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Multi-trophic-level impact of sublethal interactions between bass and omnivorous crayfish

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Abstract. We demonstrate the importance of omnivory and the importance of sublethal predator effects in the dynamics of a littoral zone food web. Using outdoor tanks (1.8 m diameter, 0.4 m depth), we examined possible cascading trophic effects of predation risk by fish (largemouth bass [*Micropterus salmoides*]) through omnivorous crayfishes (three *Orconectes* species) on benthic macroinvertebrates and macrophytes. Even in the absence of predation by bass on crayfish, crayfish mortality was 50% greater in tanks with bass relative to tanks without bass. Consistent with reduced crayfish numbers and reduced feeding by surviving crayfish in the presence of bass, macrophyte cover was lower in the absence of bass. Similarly, abundance of eight of 11 macroinvertebrate taxa was lower (three significantly so) in the absence of bass. Thus, the impact of crayfish on lower trophic levels was reduced by sublethal effects of predatory bass, partly consistent with the trophic cascade model. However, as omnivores, crayfishes directly affected more than one trophic level, detritivorous/herbivorous macroinvertebrates and macrophytes, and thus produced effects inconsistent with the trophic cascade model. Reduced macrophyte grazing by crayfish may therefore be one mechanism by which biomanipulation (addition of predatory fishes) often results in increases in macrophyte abundance, a response usually attributed solely to decreased shading by phytoplankton.

Key words: omnivory, predation, herbivory, trophic cascade, sublethal effects, crayfish, biomanipulation, *Orconectes*, bass, macrophytes, macroinvertebrates.

The impact of top-down forces on community composition and productivity, especially as incorporated in the Cascading Trophic Interactions Model (Carpenter and Kitchell 1993), has been widely discussed (e.g., Carpenter and Kitchell 1992, DeMelo et al. 1992, Hunter and Kitchell 1992, DeMelo et al. 1992, Menge 1992, Power 1992, Martin et al. 1992, Menge 1992, Power 1992, Strong 1992, Lodge et al. 1994) and increasingly applied in lake management (Gulati et al. 1990, Kitchell 1992). Studies on cascading effects in food webs have focused on numerical responses of relatively distinct trophic levels, such as the effects of piscivores on planktivorous fishes, zooplankton, and phytoplankton in pelagic food webs of lakes (Carpenter and Kitchell 1993) and effects of benthivorous fishes on insect predators, grazers, and filamentous algae in streams and rivers (Power 1990). Very little attention has been given to 1) the contribution of sublethal (non-consumptive) effects of predation to the overall outcome of predator manipulations (Carpenter et al. 1987) and 2) the role of omnivores in influ-

encing the dynamics of cascading trophic interactions (Lodge et al. 1994).

Sublethal effects of predation have been documented for many prey taxa (e.g., Werner et al. 1983, Sih et al. 1985, Holomuzki 1986, Dixon and Baker 1988, Kohler and McPeck 1989, Stamp and Bowers 1991, Short and Holomuzki 1992, Peckarsky et al. 1993), but the consequences of such interactions for lower trophic levels are not well studied (but see Power 1984, Power et al. 1985). In most demonstrations of the trophic cascade, investigators have not measured the relative contributions of lethal and sublethal effects of predators. Here, we explore possible multi-trophic-level consequences of sublethal effects by top predators on omnivorous prey.

Much of the food web literature suggests that omnivory is or should be rare (Pimm 1982, Yodzis 1984); however, considerable evidence suggests that omnivory is common and important in food webs and community dynamics (Cousins 1987, Menge and Sutherland 1987, Walter 1987, Moore et al. 1988, Sprules and Bowerman 1988, Polis 1991, Power 1992). The multi-trophic-level effects imposed by omnivory may substantially complicate attempts to predict community dynamics or manage communities using the trophic cascade model (Lodge et al.

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1994). As omnivores in lakes and streams, crayfishes can directly affect the abundances of macrophytes, periphyton, and macroinvertebrates (Lodge and Lorman 1987, Chambers et al. 1990, Hanson et al. 1990, Weber and Lodge 1990, Charlebois 1994, Lodge et al. 1994), with some of these direct effects working in opposition to other indirect effects of the same omnivore (Lodge et al. 1994). For example, crayfish reduce grazing pressure on periphyton by preying on grazers, which may allow for increases in periphyton biomass. On the other hand, crayfish themselves reduce periphyton biomass by grazing on periphyton, and also by removing macrophytes and therefore reducing available surface area for epiphytic periphyton (Charlebois 1994, Lodge et al. 1994). Existing evidence suggests that crayfish, as omnivores, play an important role in benthic community trophic interactions.

Though illuminating, previous studies examining the role of crayfish in food webs (e.g., Lodge et al. 1994) have not tested the potential effect of predatory fishes in reducing the impact of crayfish on the benthic community. Predation by fish on crayfish may reduce crayfish numbers (Saiki and Task 1979, Rach and Bills 1989, DiDonato and Lodge 1993, Garvey et al. 1994) and crayfish foraging activity (Hill and Lodge 1994) and, as a result, reduce crayfish impact on benthic flora and fauna. Here, we describe a tank experiment in which we quantified crayfish impact on macrophytes and macroinvertebrate taxa (but not periphyton) in both the presence and absence of predatory fish. In our experiment, however, we prevented direct predation by using fish that were too small to consume the crayfish used. Thus, we tested only the sublethal effects of fish predation in these trophic interactions.

Our predictions in this experiment were based on a five-trophic-level food web (Fig. 1). If no omnivorous links existed in this food web, a cascading trophic model would predict that increased bass abundance would decrease crayfish activity, increase predacious macroinvertebrates, decrease detritivorous/algivorous macroinvertebrates, and increase macrophytes. In contrast, our prediction based on previous work (e.g., Chambers et al. 1990, Hanson et al. 1990, Charlebois 1994, Lodge et al. 1994) and the omnivorous links indicated (Fig. 1), was that the presence of bass would reduce direct negative

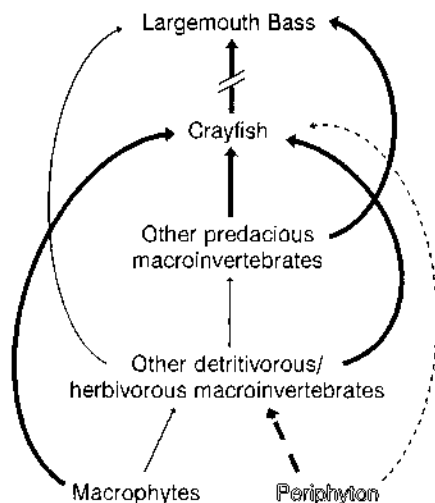


FIG. 1. Five-trophic-level food web model of energy flow on which we based predictions for interactions among predatory bass, omnivorous crayfish, other predacious macroinvertebrates, other detritivorous/herbivorous macroinvertebrates, and macrophytes. The predicted strength of various links is proportional to the thickness of lines. Periphyton (dashed lines) was not measured. The broken link represents the sublethal (non-consumptive) effect of largemouth bass on crayfish.

impact of crayfish on multiple lower trophic levels: predacious macroinvertebrate, other detritivorous/herbivorous macroinvertebrates, and macrophytes.

Methods

From 3 July to 21 August 1992, we conducted an experiment at the University of Wisconsin-Madison's Trout Lake Station to assess sublethal (non-consumptive) effects of fish predators on growth and mortality of three interacting crayfish species, *Orconectes rusticus* (Girard) (an invading species in northern Wisconsin), *Orconectes propinquus* (Girard) (an earlier invader), and *Orconectes virilis* (Hagen) (a native) (Hill 1994). During this experiment, we also quantified crayfish impact (all three species combined) on macrophytes and invertebrate fauna to test for possible multi-trophic-level effects induced by predation risk from largemouth bass (*Micropterus salmoides* [Lacépède]). Experiments were performed in ten Frigid Unit® tanks (1.8 m diameter, 0.4 m depth). Each of the ten experimental tanks contained 20 adult crayfish

per species (11 males, 9 females), or 60 crayfish (total density = 24/m²). The crayfish density used was within the range (on the high end) of measured crayfish densities in northern Wisconsin lakes (Capelli 1975, Lorman 1980, Olsen et al. 1991, Kershner 1992). Crayfish were 21–35 mm carapace length [CL], with equal size distributions in each tank.

Five of the ten experimental tanks contained largemouth bass, with bass and no-bass treatments being randomly distributed among the ten tanks. The bass tanks contained one bass for the first 2 wk and two bass for the remaining 5 wk. The second bass was added because we became concerned that one bass was not sufficient to instill a sense of predation risk. These bass were too small (15.3–19.8 cm total length [TL]) to eat the sizes of crayfishes we used. Butler and Stein (1985) found that largemouth bass would not consume crayfish of CL \geq 9.3% of bass TL. In our experiment, the smallest crayfish was 21 mm CL and the largest bass was 19.8 cm TL. Thus, all of the crayfish exceeded 10.6% of bass TL. Though the bass were too small to consume crayfish, they did orient on crayfish, inducing anti-predator behavior in the crayfish (personal observations) such as chelae displays, swimming escapes, and reduced activity (Collins et al. 1983, Garvey et al. 1994). Bass were fed about 12 minnows (schooling Cyprinidae collected by seine in Trout Lake) per tank every 1.5–2 wk. At the first bass feeding, we also put six live minnows in each no-bass tank to control for minnow effects on crayfish growth; e.g., minnows might die, enter the carrion pool, and serve as a high quality food source.

We mimicked littoral conditions of heterogeneous habitat by placing freshly collected rocks, sand, and vegetation from Trout Lake in the tanks at the beginning of the experiment. The bottom of each tank was divided into three equal areas (0.85 m² each): cobble (8–12-cm diameter rocks) on sand, macrophytes in sand, and a band of open sand between them. Water was supplied by unfiltered flow-through epilimnetic Trout Lake water (total filtered phosphorus = 1.8–8.8 μ g/L, phytoplankton < 18 μ g/L chl *a* [unpublished data, Northern Lakes LTER, John Magnuson, Principal Investigator]). Residence time of water in tanks was 6–12 h, depending on water pressure created by the pump, with the entire volume of water being replaced 2–4 times each day. The rapid turnover of water

in our tanks minimized the potential influence of nutrients excreted by bass and minnows.

We added equal amounts of macrophytes, detritus, and associated invertebrates from Trout Lake to each tank, with a goal of mimicking natural littoral species composition. Macrophytes consisted of a mixture of *Ceratophyllum demersum* L., *Elodea canadensis* (Michx.) Planchon, *Vallisneria americana* Michx., *Potamogeton amplifolius* Tuckerm, *Potamogeton richardsonii* (Benn.), and *Potamogeton robbinsii* Oakes (initial total density in macrophyte area = 70–80 shoots/m²). Thereafter, every 1.5–2 wk, macrophytes were added in equal quantities to each tank (about nine similar size shoots/tank). Detritus was collected with sweep nets from a heavy deposit of terrestrial leaf litter in Trout Lake's southeast bay. Equal amounts of detritus (500 g wet) were added to each tank at the beginning of the experiment. After two and five weeks, we added equal numbers of macroinvertebrates (minus crayfish) to each tank. Macroinvertebrates were collected using a sweep net (500 μ m mesh) for 1.5 h in Plum Lake (Vilas County, Wisconsin, 46°0'N, 89°30'W; Township 41N, Range 8E), thoroughly mixed, and evenly divided by volume among experimental tanks.

To assess whether predation risk from largemouth bass affected crayfish impact on macrophytes and macroinvertebrates, we quantified macrophytes and invertebrates remaining in each tank at the end of the 7-wk experiment. Final macrophyte abundance was measured in two ways: as percent cover and wet weight. Percent cover was estimated using a viewing box (glass bottom bucket, 25 cm diameter). The box was held 30 cm from the bottom to estimate percent cover of unrooted (*C. demersum*) and rooted (*Potamogeton* spp., *V. americana*, *E. canadensis*) macrophytes in each of four quadrants of the visual field. Macrophyte fragments and unrooted stems were excluded from percent cover estimates (but not from biomass estimates). Percent cover per tank was estimated by averaging cover estimates from two randomly chosen viewing areas within the tank's macrophyte habitat (total area sampled was 25% of macrophyte habitat).

We estimated macrophyte wet weight and macrophyte-associated macroinvertebrate abundances by harvesting all stems and fragments from each tank. Macrophytes were sieved (400 μ m mesh) to retain macroinvertebrates.

Washed macrophytes were dripped dry for five minutes and weighed.

Cobble-associated macroinvertebrates were sampled by retrieving four randomly chosen rocks from each tank and immediately washing and picking with forceps over a sieve (400 μm mesh). Counts of animals from cobble subsamples were adjusted (number of animals counted/4 \times total number of rocks in the tank) and added to macroinvertebrate counts from macrophytes for each tank. Macroinvertebrates in sand were not sampled because most macroinvertebrates available to crayfish were probably on macrophytes and cobble. Preserved (70% ethanol) animals were identified to the family or subfamily level when necessary for assigning trophic status (Merritt and Cummins 1984, Pennak 1989, Thorp and Covich 1991). Within each order, all families represented in our tanks were of the same trophic status. Animal counts were therefore grouped at the level of order for statistical analyses.

To assess the relative influence of the presence and absence of bass on crayfish impact, percent cover and wet weight of macrophytes and total abundance for each macroinvertebrate taxon were compared between bass treatments using *t*-tests ($df = 8$ for all tests). For analyses, percent cover estimates were converted to proportions and transformed (arcsin square root). The *t*-tests comparing response variables between treatments were independent of each other; therefore, we did not apply the Bonferroni correction. Given that we made 11 comparisons, we would expect only 0.55 statistically significant comparisons by chance.

Results

Despite the fact that bass could not consume the crayfish, mortality of crayfish was higher in the bass than in the no-bass treatment. In the bass treatment only 33–47% of the crayfish survived, while 52–64% survived in the no-bass treatment by the end of the experiment.

Of the eleven non-crayfish macroinvertebrate orders identified in our experiment, two consisted of predators: Odonata and Tricladida (which may also include some scavengers). The remaining nine orders consisted mainly of herbivores/detritivores: Diptera (primarily Chironomidae [Chironominae] and Simuliidae); Ephemeroptera (primarily Heptageniidae and

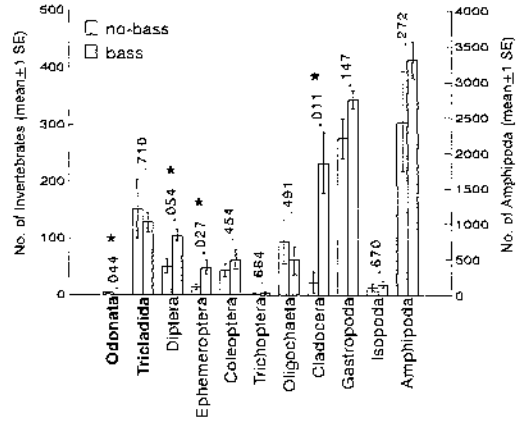


FIG. 2. Final total number per tank of each macroinvertebrate taxon in no-bass and bass treatments. The right axis is number of Amphipoda. The left axis is all other taxa. Bold taxa are predacious. Other taxa are herbivorous/detritivorous. Results of *t*-tests comparing no-bass and bass means are indicated by *p* values for each taxon. * indicates $p < 0.05$ (except Diptera $p = 0.054$).

Baetiscidae); Coleoptera (primarily Elmidae and Psephenidae); Trichoptera (primarily Hydropsycheidae); Oligochaeta; Cladocera; Gastropoda; Isopoda; and Amphipoda.

In all tanks, most macroinvertebrates sampled were found on macrophytes (94–99% of total). Four taxa of macroinvertebrates exhibited significant or near significant differences in number between the bass and no-bass treatments (Fig. 2). Odonata numbers were lower whereas benthic Cladocera, Ephemeroptera, and probably Diptera numbers were higher in the presence of bass. There were no statistically detectable differences in numbers of individuals for any other taxon.

Percent cover of intact macrophytes was higher in the bass treatment (63%) than in the no-bass treatment (47%) (Fig. 3). Macrophyte wet weight (inclusive of fragments) did not differ between predator treatments.

Discussion

Our results were consistent with expectations of reduced impact of omnivorous crayfishes on multiple trophic levels in the presence of bass. These results contradict some predictions we would have made using models of cascading trophic interactions, where the direction of

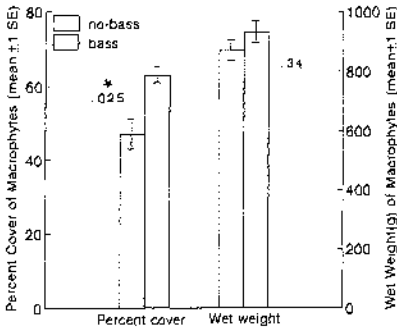


FIG. 3. Percent cover (intact shoots) (left axis) and wet weight (intact shoots plus fragments) (right axis) of macrophytes in no-bass and bass treatments. Results of *t*-tests comparing no-bass and bass means are indicated by *p* values. * indicates $p < 0.05$.

predator effects alternates down successive trophic levels (Paine 1980, Carpenter et al. 1985). Omnivores, by directly affecting more than one trophic level, have not often been considered within the classic trophic cascade model (Power 1992, Strong 1992).

Although only three macroinvertebrate taxa (crayfish prey) were significantly more abundant in the bass than no-bass treatment, the trend for each of five other taxa was consistent with expectations: more macroinvertebrates in tanks containing bass (presumably as a result of reduced crayfish predation). Potential indirect effects of reduced crayfish impact on macroinvertebrate grazer abundance might include increased macroinvertebrate grazing on macrophytes by taxa that sometimes consume macrophytes—Isopoda, Chironominae, and Trichoptera (Merritt and Cummins 1984, Pennak 1989, Thorp and Covich 1991)—but macrophyte results are inconsistent with this scenario. As a direct effect of crayfish grazing on macrophytes (rather than from a cascading effect through macroinvertebrates), we observed greater macrophyte cover in the presence of bass relative to the no-bass treatment.

We saw no differences in wet weight of macrophytes between bass and no-bass treatments because wet weight included fragments. The significant difference between treatments in percent cover but not wet weight suggests that crayfish damage of macrophytes includes much non-consumptive destruction, consistent with earlier laboratory and field results (Lodge 1991,

Olsen et al. 1991, Lodge et al. 1994). In lakes, most of these fragments would enter the detritus pool (Lodge et al. 1994).

Three possible mechanisms could account for the apparently fish-induced reduction in impact of crayfish on macrophytes and macroinvertebrates. First, nutrients released from fish (bass and minnows) might have contributed to more rapid macrophyte growth in the bass tanks. Such nutrients might also have increased periphyton available to grazers. Without an additional treatment to separate fish and crayfish effects (tanks with bass and minnows but no crayfish), we cannot completely rule out nutrient effects in bass tanks. However, given the short residence time of water (6–12 h) in our flow-through tanks, we believe the influence of fish-derived nutrients on macrophytes and periphyton was negligible. Thus, we conclude the other two alternatives are much more likely.

Second, mortality of crayfish was higher in the bass than in the no-bass treatment, so that over time there were fewer crayfish to consume or damage macrophytes and macroinvertebrates. Higher crayfish mortality in the presence of bass likely resulted from increased crayfish–crayfish aggression while competing for shelter in cobble (Hill 1994).

Third, surviving crayfish probably reduced their activity in the face of predation risk, spending more time inactive or in preferred cobble habitat and less time foraging (Hill and Lodge 1994). In keeping with earlier evidence that macrophyte and macroinvertebrate abundances are directly and negatively affected by crayfish (Chambers et al. 1990, Hanson et al. 1990, Weber and Lodge 1990, Charlebois 1994, Lodge et al. 1994), our results suggest that in natural lakes the presence of predatory fishes may reduce crayfish impact on lower trophic levels in three ways: by reducing crayfish abundance via fish predation on crayfishes (DiDonato and Lodge 1993, Garvey et al. 1994); by non-consumptively increasing crayfish mortality (results reported in this paper); and by reducing foraging activity by surviving crayfish (Hill and Lodge 1994). Our results further suggest that much of the impact of top predators on food webs may result from sublethal effects.

Macroinvertebrates may have been more abundant in the bass treatment not just because of reduced crayfish foraging activity and abundance but also because of the greater percent

cover of macrophytes in bass tanks relative to no-bass tanks. As a bottom-up feedback effect, more macrophytes would provide more cover for macroinvertebrates, especially benthic cladocerans, and would allow for greater total periphyton availability to grazers due to greater surface area for periphyton growth.

We observed one significant result for macroinvertebrate abundance that was counter to expectations based solely on crayfish responses: reduced numbers of odonates in the presence of bass. However, this outcome was not surprising given the documented preference for odonates by predatory fishes such as bass (Hodgson and Kitchell 1987, Hodgson et al. 1993). A potential indirect effect of reduced odonates was decreased predation on odonate prey, which would be consistent with the trends of increased taxa abundance we observed in bass tanks. However, we believe the observed invertebrate responses were not due to differences in odonate abundance because the number of odonates per tank was very low ($<1.5/m^2$) even in the no-bass tanks, and because all remaining odonates were very small (<5 mm in length). Thus, it is likely that the observed trends were in response to changes in crayfish number and foraging rather than changes in odonate number.

Minnows, which were not considered in our initial model, may have affected observed trends in macroinvertebrate abundances given that some minnows are benthivorous. We might have expected to see a larger impact on macroinvertebrates by minnows in the bass rather than no-bass treatment because of the much larger number of minnows added to bass tanks. However, observed trends in macroinvertebrate abundances were not consistent with this idea. An alternative possibility, consistent with observed trends, is that minnows in no-bass tanks were not subject to predation from bass, and therefore may have foraged more actively than in bass tanks, having a larger impact on macroinvertebrates in the absence of bass. However, far fewer minnows were added to no-bass than bass tanks, and no minnows were recovered at the end of the experiment, suggesting 100% minnow mortality during the experiment. Therefore, the likelihood of significant impact by minnows on macroinvertebrates relative to impact by crayfish was low. We therefore believe observed reductions in impact on mac-

rophytes and macroinvertebrates in the presence of bass were largely due to sublethal effects of predation on crayfish.

We did not include periphyton in our measurements of crayfish impact on lower trophic levels. Grazing by crayfish on filamentous algae and on macrophytes (as surface area for periphyton) can reduce the quantity of periphyton in a given area while increasing the quality of periphyton available to other grazers (Charlebois 1994, Creed 1994, Lodge et al. 1994). An opposite but indirect effect can result from predation by crayfish on snails and other grazers, releasing periphyton from grazing pressure and allowing it to increase in biomass (Weber and Lodge 1990, Lodge et al. 1994). In previous studies without predators of crayfish, the indirect positive effects of crayfish on periphyton via reduction of grazers by crayfish predation appeared to be stronger than direct negative effects of crayfish as grazers (Weber and Lodge 1990, Charlebois 1994, Lodge et al. 1994). Therefore, periphyton biomass per unit area may have been lower in bass tanks than in no-bass tanks because of lower crayfish impact on grazers in the presence of bass, but total periphyton may have been greater in bass tanks simply as a function of greater availability of macrophyte surface area. The role predacious fishes may have in influencing crayfish impact on periphyton warrants further study.

Martin et al. (1992) examined the role of the trophic cascade in a littoral zone community with relatively distinct trophic levels: sunfish (predators), snails (grazers), and periphyton and macrophytes. Macrophytes were apparently shaded out by heavy periphyton growth. The heavy periphyton growth was a trophic response to heavy predation on snails by sunfish. In cages from which sunfish were excluded, snails increased in abundance, periphyton decreased, and macrophytes increased, presumably in response to increased light availability. Unlike sunfish, crayfish as omnivores directly affect macroinvertebrates, macrophytes, and probably periphyton (see Charlebois 1994, Lodge et al. 1994), simultaneously shunting the indirect effects of largemouth bass to multiple trophic levels rather than only communicating the effects of the trophic cascade to the next trophic level. Thus, where omnivores such as crayfish are abundant, we may see responses to biomanipulation that are very different from

those in littoral communities where omnivores are less abundant.

Unlike relatively simple pelagic communities, littoral communities are structurally complex and speciose, with further complexity being introduced by the prevalence of omnivory (Lodge et al. 1988, Lodge et al. 1994). Sorting out the biotic interactions in these communities can be problematic, as evidenced by the complexities we encountered in our relatively simple model of a littoral community. Regardless of their complexity, experiments examining interactions of littoral communities can yield interesting and sometimes straightforward results, providing insight into complex littoral community dynamics (Power 1992, Lodge et al. 1994). Understanding the dynamics of complex littoral communities is essential to understanding lake-wide processes.

Our results may have relevance to lake management. The response of the littoral food web to biomanipulation may contribute to desired changes in lake biota. A common goal of food-web management is to decrease phytoplankton abundance and increase macrophyte abundance (Moss 1990, Vermaat et al. 1990, Ozimek et al. 1990, Comin et al. 1990). In lakes that have abundant crayfish and that are stocked with predatory fishes, an increase in macrophytes may result not only from decreased light competition with phytoplankton (as a result of cascading trophic interactions among piscivores, planktivores, zooplankton, and phytoplankton), but also from decreased herbivory on macrophytes by crayfish. The potential of such interactive effects of pelagic and benthic food webs needs to be carefully considered in lake management plans.

In the littoral food web, omnivory may blur the lines of the trophic cascade by directly affecting more than one trophic level. With the realization that omnivory is much more common than previously believed (Cousins 1987, Polis 1991), it is essential that we explore the role of omnivores in communities and how they may affect prediction and management strategies within the trophic cascade model.

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