibly the impact of the dispersal treatment on trophic structure as well (Shurin et al. 2000). Zooplankton for the high-dispersal treatment were collected from a mean of 8.2 ponds within an area of $\sim 100 \text{ km}^2$. Since the distances over which species disperse is unknown, the spatial extent of the regional pool could not be reliably defined. However, previous work (Shurin 2000a) suggested high rates of dispersal among eleven ponds within a 100 km^2 region.

Indirect facilitation of small species by fish took place either through suppression of competitors or intermediate predators, or by some combination of the two. The species that declined in the fish treatment were almost entirely large cladocerans and cyclopoid copepods (Figs. 1 and 2). Large zooplankton consume a broader size spectrum of particles and have lower threshold food density below which they cannot maintain metabolic demands (Burns 1968, Hall et al. 1976, Gliwicz 1990). Cyclopoids such as *Acanthacyclops vernalis* and *Eucyclops agilis* are omnivorous, preying on protozoans and rotifers as adults, however most stages are primarily herbivorous (Adrian and Frost 1993). In addition, fish enhanced phytoplankton biomass, suggesting that more resources were available to invaders in the fish treatment (Fig. 3H).

The new species found in the high-dispersal treatment were not simply sink populations in the process of going extinct. The species that accounted for the increased diversity in the high-dispersal treatment were introduced in very low numbers. For instance, the seven species that were found exclusively in the high-dispersal treatment (*Macrothrix laticornis*, *Brachionus angularis*, *B. quadridentatus*, *Lecane leontina*, *Monostyla bulla*, *Ploesoma hudsoni*, *Polyarthra vulgaris*) were added in mean densities of 0.12/L (range 0.001–0.58/L; see Appendix). Of these, *Polyarthra vulgaris* was added in the greatest numbers (0.58/L; see Appendix); however, it was only found in the high-dispersal treatment in the presence of fish (Fig. 2). In addition, its mean density in the high-dispersal treatment with fish was 2.4 animals/L (Fig. 2), indicating that the population generally increased in the presence of fish. Finally, many species that were introduced in the greatest densities were unaffected by the dispersal treatment (e.g., *Bosmina longirostris*, *Daphnia dubia*, *Diaphanosoma brachyurum*, *Mesocyclops edax*, *Tropocyclops prasinus*, *Polyarthra major*; Fig. 2; see Ap-

pendix). These results indicate that the patterns associated with the dispersal treatment resulted from invasions by new species and not from sink effects due to the individuals added in the inoculum.

The two predators influenced planktonic community structure and invasibility differently, indicating that fish and notonectids are functionally distinct in their effects on lower trophic levels (*sensu* Morin 1995). Fish had greater impacts on the densities of large zooplankton (Figs. 1 and 2) and reduced mean body size to a greater extent (Fig. 3D). These effects resulted in a larger increase in phytoplankton biomass (Fig. 3H) and greater facilitation of invaders in the dispersal treatment (Fig. 1). Fish and notonectids had nonadditive effects on zooplankton body size (i.e., the effects of the two predators together were smaller than expected based on their independent effects, Table 4). This likely reflects a reduced impact of notonectids in the presence of fish, probably due to consumption of juvenile notonectids by fish. Although both predators are size selective, preferentially consuming large-bodied zooplankton, the magnitude of the effects of fish were generally greater, indicating that fish may be more important than notonectids in promoting regional coexistence among zooplankton.

This study suggests that regional processes play an important role in determining the outcome of local interactions such as predation in communities. Studies of the effects of species diversity on ecosystem function and response to environmental change have focused largely on the importance of diversity at the local scale (e.g., Hooper and Vitousek 1997, McGrady-Steed et al. 1997, Tilman 1999). However, immigration from a pool of species with diverse traits may buffer local communities against environmental changes such as the invasion of predators (Leibold et al. 1997). For instance, Hairston (1996) suggested that zooplankton egg banks represent reserves of genetic and species diversity that may be important for regulating the response of lake ecosystems to environmental fluctuations. Spatial heterogeneity in local conditions, such as refugia from predators, may serve a similar function. In the present study, dispersal by species from the regional pool reversed the negative effects of predators on local zooplankton diversity. Ecologists have long debated the question of what properties of communities influence their response to environmental perturbations. I argue that regional species diversity and composition affect local zooplankton assemblages and may therefore be important for determining the long-term effects of changes such as predator invasions. The isolation of local communities, for instance through habitat fragmentation, may therefore alter the impact of extrinsic perturbations even if it has no direct effect on the local biota.

ACKNOWLEDGMENTS

I thank Galeet Cohen for help in the field and Michael Fraker for assistance counting zooplankton samples. Jon

Chase and Amy Downing allowed access to their unpublished pond survey. Comments by John Alroy, Joy Bergelson, Amy Downing, Sarah Gergel, Pierre Legendre, Mathew Leibold, Jonathan Levine, Craig Osenberg, Scott Peacor, Cathy Pfister, David Post, Alan Tessier, Tim Wootton, and the reviewers greatly improved the manuscript. Funding was provided by NSF (DEB 95-09004 to M. Leibold and Dissertation Improvement Grant DEB 99-72656 to the author). Kellogg Biological Station in general, and Gary Mittelbach and Alan Tessier in particular, generously provided access to facilities. This experiment was performed under Michigan State University's All-University Committee on Animal Use and Care project number 08/98-125-00. This is Kellogg Biological Station contribution #948.

LITERATURE CITED

- Adrian, R., and T. M. Frost. 1993. Omnivory in cyclopoid copepods—comparisons of algae and invertebrates as food for 3, differently sized species. *Journal of Plankton Research* **15**:643–658.
- Arner, M., S. Koivisto, J. Norberg, and N. Kautsky. 1998. Trophic interactions in rockpool food webs: regulation of zooplankton and phytoplankton by *Notonecta* and *Daphnia*. *Freshwater Biology* **39**:79–90.
- Arnott, S., and M. Vanni. 1993. Zooplankton assemblages in fishless bog lakes: influence of biotic and abiotic factors. *Ecology* **74**:2361–2380.
- Bendell, B. E. 1986. The effects of fish and pH on the distribution and abundance of backswimmers (Hemiptera: Notonectidae). *Canadian Journal of Zoology* **64**:2696–2699.
- Bennett, D. V., and F. A. Streams. 1986. Effects of vegetation on *Notonecta* (Hemiptera) distribution in ponds with and without fish. *Oikos* **46**:62–69.
- Brett, M. T., and C. R. Goldman. 1997. Consumer versus resource control in freshwater pelagic food webs. *Science* **275**:384–386.
- Brooks, J. L., and S. I. Dodson. 1965. Predation, body size, and composition of the plankton. *Science* **150**:28–35.
- Burns, C. W. 1968. The relationship between body-size of filter-feeding zooplankton and the maximum size of particle ingested. *Limnology and Oceanography* **13**:675–678.
- Carpenter, S. R., and J. F. Kitchell. 1993. *The trophic cascade in lakes*. Cambridge University Press, Cambridge, UK.
- Carson, W. P., and R. B. Root. 2000. Herbivory and plant species coexistence: community regulation by an outbreaking phytophagous insect. *Ecological Monographs* **70**:73–99.
- Chase, J. M., M. A. Leibold, A. L. Downing, and J. B. Shurin. 2000. Grassland food web patterns and processes: Empirical evaluation of three models. *Ecology* **81**:2485–2497.
- Crawley, M. J. 1989. The relative importance of vertebrate and invertebrate herbivores in plant population dynamics. Pages 41–557 in E. Bernays, editor. *Insect plant interactions*. CRC Press, Boca Raton, Florida, USA.
- Dodson, S. I. 1970. Complementary feeding niches sustained by size-selective predation. *Limnology and Oceanography* **15**:131–137.
- Dodson, S. I. 1974. Zooplankton competition and predation: an experimental test of the size-efficiency hypothesis. *Ecology* **55**:605–613.
- Elser, J. J., T. H. Chrzanowski, R. W. Sterner, and K. H. Mills. 1998. Stoichiometric constraints on food-web dynamics: a whole-lake experiment on the Canadian shield. *Ecosystems* **1**:120–136.
- Fritts, T. H., and G. H. Rodda. 1998. The role of introduced species in the degradation of island ecosystems: A case history of Guam. *Annual Review of Ecology and Systematics* **29**:113–140.
- Giguère, L. 1979. An experimental test of Dodson's hypothesis that *Ambystoma* (a salamander) and *Chaoborus* (a

- phantom midge) have complementary feeding niches. *Canadian Journal of Zoology* **57**:1091–1097.
- Gliwicz, Z. M. 1990. Food thresholds and body size in cladocerans. *Nature* **343**:638–640.
- Gough, L., and J. B. Grace. 1998. Herbivore effects on plant species density at varying productivity levels. *Ecology* **79**:1586–1594.
- Hairston, N. G., F. E. Smith, and L. B. Slobodkin. 1960. Community structure, population control, and competition. *American Naturalist* **44**:421–425.
- Hairston, N. G., Jr. 1996. Zooplankton egg banks as biotic reservoirs in changing environments. *Limnology and Oceanography* **41**:1087–1092.
- Hall, D. J., S. T. Threlkeld, C. W. Burns, and P. H. Crowley. 1976. The size-efficiency hypothesis and the size structure of zooplankton communities. *Annual Review of Ecology and Systematics* **46**:177–208.
- Holt, R. D. 1993. Ecology at the mesoscale: The influence of regional processes on local communities. Pages 77–88 in R. E. Ricklefs and D. Schluter, editors. *Species diversity in ecological communities*. University of Chicago Press, Chicago, Illinois, USA.
- Holt, R. D. 1997. From metapopulation dynamics to community structure: some consequences of spatial heterogeneity. Pages 149–164 in I. Hanski and M. E. Gilpin, editors. *Metapopulation biology: Ecology, genetics and evolution*. Academic Press, San Diego, California, USA.
- Holt, R. D., J. Grover, and D. Tilman. 1994. Simple rules for interspecific dominance in systems with exploitative and apparent competition. *American Naturalist* **144**:741–771.
- Hooper, D. U., and P. M. Vitousek. 1997. The effects of plant composition and diversity on ecosystem processes. *Science* **277**:1302–1305.
- Hunter, M. D., and P. W. Price. 1992. Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. *Ecology* **73**:724–732.
- Jenkins, D. G., and A. L. J. Buikema. 1998. Do similar communities develop in similar sites? A test with zooplankton structure and function. *Ecological Monographs* **68**:421–443.
- Jongman, R. H. G., C. J. F. ter Braak, and O. F. R. van Tongeren. 1995. *Data analysis in community and landscape ecology*. Cambridge University Press, Cambridge, UK.
- Kerfoot, W. C., and A. Sih, editors. 1987. *Predation: direct and indirect impacts on aquatic communities*. University Press of New England, Hanover, New Hampshire, USA.
- Legendre, P., and M. J. Anderson. 1999. Distance-based redundancy analysis: testing multispecies responses in multifactorial ecological experiments. *Ecological Monographs* **69**:1–24.
- Legendre, P., and L. Legendre. 1998. *Numerical ecology*. Elsevier, Amsterdam, The Netherlands.
- Leibold, M. A. 1996. A graphical model of keystone predators in food webs: trophic regulation of abundance, incidence, and diversity patterns in communities. *American Naturalist* **147**:784–812.
- Leibold, M. A., J. M. Chase, J. B. Shurin, and A. L. Downing. 1997. Species turnover and the regulation of trophic structure. *Annual Review of Ecology and Systematics* **28**:467–494.
- Lubchenco, J. 1978. Plant species diversity in a marine intertidal community: importance of herbivore food preference and algal competitive abilities. *American Naturalist* **112**:23–39.
- Lynch, M. 1980. The evolution of cladoceran life histories. *Quarterly Review of Biology* **55**:23–42.
- McCauley, E. 1984. The estimation of the abundance and biomass of zooplankton in samples. Pages 228–265 in J. A. Downing and F. H. Rigler, editors. *A manual on methods for the assessment of secondary productivity in fresh waters*. Blackwell Scientific, Oxford, UK.
- McGrady-Steed, J., P. M. Harris, and P. J. Morin. 1997. Biodiversity regulates ecosystem predictability. *Nature* **390**:162–165.
- McPeck, M. A. 1998. The consequences of changing the top predator in a food web: a comparative experimental approach. *Ecological Monographs* **68**:1–23.
- Mittelbach, G. G. 1988. Competition among refuging sunfishes and effects of fish density on littoral-zone invertebrates. *Ecology* **69**:614–623.
- Mittelbach, G. G., A. M. Turner, D. J. Hall, J. E. Rettig, and C. W. Osenberg. 1995. Perturbation and resilience: a long-term, whole-lake study of predator extinction and reintroduction. *Ecology* **76**:2347–2360.
- Morin, P. J. 1987. Salamander predation, prey facilitation, and seasonal succession in microcrustacean communities. Pages 174–187 in W. C. Kerfoot and A. Sih, editors. *Predation: direct and indirect impacts on aquatic communities*. University Press of New England, Hanover, New Hampshire, USA.
- Morin, P. J. 1995. Functional redundancy, nonadditive interactions, and supply-side dynamics in experimental pond communities. *Ecology* **76**:133–149.
- Murdoch, W. W., M. A. Scott, and P. Ebsworth. 1984. Effects of the general predator *Notonecta* (Hemiptera) upon a freshwater community. *Journal of Animal Ecology* **53**:791–808.
- Oksanen, L., S. D. Fretwell, J. Arruda, and P. Niemela. 1981. Exploitation ecosystems in gradients of primary productivity. *American Naturalist* **118**:240–261.
- Osenberg, C. W., E. E. Werner, G. G. Mittelbach, and D. J. Hall. 1988. Growth-patterns in bluegill (*Lepomis macrochirus*) and pumpkinseed (*Lepomis gibbosus*) sunfish—environmental variation and the importance of ontogenetic niche shifts. *Canadian Journal of Fisheries and Aquatic Sciences* **45**:17–26.
- Pacala, S. W., and M. J. Crawley. 1992. Herbivores and plant diversity. *American Naturalist* **140**:243–260.
- Pace, M. L. 1984. Zooplankton community structure, but not biomass, influences the phosphorus–chlorophyll *a* relationship. *Canadian Journal of Fisheries and Aquatic Sciences* **41**:1089–1096.
- Paine, R. T. 1966. Food web complexity and species diversity. *American Naturalist* **100**:65–75.
- Paine, R. T., and R. L. Vadas. 1969. The effects of grazing by sea urchins, *Strongylocentrotus* spp., on benthic algal populations. *Limnology and Oceanography* **14**:710–719.
- Persson, L. 1999. Trophic cascade: abiding heterogeneity and the trophic level concept at the end of the road. *Oikos* **85**:385–397.
- Polis, G. A., and D. R. Strong. 1996. Food web complexity and community dynamics. *American Naturalist* **147**:813–846.
- Proulx, M., and A. Mazumder. 1998. Reversal of grazing impact on plant species richness in nutrient-poor vs. nutrient-rich ecosystems. *Ecology* **79**:2581–2592.
- Pulliam, H. R. 1988. Sources, sinks, and population regulation. *American Naturalist* **132**:652–661.
- Schneider, D. W., and T. M. Frost. 1996. Habitat duration and community structure in temporary ponds. *Journal of the North American Benthological Society* **15**:64–86.
- Schoener, T. W. 1989. Food webs from the small to the large. *Ecology* **70**:1559–1589.
- Schoener, T. W., and D. A. Spiller. 1996. Devastation of prey diversity by experimentally introduced predators in the field. *Nature* **381**:691–694.
- Shurin, J. B. 2000a. Dispersal limitation, invasion resistance, and the structure of pond zooplankton communities. *Ecology* **81**:3074–3086.

- Shurin, J. B. 2000*b*. Local and regional influences on the structure of freshwater zooplankton communities. Dissertation. University of Chicago, Chicago, Illinois, USA.
- Shurin, J. B., J. E. Havel, M. A. Leibold, and B. Pinel-Alloul. 2000. Local and regional zooplankton species richness: a scale-independent test for saturation. *Ecology* **81**:3062–3073.
- Sih, A., P. Crowley, M. McPeck, J. Petranka, and K. Strohmeyer. 1985. Predation, competition, and prey communities: a review of field experiments. *Annual Review of Ecology and Systematics* **16**:269–311.
- Soranno, P. A., S. R. Carpenter, and X. He. 1993. Zooplankton biomass and body size. Pages 172–188 in S. R. Carpenter and J. F. Kitchell, editors. *The trophic cascade in lakes*. Cambridge University Press, Cambridge, UK.
- Spencer, M., and P. H. Warren. 1996. The effects of energy input, immigration and habitat size on food web structure: A microcosm experiment. *Oecologia* **108**:764–770.
- Spiller, D. A., and T. W. Schoener. 1998. Lizards reduce spider species richness by excluding rare species. *Ecology* **79**:503–516.
- Sprules, W. G. 1972. Effects of size-selective predation and food competition on high altitude zooplankton communities. *Ecology* **53**:375–386.
- Stemberger, R. S., and J. J. Gilbert. 1985. Body size, food concentration, and population growth in planktonic rotifers. *Ecology* **66**:1151–1159.
- Strong, D. R. 1992. Are trophic cascades all wet? Differentiation and donor control in speciose ecosystems. *Ecology* **73**:747–754.
- ter Braak, C. J. F., and P. Smilauer. 1999. CANOCO for Windows 4.02. Centre for Biometry. Wageningen, The Netherlands.
- Tilman, D. 1999. The ecological consequences of changes in biodiversity: a search for general principles. *Ecology* **80**:1455–1474.
- Tonn, W. M., and J. J. Magnuson. 1982. Patterns in the species composition and richness of fish assemblages in northern Wisconsin lakes. *Ecology* **63**:1149–1166.
- Vanni, M. J. 1988. Freshwater zooplankton community structure: introduction of large invertebrate predators and large herbivores to a small-species community. *Canadian Journal of Fisheries and Aquatic Science* **45**:1758.
- Warren, P. H. 1996. The effects of between-habitat dispersal rate on protist communities and metacommunities in microcosms at two spatial scales. *Oecologia* **105**:132–140.
- Wellborn, G. A., D. K. Skelly, and E. E. Werner. 1996. Mechanisms creating community structure across a freshwater habitat gradient. *Annual Review of Ecology and Systematics* **27**:337–363.
- Welschmeyer, N. 1994. Fluorometric analysis of chlorophyll *a* in the presence of chlorophyll *b* and phaeopigments. *Limnology and Oceanography* **39**:1985–1992.
- Werner, E. E., and M. A. McPeck. 1994. The roles of direct and indirect effects on the distributions of two frog species along an environmental gradient. *Ecology* **75**:1368–1382.
- Zaret, T. M. 1980. *Predation and freshwater communities*. Yale University Press, New Haven, Connecticut, USA.
- Zimmer, K. D., M. A. Hanson, and M. G. Butler. 2000. Factors influencing invertebrate communities in prairie wetlands: a multivariate approach. *Canadian Journal of Fisheries and Aquatic Sciences* **57**:76–85.

APPENDIX

A table containing taxa and numbers of individuals introduced to each tank in the high-dispersal treatment is available in ESA's Electronic Data Archive: *Ecological Archives* E082-039.