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Biotic interactions in freshwater benthic habitats

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Abstract. We summarized studies on the impacts and scale effects of negative (competition, predation, parasitism, herbivory) and positive (mutualism, commensalism, indirect facilitation) species interactions in freshwater benthic habitats since ~1986 and focused on organisms with mainly or entirely aquatic life cycles. Benthologists publishing in *J-NABS* have contributed robustly to our overall knowledge of predation and herbivory but less so of other species interactions. Predators can limit the abundance of benthic prey and affect prey size or age structure, behavior, and morphology, and these effects can be transmitted through food webs and ecosystems. Herbivores can limit biomass of benthic algae, alter physiognomy, species composition and diversity, and stoichiometry, and exert strong indirect effects within food webs and nutrient cycles. Parasites can alter host behavior or morphology, but few studies have shown that lethal/sublethal effects of parasites on their hosts have population- or community-scale consequences. Fishes and macroinvertebrates occasionally experience competition, but the effect of competition on demographics and assemblages appears restricted to local scales, perhaps because competition can be modulated by many biotic (bioenergetic efficiency, parasitism, predation) and abiotic (floods, drought, resource distribution) factors. Positive interactions have been the least studied species interaction by benthologists, but interest is growing. Future study of population-scale positive interactions and nontraditional interactions at larger scales (e.g., riparian effects on benthic habitat stabilization, cross-system recruitment of different life stages) will improve our understanding of freshwater benthic ecosystems and their conservation. We urge benthologists to explore how populations evolve in response to biotic interactions embedded in benthic communities and to assess how these responses might redefine trophic and community structure and their emergent properties.

Key words: historical review, competition, predation, parasitism, herbivory, positive interactions, indirect interactions, spatiotemporal effects, impact modulators.

A Brief History

Interest in biotic interactions might have originated with Malthus' (1798) projections that food competition arises from geometrical increases in populations. Darwin (1859) argued that a "struggle for existence" would inevitably follow population increases, until

competitors, enemies, or epidemics resumed "a limiting check". Many statisticians and naturalists between 1870 and 1940 were interested in how natality, mortality, and dispersion affected population cycles in a variety of organisms (reviewed by Allee et al. 1949). Lotka (1925) and Volterra (1926) mathematically incorporated the limiting effects of competition, predation, and parasitism into population growth models, and Pearl (1930) and others emphasized that analysis of population density and its end effects were of "significant biological importance". Smith (1935)

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proposed the now-familiar, self-defining terms “density dependent” and “density independent”, and Elton (1949, p. 19) articulated the meaning and importance of density-dependent mortality factors:

“It is becoming increasingly understood by population ecologists that the control of populations...is brought about by density-dependent factors, either within the species or between species. The chief density-dependent factors are intraspecific competition for resources, space, or prestige; and interspecific competition, predators or parasites; with other factors affecting the exact intensity and level of operation of these processes.”

An awareness also was growing that mixed-species interactions could produce “intra-community events,” such as organizational and successional changes in the community, and changes in the physical environment (Allee et al. 1949).

From ~1900 to 1975, interest in competition took priority over other biotic interactions, in part because of the view that predators and herbivores consumed virtually anything and, hence, were unrestricted by food (Macan 1963). This precedence also was influenced by Grinnell (1904), Monard (1920), and Gause (1934) who argued that 2 species with a similar ecology cannot co-occur; a concept reiterated by Hardin (1960) in the competitive exclusion principle. A few early benthologists tested this thesis. Beauchamp and Ullyott (1932) reported finding *Planaria montenegrina* in upper stream reaches near cold springs (16–17°C) in the Balkans and *Planaria gonocephala* in warmer lower reaches (21–23°C), and suggested that competitive superiority of each species in these temperature ranges restricted their distributions. Similarly, Geijskes (1935) found that when *Cordulegaster bidentatus* and *Cordulegaster annulatus* dragonfly nymphs occurred sympatrically, *C. bidentatus* inhabited cold springs, whereas *C. annulatus* resided in lower reaches of small streams. However, in parts of northern Germany where *C. annulatus* was absent, *C. bidentatus* could extend far downstream, a result suggesting that *C. bidentatus* outcompeted its rival only in cold spring waters (Illies 1952). These studies might be the first examples in freshwater benthic systems of condition-specific competition, wherein competitive dominance depends upon environmental conditions.

Freshwater benthologists also invoked competition to explain behaviors and abundance patterns of other organisms. Müller (1954) and Waters (1961) argued that drift resulted from overcrowding, and Macan and Mackereth (1957) inferred density-dependent emigration when explaining that *Gammarus pulex* amphipods

moved downstream at high densities to avoid “mutual disturbance”. Competition also was suggested to drive successional changes in lotic diatom assemblages, although limiting resources were not identified (Patrick et al. 1954, Yount 1956). Interference competition in the form of intra- and interspecific territoriality was documented in fishes (e.g., Smyly 1957, Winn 1958). Nilsson (1955) observed that coexisting *Salvelinus alpinus* (char) and *Salmo trutta* (brown trout) used different depths in lakes to feed on bottom fauna at different times; however, in lakes without trout, char used both deep and shallow waters. Davis and Warren (1965) documented that in streams *Acroneuria pacifica* stoneflies can outcompete *Cottus perplexus* sculpins for midge prey.

Macan (1963) observed an increase in densities of the predatory flatworm *Polycelis felina* that coincided with a decline of several species of epibenthic-feeding mayflies in a nutrient-enriched stream. However, invertebrate prey residing under stones were unaffected because motile *Polycelis* traps its prey with mucus strings laid over stone surfaces. This interaction might be the first documentation of apparent competition, an indirect predator effect that occurs when multiple noncompeting prey species elevate predator abundance, which, in turn, reduces prey abundance (Holt 1977). Competition is “apparent” because resources are not limited and the interaction is negative for both prey (Fig. 1A).

Relatively few freshwater ecologists studied species interactions between ~1900 to 1975. A prevailing belief of the time was that biological control of populations is rare because the high densities needed to make competition or predation important were seldom attained (Mayr 1948, Andrewartha and Birch 1954). Species interactions were absent in Ruttner’s (1963) *Fundamentals of Limnology*, and competition, predation, and disease were covered in only 2½ pages as “other biotic factors” in Hynes’ (1970) seminal text, *The Ecology of Running Waters*. Hynes (1970) also discussed symbiosis and host-parasite relationships in a 2½-page subsection termed “peculiar associations,” and suggested these associations might be important only when a species is at its geographical limits away from normal competitors. Similarly, herbivory in freshwater benthic ecosystems was essentially unexplored over this period, although Douglas (1958) documented a negative correlation between larval abundance of the caddisfly *Agapetus fuscipes* and amount of *Achnanthes* diatoms on stream stones, patterns suggesting potential resource depression and competition.

Interest in biotic interactions grew in the 1970s as ecologists working in the rocky intertidal zone

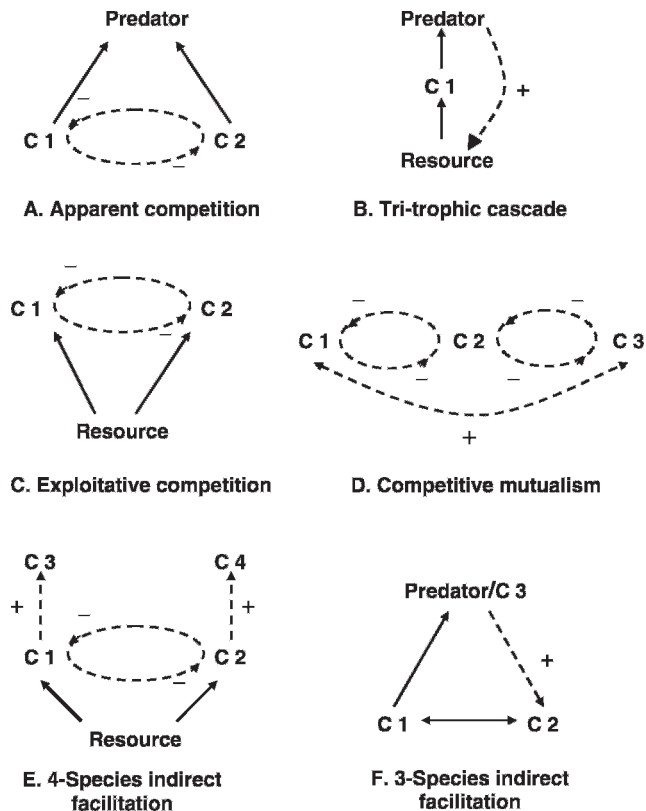


FIG. 1. Six common indirect species interactions. Dashed lines are indirect interactions; solid lines are direct consumer (C)–resource or C–C interactions. + and – represent positive and negative impacts, respectively. A.—Noncompeting prey species can increase the abundance of a shared predator to the detriment of the prey (Holt 1977). B.—Producer resource indirectly benefits when a predator suppresses a consumer (herbivore). C.—Two consumers sharing a common resource might compete indirectly during resource depression. D.—C 1 and C 3 indirectly facilitate each other by inhibiting the other’s competitor, C 2, when all 3 consumers are on the same trophic level. E.—C 3 and C 4 indirectly interact, and as C 3 decreases C 1, its competitor (e.g., for space) C 2 increases to the benefit of C 4. F.—Predator/C 3 and C 2 do not directly interact, but more resources are available to C 2 as C 1 is consumed. This interaction also represents keystone predation or competition *sensu* Paine (1980).

demonstrated how biotic interactions were influenced by the physical harshness of the environment (e.g., Connell 1970, Lubchenco and Menge 1978). Biotic interactions were a focus of freshwater benthologists at the Provo, Utah, meeting of the North American Benthological Society (NABS) in 1981 when its first symposium in community ecology was held. An outcome of the symposium was the book *Dynamics of Lotic Ecosystems* (Fontaine and Bartell 1983), in which Peckarsky (1983; Fig. 2) hypothesized that the

importance of biotic interactions in stream communities varied along a harsh–benign physical gradient. McAuliffe (1984; Fig. 2) showed empirically that flood disturbance can disrupt competitive hierarchies in a stream community, and Power et al. (1988b¹) echoed the theme that biotic interactions were inextricably linked to variation in abiotic factors in the *J-NABS* special issue “Community structure and function in temperate and tropical streams” (volume 7, issue 4). Poff and Ward’s (1989) 78-stream meta-analysis further suggested that hydrologic variability might override effects of biotic interactions on population and community patterns. Gregory (1983; Fig. 2) documented the importance of benthic producers to the trophic economy of a stream and formalized the idea of top-down control of benthic producers by grazers. Lamberti and Resh (1983; Fig. 2) experimentally demonstrated that a benthic herbivore could regulate periphyton standing crops and that periphyton patchiness could determine herbivore distributions. Individual chapters were devoted to resource competition and herbivory as regulators of benthic producers in streams and wetlands in Stevenson et al. (1996), and to these interactions and predation in Allan’s (1995) and Allan and Castillo’s (2007) text *Stream Ecology: the Structure and Function of Running Waters*.

Interest in interactions involving ≥ 3 species or trophic guilds was stimulated by Carpenter et al. (1987) who showed that lake primary production could be affected by strong consumptive effects of top predators. This top-down model of trophic control was first introduced by Hairston et al. (1960) in their “world is green” paper in which they argued that organisms at the tops of food chains are food limited, whereas organisms at successive lower levels are alternately predator and food limited. Power (1990b) provided experimental evidence of top-down linkages among stream fishes, small predaceous insects, herbivores, and algae. Strong (1992) suggested that top-down control of trophic structure is “all wet” and uncommon in nonaquatic food webs. Empirical work suggested that trophic cascades of ≥ 3 levels were uncommon in small streams where high spatial complexity dampens predator or competitor effects (Holomuzki and Stevenson 1992). Power (1992b; Fig. 2) modeled how interference and exploitative competition and loss of nutritious, accessible prey could mediate top-down forces in food chains.

Trophic cascades are a kind of density-mediated indirect interaction (DMII; Wootton 2002) that arise when direct effects on 2 species or guilds affect a 3rd

¹ Boldface indicates paper was published in *J-NABS*

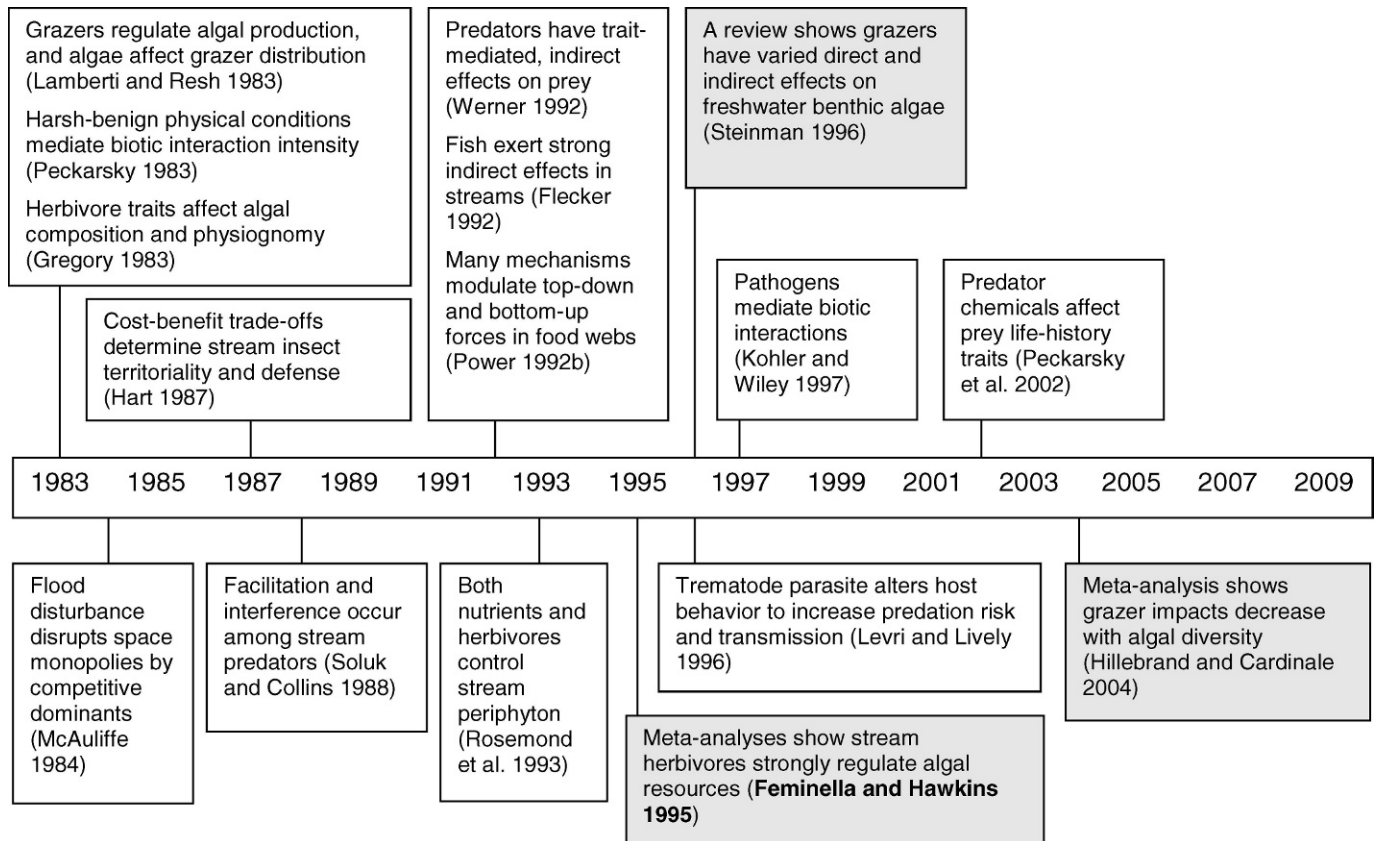


FIG. 2. Timeline of pivotal papers published on biotic interactions in freshwater benthic habitats from 1983 to 2004. White-filled boxes are empirical or conceptual papers, whereas gray-filled boxes are reviews or meta-analyses. Boldface indicates paper was published in *J-NABS*.

in an interaction chain (Fig. 1B). Freshwater benthologists have provided salient examples of another type of indirect effect that arises when a species modifies a trait in 1 of 2 interacting species or the environmental context in which 2 species interact. Trait-mediated indirect interactions (TMIs; Werner 1992; Fig. 2) include predator-induced changes in activity levels of their prey, which, in turn, might affect prey foraging rate (Wissinger and McGrady 1993) or susceptibility to other predators (Soluk and Collins 1988; Fig. 2). An “environment-mediated interaction modification” (Wootton 2002) includes reduction of predation risk on prey because of the presence of refugia, such as macrophytes (Kelly and Hawes 2005).

Recognizing that species interactions are not fixed, benthic ecologists have begun to study how ecological context and trait plasticity shape outcomes of species interactions. For example, Dahl and Peckarsky (2002) showed that waterborne trout chemicals induce a thicker exoskeleton and longer caudal filaments in *Drunella* mayflies and suggested that graded plasticity in such traits increases survivorship by increasing

handling time and escape probability during predation events. Benthologists also are asking how interaction intensity changes over time (Berlow et al. 1999) and are devising ways to quantify the magnitude of species interactions through multifactorial studies, single-factor analyses along environmental gradients, meta-analysis, and path analysis (Wootton 1994a). Multiscale approaches to these studies are helping benthic ecologists determine the scale at which biotic interactions are important, and whether such interactions structure metacommunities (Van de Meutter et al. 2007). Benthic ecologists also have explored how multiple competitors or predators might alter individual behaviors or habitat selection processes (Peckarsky et al. 1997).

Competition

Competition can be real or apparent. Real competition can occur directly through interference competition or indirectly through resource exploitation (Fig. 1C) within or between species. Data often interpreted as evidence for competition include

negative correlations between density and mean individual size, increased densities and growth or survival from resource supplementation, resource-based emigration, territoriality, habitat-use restrictions, and niche expansion or density compensation by 1 species when a 2nd is absent or experimentally reduced (e.g., Richardson 1991, Kohler and Wiley 1997). Just as consumer species can reciprocally reduce each other's abundance by depleting a shared resource, prey species can sometimes indirectly depress each other by increasing the abundance of a shared predator, an effect called apparent competition (Holt 1977). Holt's theoretical analysis stimulated a large number of field studies, but relatively few have been done in freshwater benthic systems.

Competitor type and responses

The effect of real competition on abundance patterns of the freshwater benthos varies among developmental stages, taxa, and guilds. For predaceous fishes, asymmetric intraspecific competition between size/age classes can decrease growth, increase mortality, or increase variance in size distribution, but age-0 individuals typically are more affected than are individuals older than age 1 (e.g., brook trout, Fausch and White 1986; crucian carp, Tonn et al. 1994; brown trout, Jenkins et al. 1999; banded sculpin, Koczaja et al. 2005). Competition also can occur interspecifically between juveniles and can be qualitatively asymmetrical. For example, mottled sculpins (*Cottus bairdi*) experience reduced growth, whereas fantail darters (*Etheostoma flabellare*) suffer decreased relative condition, when sympatric juveniles compete for invertebrate prey (Resetarits 1997). However, adult fish also can experience density-dependent decreases in growth from food competition (Davey et al. 2006) or territorial defense (Zimmerman and Vondracek 2006).

Among macroinvertebrates, herbivorous snails and larval caddisflies can exert especially strong exploitative effects. Consequences of periphytic food depletion by pleurocerid snails (*Elimia*, *Juga*) include reductions in individual growth of competitors (Hill et al. 1995, Lamberti et al. 1995), decreases in competitor abundance (e.g., nontanypodine chironomids, Harvey and Hill 1991; caddisflies, Lamberti et al. 1995), or changes in overall consumer diversity (Hawkins and Furnish 1987, Rosemond et al. 1993 [Fig. 2]). Herbivory by the hydrobiid New Zealand mudsnail *Potamopyrgus antipodarum* slows prepupation rates of *Pycnocentroides* caddisflies and emergence rates of subimago *Deleatidium* mayflies, but mudsnail growth and foraging appear unaffected by these

potential competitors (Holomuzki and Biggs 2006a). Invasive populations of *Potamopyrgus* (~300,000 snails/m²) appear to exert similar amensalistic effects (0, -) on lotic grazers in the western US (Kerans et al. 2005). Dominance of *Potamopyrgus* over native and nonnative grazers might result from their ability to feed either on surface periphyton or subsurface heterotrophic biofilms (Rounick and Winterbourn 1983), from potential facilitation by other grazers (Riley et al. 2008), or from their high bioenergetic efficiencies (Broekhuizen et al. 2002). Conversion efficiency of food into tissue growth might be as important as resource uptake or exploitative ability in determining competitive outcomes, but is rarely examined (Ricciardi and Whoriskey 2004).

Density-dependent grazing by larval *Helicopsyche* caddisflies can depress periphyton abundance, which subsequently decreases grazer growth, pupation rates, pupal size, and net rate of population recruitment (Lamberti et al. 1987b, Feminella and Resh 1990). Glossosomatid caddisflies can exclude benthic competitors exploitatively (Kohler 1992), as evidenced by marked increases in abundance of periphyton and most grazers and filter feeders after catastrophic declines of *Glossosoma* by microsporidian infection (Kohler and Wiley 1997; Fig. 2). It is less clear how sublethal parasite/pathogen infections alter competitive hierarchies and allow persistence of inferior competitors. Experimental removals of *Glossosoma penitum* similarly cause significant increases in epilithic algae and primary consumer biomass (McNeely and Power 2007), further indicating glossosomatids as strong interactors.

Net- or tube-building larval insects restricted to swift-flowing sections of streams aggressively defend high-current-velocity patches with high-resource profitability (e.g., blackflies and psychomyids, Hart 1987 [Fig. 2]; hydropsychids, Englund 1991; hydroptilids, Hart and Robinson 1990). Contests over space can occur within or between trophic guilds and are usually settled by size and ownership status. For example, among filter-feeders, *Hydropsyche* caddisflies can restrict distributions of *Simulium* blackflies, except in winter when flood-induced mortality mediates competition (Hemphill 1991). Interference competition ("nipping") by *Simulium virgatum* causes significant decreases in foraging and ingestion rates by the grazing midge *Blepharicera micheneri*, resulting in decreased growth and increased mortality and time to pupation (Dudley et al. 1990). Similarly, tube-bound deposit feeders compete aggressively for food, space, and tube-building materials, and this competition can lead to density-dependent mortality (Ball and Baker 1995) and emigration (Wiley and Warren

1992). However, dispersion of resource patches can de-aggregate individuals to mitigate competition (Silver et al. 2000).

Resource limitation appears to be uncommon in native, suspension-feeding bivalves (DiDonato 1998), except during invasive species outbreaks when food levels become too low to support reproduction and survival (Strayer 1999). Likewise, few studies show food or habitat limitation for shredding detritivores (Smock et al. 1989, Richardson 1991, Dobson and Hildrew 1992), perhaps because of plentiful food subsidies from terrestrial habitats (Webster et al. 1995), synchrony of life and resource cycles (Feminella and Stewart 1986), rapid switches to available secondary resources (Costantini and Rossi 1998), and the avoidance of resource patches with heterospecific competitors (Abós et al. 2006).

Benthic algae might compete for nutrients, light, and space when control by grazers or physical disturbance (e.g., flooding) is unimportant (Biggs et al. 1998). N-, P-, and N+P colimitation occur in many benthic habitats (reviewed by Borchardt 1996, Francoeur 2001). Competitively dominant species are typically those with extended growth forms (mucilaginous stalks, filaments) or motility enabling individuals to acquire nutrients and light supplied from the overlying water. McCormick and Stevenson (1991) showed that algal succession occurs when stalked diatoms (*Cymbella* sp., *Gomphonema olivaceum*) reduce reproductive rates of low-lying, early-successional species (*Meridion circulare*), presumably by an indirect competitive mutualism (facilitation) (Fig. 1D). Luxury uptake of nutrients during times of high availability might alleviate competition in variable nutrient environments (Stevenson and Stoermer 1982), although how frequently and in what taxa this response occurs are unclear. Sometimes grazing pressure supersedes nutrient limitation (Rosemond et al. 1993, Flecker et al. 2002). Stevenson (1997) suggested that diatoms are regulated by competition for nutrients and light only above some herbivory threshold, a resource condition in which algal accrual and grazing rates are equal. Determining this threshold under various environmental conditions might help us better assess the role of competition in structuring benthic algae.

Spatiotemporal effects and the environmental context of competitive outcomes

Many benthic species appear to experience competition occasionally, although whether short-term competitive bouts affect long-term demographic structure or assemblage patterns is unclear. Whether

“carry-over effects” of sublethal competition among adults reduce offspring quality or fitness also is unclear (Feminella and Resh 1990). Moreover, effects of competition on demographic assemblage structure seem restricted to local scales for both fishes (Jackson et al. 2001) and macroinvertebrates (Peckarsky et al. 1997). However, the spatial and ecological importance of competition might hinge on resource-mediating factors, such as regional climate change, land use change, or the appearance of competitively superior invasive species.

Specific environmental conditions can determine the competitive outcomes of closely matched species. For example, water temperature can determine competitive superiority and, hence, altitudinal separations of stream char by affecting individual aggressiveness, food intake, and growth (Taniguchi and Nakano 2000). Macrophyte abundance, which mediates environment-specific feeding efficiencies, can determine survival differences and, thus, local distributions of competing *Notonecta* hemipterans (Briers and Warren 1999). More experimental field studies are needed to determine the extent to which different competitive outcomes might manifest over time across sets of ecologically distinct locations.

Both intra- and interguild predation can greatly affect competition intensity. Size-specific cannibalism on smaller individuals might decrease exploitative competition among odonate larvae, notonectids, planaria, and crayfish (reviewed by Polis et al. 1989). Cannibalism among same-sized detritivorous larval caddisflies is necessary for completion of development in food-poor, seasonal wetlands (Wisinger et al. 1996). Asymmetric intraguild predation can alleviate competition between young bass and bluegill for invertebrate prey when bass grow to a size-piscivory threshold and eat bluegill (Olson et al. 1995). Interguild predation by fish can alleviate food or space competition between snails (Hershey 1990), net-spinning caddisflies (Lancaster et al. 1988), and crayfish (Garvey et al. 1994). Particularly strong lethal effects can cause DMIs that change competition intensity on noncontiguous trophic levels. Insectivorous stream fishes release tuft-weaving chironomids from predation by consuming small predators, such as aeshnid odonates, and allow midges to suppress algae and create the prerequisite food limitation necessary for competition among grazers (Power 1992a). Predators also can nonlethally modify competitive interactions through TMIs. For example, *Baetis* mayflies and *Glossosoma* are strong exploitative competitors in northern Japanese streams. However, when *Cottus nozawae* sculpins are present, *Baetis* decreases surface grazing, which significantly reduces

mayfly growth, whereas growth and behavioral responses of armored glossosomatids to sculpins are negligible (Kuhara et al. 1999). The influence of DMIs vs TMIs on the effects of competition on population or community dynamics is context-dependent. Thus, understanding the context will help us determine the relative influence of each.

Apparent competition

The overall prevalence and importance of apparent competition among the benthos remains unclear, although a few cases have been documented. Densities of the invasive dragonfly *Cordulegaster boltonii* increase at the expense of decreasing densities of its noncompeting caddisfly and stonefly prey (Woodward and Hildrew 2001). Baxter et al. (2004) suggested that apparent competition between aquatic and terrestrial invertebrates occurs in Japanese streams when introduced rainbow trout usurp both benthic and terrestrial prey that would have been used by native charr (*Salvelinus malma*). In lakes, feeding by omnivorous fishes in pelagic and benthic habitats can increase fish production and cause apparent competition between pelagic and benthic invertebrate prey (Vander Zanden and Vadeboncoeur 2002). Similarly, feeding by piscivores on benthic-feeding roach (*Rutilus rutilus*) and zooplanktivorous perch (*Perca fluviatilis*) can cause apparent competition between these noncompeting fish (Persson 1997). If shared resources do become limited when predator abundance is high, then real competitors might be even more disadvantaged because they would experience the double jeopardy of high predation risk and high resource competition. Studies designed specifically to test apparent competition are needed to assess its effect on the dynamics of real competition in benthic habitats.

Predation

In some contexts, freshwater predators can limit prey abundances, alter prey size or age structure, behavior or other traits, and exert indirect effects that cascade through food webs and ecosystems. Predator effects depend on prey and predator traits and the environmental context of the interaction, and clearly increase with predator densities and per capita killing rates.

Prey traits

Prey reduce their vulnerability to predators with their use of space, morphologies, or behaviors. Potential prey can avoid consumption by living

where predators cannot hunt effectively, such as in sediment crevices (Suttle et al. 2004, **Fairchild and Holomuzki 2005**), dense weed beds (**Kelly and Hawes 2005**), deep water where wading or diving birds are ineffective (Power et al. 1989, Steinmetz et al. 2008), or fast flows (Hart and Merz 1998, Hart and Finelli 1999). More accessible prey can escape or survive predation by means of morphologies (e.g., armor, spines) or behaviors (e.g., sedentary life style, retreat construction) (Hershey 1987, **Li and Gregory 1989, Fuller and Rand 1990, Holomuzki and Biggs 2006b**) that reduce risk. Trait-mediated defenses (i.e., direct, nonconsumptive predator effects; Peckarsky et al. 2008) occur when exposure to a predator causes individual prey to change behavior (Peacor and Werner 2004), morphology (Hoverman and Relyea 2007), or a chemical trait that reduces prey vulnerability, but these responses also might reduce resource allocation toward growth or reproduction (**Abrams 1997**). Freshwater benthologists have provided striking examples of predator-induced trait-mediated defenses. For example, when mayfly nymphs in Colorado streams are exposed to trout or to experimental introductions of fish-tainted water in fishless streams, nymphs mature at smaller sizes and suffer reduced fecundity (Peckarsky et al. 2002; Fig. 2). Nonvisual (chemical or mechanical) cues induce defensive responses (e.g., reduced movement, greater drift, spines) in a wide variety of the freshwater benthos (see “Symposium: Non-Visual Cues in Antipredator Behaviour” special series in *J-NABS* 13:266–325).

Vulnerability to predators often changes markedly with size and age in benthic-feeding fishes (Power 1987, Steinmetz et al. 2008) and invertebrates (Havel et al. 1993, **Tyrrell and Hornbach 1998**). Newly hatched prey (e.g., mussels) might be virtually invisible or unprofitable initially, but become vulnerable at intermediate sizes until they outgrow gape-limited predators (**MacIsaac 1994**). However, growth also might produce changes in antipredatory responses. Small prey generally accept more risk than larger individuals when feeding involves greater exposure to predation, perhaps to speed their growth through vulnerable size stages (Werner and Gilliam 1984). Food-limited armored catfish generally avoid algal mats along Panamanian stream margins where fish are at risk of bird predation; however, smaller species and size classes venture into shallower areas more often than larger fish, but usually at night when birds are inactive (Power 1984). Small baetid mayfly nymphs show weak or no diel periodicity in use of stone surfaces, whereas larger nymphs graze on surfaces only at night,

apparently to avoid daytime-feeding fishes (Culp and Scrimgeour 1993). However, food reward can influence size-specific antipredatory responses. Relative to smaller baetids, large nymphs reduce their drift reaction, and hence, accept more risk from minnow predation, to forage in food-rich patches (Scrimgeour et al. 1994). The best fit in tests of 4 theoretical models predicting risk/growth rate trade-offs for minnow prey under predation risk from green sunfish was from a model that accounted for minimizing risk/growth ratios and for a parameter from dynamic modeling that represented change in the reproductive value of the potential prey over time (Skalski and Gilliam 2002). Tests of similar models with benthic invertebrate foragers and further exploration of risk as a dynamic variable that changes with prey size would be useful (Brodin and Johansson 2004).

Predator traits and density

Predator per capita effects depend on predator voracity (inversely related to satiation levels and handling time per prey) and efficiency in tracking and capturing prey in heterogeneous environments (Power 1992a). Collective effects of benthic predators also depend on their densities and those of their prey (predator/prey ratios), but these ratios hardly ever change in a simple linear fashion. Fish are voracious when food is abundant, yet can endure reduced rations, and even prolonged starvation, without dying (Schindler et al. 1997). Several experiments have detected a presence/absence rather than a constant per capita effect of fish on prey density—prey are suppressed to constant levels across a range of predator densities (e.g., perch preying on chironomids in lake enclosures, Diehl 1995; bass preying on minnows in stream pools, Power et al. 1985; steelhead trout preying on minnows in river enclosures, Power et al. 2008). Schindler et al. (1997) found that individual feeding specializations by largemouth bass are most intensely expressed (i.e., individuals have more overlap with their own previous diets than other bass) during periods of high bass density and prey scarcity, a result suggesting that bass total impacts on prey are more complex than the simple sum of mean individual impacts. How individual feeding specializations enable predators like bass to maintain collective impacts strong enough to change lake (and stream) foodweb structure requires more study (Schindler et al. 1997).

When different species of predators simultaneously hunt prey in different ways, they might enhance prey mortality (predator facilitation, Soluk and Collins

1988, Steinmetz et al. 2008), cause simple additive mortality (Fairchild and Holomuzki 2005), or decrease mortality (predator interference; Englund et al. 1992, Wissinger and McGrady 1993, Diehl 1995, Vance-Chalcraft et al. 2004). Stronger-than-expected collective impacts can occur over short behavioral time scales when hunted prey leave ‘the frying pan for the fire’ (Turner et al. 1999, McIntosh and Peckarsky 1999). Soluk and Collins (1988) suggested that asymmetric facilitation between stoneflies and sculpins (enjoyed by sculpins) resulted from stoneflies driving ephemereid mayflies from under stones to where sculpins could eat them. Experimental disabling of the ability of a top predator to kill prey (e.g., stitching shut the mouths of sculpins, Soluk and Collins 1988; “de-menting” dragonfly nymphs, Wissinger and McGrady 1993) shows that these impacts can be mediated solely by behavioral modification of prey or the subordinate (intermediate) predator. Predators exert weaker-than-expected collective effects if one predator is inhibited by risk of intraguild predation (Wissinger and McGrady 1993) or if one predator induces an antipredatory response that is effective against other predators (Diehl 1995). In Soluk and Collins’s (1988) experiments, fewer baetid mayflies than expected were eaten by stoneflies in the presence of sculpins because stoneflies avoided tops and sides of rocks.

Facilitation and interference between predators typically are mediated by spatial heterogeneity, which alters foraging efficiency and prey encounter rates. Predation by bluegill sunfish and libellulid dragonfly nymphs on larval mayflies exceeds additivity in structurally simple microcosms, where fish predation is increased by odonates (net facilitation), but impacts are additive in more complex arenas with refugia (Swisher et al. 1998). If added structure allows dragonfly nymphs and sunfish to partition their hunting areas, and if prey do not move between these areas, independent predator impacts should be simply additive. However, movement of either prey or predators between patches probably would make independent effects of predators in each patch multiplicative—the proportion of prey surviving a trial with both predators would reflect the probability of surviving one predator times the probability of surviving the other. Thus, refuge use determines the nature of the statistical model used to evaluate predator interactions. Synergistic “interaction modifications” are common in freshwater systems (Wootton 1994a), so a multiplicative model (as used by Soluk and Collins 1988) is usually more appropriate than an additive model to test for independence of predator effects (Wootton 1994b).

Spatial, temporal, and biotic context of predator impacts

Benthic predator impacts on prey have been detected at the scale of microhabitat patches (**Kershner and Lodge 1995**, **Fairchild and Holomuzki 2005**), macrohabitats (stream reaches, Peckarsky et al. 2002; stream pools, Power et al. 1985, Wiseman et al. 1993), and entire systems (small ponds or lakes, **Carlisle and Hawkins 1998**, **Venturelli and Tonn 2005**). However, evaluations of predator impacts often must be done in enclosures, which can impose scale-dependent artifacts related to dispersal rates of organisms into and out of enclosures (Cooper et al. 1990, Carpenter 1996, Englund and Cooper 2003). Thus, when doing enclosure experiments, researchers must allow for unrestricted prey migration into and out of appropriately sized enclosures to extrapolate results to larger scales (**Bartsch et al. 2005**). Furthermore, predator impacts might vary among spatial scales depending on natural transitions in predator and prey types along gradients of hydrologic permanence and habitat size (lentic systems: small ephemeral pools to large lakes; lotic systems: intermittent tributaries to large rivers; reviewed by Wellborn et al. 1996, **Creed 2006**). For example, predator impacts might be undetectable where prey adaptations allow coexistence with certain predators, but quite strong when prey move from one size/permanence habitat to another (e.g., small tributary to perennial river) where they have not coevolved with resident predators (Fraser and Gilliam 1992, Fraser et al. 1995, **Creed 2006**).

Predator impacts can be short- or long-term. On behavioral time scales, predators can trigger reductions in movement or drift reactions by invertebrate prey (Holomuzki and Hoyle 1990, **Scrimgeour et al. 1994**). In California and New Zealand streams, effects of predatory fish are strong enough to cascade down food chains to influence algal biomass several months after scouring floods (Power 1990b, Biggs et al. 2000). Over generations, predation can influence evolution of traits, such as morphological shifts that confer faster size-specific swimming speed on damselflies invading lakes with dragonfly predators (McPeck et al. 1996).

Shifts in the biotic environment, such as availability of food for prey, also affect predator impacts. For example, when *Epitheca* dragonflies are confined with sunfish in large enclosures, their life histories change from univoltine to semivoltine because of reduced foraging and intensified competition with small predators (**Martin et al. 1991**). However, in subsequent similar experiments, sunfish predation on dragonfly nymphs released survivors from density-

dependent competition and allowed higher per capita feeding rates that promoted the univoltine life history (Johnson et al. 1995). The authors hypothesized that the contrasting outcomes in the later experiment occurred during periods of higher chironomid and ostracod prey availability for dragonflies. The impact of sunfish predation on dragonfly life history has large fitness consequences because semivoltine dragonflies must postpone reproduction and endure aquatic predation for twice as long as univoltine conspecifics (Johnson et al. 1995).

Indirect impacts of predators

Benthic predators influence benthic algal or plant biomass indirectly through chains in food webs in experimental tanks (**Hill and Lodge 1995**), lakes (Martin et al. 1992), ponds (Brönmark 1994), and rivers (Power et al. 1985, Power 1990c). By limiting dispersal or foraging by prey in certain habitats, predators can create spatial refugia for their prey's prey, e.g., exclusion of fish by fishing birds creates shallow-water refugia for snails or algae (Matthews et al. 1986, Power et al. 1989, Steinmetz et al. 2003). Predation also can modify ecosystem functions provided by prey. Litter processing in experimental channels (Hamish and McIntosh 2006) and in natural streams (Malmqvist 1993) decreases in the presence of trout and stonefly predators, respectively, because of lethal and nonlethal predator effects on invertebrate shredders. On larger scales, benthic predators feeding in one habitat but defecating or dying in another transfer nutrients, energy, or pollutants across habitat boundaries (Nakano and Murakami 2001, Sanzone et al. 2003, Baxter et al. 2005, **Lamberti et al. 2010**). Studies are needed that examine how these transfers affect general ecosystem processes, such as primary production, community composition, and system stability.

Host-Parasite Interactions

Like predators, parasites consume prey resources (host tissues), but unlike predators, typically do not kill their host (Jokela et al. 1999). Some parasites cause relatively little harm to their host, e.g., freshwater mussel glochidia temporarily infesting fish (Watters 2006). However, many hosts incur sizable costs when infested by macro- or microparasites. For example, attack and parasitic feeding by adult *Petromyzon* lampreys on lake and riverine fishes causes considerable tissue and fluid loss, which might lead indirectly to chronic stress, secondary infection of wounds, and even death (Bergstedt et al. 2001). Similarly, leech infestations on fish can cause chronic

anemia and might lead to secondary bacterial and fungal infections at attachment sites (Davies and Govedich 2001). Naidid oligochaetes parasitizing invading populations of dreissenid mussels feed on the mantle, gill epithelia, and ovarian oocytes and tissues (Conn et al. 1995), whereas parasitic larval mites and trematodes infecting unionid mussels might reduce mussel glycogen stores and reproductive output (Gangloff et al. 2008). Gravid female *Asellus aquaticus* isopods exposed to the acanthocephalan parasite, *Acanthocephalus lucii*, are at higher risk of mortality and bear smaller offspring than do nonparasitized females (Hasu et al. 2006). However, even in nonparasitized, resistant females, offspring size is reduced by parasite exposure, a result suggesting that resistant females have fewer resources directed toward parental investment after their immune systems have been compromised by parasites (Hasu et al. 2006).

Parasite effects on host behavior, color, and morphology

Parasites are capable of altering host behavior, ostensibly for transmission to the next host. *Microphallus* (trematode)-parasitized *Potamopyrgus*, unlike nonparasitized snails, remain active on tops of rocks even in low- or no-food conditions, particularly in early morning when risk of consumption by the parasite's final host (waterfowl) is highest (Levri and Lively 1996 [Fig. 2], Levri 1999). Compared to uninfected individuals, *Echinogammarus stammeri* amphipods infected by the acanthocephalan *Pomphorhynchus laevis* remain highly active in the presence of predatory fish odors, a behavior that enhances host vulnerability to fish predation and, hence, likelihood of parasite transmission (Dezfuli et al. 2003). However, determining whether a behavioral change is adaptive for parasite transmission or is a nonadaptive, pathological byproduct of infection is often challenging. Some parasite-induced behavioral changes seem to increase risk of predation by the wrong (nonhost) predator rather than increase transmission to the next correct host. Mermithid (nematode)-infected *Deleatidium* mayfly larvae in a New Zealand stream have a higher propensity to drift than do uninfected larvae and, thereby, face higher predation from drift-feeding trout; however, mermithids die if ingested by fish (Williams et al. 2001, see also Vance and Peckarsky 1997). These studies suggest that behavioral effects on hosts might be a generalized response to parasitism and only coincidentally beneficial for parasite transmission.

For many parasites, ability to manipulate host behavior might have evolved from adaptations

exploiting the host's immune-neural connections (Adamo 2002). Under normal conditions, neuromodulators can resculpt neural circuits. This resculpting confers on a host the behavioral flexibility to survive in a complex, changing environment (Thomas et al. 2005), but also provides parasites with a means of altering host behavior to increase transmission. The acanthocephalan *Polymorphus paradoxus* reduces predator escape behavior by its host *Gammarus lacustris*, apparently through alterations of the host's serotonergic system (Maynard et al. 1996). Exogenously supplied serotonin can mimic effects of parasitism on some host behaviors (Helluy and Holmes 1990). The trematode *Trichobilharzia ocellata* inhibits egg-laying in its snail host *Lymnaea stagnalis* by inducing host production of schistosomin, which inhibits electrical excitability of caudodorsal cells necessary for oviposition (Hordijk et al. 1992). In addition, the parasite exerts a direct effect on gene expression of neuropeptide Y in the snail's nervous system, which also depresses egg laying (de Jong-Brink et al. 1999).

Parasites also can induce color and morphological changes in their hosts. Parasitic endosymbionts can cause fluorescing of metabolic products in Zenker cells of *Asellus* isopods, thereby increasing the isopod's visibility and vulnerability to predation by three-spined sticklebacks (*Gasterosteus aculeatus*) (Zimmer et al. 2002). Similarly, the acanthocephalan worm *Pomphorhynchus laevis* induces its intermediate host *Gammarus pulex* to change from light gray to orange, making it more conspicuous to its final host (sticklebacks) (Bakker et al. 1997). Heavy trematode (*Diplostomum*) infection causes darkening of brown trout (*S. trutta*) and salmon (*Salmo salar*), although the significance of this color change for both host fish and parasite is unclear (Rintamäki-Kinnunen et al. 2004). Parasite-induced change in host morphology is highly varied. *Microphallus*-infected *Potamopyrgus* are less spiny and have wider shells than do their uninfected counterparts (Levri et al. 2005). Digenean (*Proterometra*)-infected *Elimia* snails are larger than uninfected conspecifics, apparently because of parasite-induced increases in growth rate (gigantism; Krist 2000). Parasitism of adult *Baetis bicaudatus* mayflies by the mermithid nematode *Gasteromermis* sp. causes infected males to develop feminized external genitalia, and some even undergo complete sex reversal (Vance 1996). Mermithid nematodes often castrate their insect hosts (Baudoin 1975), as do *Potamopyrgus* and *Elimia* snail parasites (Levri and Lively 1996, Krist 2001). However, unparasitized *Lymnaea* snails can recognize castrated individuals and prefer to inseminate uninfected partners, presumably to avoid wasting gametes on a castrated mate (de Jong-Brink 1990).

Host–parasite systems and the environment

Host–parasite systems are strongly interwoven with the environment. Yet, parasite-induced phenotypic changes to hosts often are studied without considering the environmental context of the interaction, thus hampering our understanding of the selective pressures experienced by both symbionts (de Jong-Brink and Koene 2005). Local populations of hosts and parasites develop and overcome resistance, respectively, in an ongoing coevolutionary struggle, e.g., *Microphallus* is better adapted to infect *Potamopyrgus* with a local genotype than *Potamopyrgus* with a genotype from a different population (Osnas and Lively 2004). However, local selection pressures driving coevolutionary processes surely will change as local climate change alters rates of physicochemical processes over various temporal scales. For hosts, such changes probably will affect basic life histories, and their distributions and abundances will become increasingly complex and context dependent. For parasites, changes in water temperature, level, or chemistry might cause a breakdown of host specificity, which could arise from host rarity or shifts in reproductive phenologies (Marcogliese 2001). In multiple-parasite systems, environmental change might alter cooperative and conflicting relationships between sympatric parasites sharing a host. For hosts, stress induced by local climate change might result in immunosuppression and increased susceptibility to parasites, which in turn could increase adult parasite growth, fecundity, and survival, and thus, enhance transmission potential and pathogenicity (Poulin 2006). Freshwater clams stressed by low O₂ levels are more prone to parasitism by the ergasilid copepod *Paraergasilus*, which slows clam growth and lowers reproduction and survival, than are unstressed clams (Saarinen and Taskinen 2005). Thus, changes in host–parasite interactions might be an early-warning signal of ecosystem alteration.

Large-scale effects of parasites

Most host–parasite studies have focused on the intricacies of the interaction at the individual level, but some studies have shown that parasites can have population-scale consequences on their hosts. Lethal effects of lampreys have devastated commercial fishes (e.g., lake trout, walleye) in the Laurentian Great Lakes (Schneider et al. 1996). Furthermore, sublethal infections of metacercarial trematodes slow the growth of European minnows (*Phoxinus phoxinus*), an effect that indirectly alters host population dynamics by allowing large shoaling fishes to

outcompete smaller infected fishes for food (Pitcher and Hart 1982, Müller 1995). Microsporidian infection (*Pleistophora mulleri*) significantly reduces aggressiveness of the amphipod *Gammarus duebeni*, making it more vulnerable to intraguild predation by the invasive *Gammarus pulex* (Fielding et al. 2005). *Pleistophora* also indirectly regulates its host abundance through asymmetric cannibalism, with parasitized individuals being much more likely to be cannibalized than unparasitized individuals (MacNeil et al. 2003). Predatory effects on *G. duebeni* might have community-wide consequences because these amphipods can function as a keystone species in lentic systems (Kelly et al. 2003). Declines in *Astacus* crayfish follow immune system failure after infections by the parasite *Psorospermium haeckeli* (Söderhäll and Cerenius 1992). These population losses might have large-scale effects because crayfish can act as ecosystem engineers (Creed and Reed 2004). Depending on environmental context, chytrid fungus infection either can increase or decrease diatom proliferation, thereby affecting outcomes of interspecific competition and algal community succession (Ibelings et al. 2004). Bacterial infection can alter diatom species composition and abundance, and hence primary production and presumably grazer abundance (Peterson et al. 1993).

Herbivory

Grazers wholly or partially eat multiple live producers, such as photosynthetic bacteria, algae, or plants, over their lifetimes. A revealing meta-analysis by Feminella and Hawkins (1995; Fig. 2) concluded that grazers strongly regulate producer biomass and assemblage in streams and contradicted a widely held view that herbivory was unimportant in lotic systems. A review by Steinman (1996; Fig. 2) of herbivore impacts in freshwater lotic and lentic systems added that producer responses to grazing depended largely on producer traits and grazer type. Effects of freshwater grazers can ramify through food webs, depending on the environmental context of the herbivore–producer interaction.

Producer traits and responses

A producer's morphology and chemistry can affect its risk of consumption by herbivores. Algae with spiny armament or a low-lying, prostrate growth form, or young macrophyte leaves that are tightly packed at the shoot apex, are difficult to consume (Jacobsen and Sand-Jensen 1995, Lürling and Beekman 1999). More accessible algae or macrophyte parts might have chemicals to escape herbivory. For

example, some cyanobacteria produce microcystins or saxitoxins, and macroalgae, such as *Chara* and *Cladophora*, produce secondary metabolites that deter some, but not all, herbivores (Camacho and Thacker 2006, Camacho 2008). Likewise, some aquatic macrophytes harbor secondary metabolites, including phenolics or subclasses of phenolics, such as tannins or lignins, that effectively reduce herbivory (Burks and Lodge 2002). Trait-mediated, phenotypically plastic defenses have been documented in a few algae. Grazing by the rotifer *Brachionus* can induce unicellular *Scenedesmus* chlorophytes to form an 8-celled coenobium (colony), which provides a size refugium from micrograzers (Van der Stap et al. 2006). Coenobium formation also can be induced by chemical cues of some micrograzers (Lürling 2003a). A coenobium's mucilaginous matrix also might provide a defense against herbivory (Malej and Harris 1993). In addition, herbivorous zooplankters can induce spine formation that reduces consumption in single-celled *Scenedesmus* and *Desmodesmus* (Lürling and Beekman 1999). Inducible defenses and infochemical responses of algae to herbivores might be much more widespread than assumed (Lürling 2003b).

Structural and functional responses of producers to herbivory are wide-ranging. For periphyton, biomass removal is tightly associated with periphyton abundance potentially available to grazers, and even in highly productive systems, some grazers can limit producer biomass to extremely low levels (**Feminella and Hawkins 1995**) until periphyton reaches a spatial refuge from herbivory (**Lamberti et al. 1987a**, McIntire et al. 1996). In addition, herbivores frequently alter assemblage structure, physiognomy, and stoichiometry of producers. For example, grazing minnows, caddisflies, and snails can eliminate filamentous chlorophytes from algal communities (e.g., Lamberti and Resh 1983, Power et al. 1985, Gelwick and Matthews 1992). Consumption of upright, overstory or loosely attached algal taxa by grazers often shifts benthic assemblages toward prostrate, understory forms (Hill et al. 1992, Holomuzki and Biggs 2006a), which avoid grazing because of their physiognomy, or thrive because of competitive release (Power et al. 1988a, Graham and Vinebrook 1998). Even so, grazers might have little effect on producer succession during post-grazing recovery (Holomuzki et al. 2006, but see Wellnitz and Poff 2006). Grazing also can decrease epilithon C:P (**Frost et al. 2002**), in part by increasing per capita availability of nutrients to remaining autotrophs (Urabe 1993) or increase it if algal P is efficiently assimilated by grazers and P excretion is greatly reduced (Liess and Kahlert 2007).

Generalizations regarding herbivore effects on producer diversity are tenuous because grazed assemblages can show higher or lower diversity than ungrazed assemblages. Directions of such patterns depend on grazer density, mobility, and life history (Holomuzki et al. 2006), and on biotic attributes of producer assemblages, such as strength of competitive hierarchies (Steinman 1996). In a meta-analysis including a wide range of aquatic grazers and systems, Hillebrand and Cardinale (2004; Fig. 2) reported that effects of grazers decrease with increasing algal diversity, a result suggesting that community diversity influences inedibility. Effects of herbivores on producer productivity measured by area-specific productivity (ASP) and biomass-specific productivity (BSP) strongly differ. Typically, benthic grazers reduce ASP because they reduce producer biomass (Gregory 1983, Rosemond et al. 1993), but whether grazers increase or decrease BSP varies with grazing intensity, environmental productive capacity, and age and condition of producers (Lamberti et al. 1989, Hill et al. 1992).

Herbivore type, traits, and density

Grazer feeding modalities include rasping (e.g., snails), gathering or brushing (e.g., heptageniid and leptophlebiid mayflies), cutting (e.g., conoesucid caddisflies), and scraping (e.g., glossosomatid caddisflies, stonerollers, armored catfish) (Power et al. 1988a, Wellnitz and Ward 2000, Holomuzki et al. 2006), and feeding modality influences what algal species and physiognomies are consumable. Stalked, erect, and filamentous growth forms often are vulnerable to most herbivores, whereas prostrate forms often are vulnerable only to raspers and scrapers. Rasping and scraping grazers typically have a greater effect on periphyton biomass and assemblage structure than do other grazer types (Kohler and Wiley 1997, Gelwick and Matthews 1992, Holomuzki et al. 2006) because of their feeding mode and because they dislodge overstory forms when maneuvering through biofilms (Rosemond et al. 2000). Even similar grazers can have disparate influences on physiognomy. Foraging *Ecdyonurus* mayflies reduce stalked growth forms, whereas *Baetis* mayflies reduce erect and filamentous algae, but neither species affects prostrate diatoms (Wellnitz and Ward 1998).

Motility and foraging behavior also influence grazer effects on producers. Some snails forage slowly and graze algae almost down to bare rock ("diggers"), whereas faster-moving grazers leave behind large algal residues (Wilson et al. 1999). The latter behavior increases the likelihood that a recently grazed patch

will be revisited by herbivores and can facilitate coexistence of multiple grazers on a single resource (Wilson et al. 1999). If a tradeoff between area-extensive vs area-intensive grazing (i.e., moving fast and grazing a large area per unit time vs digging deep at a small spatial scale) is common in benthic systems, knowledge of its frequency could provide predictive insight into patterns and causes of density dependence and species persistence (Schmitt 1996).

The influence of a particular herbivore on periphytic community structure also will depend on total herbivore biomass and density (Holomuzki et al. 2006) and productive capacity of the system to accrue biomass (Lamberti et al. 1989). Most studies report grazer-induced decreases in producer biomass as a direct function of grazer density (Hill and Knight 1987, **Steinman et al. 1987**, Rosemond et al. 1993, Hill et al. 1992), but exceptions exist (McCormick 1990, Darcy-Hall 2006). Moreover, grazer density–algal depletion relationships might be nonlinear when algal biomass is very low or when disproportionate increases in nonconsumptive losses occur from overstory dislodgment (Scrimgeour et al. 1991).

Meiofauna (benthic rotifers, nematodes, copepods, protozoans) can exert strong pressure on producer assemblages (**McCormick 1991**, **Borchardt and Bott 1995**, **Caramujo et al. 2005**), particularly when macrograzer abundance is low (**Peters et al. 2007**). Abundances of algae and meiofaunal grazers can be tightly coupled in lakes (Hillebrand et al. 2002), but relatively little is known about factors mediating this relationship within benthic habitats in general.

Spatiotemporal effects and environmental context of herbivore effects

Herbivore effects on producers have been detected at fine (individual particles, Power et al. 1988a), intermediate (habitat units, Feminella et al. 1989; stream reaches, Taylor et al. 2002), and large (lakes, Carpenter et al. 1991; rivers, Caraco et al. 1997) spatial scales. Even within scales, grazer effects on algal biomass often are patchy (Kahlert et al. 2002, Villanueva and Modenutti 2004). Finlay et al. (1999) used $\delta^{13}\text{C}$ analyses to show that most algivores rely on local production and that the importance of algal-derived C to river food webs is greatly underestimated. Herbivore effects typically are tested in small-scale experiments that often underestimate grazer impacts (**Feminella and Hawkins 1995**, Kohler and Wiley 1997, Taylor et al. 2002). These experiments generally show that grazers can significantly reduce algal biomass over short time scales (day to a few weeks) (DeNicola et al. 1990, Feminella and Resh 1991,

Rosemond et al. 2000, Taylor et al. 2002), but with exceptions (Vaughn et al. 1993, Holomuzki and Biggs 2006a). Low grazer bioenergetics and ambient light and nutrient conditions, availability of alternative food sources, and algal recruitment can delay or nullify grazer effects (Feminella et al. 1989, Lamberti et al. 1989, Hill et al. 1992, Holomuzki and Biggs 2006a).

Grazer effects on algae are highly variable and differ with spatial heterogeneity in substrate, nutrient, or hydrodynamic conditions (**Peters et al. 2007**). Turbidity or shading can decrease primary production and thereby facilitate grazer control in lakes (Liboriussen et al. 2005) and rivers (Caraco et al. 1997). In low-productivity lakes, nutrient limitation might override grazing pressure and select for grazer-vulnerable, superior nutrient competitors (Darcy-Hall 2006). Similarly, grazers might be unable to reduce algal biomass in streams when periphyton growth is not nutrient limited (Dubé et al. 1997, but see Stewart 1987). Catchment geology, as it relates to enrichment potential, often might modulate herbivore effects in streams (Biggs and Gerbeaux 1993). In enriched stream reaches, omnivorous fish can control primary production only after seasonal floods reduce algal biomass (Pringle and Hamazaki 1997). Periodic disturbance also might alter taxonomic composition and reduce densities of lotic filter-feeders and nullify their effect on algal productivity (Cardinale and Palmer 2002).

Predators typically have strong effects on herbivores, but the magnitude of impacts can vary. Direct lethal effects of predators can mediate herbivore impacts on benthic producers in streams (McIntosh and Townsend 1996, Huryn 1998), lakes (Brönmark 1989), and wetlands (Batzer and Resh 1991). However, indirect effects of predators on periphyton biomass might be weakened when grazers are armored (**Ruetz et al. 2004**) or have access to spatial refugia (Rosenfeld 2000). Trophic cascades in freshwater systems typically are attenuated at the herbivore–producer interface (Shurin et al. 2002).

Indirect impacts of herbivores

Direct effects of herbivores on producers can ramify through interaction chains. Algal and detrital-feeding fishes can have strong indirect effects on benthic invertebrate community structure and distributions (Flecker 1992; Fig. 2). Macrograzers can significantly depress algal biomass and, in so doing, decrease abundance and alter community composition of epilithic meiofauna (**Peters et al. 2007**). Grazers also can indirectly determine algal dominance. Large

Orconectes crayfish can exclude *Cladophora* from deep habitats and open space for colonizing diatoms and sessile grazing insects that eat diatoms (Creed 1994; Fig 1E). Reduction of stream diatom turfs by grazing minnows facilitates dominance of cyanobacterial felts (Power et al. 1988a). Invasive *Marisa cornuarietis* (giant rams-horn snail) can effectively mow entire macrophyte beds in Texas lakes and rivers (Horne et al. 1992), which can decrease faunal habitat suitability and increase nutrient and turbidity levels (Carr et al. 2003).

Herbivory sometimes can have an indirect stimulatory effect on grazed periphytic residues by increasing space availability and light and nutrient penetration (Brönmark 1989, McCormick and Stevenson 1989, McCormick 1994, Flecker et al. 2002). Grazers change the movement of chemical elements for autotrophic uptake and alter producer stoichiometric ratios (Frost et al. 2002, Hillebrand et al. 2004), which might affect producer growth form (i.e., fast- vs slow-growing) in the post-grazing assemblage (Liess and Hillebrand 2006). In addition, nutrients from grazer excretions can produce patchy stimulatory effects and reduce C:N:P in algal communities (Hillebrand and Kahlert 2001). At larger scales, reductions of periphyton biomass by grazers affect hydraulic characteristics and can increase transient storage and internal nutrient cycling in streams (Power et al. 1988a, Mulholland et al. 1994). Knowledge of the factors influencing the interaction between herbivory and contrasting abiotic factors (e.g., light, nutrient, flow-disturbance) when determining producer species composition, diversity, and assemblage structure will help us understand the spatiotemporal dynamics of top-down and bottom-up forces in freshwater benthic habitats.

Positive Interactions

Positive interactions have received far less attention from freshwater benthologists than have interactions with competitors or enemies (Kareiva and Bertness 1997, Stachowicz 2001). Below we highlight examples of positive interactions in the freshwater benthos in the context of conspecific Allee effects (i.e., positive relationship between population density and individual survival and reproduction), tight 2-species mutualisms, positive indirect interactions in foodweb fragments, and organismal amelioration of habitats and ecosystems.

Conspecific facilitation and Allee effects

Many benthic invertebrates and fishes aggregate at some life stage, and aggregation might saturate

predators and increase the probability of fertilization (Liermann and Hilborn 2001). Some caddisflies aggregate during diapause or pupation (Martin and Barton 1987, McCabe and Gotelli 2003) for protection from predators. Aggregations are more likely to be encountered by predators, but the per capita risks for individual pupae are lower in aggregations than for solitary individuals because the protective benefit of predator dilution outweighs the higher encounter risk (Wrona and Dixon 1991). Aggregations also might confer a mate-finding advantage and counter an Allee effect (i.e., reduced likelihood of finding a mate in low population densities), if aggregated males and females emerge synchronously. Reproductive advantages have not yet, to our knowledge, been documented for aquatic emergence from pupal aggregations, but the use of new genetic tools (e.g., mitochondrial and nuclear ribosomal deoxyribonucleic acid [DNA] sequencing; Zhou et al. 2007) might illuminate this research area.

2-species symbioses

In freshwater benthic systems, relatively few obligate species-specific mutualisms are known, but several fascinating examples have been documented. Coccoid, endosymbiotic cyanobacteria living within diatoms (*Epithemia* spp., *Rhopalodia* spp.) of the family Rhopalodiaceae (Floener and Bothe 1980) can fix N₂, which subsequently helps these diatoms become dominant in N-limited environments (e.g., Mulholland et al. 1991, Peterson and Grimm 1992, Marks and Power 2001). In another benthic endosymbiosis, the cyanobacterium acts as the host. The cyanobacteria *Nostoc parmelioides* (Dodds and Marra 1989) and *Nostoc verrucosum* (Sabater and Munoz 2000) are colonized by larval midges (*Cricotopus* sp.), which graze the colony from the inside. Food and protection provided by the cyanobacterium are reciprocated by the midge resculpting *N. parmelioides* from a spherical to an ear-like form, which enhances per biomass exposure to photon and nutrient flux (Brock 1960, Ward et al. 1985). In addition, the midge resecures detached *Nostoc* to substrates, potentially decreasing export of colonies during scouring floods (Brock 1960). Challenges remain in assessing whether these positive effects adequately compensate *Nostoc* for biomass lost to grazing. To evaluate whether the association is mutualistic or parasitic—the relationship might grade between these states in different environmental contexts—colony growth and output and survival of vegetative and reproductive structures both from colonized and uncolonized hosts must be compared.

A common, cosmopolitan freshwater sponge, *Spongilla lacustris*, hosts zoochlorellae when it occurs on sunlit substrates. Photosynthetic products from these endosymbionts supplement sponge growth, which is otherwise supported solely by filtering particles (Sand-Jensen and Pedersen 1994). Brown et al. (2002) demonstrated faster growth and lower mortality for crayfish when ectocommensal branchiobdellids were present to clean debris and epibionts from crayfish gills.

Indirect facilitation in foodweb fragments

Processing chains of consumers that eat each other's byproducts (e.g., fecal pellets or comminuted crumbs from feeding; Heard 1994) have been reported for various benthic invertebrates (Wallace and Webster 1996). After being colonized by bacteria, chironomid fecal pellets are relatively high in food value, but too large for midges to reingest (McLachlan et al. 1979). However, when pellets are gnawed by cladocerans, particles small enough for midges to ingest are produced. The authors infer that this trophic facilitation supports an organic matter-based food web that otherwise would be highly refractory. Similar microbe- or size-mediated reciprocal trophic benefits involving fecal pellets also occur between oligochaetes (Milbrink 1993). At larger scales, shredding shrimp in upstream pools increase fine particle export (and dissolved C and N) to downstream filter-feeding shrimp by consuming leaf detritus introduced by hurricane-level storms (Crowl et al. 2001). Rigorous evaluations of food limitation and food sources are needed to test whether benthic consumers actually benefit from processing chains per se (Heard and Richardson 1995).

Organisms can benefit indirectly from substrate clearing by grazers. For example, the snail *Radix* bulldozes epilithon from mesocosm substrates and facilitates settlement of filter-feeding simuliids (Ledger et al. 2006) (Fig. 1F). By removing silt or epiphytic overgrowth, benthic grazers can release understory epilithic algae (Power 1990c) or epiphytized macroalgae (Dudley 1992) from light or nutrient limitation. Grazing of overstory diatoms by fishes in Ozark and Andean streams can uncover underlying N-fixing cyanobacteria (*Calothrix*) that might enhance N loading (Power et al. 1988a, Flecker 1996, Flecker and Taylor 2004). Removal of the filamentous macroalga *Cladophora* by grazing *Gumaga* caddisflies enhances the supply of understory epilithic diatoms preferred by another grazing caddis, *Helicopsyche* (Feminella and Resh 1991) (Fig. 1E).

Habitat amelioration at various scales

Benthic organisms might facilitate each other by ameliorating stressful physical conditions, such as fluid shear stress, bed scour, desiccation, and anoxia. Caddisfly pupal cases roughen substrates, and facilitate colonization and local persistence by other benthic species (Nakano et al. 2007). However, the scale of such effects is not always small. Caddisfly-dominated mounds that are 9 m high and 40 m in diameter have been excavated from Eocene lakeshores in Wyoming, where caddisfly cases on mudflats provided nucleation (phase transition) sites for microbial mats (Leggitt and Cushman 2001). As the complex grew as a carbonate-containing stromatolite-like structure, it apparently added benthic stability and topographic heterogeneity to a soft-bottomed lakeshore.

Similarly, aquatic macrophytes (*Justicia*) aid unionid mussels by stabilizing the streambed and enhancing local influx of fine organic particles (Fritz et al. 2004). Sedge tussocks (*Carex nudata*) growing in and along the active channel shield guest plants growing within tussocks from scour and export during winter floods and from herbivory during summer low flows (Levine 2000). In slow-flowing lentic or wetland environments where hypoxia can stress infauna or rooted plants, aerenchymous plants can facilitate neighbors by oxygenating sediments (Callaway and King 1996). Floating mats of algae or macrophytic vegetation provide food-rich, warm incubators that enhance development, survival, and emergence of aquatic insects (Power 1990a), and hide juvenile fish from predators (Sazima and Zamprogno 1985).

At ecosystem scales, certain freshwater fishes and benthic invertebrates benefit from the added habitat heterogeneity generated by ecosystem-engineering beavers (Naiman et al. 1988, Wright et al. 2002). In addition, the importance of forest cover to stream habitat structure and to retentiveness, temperature, and wood and sediment loading regimes that favor salmonids is widely recognized (Harvey 1998, Welty et al. 2002). Hydraulic lift by large trees that access deep ground water and leak some of it into shallow soils (Callaway 1990) might play a crucial, but overlooked, role in maintaining stream runoff during drought (Jung-Eun Lee et al. 2005).

Role of *J-NABS* and the Future

Since its origin in 1986, 15% of all articles published in *J-NABS* have focused on biotic interactions (7 to 33%/y). Despite some difficulty in pigeonholing these articles, we estimate that ~70% have focused on

predation and herbivory, a percentage that has changed little since 1995 (Fig. 3B, C). *J-NABS* has contributed much to our knowledge of direct, nonconsumptive effects of predators on prey traits and of the scale-dependent effects predators have on prey assemblages. *J-NABS* has also illuminated the striking indirect effects herbivores can have on community structure and biophysical processes and the effects meiofauna can have on producer assemblages. We urge benthologists to further our overall knowledge of predation and herbivory by studying how: 1) predators and herbivores induce trait plasticity in prey and producers, respectively, 2) the ecological and evolutionary importance of predation and herbivory varies along environmental gradients (e.g., climate), and 3) indirect effects are modified by environmental resources and conditions. Benthic ecosystems also are excellent systems for testing general hypotheses about the influence of competition, parasitism, and positive interactions, topics that have received comparatively less attention in *J-NABS* (Fig. 3A, D, E). Future work should examine the time-varying effects of competition on population structure, and should determine whether short-term competitive experiences affect long-term demographic rates and structure. For example, are terrestrial adults independent of the density-dependent growth and mortality dynamics that manifest in larval aquatic stages? If not, are local effects of competition homogenized over the system or metacommunity by adult reproduction and recruitment? Peckarsky et al.'s (1997) plea for researchers to examine how competitors or enemies affect gene flow through dispersing adults has largely been ignored, so additional information will help answer these questions. Collaborative research with population geneticists will undoubtedly help us understand the evolutionary consequences of biotic interactions in complex multispecies systems. Furthermore, collaborations between benthologists and parasitologists probably will provide new insight into organizational mechanisms of benthic systems, given that parasites can affect the functional roles of their hosts. Studies are needed that determine how lethal/sublethal effects of parasites affect host demographics and whether these effects have larger-scale consequences. *J-NABS* could be a key venue for these studies and others that explore how aquatic host–microparasite coevolutionary processes change with climate-driven changes in local selection pressures.

Interest in positive biotic interactions is only beginning to grow, despite a long recognition of its importance in structuring natural communities (e.g., Clements 1916). Like Halpern et al. (2007), we believe

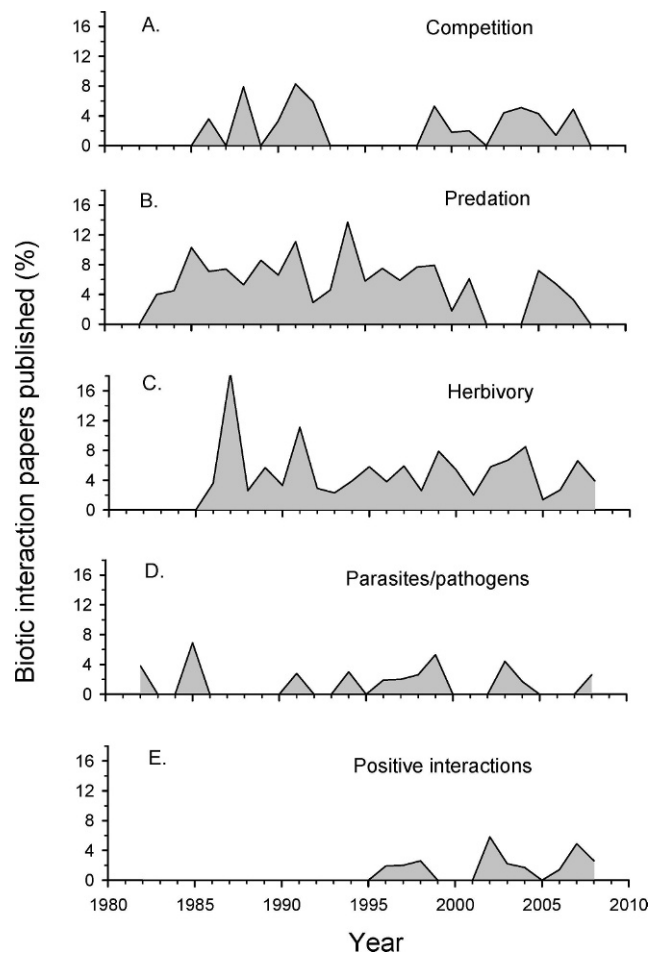


FIG. 3. Area plots of the percentage of total articles published in *J-NABS* and *Freshwater Invertebrate Biology* that addressed competition (A), predation (B), herbivory (C), parasites/pathogens (D), and positive interactions (E) since 1982. *J-NABS* developed from *Freshwater Invertebrate Biology* in 1986.

that studying population-scale positive interactions, as well as nontraditional, larger-scale interactions (e.g., riparian subsidies into streams and their effects on benthic habitat stabilization, or cross-system recruitment of life stages) will greatly increase our understanding of how freshwater benthic ecosystems operate and our ability to conserve or restore them. Last, we urge benthologists to explore how populations will evolve in response to a diverse array of biotic interactions embedded in benthic communities and, in turn, how these evolutionary responses will redefine trophic and community structure and their emergent properties, such as connectivity, stability and resilience. The high rate at which human actions are currently changing the mix of species in many freshwater communities greatly accelerates our need to understand the degree to which biotic interactions

affect population demographics, community structure, and ecosystem function.

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