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Independent and interactive effects of crayfish and darters on a stream benthic community

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Abstract. A growing body of research suggests that direct and indirect interactions among consumers can have strong effects on the abundance of their prey. We examined the independent and interactive effects of 2 common freshwater consumers, crayfish (*Orconectes propinquus*) and rainbow darters (*Etheostoma caeruleum*), on benthic macroinvertebrates in a southern Michigan, USA, stream. A secondary goal was to assess the effects of crayfish and darters on the basal trophic level (periphyton) in the system. Presence and absence of crayfish and darters were manipulated in situ in wire mesh cages (0.2 m², 6-mm mesh) using a 2 × 2 factorial, randomized block design. Invertebrates and periphyton (for chlorophyll *a* analysis) were sampled biweekly for 6 wk from artificial rock substrates within these cages. Neither consumer significantly affected chlorophyll *a* accumulation. Darters alone had no significant effects on total invertebrate abundance. Crayfish alone caused, on average, a 58% reduction in total invertebrate abundance relative to exclosures, and most common invertebrate taxa were negatively affected. In the presence of darters, however, crayfish reduced invertebrate numbers by only 29% relative to exclosures. Darters apparently modified the ability of crayfish to suppress invertebrate abundance, although the mechanism is unclear. Evaluations of community structure based on manipulations of individual consumer species may be misleading when interaction modifications such as these occur.

Key words: indirect effects, crayfish, darter, benthic invertebrates, Michigan, field experiment.

The importance of indirect effects in food webs has been demonstrated in several types of communities (Soluk and Collins 1988, Flecker 1992, Soluk 1993, Wissinger and McGrady 1993, Wootton 1993, Morin 1995, Ferguson and Stiling 1996, McIntosh and Townsend 1996), and the body of theory addressing indirect effects continues to grow (Hairston et al. 1960, Oksanen et al. 1981, Miller and Kerfoot 1987, Werner 1992, Billick and Case 1994, Wootton 1994). Wootton (1993) distinguished between 2 types of indirect effects: interaction chains and interaction modifications. Interaction chains refer to a string of 2 or more direct effects in a food web. Interaction modifications are a type of higher-order interaction that results when a species qualitatively changes the direct interaction between 2 other species (or groups) without affecting the abundance of the focal species (e.g., 1 type of consumer modifies the interaction between another consumer and its prey). When interaction modifications occur in communities, it may not be possible to predict the combined effects of 2 or more consumers based on manipulations of individual consumer species.

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Indirect effects resulting from strong biotic interactions can influence invertebrate community structure in running waters (Flecker 1992, Hart 1992, Power 1992, Creed 1994, Lamberti 1996). Strong direct and indirect effects of certain consumers (large crustaceans, detrital-feeding fish) are commonly observed (Flecker 1992, 1997, Hart 1992, Creed 1994). Strong direct effects of insect predators on their prey have also been observed (Peckarsky and Dodson 1980, Walde 1986, Lancaster 1990). There is conflicting evidence, however, on whether predatory fish have strong direct (and indirect) effects on stream benthic communities. Several studies have failed to show strong effects of fish predation in streams (Allan 1982, Flecker and Allan 1984, Reice and Edwards 1986, Culp 1986), whereas others have shown that fish can have strong effects on their prey (Flecker 1984, Gilliam et al. 1989, Schlosser and Ebel 1989, Harvey and Hill 1991, Power 1992, Wiseman et al. 1993). Many of the previous studies addressing the effects of fish and invertebrate consumers in streams have been done by manipulating single consumers (e.g., Peckarsky and Dodson 1980, Culp 1986, Gilliam et al. 1989, Lancaster 1990, Wiseman et al. 1993). Few studies (see Soluk and Collins 1988, Soluk 1993) have addressed

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the independent and interactive effects of multiple consumers on lotic benthic communities.

Crayfish are found in many freshwater habitats worldwide and can have strong direct and indirect effects on lower trophic levels in lakes (e.g., Lodge et al. 1994) and streams (Hart 1992, Creed 1994, Charlebois and Lamberti 1996, Perry et al. 1997). Crayfish are omnivorous, and typically feed on algae, other plants, and invertebrates (Capelli 1980, Hart 1992, Creed 1994, Charlebois and Lamberti 1996). Crayfish are relatively large and active consumers, so they can potentially modify their local habitat, e.g., by substrate rolling. The tendency of crayfish to physically alter their habitat may have consequences for benthic invertebrates and periphyton. Darters, which commonly co-occur with crayfish in North American streams, feed almost exclusively on invertebrates (Martin 1984, Page 1983), but appear to have weak effects on invertebrate populations (Milstead and Threlkeld 1986). Crayfish and rainbow darters prefer coarse substrates (large gravel to cobble) in streams (Schlosser and Toth 1984, Fisher and Pearson 1987, Hobbs and Jass 1988). When crayfish and darters occur in close proximity, crayfish influence darter behavior and even consume darters (Rahel and Stein 1988). Because of their similar habitat use and food preferences, crayfish and darters are likely to interact directly (e.g., interference competition, predation) and indirectly (e.g., exploitative competition) in streams.

We experimentally manipulated crayfish (*Orconectes propinquus*) and rainbow darters (*Etheostoma caeruleum*) in flow-through mesocosms in a midwestern stream. Our goals were to compare the individual effects of crayfish and darters on lower trophic levels, and to determine if crayfish and darters had interactive effects on benthic invertebrates. Our specific predictions were: 1) crayfish and darters will have negative effects on the abundances of benthic invertebrates, and 2) through interference competition, crayfish will reduce the ability of darters to suppress benthic invertebrate abundance.

Methods

Study Site

Our study was conducted in Mill Creek, a 3rd-order, stony-bottom stream in southwestern Michigan, USA (lat 41°50'N, long 85°45'W) during July to September 1995. The stream contains a large population (mean density = $2/m^2$, maximum density = $10/m^2$) of rainbow darters. Blacknose dace (*Rhinichthys atratulus*), sculpin (*Cottus* spp.), and johnny darters (*Etheostoma nigrum*) also occur in riffles, but in relatively low numbers. Crayfish are also abundant (mean density = $1/m^2$, maximum density = $5/m^2$).

Experimental design

Crayfish and darter abundances were manipulated in situ in wire mesh cages (53 cm L × 38 cm W × 20 cm D, $0.20 m^2$, 6-mm mesh), 3/4 submersed in a 50-m long, unshaded riffle (0.3–0.5 m/s water velocity, 15–20 cm depth). We used a 2 × 2 factorial design with the following treatments: 1) no crayfish or darters (exclosures), 2) 1 crayfish (= $5/m^2$), 3) 2 darters (= $10/m^2$), and 4) 1 crayfish + 2 darters. Our treatments thus were at the high end of the range of consumer densities observed in the stream. Each treatment was replicated 5 times in a randomized block design. Cages were arranged in a 4 × 5 matrix, with longitudinal stream position as the blocking factor. Blocks were ~7 m apart and cages were staggered to minimize upstream cage effects. Treatments were assigned randomly to cages within each block. The relatively large mesh size of the cages enclosed the crayfish (23–28 mm carapace length) and darters (52–58 mm total length) but presumably allowed most other invertebrates to move freely in and out of the cages. Most other fish species were excluded from the cages.

Each cage was lined with 4 L of mixed gravel (1–3 cm diameter) to a depth of 2 cm. The gravel was obtained from a local quarry and was allowed to precolonize in the stream for 2 wk prior to the start of the experiment. Twenty egg-shaped artificial substrates (each 100 cm^2 surface area) were placed in the stream for leaching and periphyton colonization 6 wk prior to the experiment, and were then placed on top of the gravel. The substrates were made of unglazed ceramic that mimicked natural rocks in the riffle, while providing the advantages of uniform surface area and reproducibility among treatments. Substrates were lightly scrubbed with a brush before they were placed in the cages to minimize initial differences in algal and invertebrate accumulation, while retaining a thin bio-

film. Crayfish and darters were added to the cages 1 d after the substrates were added. The cages were cleaned daily to minimize flow obstruction. Crayfish and darters within cages were censused every 4–5 d by snorkeling, and any that had perished or escaped (<10% of total) were replaced. Young-of-the-year crayfish and darters were occasionally observed in cages beginning midway through the experiment, and were removed when possible.

Sampling approach

The artificial substrates were sampled for invertebrates and periphyton 1 d prior to consumer addition, to determine whether initial abundances of invertebrates and periphyton were similar among cages. Thereafter, substrates were sampled biweekly (3 times) throughout the 6-wk experiment. Two substrates were randomly sampled for invertebrates and 1 for chlorophyll *a* from each cage on every sampling date except for the final date, when 5 substrates were sampled for invertebrates, 2 for chlorophyll *a*, and 1 for periphyton biomass (as ash-free dry mass, AFDM). When possible, a Nitex® net (100-μm mesh) was used to catch invertebrates that fell off the substrates during their removal from the cages. The entire surface of the substrate was sampled for each analysis. The artificial substrates were representative of natural substrates in the stream in terms of algal cover after day 12. Sampled substrates were replaced with new, clean substrates.

Substrates collected for invertebrate analysis were preserved in 70% ethanol. Invertebrates were sorted and enumerated using a Leica MZ12 dissecting microscope at 10×. Only invertebrates from the final sampling date were identified, to family in most cases. Substrates collected for chlorophyll *a* analysis were placed on ice in the field, frozen in the laboratory overnight, and the entire substrates were extracted in 95% ethanol (Hansson 1988). Chlorophyll *a*, corrected for phaeophytin, was measured with a Perkin-Elmer Lambda 6 spectrophotometer using the acidification method (APHA 1992). Biomass of periphyton brushed from artificial substrates was determined as the loss in mass on ignition at 500°C. Darters were collected from cages at the end of the experiment and preserved in 70% ethanol for analysis of gut contents. Darters were dissected and inverte-

brates were identified to family under 10× magnification and enumerated. Crayfish were collected for gut analysis but the samples were lost because of freezer malfunction.

Data analysis

We used a 2-way repeated measures ANOVA (rmANOVA) on log-transformed total macroinvertebrate abundance and chlorophyll *a* to assess if the combined effect of crayfish and darters on their prey was a multiplicative function of the individual effects. Given no interaction between consumers, the effect of 2 consumers on their prey is more likely to be a multiplicative process (sensu Wootton 1994) than an additive one. Additive models can lead to implausible predictions for the combined effects of 2 predators (Wootton 1994). For example, 2 predators that each deplete 80% of their prey when in isolation would be expected, in combination, to lead to negative prey abundances given a simple additive model. By log-transforming invertebrate abundance and chlorophyll *a*, we were able to test a multiplicative rmANOVA model. Because algal biomass was sampled only on the final date, a 2-way ANOVA (no repeated measures) was conducted for that date. The response of specific invertebrate taxa to crayfish and darters from the final sampling date was evaluated with 1-way ANOVA on each common invertebrate taxon, followed by Fisher's LSD test to determine which treatments differed significantly from the exclosures. The α-level for significance in the Fishers' LSD tests was uncorrected for the multiple ANOVAs. The *p*-values were used as an index of effect strength for specific taxa but not as hypothesis tests per se. Percent reduction was used to describe the effect of consumers on benthic invertebrates relative to exclosure cages. Percent reduction was calculated by dividing the difference between exclosure and enclosure mean invertebrate abundance by the exclosure mean for a given date. Percent reductions are means across the 3 sampling dates (not including the initial sampling date).

To determine the directionality of the crayfish-darter interaction, we also compared invertebrate densities when crayfish and darters co-occurred to the expected density given no interaction between consumer species. The expected number of invertebrates (N) remaining
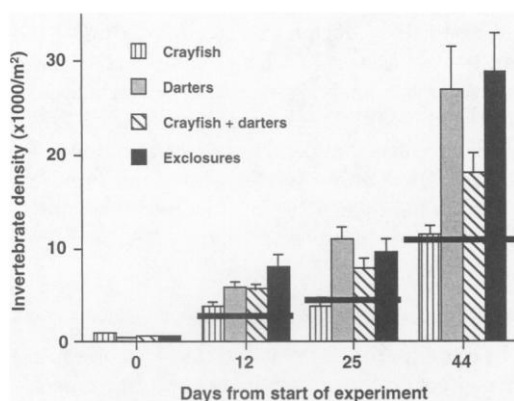
FIG. 1.   Response of total macroinvertebrate abundance to the presence of crayfish and darters (mean + 1 SE, n = 5). Horizontal lines indicate expected macroinvertebrate density in crayfish + darter cages assuming a multiplicative model of no interaction between crayfish and darters (equation 1). SEs on day 0 are too small to be seen.
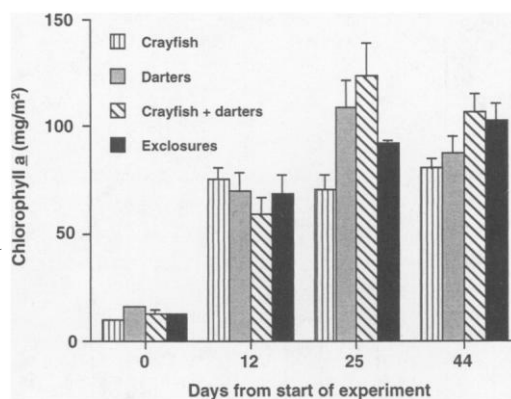

FIG. 2.   Response of periphyton chlorophyll a to the presence of crayfish and darters (mean + 1 SE, n = 5). A repeated measures 2-way ANOVA on log-transformed periphyton abundance revealed that $p > 0.2$ for crayfish and darter main effects and the crayfish × darter interaction.

in a cage for the crayfish + darter treatment was calculated after Fowler and Rausher (1985) as:

$$N = 10 \times \exp\left(\log X_c - \sum_{i=1}^{m} (\log X_c - \log X_i)\right) \text{ [1]}$$

where X_c is the total invertebrate abundance in exclosures (controls) and X_i is the total invertebrate abundance for the m single-consumer treatments where m = 2 (crayfish or darters).

Results

In the treatment with crayfish alone, total invertebrate abundance was reduced by 58% compared with exclosures (Fig. 1), and the crayfish main effect was highly significant ($p < 0.001$, Table 1). In contrast, total invertebrate abundance was reduced by only 7% in the darters

alone treatment (Fig. 1), and the darter main effect was not significant (Table 1). Crayfish and darters together reduced invertebrates by 29% relative to exclosures (Fig. 1). The 2 consumers together, however, reduced invertebrate abundance less than expected from a simple multiplicative model of no interactive effect for all 3 sampling dates (Fig. 1). Furthermore, the rmANOVA indicated that the effect of crayfish on benthic invertebrates was influenced by the presence of darters ($p = 0.023$, Table 1).

Neither crayfish nor darters significantly affected chlorophyll a accumulation when all dates were considered together (Fig. 2, $p > 0.4$ for all between-subject factors for rmANOVA). On day 25, darters had a significant main effect on chlorophyll a (Fig. 2, $p = 0.028$, 2-way ANOVA). Neither consumer significantly affected algal biomass on the final sampling date, although there was a nonsignificant trend of lower AFDM in treatments with consumers (Fig. 3).

TABLE 1.   Results of between-subjects repeated measures ANOVA on log-transformed total invertebrate abundance.

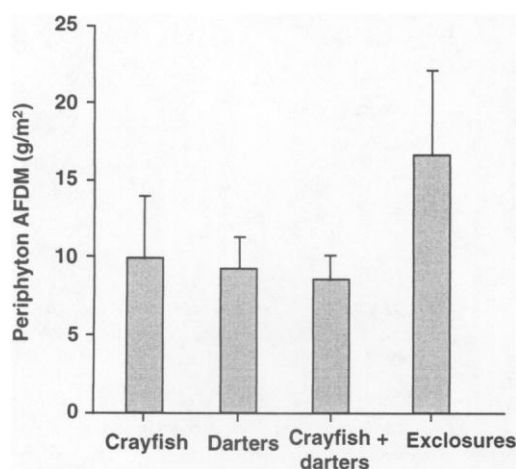| Source of variation	SS	df	MS	F	p
block	1.360	4	0.340	1.292	0.327
Crayfish	5.484	1	5.484	20.848	<0.001
Darters	1.110	1	1.110	4.218	0.062
Crayfish × Darters	1.768	1	1.768	6.721	0.023
Error	3.157	12	0.263		

FIG. 3. Periphyton ash-free dry mass (AFDM) on the final sampling date (day 44) (mean +1 SE, $n = 5$). A 2-way ANOVA revealed that $p > 0.3$ for crayfish and darter main effects and the crayfish × darter interaction.

Responses of common invertebrate taxa (>1.5% of total) to crayfish and darters are presented as the directional difference from exclosure means within each block for the final sampling date (Fig. 4). Chironomid larvae, baetid mayflies, and hydroptilid caddisflies were the dominant invertebrate taxa on the final sampling date, composing 67%, 8%, and 4% of all invertebrates (total number = 21, 514), respectively. Crayfish alone negatively affected 3 of the 6 most abundant invertebrate taxa when compared to exclosures (Fig. 4). Crayfish and darters together reduced baetid abundance relative to exclosures, but had no effect on other taxa. Darters alone increased tricorythid mayfly abundance relative to exclosures.

Darter mortality was substantially higher in cages with crayfish (9 darter mortalities) than in cages lacking crayfish (3 mortalities). In 7 of the 9 mortalities in the crayfish + darter treatment, the darter was partially eaten, presumably by the crayfish. On 1 occasion, a crayfish was observed consuming a darter in 1 of the cages.

Darter guts only contained invertebrates (total number = 458), 86% of which were chironomids. Other taxa in guts included black flies (10% of total), hydropsychid caddisflies (2%), and baetid mayflies (1%). The number of invertebrates in darter stomachs did not differ between the darter alone (35 ± 10, mean ± SE)

and crayfish + darter treatments (42 ± 20) (t-test, $p > 0.75$, $n = 3$). These results are consistent with gut analyses of rainbow darters collected from Mill Creek during the fall of 1994, which revealed that darter guts (total number = 12) contained only invertebrates (total number = 266), most of which (78%) were chironomids (R. S. Stelzer, unpublished data).

Discussion

In our experiment, crayfish had a strong negative effect on the abundance of epilithic macroinvertebrates in enclosures. In contrast, darters had no independent effects on macroinvertebrate abundance. We found a significant interaction between crayfish and darters, however, such that the crayfish effect on total macroinvertebrate abundance was reduced in the presence of darters. The effect of crayfish alone was likely a result of both crayfish consumption of invertebrates and invertebrate emigration caused by crayfish movements in the cages. Several potential mechanisms may have led to the interactive effect of crayfish and darters on their prey. First, darters may have caused invertebrate prey to move into refugia underneath the substrates (e.g., Kohler and McPeek 1989) making them less susceptible to predation by crayfish or emigration (e.g., drift) induced by crayfish activity. Second, crayfish and darters may have engaged in interference competition, which may have reduced the time crayfish spent pursuing or consuming invertebrates. If interference competition occurred, it is likely that it was asymmetrical, favoring crayfish; crayfish probably pose more of a direct physical threat to darters, than darters do to crayfish. Third, darters, as an alternative food resource for crayfish (Rahel and Stein 1988), may have reduced the amount of time crayfish spent foraging for invertebrates and thus lessened the total effect on invertebrates when both consumers were present. These 3 mechanisms all represent interaction modifications in that a 3rd organism (darters) affected a pairwise interaction between 2 other organisms (or groups of organisms—crayfish and other invertebrates) without directly affecting the abundance of either group. More information is needed about how crayfish, darters, and their prey interact to determine the mechanisms responsible for our results.

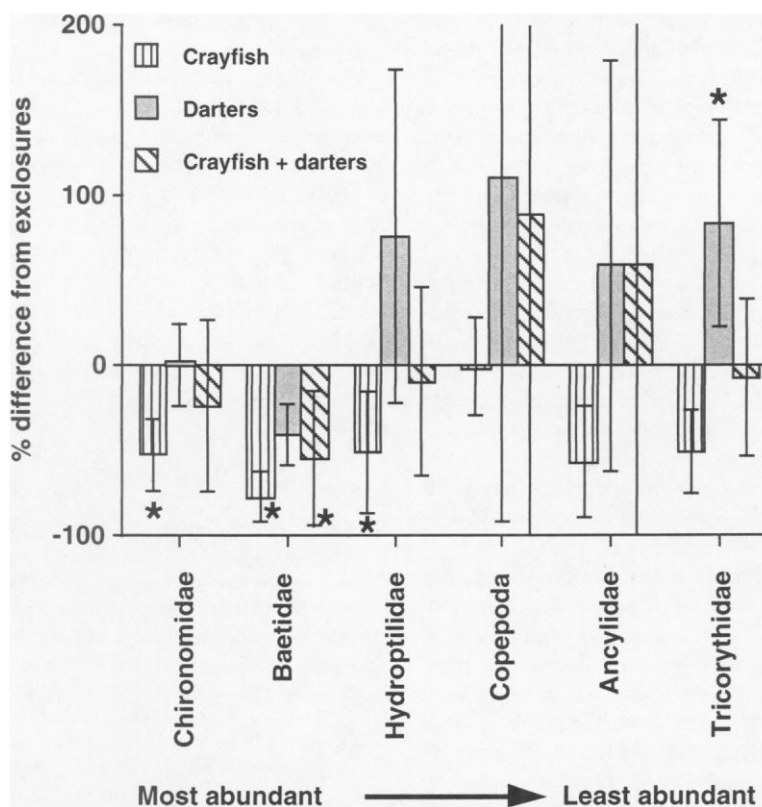In Mill Creek, crayfish alone reduced the den-

FIG. 4.   Percent difference in macroinvertebrate abundance relative to exclosures (no crayfish or darters) within experimental blocks after 44 d (means and 90% CIs, $n = 5$). Invertebrate taxa shown each composed >1.5% of total macroinvertebrates. Asterisks indicate treatments with invertebrate abundances significantly different ($p < 0.05$) from exclosures based on Fisher's LSD multiple comparison test.

sity of most of the common macroinvertebrate taxa. Crayfish and darters, when coexisting, had weak effects on most individual invertebrate taxa. These results differed from those of Hart (1992) and Creed (1994), who reported that *O. propinquus* in another Michigan stream had positive indirect effects on the abundance of some grazers (e.g., *Leucotrichia* sp. and *Psychomyia* sp.) through the ability of crayfish to reduce the biomass of the filamentous alga *Cladophora glomerata*. Crayfish did not significantly reduce periphyton biomass (much of which consisted of *Cladophora*) in our enclosures, and thus the lack of an indirect positive effect on grazers such as *Hydroptila* spp. (like *Leucotrichia* sp., a micro-caddisfly), is not surprising. Our results are more consistent with those of Charlebois and Lamberti (1996), who found that crayfish (*O. rusticus*) alone reduced the abundance of most com-

mon macroinvertebrate taxa, except for *Leucotrichia*, in a northern Michigan stream.

The effect of crayfish on periphyton chlorophyll *a* or biomass accumulation was not statistically significant, although crayfish appeared to have a weak negative effect on chlorophyll *a* and AFDM near the end of the experiment (Figs 2, 3). Perhaps indirect positive effects of crayfish on periphyton abundance, mediated through reductions in grazer abundance (e.g., *Baetis* spp., *Hydroptila* spp., and ancylid limpets; Fig. 4.), counteracted any direct negative effect of crayfish grazing on periphyton. Charlebois and Lamberti (1996) also found that crayfish had weak effects on periphyton (mostly diatoms) whereas Hart (1992) and Creed (1994) showed that crayfish had strong negative effects on *Cladophora* abundance.

Darters had no direct effects on total mac-

roinvertebrate abundance, despite their strictly invertivorous diet. Milstead and Threlkeld (1986) showed that the orangethroat darter (*E. spectabile*) also had weak effects on a population of the amphipod *Hyalella azteca* in a spring pool. In our study, tricorythid mayflies increased in abundance in the presence of darters but the mechanism for this pattern is unclear.

The invertebrate consumer in our study had a much greater impact on benthic macroinvertebrates than the vertebrate consumer. This difference is consistent with the meta-analysis of Wooster (1994), who showed that invertebrate predators tend to have greater negative effects on benthic invertebrate prey in streams than do vertebrate predators (mostly fish). However, because crayfish are large invertebrates and darters are small fish, these organisms are not necessarily typical of their groups.

Our finding that darters had no independent effects on total invertebrate abundance is consistent with several other experiments that showed little or no effect of fish predation on invertebrates in stony-bottom streams (Allan 1982, Flecker and Allan 1984, Culp 1986, Reice and Edwards 1986, but see Flecker 1984 for an exception). The abundant crevices between rocks in such streams may provide invertebrates with refugia from fish, thereby dampening the effect of fish on invertebrates. A 2nd possible explanation is high prey exchange in streams, which can overwhelm predation effects (Cooper et al. 1990, Mackay 1992). Others, however, have shown that when prey emigration is a large component of prey exchange, prey exchange is often positively associated with local predator impact (Bechara et al. 1993, Forrester 1994, Sih and Wooster 1994).

In summary, crayfish had strong negative effects on macroinvertebrate abundance in Mill Creek at the scale of our enclosures. Although darters had no apparent direct effects on invertebrate abundance, it appears that when coexisting with crayfish, darters modified the ability of crayfish to depress invertebrate abundance for reasons that remain unclear. The combined effect of crayfish and darters on benthic macroinvertebrates would have been overestimated if measured from experiments solely addressing the pairwise interactions between consumers and prey. Clearly, interaction modifications among consumers need more exploration in benthic ecosystems.

Literature Cited

ALLAN, J. D. 1982. The effects of reduction in trout density on the invertebrate community of a mountain stream. Ecology 63:1444–1455.

APHA (AMERICAN PUBLIC HEALTH ASSOCIATION). 1992. Standard methods for the examination of water and wastewater. 18th edition. American Public Health Association, Washington, DC.

BECHARA, J. A., G. MOREAU, AND L. HARE. 1993. The impact of brook trout (*Salvelinus fontinalis*) on an experimental stream benthic community: the role of spatial and size refugia. Journal of Animal Ecology 62:451–464.

BILLICK, I., AND T. J. CASE. 1994. Higher order interactions in ecological communities: what are they and how can they be detected? Ecology 75:1529–1543.

CAPELLI, G. M. 1980. Seasonal variation in the food habits of the crayfish *Orconectes propinquus* (Girard) in Trout Lake, Vilas County, Wisconsin, U.S.A. (Decapoda, Astacidea, Cambaridae). Crustaceana 38:82–86.

CHARLEBOIS, P. M., AND G. L. LAMBERTI. 1996. Invading crayfish in a Michigan stream: direct and indirect effects on periphyton and macroinvertebrates. Journal of the North American Benthological Society 15:551–563.

COOPER, S. D., S. J. WALDE, AND B. L. PECKARSKY. 1990. Prey exchange rates and the impact of predators on prey populations in streams. Ecology 71:1503–1514.

CREED, R. P. 1994. Direct and indirect effects of crayfish grazing in a stream community. Ecology 75:2091–2103.

CULP, J. M. 1986. Experimental evidence that stream macroinvertebrate community structure is unaffected by different densities of coho salmon fry. Journal of the North American Benthological Society 5:140–149.

FERGUSON, K. I., AND P. STILING. 1996. Non-additive

effects of multiple natural enemies on aphid populations. Oecologia 108:375–379.

FISHER, W. L., AND W. D. PEARSON. 1987. Patterns of resource utilization among four species of darters in three central Kentucky streams. Pages 69–76 *in* W. J. Matthews and D. C. Heins (editors). Community and evolutionary ecology of North American stream fishes. Oklahoma Press, Norman, Oklahoma.

FLECKER, A. S. 1984. The effects of predation and detritus on the structure of a stream insect community: a field test. Oecologia 64:300–305.

FLECKER, A. S. 1992. Fish trophic guilds and the structure of a tropical stream: weak direct vs. strong indirect effects. Ecology 73:927–940.

FLECKER, A. S. 1997. Habitat modification by tropical fishes: environmental heterogeneity and the variability of interaction strength. Journal of the North American Benthological Society 16:286–295.

FLECKER, A. S., AND J. D. ALLAN. 1984. The importance of predation, substrate and spatial refugia in determining lotic insect distributions. Oecologia 64:306–313.

FORRESTER, G. E. 1994. Influences of predatory fish on the drift dispersal and local density of stream insects. Ecology 75:1208–1218.

FOWLER, N. L., AND M. D. RAUSHER. 1985. Joint effects of competitors and herbivores on growth and reproduction in *Aristolochia reticulata*. Ecology 66:1580–1587.

GILLIAM, J. F., D. F. FRASER, AND A. M. SABAT. 1989. Strong effects of foraging minnows on a stream benthic invertebrate community. Ecology 70:445–452.

HAIRSTON, N. G., F. E. SMITH, AND L. B. SLOBODKIN. 1960. Community structure, population control, and competition. American Naturalist 94:421–425.

HANSSON, L. 1988. Chlorophyll *a* determination of periphyton on sediments: identification of problems and recommendation of method. Freshwater Biology 20: 347–352.

HART, D. D. 1992. Community organization in streams: the importance of species interactions, physical factors, and chance. Oecologia 91:220–228.

HARVEY, B. C., AND W. R. HILL. 1991. Effects of snails and fish on benthic invertebrate assemblages in a headwater stream. Journal of the North American Benthological Society 10:263–270.

HOBBS, H. H., AND J. P. JASS. 1988. The crayfishes and shrimp of Wisconsin. Milwaukee Public Museum, Milwaukee, Wisconsin.

KOHLER, S. L., AND M. A. MCPEEK. 1989. Predation risk and the foraging behavior of competing stream insects. Ecology 70:1811–1825.

LAMBERTI, G. A. 1996. The role of periphyton in benthic food webs. Pages 533–572 *in* R. J. Stevenson,

M. L. Bothwell, and R. L. Lowe (editors). Algal ecology: freshwater benthic ecosystems. Academic Press, San Diego.

LANCASTER, J. 1990. Predation and drift of lotic macroinvertebrates during colonization. Oecologia 85:48–56.

LODGE, D. M., M. W. KERSHNER, J. E. ALOI, AND A. P. COVICH. 1994. Effects of an omnivorous crayfish (*Orconectes rusticus*) on a freshwater littoral food web. Ecology 75:1265–1281.

MACKAY, R. J. 1992. Colonization by lotic macroinvertebrates: a review of processes and patterns. Canadian Journal of Fisheries and Aquatic Sciences 49:617–628.

MARTIN, F. D. 1984. Diets of four sympatric species of *Etheostoma* (Pisces: Percidae) from southern Indiana: interspecific and intraspecific multiple comparisons. Environmental Biology of Fishes 11: 113–120.

MCINTOSH, A. R., AND C. R. TOWNSEND. 1996. Interactions between fish, grazing invertebrates and algae in a New Zealand stream: a trophic cascade mediated by fish-induced changes to grazer behaviour? Oecologia 108:174–181.

MILLER, T. E., AND W. C. KERFOOT. 1987. Redefining indirect effects. Pages 33–37 *in* T. E. Miller and W. C. Kerfoot (editors). Predation: direct and indirect impacts on aquatic communities. University Press of New England, Hanover, New Hampshire.

MILSTEAD, B., AND S. T. THRELKELD. 1986. An experimental analysis of darter predation on *Hyalella azteca* using semipermeable enclosures. Journal of the North American Benthological Society 5:311–318.

MORIN, P. J. 1995. Functional redundancy, non-additive interactions, and supply-side dynamics in experimental pond communities. Ecology 76:133–149.

OKSANEN, L., S. D. FRETWELL, J. ARRUDA, AND P. NIEMELA. 1981. Exploitation ecosystems in gradients of primary productivity. American Naturalist 118: 240–261.

PAGE, L. P. 1983. Handbook of darters. TFH Publications, Hong Kong.

PECKARSKY, B. L., AND S. I. DODSON. 1980. Do stonefly predators influence benthic distributions in streams? Ecology 61:1275–1282.

PERRY, W. L., D. M. LODGE, AND G. A. LAMBERTI. 1997. Impact of crayfish predation on exotic zebra mussels and native invertebrates in a lake-outlet stream. Canadian Journal of Fisheries and Aquatic Sciences 54:120–125.

POWER, M. E. 1992. Habitat heterogeneity and the functional significance of fish in river food webs. Ecology 73:1675–1688.

RAHEL, F. J., AND R. A. STEIN. 1988. Complex predator-prey interactions and predator intimidation

among crayfish, piscivorous fish, and small benthic fish. Oecologia 75:94–98.

REICE, S. R., AND R. L. EDWARDS. 1986. The effect of vertebrate predation on lotic macroinvertebrate communities in Quebec, Canada. Canadian Journal of Zoology 64:1930–1936.

SCHLOSSER, I. J., AND K. K. EBEL. 1989. Effects of flow regime and cyprinid predation on a headwater stream. Ecological Monographs 59:41–57.

SCHLOSSER, I. J., AND L. A. TOTH. 1984. Niche relationships and population ecology of rainbow (*Etheostoma caeruleum*) and fantail (*E. flabellare*) darters in a temporally variable environment. Oikos 42:229–238.

SIH, A., AND D. E. WOOSTER. 1994. Prey behavior, prey dispersal, and predator impacts on stream prey. Ecology 75:1199–1207.

SOLUK, D. A. 1993. Multiple predator effects: predicting combined functional response of stream fish and invertebrate predators. Ecology 74:219–225.

SOLUK, D. A., AND N. C. COLLINS. 1988. Synergistic interactions between fish and stoneflies: facilitation and interference among stream predators. Oikos 52:94–100.

WALDE, S. J. 1986. Effect of an abiotic disturbance on a lotic predator-prey interaction. Oecologia 69: 243–247.

WERNER, E. E. 1992. Individual behavior and higher-order species interactions. American Naturalist 140:S5–S32.

WISEMAN, S. W., S. D. COOPER, AND T. L. DUDLEY. 1993. The effects of trout on epibenthic odonate naiads in stream pools. Freshwater Biology 30: 133–145.

WISSINGER, S., AND J. MCGRADY. 1993. Intraguild predation and competition between larval dragonflies: direct and indirect effects on shared prey. Ecology 74:207–218.

WOOSTER, D. 1994. Predator impacts on stream benthic prey. Oecologia 99:7–15.

WOOTTON, J. T. 1993. Indirect effects and habitat use in an intertidal community: interaction chains and interaction modifications. American Naturalist 141:71–89.

WOOTTON, J. T. 1994. Putting the pieces together: testing the independence of interactions among organisms. Ecology 75:1544–1551.