4-1997

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Abstract

We experimentally reduced densities of predatory fish in replicated 2 m^2 areas of the littoral zone in two ponds to test whether density and biomass of invertebrates would respond to release from fish predation. The ponds are of similar size and in close proximity, but support different fish assemblages: bluegills (*Lepomis macrochirus* Rafinesque) and largemouth bass (*Micropterus salmoides* (Lacepede)) in one pond, and bluespotted sunfish (*Enneacanthus gloriosus* (Holbrook)) and chain pickerel (*Esox niger* Lesueur) in the other. Fish densities were reduced to less than 15% of ambient levels in both experiments. In the bluegill–bass pond, density and biomass of most invertebrate taxa and size classes were unaffected by the fish manipulation. Total invertebrate densities did not differ significantly between fish treatments, but total invertebrate biomass was significantly greater where fish density was reduced, averaging 30% higher over the course of the study. Likewise, manipulation of fish in the bluespotted sunfish–pickerel pond had few significant effects on individual taxa and size classes. There were no significant effects on total invertebrate abundance in the bluespotted sunfish–pickerel pond. Our results provide direct experimental evidence consistent with the collective evidence from previous work, suggesting that the impact of fish predation on density and biomass of invertebrate prey in littoral habitats is variable, but generally weak. Invertebrates that coexist successfully with fish in littoral systems probably are adept at taking advantage of refugia offered by the structurally complex physical environment.

Response of littoral invertebrates to reduction of fish density: simultaneous experiments in ponds with different fish assemblages

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SUMMARY

1. We experimentally reduced densities of predatory fish in replicated 2 m^2 areas of the littoral zone in two ponds to test whether density and biomass of invertebrates would respond to release from fish predation. The ponds are of similar size and in close proximity, but support different fish assemblages: bluegills (*Lepomis macrochirus* Rafinesque) and largemouth bass (*Micropterus salmoides* (Lacepede)) in one pond, and bluespotted sunfish (*Enneacanthus gloriosus* (Holbrook)) and chain pickerel (*Esox niger* Lesueur) in the other. Fish densities were reduced to less than 15% of ambient levels in both experiments.

2. In the bluegill–bass pond, density and biomass of most invertebrate taxa and size classes were unaffected by the fish manipulation. Total invertebrate densities did not differ significantly between fish treatments, but total invertebrate biomass was significantly greater where fish density was reduced, averaging 30% higher over the course of the study. Likewise, manipulation of fish in the bluespotted sunfish–pickerel pond had few significant effects on individual taxa and size classes. There were no significant effects on total invertebrate abundance in the bluespotted sunfish–pickerel pond.

3. Our results provide direct experimental evidence consistent with the collective evidence from previous work, suggesting that the impact of fish predation on density and biomass of invertebrate prey in littoral habitats is variable, but generally weak. Invertebrates that coexist successfully with fish in littoral systems probably are adept at taking advantage of refugia offered by the structurally complex physical environment.

Introduction

The question of whether freshwater fish play an important role in shaping and regulating invertebrate prey communities has generated considerable attention, and is of interest both from the perspective of how species interactions influence community structure, and the regulation of fish production. Early studies in small lakes (Ball & Hayne, 1952; Hayne & Ball, 1956; Macan, 1966) suggested that fish control densities and biomass of some macroinvertebrate taxa, and production–consumption estimates (Gerking,

1962) tended to support these findings. Hall, Cooper & Werner's (1970) landmark experimental pond study showed that bluegills caused a shift toward smaller limnetic zooplankton, as had been shown in other zooplankton–zooplanktivore systems (Hrbacek *et al.,* 1961; Brooks & Dodson, 1965), but had little effect on benthic invertebrates. More recent studies have shown widely ranging effects of fish predation on littoral benthos, from strong negative effects on total biomass (Crowder & Cooper, 1982) and density (Morin, 1984;

Mittelbach, 1988), to studies indicating weak or variable effects (Bohanan & Johnson, 1983; Gilinsky, 1984; Hershey, 1985; Hambright *et al.*, 1986; Diehl, 1992; Bronmark, 1994; Johnson *et al.*, 1996), and other studies showing little or no effect (Thorp & Bergey, 1981a,b; Hanson & Leggett, 1986).

Thus, with some exceptions, evidence that fish interact strongly in regulating benthic, freshwater invertebrate prey communities is scant (Thorp, 1986), but the mixture of experimental results suggests that the strength of these interactions may actually be quite variable. Between-site variation in fish assemblages, fish density, invertebrate assemblages, and environmental variables such as substrate structural complexity and turbidity may be important determinants of how fish predation affects invertebrate communities. Furthermore, differences in experimental methodology, such as type of manipulation (i.e. enclosures, exclosures, replicated ponds), size of experimental units and sampling methods, as well as geographical and temporal variation, may complicate comparisons. Studies that encompass a wider range of potentially important variables with comparable methodology will increase our understanding of their influence.

The purpose of this study was to test whether reduction of fish density in areas of the shallow littoral zone would affect abundance of invertebrate prey. We ran simultaneous experimental manipulations using identical methodology in two ponds of similar size and in close proximity, but supporting different fish assemblages. Densities and biomass of invertebrate populations were sampled for several months, providing evidence for the degree of influence fish predation has on these communities over a substantial portion of a single season, and directly comparable results from systems with different predator assemblages.

Materials and methods

Study sites

We conducted one of the experiments in Farm Pond, located on the Patuxent Wildlife Research Centre site (U.S. Fish and Wildlife Service) (39° 2′N, 76°47′W) in Prince George's County, Maryland, U.S.A. Farm Pond has a surface area of 0.33 ha and a maximum depth of 2 m. The littoral zone has a dense band of rushes (*Eleocharis quadrangulata* Michx.) from the shoreline to about the 0.5 m depth contour, with water shield

(*Brasenia schreberi* Gmelin) extending out to roughly the 1 m depth contour. Macrophyte biomass in June 1983 averaged 211 g m^{-2} (dry) at the 0.3 m depth contour.

Bluegills (*Lepomis macrochirus* Rafinesque) and largemouth bass (*Micropterus salmoides* Lacepede) are abundant in Farm Pond, and are the only fish species present. Bluegills feed on a variety of small-bodied littoral invertebrates (Sadzikowski & Wallace, 1976; Keast, 1978); largemouth bass eat a variety of small-bodied invertebrates during their first year, typically switching to fish and large-bodied invertebrates (e.g. crayfish) after the first year (Keast, 1985).

We ran the other experiment in Bluegill Pond, also located on the Patuxent Wildlife Research Centre site and 1 km from Farm Pond. Bluegill Pond has a surface area of 0.54 ha and a maximum depth of 1.5 m. Littoral vegetation in Bluegill Pond consists of discontinuous patches of water shield intermixed with *Sphagnum* sp. and *Utricularia* sp., averaging 85 g m^{-2} (dry) at the 0.3 m depth contour.

Bluegill Pond contains bluespotted sunfish (*Enneacanthus gloriosus* (Holbrook)), a small centrarchid species restricted to the Atlantic coastal plain of North America (Lee *et al.*, 1980), and chain pickerel (*Esox niger* Lesueur)—but does not contain bluegills or any other species. Bluespotted sunfish feed on a variety of small-bodied littoral invertebrates (Flemer & Woolcott, 1966). Chain pickerel, like largemouth bass, feed predominantly on small-bodied invertebrates during their first year, switching to a diet of mostly fish thereafter (Flemer & Woolcott, 1966; Scott & Crossman, 1973). To avoid potential confusion from the unfortunate mismatch between pond name and species composition, Bluegill Pond will hereafter be referred to as BSPP ('bluespotted sunfish–pickerel pond'). Likewise, Farm Pond will be referred to as BBP ('bluegill–bass pond').

Experimental pens

To manipulate densities of fish, we installed three identical 2 × 4 m screen pens in the littoral zone of each pond. Pens were divided into four 1 × 2 m compartments extending 2 m out from the shoreline to a depth of 0.6–0.7 m. Pens were constructed of aluminium window screen (1.5 mm mesh) stapled to wooden corner stakes. Bottom edges extended 10–15 cm into the substrate. Two compartments in each

pen were randomly designated as fish exclosures. The other two were used as controls, with 80×20 cm 'windows' of screen removed below the water line on the offshore side for fish to pass freely in and out. This design allowed natural onshore/offshore movements of fish and assured natural predation pressure in control compartments while providing an effective barrier to fish in exclusion compartments with nearly identical pen structure. Unenclosed areas immediately adjacent to pens were monitored to control for potential enclosure effects.

We installed the pens in April 1983, but allowed several weeks for recovery from the disturbance before sampling invertebrates. Only small fish (< 50 mm) were present in exclusion compartments after installation, and we removed them with minnow traps over a period of about 3 weeks. Traps were maintained continuously in exclusion compartments and checked regularly during this period, and compartments were judged 'fish-free' after traps yielded no fish on four consecutive days and no other fish were seen in compartments.

Invertebrate abundance

We began invertebrate sampling in late May (BBP) and early June (BSPP) 1983, and sampled at approximately monthly intervals until early September. Receding water in BBP in late September prevented further sampling there, but stable water level in BSPP allowed an additional sampling date in late November.

Macroinvertebrates (insects, isopods, oligochaetes) were sampled with a Hess sampler (Southwood, 1978; 0.5 mm mesh, area sampled = 0.035 m^2) between 10.00 and 12.00 h, and microinvertebrates (microcrustaceans, rotifers, mites) were sampled with inverted-funnel samplers (Brakke, 1976; area sampled = 0.013 m^2) in place for 24 h prior to macroinvertebrate sampling. Samples were taken at depths of ≈ 0.3–0.4 m, and paired macro- and microinvertebrate samples were taken from the same locations. Sample locations were determined haphazardly (never next to pen edges), but samples on successive dates were taken from different locations. Specimens were preserved in the field (70% ethanol), and in the laboratory were identified, measured (body length) to the nearest 0.01 mm for conversion to biomass (Benke, 1972; Dumont, van de Velde & Dumont, 1975; Smock, 1980), and enumerated. In addition to taxonomic identity,

specimens were assigned to one of the following size classes based on body length: 0–<2 mm, 2–<4 mm, 4–<6 mm, 6–<8 mm, 8–<10 mm, ⩾10 mm. A more detailed description of sampling procedures and sample processing is available elsewhere (Pierce *et al.*, 1987).

On each sampling date, one macroinvertebrate sample and one microinvertebrate sample were taken from each experimental compartment and one adjacent unenclosed location per pen. Thus, there were six replicates per date for the fish exclosures and controls, and three replicates per date for the enclosure controls in each pond.

Fish abundance

We estimated absolute abundance of small fish in the vegetated littoral zone areas of each pond once in early May using unbaited minnow traps and the Peterson mark–recapture method (Ricker, 1975). These data allow comparisons with littoral fish abundances reported in other studies.

To determine the effectiveness of the experimental manipulations, we monitored relative abundance of small fish by placing single, unbaited minnow traps in all experimental compartments and unenclosed sampling areas for 24 h mid-way during the last two sampling intervals in BBP and last three intervals in BSPP. Bluegills and bluespotted sunfish up to 60 mm (total length) and largemouth bass up to 70 mm were sampled in this manner. These data provide catch-per-unit-effort comparisons among treatments and between ponds.

Statistical analysis

The invertebrate response variables analysed were density (no. m^{-2}) and biomass (g dry mass m^{-2}) of individual taxa, individual size classes, and total invertebrates. The experiment in each pond was analysed separately. Pen locations were treated as blocks. Density and biomass in fish exclusion and control compartments were compared statistically, and data from unenclosed areas (enclosure controls) are presented to confirm the general absence of enclosure effects. We used split-plot ANOVAs, because the same experimental units (individual compartments) were sampled repeatedly at monthly intervals (Littell, Freund & Spector, 1991; Maceina, Bettoli & DeVries, 1994). No
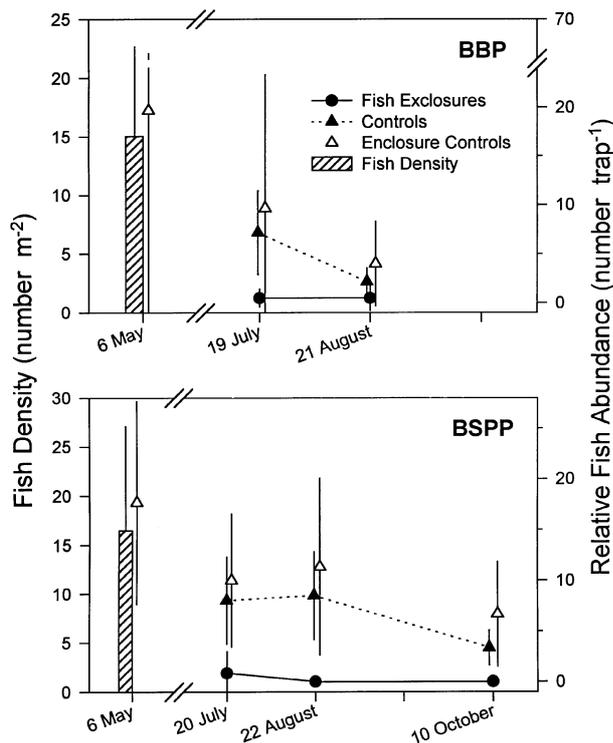
Fig. 1 Pre-experiment fish densities (± 95% CI) and relative abundance (mean ± 95% CI) of fish in fish exclosures, controls, and enclosure control (unenclosed) areas during fish reduction experiments in two ponds. Density axes on the left; relative abundance axes on the right. Symbols labelled in upper panel.

significant treatment (fish)–block (pen) interactions were detected, so sums of squares (SS) associated with treatment–block interactions were pooled with the whole-plot error (treatment × block × replicate) SS for testing treatment effects. Data were transformed as $\log_{10}(x + 1)$ to stabilize variances.

To compare relative fish abundances, we analysed transformed ($\log_{10}(x + 1)$) trap catches by separate two-way ANOVAs (treatment × block) for each date, including data from adjacent unenclosed areas. Differences among treatments were evaluated with GT2 tests. All statistical analyses were performed using SAS (SAS Institute Inc., 1988).

Results

Fish abundance

The Peterson mark–recapture estimates from early May indicated very similar pre-experiment densities of small fish in the vegetated littoral areas of the two ponds (Fig. 1). Relative abundance estimates from

mean pre-experiment trap catches in unenclosed areas (labelled as enclosure controls in Fig. 1) were likewise very similar in the two ponds.

In BBP, mid-July trap catches averaged near zero in fish exclosures—significantly lower than in either control compartments or enclosure control areas ($\alpha = 0.05$, GT2 test), which did not differ (Fig. 1). Catches in fish exclosures remained near zero in mid-August, but overall catches in the littoral zone declined by roughly 50%. Control and enclosure control catches were still similar, but only the enclosure control catches differed significantly from fish exclosures in August ($\alpha = 0.05$). There were no significant differences among blocks (pens) on either date ($P > 0.05$, F-test). Bluegills and largemouth bass were in roughly equal abundance in trap catches, and both reflected the overall pattern of abundance among treatments.

In BSPP, fish exclosure trap catches averaged at or near zero in July, August and October, and were significantly lower than catches in controls or enclosure control areas on all three dates ($\alpha = 0.05$; Fig. 1). Control catches were similar to enclosure control areas in July and August, but significantly lower in October ($\alpha = 0.05$). There were no significant differences among blocks (pens) in July or August ($P > 0.05$), but pen location did account for significant trap-catch variation in October ($P = 0.039$, $F_{2,6} = 5.86$). Trap catches in BSPP consisted only of bluespotted sunfish.

Adult bluegills and bass were routinely seen in control compartments and adjacent unenclosed areas in BBP, but we observed no abnormal congregation in or avoidance of pens. Chain pickerel were seen infrequently in BSPP, and observed only twice in control compartments. No bluespotted sunfish larger than those caught in traps were ever seen in BSPP. After the initial 3-week removal period, we never observed fish in exclusion compartments in either pond. The few fish that were subsequently caught in traps in exclusion compartments were released outside pens. Fish caught in controls and enclosure control areas were released where they were caught. Abundances of fish in exclusion compartments relative to controls, as estimated by the trap data, ranged from 6 to 14% in BBP and 0 to 5% in BSPP (Fig. 1). Thus, the fish manipulations were not 100% effective, but sampling data and periodic visual inspection indicated that fish were reduced in exclusion compartments to a small fraction of their natural density.

Table 1 Summary of ANOVAs testing the effects of fish reduction and sampling date on density and biomass of littoral invertebrates in two ponds (BBP, bluegill–bass pond; BSPP, bluespotted sunfish–pickerel pond). Groups tested include individual invertebrate taxa, invertebrate size classes, and total invertebrates. Asterisks indicate significant sources of variation: NS, $P \geq 0.05$; *$0.05 > P \geq 0.01$; **$0.01 > P \geq 0.001$; ***$0.001 > P \geq 0.0001$; ****$P < 0.0001$

| | BBP | | | | | | BSPP | | | | | |
| | Density | | | Biomass | | | Density | | | Biomass | | |
Group	Fish (F)	Date (D)	F × D	Fish	Date	F × D	Fish	Date	F × D	Fish	Date	F × D
Chironomidae	NS	****	NS	NS	****	NS	NS	*	NS	NS	NS	NS
Ceratopogonidae	NS	NS	NS	NS	NS	NS	**	****	****	**	****	**
Tabanidae	*	**	NS	NS	**	NS	NS	*	NS	NS	NS	NS
Ephemeroptera	NS	****	NS	NS	****	NS	NS	**	NS	NS	*	NS
Zygoptera	NS	***	NS	NS	NS	NS	NS	**	NS	NS	*	NS
Anisoptera	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
Coleoptera	NS	**	NS	NS	***	NS	NS	NS	NS	NS	NS	NS
Oligochaeta	NS	**	NS	NS	****	*	NS	*	NS	NS	*	NS
Isopoda	–	–	–	–	–	–	NS	***	NS	NS	**	NS
Cladocera	NS	*	NS	NS	****	NS	NS	****	NS	NS	***	NS
Copepoda	NS	****	NS	NS	****	NS	NS	**	*	NS	NS	NS
Ostracoda	NS	***	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
Rotifera	NS	NS	NS	NS	**	NS	NS	****	NS	NS	**	NS
0–<2 mm	NS	NS	NS	–	–	–	NS	****	NS	–	–	–
2–<4 mm	NS	***	NS	–	–	–	NS	***	NS	–	–	–
4–<6 mm	NS	*	NS	–	–	–	NS	NS	NS	–	–	–
6–<8 mm	NS	NS	NS	–	–	–	*	**	NS	–	–	–
8–<10 mm	NS	***	*	–	–	–	NS	**	NS	–	–	–
≥10 mm	NS	NS	NS	–	–	–	NS	NS	NS	–	–	–
Total	NS	NS	NS	**	***	NS	NS	****	NS	NS	NS	NS

Invertebrate abundance in BBP

There were very few significant differences in abundance of individual taxa and size classes associated with the fish manipulation in BBP (Table 1). Tabanid density was significantly elevated in the absence of fish, averaging 25% higher in fish exclosures than controls over the four sampling dates. There was a significant fish–date interaction with oligochaete biomass, resulting from greater relative abundance alternating between fish exclosures and controls on each successive sampling date. A significant fish–date interaction with density of the 8–<10 mm size class reflected greater abundance in fish exclosures on the first sampling date, but greater abundance in controls on subsequent dates. Density and biomass estimates of other taxa did diverge substantially between fish treatments on occasion, but consistent patterns were lacking, and high sample variation (Table 2) makes these differences difficult to interpret.

Over the course of the experiment in BBP, total

invertebrate densities averaged 52 696 m^{-2} in fish exclosures, 42 421 m^{-2} in controls, and 61 063 m^{-2} in unenclosed areas. Total biomass (dry mass) averaged 2.6 g m^{-2} in fish exclosures, 2.0 g m^{-2} in controls, and 1.9 g m^{-2} in unenclosed areas. Total invertebrate densities showed no statistically significant pattern with respect to the fish manipulation (Fig. 2, Table 1). However, total biomass was significantly greater in fish exclosures (Table 1), averaging 30% higher than in controls over the four dates (Fig. 2).

Densities and biomass of several taxa and size classes changed greatly over the course of the study (Tables 1 and 2), reflecting individual seasonal phenologies. There was an overall pattern of decline in both density and biomass of total invertebrates over time (Fig. 2). Generally, density and biomass estimates from adjacent unenclosed areas overlapped broadly with controls (e.g. Fig. 2), indicating that natural seasonal patterns of abundance were mimicked in experimental pens. There were some exceptions, but these apparent enclosure effects were relatively few and there

Table 2 Mean density (no. m^{-2}) and biomass (mg dry mass m^{-2}) of invertebrate taxa, size classes, and total invertebrates in the littoral zone of two ponds (BBP, bluegill–bass pond; BSPP, bluespotted sunfish–pickerel pond). Tabled values are averaged over treatments. The mean CV for treatment means is 99%

Group	Response variable	BBP				BSPP				
		27 May	29 June	6 Aug.	3 Sept.	2 June	30 June	7 Aug.	4 Sept.	26 Nov.
Chironomidae	Density	3258	2785	3936	1699	885	1832	1792	1467	1355
	Biomass	924	630	742	321	245	368	350	358	289
Ceratopogonidae	Density	60	119	185	331	627	277	73	100	268
	Biomass	2	6	4	5	17	11	2	2	4
Tabanidae	Density	227	87	100	162	38	46	31	114	67
	Biomass	178	58	68	153	218	31	38	48	58
Ephemeroptera	Density	241	1014	343	77	85	6	27	12	17
	Biomass	110	167	69	14	23	2	7	1	3
Zygoptera	Density	29	204	144	231	0	0	27	25	19
	Biomass	54	44	41	34	0	0	4	4	15
Anisoptera	Density	102	135	191	110	62	37	60	44	31
	Biomass	361	450	405	600	504	260	170	99	443
Coleoptera	Density	391	422	210	254	10	2	13	15	2
	Biomass	1541	271	365	331	1	2	72	103	2
Oligochaeta	Density	268	35	27	54	56	73	79	135	31
	Biomass	75	12	3	2	17	27	36	22	5
Isopoda	Density	0	0	0	0	514	712	393	67	83
	Biomass	0	0	0	0	73	115	57	13	134
Cladocera	Density	24 650	1637	392	3703	5338	1338	1297	9389	1708
	Biomass	108	3	0	6	4	1	1	4	1
Copepoda	Density	59 213	4764	2823	6005	11 692	16 794	11 329	19 512	3528
	Biomass	72	4	2	5	30	7	7	18	8
Ostracoda	Density	846	1797	4777	15 313	146	82	82	51	0
	Biomass	4	7	21	14	1	<1	<1	<1	0
Rotifera	Density	6241	15 120	10 907	12 489	11 115	3708	5423	17 410	18651
	Biomass	1	2	1	2	4	1	1	3	2
0–<2 mm	Density	92 938	25 557	22 076	39 586	29 434	22 952	21 006	49 764	24 859
2–<4 mm	Density	1184	1846	1445	585	881	1178	853	285	410
4–<6 mm	Density	1594	830	964	679	447	537	341	319	273
6–<8 mm	Density	87	202	162	181	525	137	92	175	183
8–<10 mm	Density	37	79	114	52	40	108	29	17	56
≥10 mm	Density	79	52	40	79	44	42	46	23	50
Total	Density	96 185	28 714	24 766	41 197	31 790	25 036	22 420	50 700	25 843
	Biomass	3474	1920	1909	1457	1339	836	911	697	989

appeared not to be any systematic bias upward or downward.

Invertebrate abundance in BSPP

As was the case in BBP, fish reduction produced few significant differences in abundance of individual taxa or size classes in BSPP (Table 1). There were significant fish–date interactions with ceratopogonid density and biomass (Table 1), resulting from different population trajectories in fish exclosures and controls; abundance in exclosures declined over the course of the experi-

ment to near zero, whereas abundance in controls declined similarly over the first three sampling dates but rebounded strongly over the last two dates. Ceratopogonid trends in enclosure control areas were similar to controls, suggesting either possible enhancement by fish or reduced colonization of fish exclosures during the later stages of the experiment. Copepod densities alternated between greater abundance in controls on the first two sampling dates and greater abundance in fish exclosures on the last three dates, resulting in a significant fish–date interaction. Density of the 6–<8 mm size class was significantly increased
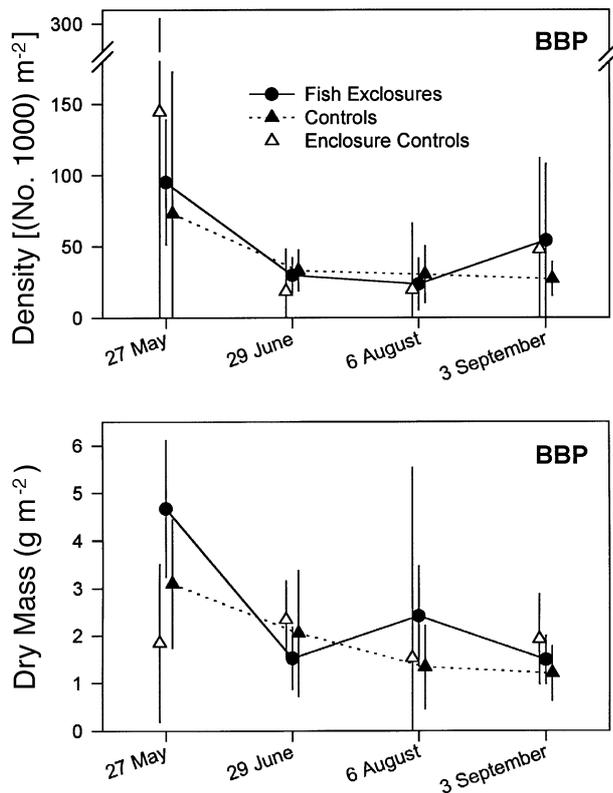
Fig. 2 Density and biomass (mean ± 95% CI) of total invertebrates in fish exclosures, controls, and enclosure control (unenclosed) areas during the fish reduction experiment in BBP. Symbols labelled in upper panel.

Fig. 3 Density and biomass (mean ± 95% CI) of total invertebrates in fish exclosures, controls, and enclosure control (unenclosed) areas during the fish reduction experiment in BSPP. Symbols labelled in lower panel.

in the presence of fish, averaging 24% higher in controls than in fish exclosures over the five sampling dates.

Over the course of the experiment in BSPP, total invertebrate densities averaged $31\,843\,\mathrm{m}^{-2}$ in fish exclosures, $26\,230\,\mathrm{m}^{-2}$ in controls, and $39\,163\,\mathrm{m}^{-2}$ in unenclosed areas. Total biomass (dry mass) averaged $1.1\,\mathrm{g\,m}^{-2}$ in fish exclosures, $0.9\,\mathrm{g\,m}^{-2}$ in controls, and $0.8\,\mathrm{g\,m}^{-2}$ in unenclosed areas. Overall, there were no statistically significant differences in either density or biomass of total invertebrates with respect to the fish manipulation in BSPP (Fig. 3, Table 1).

As in BBP, densities and biomass of several taxa and size classes changed significantly over the course of the study in BSPP (Tables 1 and 2), reflecting individual seasonal phenologies. Unlike in BBP, however, total density tended to increase over time until the last sampling date, whereas total biomass remained fairly constant (Fig. 3, Tables 1 and 2). In general, density and biomass estimates from adjacent unen-
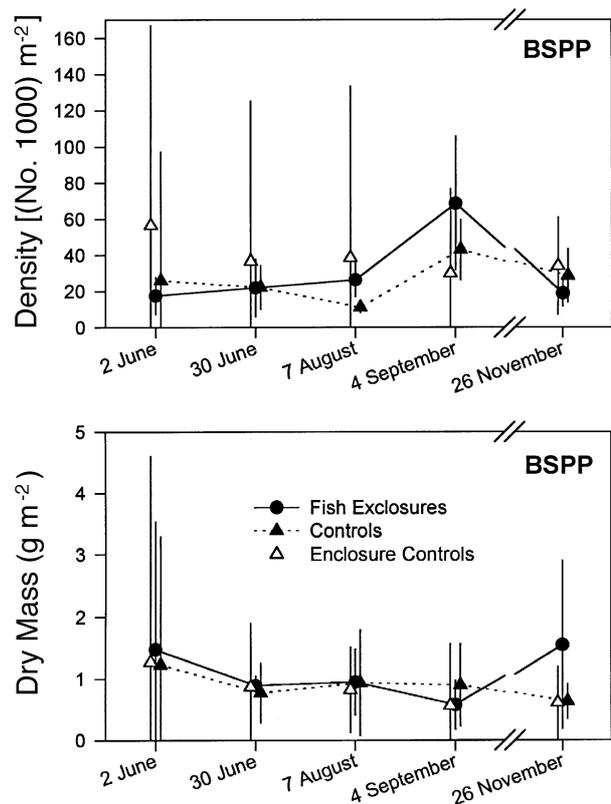
closed areas corresponded roughly with estimates from controls.

Discussion

Despite having been reduced to levels less than 15% of natural density over several months, removal of fish from areas of the shallow littoral zone in two ponds had little or no detectable effect on densities and biomass of most invertebrate prey taxa and size classes. Responses of the invertebrate communities as a whole differed, however, with the bluespotted sunfish/chain pickerel assemblage showing no evidence of control in BSPP, but significantly elevated total biomass resulting from exclusion of bluegills and largemouth bass in BBP.

The results of previous studies are similarly equivocal. Thorp & Bergey (1981a,b) reported no significant effects on benthic macroinvertebrates in response to exclusion of several centrarchid species. Crowder &

Cooper (1982), although only sampling the vegetation, found that invertebrate biomass decreased in the presence of bluegills relative to fish-free controls. However, densities actually increased through selective removal of large invertebrate predators and corresponding increases in smaller taxa. Bohanan & Johnson (1983) and Gilinsky (1984) both reported reductions in density of benthos in response to bluegills, but only on occasional sampling dates. Morin (1984) reported significant increases in anisopteran densities after exclusion of bluegills and largemouth bass from screen-bottomed cages in a small pond, and also found that numerical dominance shifted from small to intermediate sized species in the absence of fish. Hershey (1985) found that sculpins reduced benthic chironomid densities in an arctic lake, but only in the absence of macrophyte cover. Hanson & Leggett (1986) manipulated densities of pumpkinseeds (*Lepomis gibbosus* (L.)) and yellow perch (*Perca flavescens* (Mitchell)) in the littoral zone of a large lake, and found no effects on benthic invertebrate density or biomass. Mittelbach (1988) reported a strong negative correlation between densities of centrarchids (bluegills and pumpkinseeds) and large invertebrate prey in small lake; no relationship existed between densities of centrarchids and small prey. Diehl (1992) manipulated densities of perch (*Perca fluviatilis* (L.)) in a small pond and found significant reductions only in large, predatory invertebrate taxa. Bronmark (1994) later reported weak effects of perch and tench (*Tinca tinca* (L.)) on non-molluscan benthic invertebrates in the same small pond. Johnson *et al.* (1996) reported significant reduction of four taxa by juvenile *Lepomis* sunfish, but non-significant responses of nine other taxa; an analysis of total invertebrates was not presented.

Interestingly, with some exceptions (Hershey, 1985; Mittelbach, 1988), the previous studies showing the strongest fish effects were ones in which benthic substrates were not sampled directly (Crowder & Cooper, 1982; Morin, 1984). It could be argued that discrepancies among results of previous studies might be the result of different methodologies, or perhaps geographical and temporal differences. These concerns do not apply in the present context of concurrent, parallel experiments however, and thus our results provide support for the collective evidence from previous work in suggesting that the effects of fish predators on invertebrate prey in littoral systems vary between systems, and are probably a function of fish assem-

blage and density as well as a variety of potentially important environmental variables.

A study of littoral prey production and consumption by fishes in a large lake indicated that fish exploit a very small fraction of the available invertebrate prey biomass—$\approx 1\%$ per day (Boisclair & Leggett, 1985). If this figure is even roughly generalizable to other littoral systems, it probably means that these relatively small reductions by fish will almost certainly be swamped out by the much greater between-sample variation inherent in benthic communities (Allan, 1984) when using existing sampling techniques. For this reason, failure to detect strong responses to release from fish predation should not necessarily lead to the conclusion that fish abundance or growth is limited by factors other than prey abundance. Strong density-dependent reduction in fish growth has been demonstrated experimentally, with no evidence that the fish had any effect on invertebrate prey abundance (Hanson & Leggett, 1985, 1986). The fraction of total prey that is available to fish at any given time may be small, but nonetheless of great importance to the fish populations it supports (Boisclair & Leggett, 1985). New techniques to discriminate between functional and apparent prey availability, and to identify factors that affect the relationship between functional and apparent prey availability, are needed to extend our understanding of fish–invertebrate interactions in littoral systems.

Allan (1982) proposed three hypotheses to explain the lack of response of a stream invertebrate community to reduction in trout density:

1 lack of a competitive dominant;
2 substrate refuges reduced the foraging efficiencies of fish;
3 prey were well adapted to avoid fish predation.

There is considerable evidence for the latter two hypotheses in explaining similarly weak interactions in lentic systems. Both theoretical (Glass, 1971; Ware, 1973) and experimental (Savino & Stein, 1982) studies have shown that fish forage more efficiently as habitat structural heterogeneity is reduced (but see Tomcko, Stein & Carline, 1984). Sculpins were shown to significantly reduce chironomid densities in an arctic lake only in bare sediments (Hershey, 1985). The structural heterogeneity within macrophyte beds apparently offered chironomids refuge from predation. Similar patterns have been shown in lotic systems (Wilzbach, Cummins & Hall, 1986) and in several marine studies

(Vince *et al.*, 1976; review in Orth, Heck & van Montfrans, 1984; Leber, 1985). The littoral macrophyte growth and benthic detritus accumulations in ponds such as BBP and BSPP no doubt provide considerable refugia for prey in these systems. Interestingly, prey response was greater in BBP, having much higher macrophyte density (as measured by dry mass) than BSPP, contrary to expectations based on the effects of structural heterogeneity on predator efficiency.

There is abundant evidence that many prey species are adapted to minimize risk of predation via defences such as spines or setae (Hershey & Dodson, 1987; Morgan, 1989), camouflage (Otto & Svensson, 1980), and microhabitat and behavioural shifts (reviewed in Dill, 1987). In freshwater lentic systems, such predator avoidance behaviour has been demonstrated in crayfish (Stein & Magnuson, 1976; Collins *et al.*, 1983), zooplankton (reviewed in Zaret, 1980), chironomids (Hershey, 1987; Macchiusi & Baker, 1991), *Chaoborus* (von Ende, 1979), notonectids (Cook & Streams, 1984), damselflies (Heads, 1985; Dixon & Baker, 1988), and dragonflies (Wellborn & Robinson, 1987; Pierce, 1988). Strong predator avoidance behaviours have been shown in *Epitheca* (*Tetragoneuria*) *cynosura* (Say) and *Ladona deplanata* Needham, the dominant dragonfly species in BBP and accounting for roughly 25% of the littoral invertebrate biomass in BBP (Pierce, 1988). Antipredator adaptations probably function in concert with the abundant spatial refugia to significantly reduce the potential impact of fish predation on invertebrate populations in the littoral zone.

Taking a unique approach, Collins (1989) estimated potential exposure to fish predators in littoral zone areas of two lakes with underwater video cameras. Although his overall exposure rates were high, indicating that potential risk of predation should be considerable, he also found that exposure rates were highly variable between lakes, among locations within lakes, and over time. These results suggest another potential explanation, variation in fish activity, for variable effects of predators among systems and in different studies.

Despite all the experimental evidence suggesting that fish do not strongly regulate their benthic prey populations, invertebrate assemblages do differ markedly between fishless habitats and those containing fish (Wright, 1943; von Ende, 1979; Johnson & Crowley, 1980; Cook & Streams, 1984; Bendell &

McNicol, 1987; McPeek, 1990). These observations may seem paradoxical to the above conclusions, but they actually reflect an entirely different phenomenon. Thorp (1986) distinguished between causation and maintenance of community structure as distinctly different roles for predators in freshwater systems, and suggested that past failures to recognize this distinction have hampered efforts to synthesize the considerable body of data. This distinction suggests that experiments where fish predators are introduced to systems where they do not normally occur (e.g. Bronmark, 1994) are not directly comparable with fish exclusion experiments such as the present study, because the underlying interactions and prey assemblages are fundamentally different. Further advances in this area will probably not be realized until a new approach is taken, considering the type of interaction (*sensu* Thorp, 1986), the full range of direct and indirect effects occurring throughout the food web (*sensu* Diehl, 1995; Johnson *et al.*, 1996), and the discrepancy between functional prey availability to predators and the apparent availability of prey as measured by existing sampling techniques.

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