The Role of Benthic Invertebrate Species in Freshwater Ecosystems

Zoobenthic species influence energy flows and nutrient cycling

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Small invertebrates are functionally important in many terrestrial and aquatic ecosystems (Wilson 1992, Freckman et al. 1997, Palmer et al. 1997, Postel and Carpenter 1997). In freshwater sediments, benthic invertebrates are diverse and abundant, but they are often patchily distributed and relatively difficult to sample, especially when they live in deep subsurface sediments. Thus, the species richness and functional importance of freshwater benthic invertebrates generally go unnoticed until unexpected changes occur in ecosystems. Unanticipated changes in freshwater ecosystems are often due to alterations in the complex connections among sediment-dwelling species and associated food webs (e.g., Goedkoop and Johnson 1996, Lodge et al. 1998b, Stockley et al. 1998) or to disturbances, such as floods or drought (e.g., Covich 1993, Power 1995, Johnson et al. 1998), that alter the species composition of the benthos. In addition, benthic species can themselves constitute a distur-

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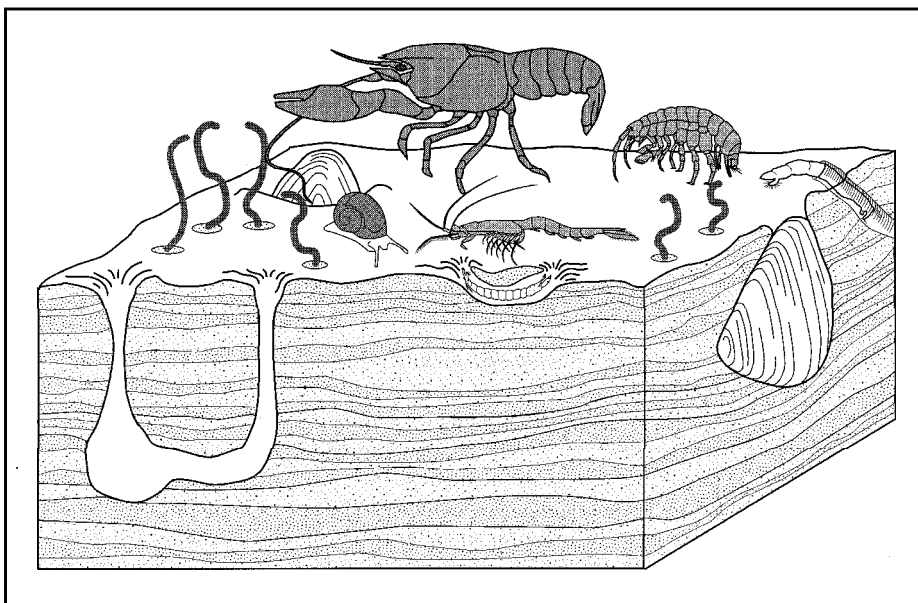
> **The integrity of the freshwater supply depends on how various benthic species make their living and contribute to complex food webs**

bance, such as when they transmit diseases. For example, certain benthic invertebrate species (e.g., *Tubifex tubifex*) serve as parasite-transmitting vectors; if these invertebrates increase in abundance in stream sediments, they may spread a lethal disease to trout, causing trout populations to decline (Brinkhurst 1997). Fish kills may also occur because of increased accumulation of nutrients, which cause formation of toxic algal blooms, deoxygenation of deeper, density-stratified waters, and high concentrations of ammonia or hydrogen sulfide (Covich 1993).

The bottom muds of lakes and streams may at first glance appear to be uniform and, therefore, unlikely habitats for high biodiversity. However, physical, chemical, and biological processes create significant horizontal and vertical heterogeneities in the substrata (Figure 1) that provide a physical template for distinct niches (Hutchinson 1993). These sedimentary processes include changes in direction and rates of

flows, differential deposition of sediment grain sizes and dead organisms, growth and death of roots, burrowing and sediment reworking, and fecal production by benthic consumers. Microhabitats are also created by chemical gradients and microzonation in concentrations of dissolved oxygen, hydrogen sulfide, ammonia, phosphorus, and other critical chemicals (Groffman and Bohlen 1999). Colwell (1998) emphasizes that such "biocomplexity" of habitats and biological relationships is an important aspect of biodiversity. Bioturbation and other biotic interactions create extensive biocomplexity in freshwater sediments (Charbonneau and Hare 1998). These biocomplexities must be better understood if clean drinking water and recreational uses of fresh waters are to be maintained. Science-based policies require an ecosystem perspective on the multiple roles of many diverse benthic species.

Previous studies have often dealt with the "goods" produced by benthic species, such as the quantity of prey items consumed by fish. These goods are clearly important components of food webs, but how their functional relationships respond to changes in species composition are also important. In this article, we highlight examples of how some species have a disproportionately large impact on food-web dynamics and how particular species provide essential ecosystem services. These ecosystem functions include sediment mixing, nutrient cycling, and energy flow through food webs.

Figure 1. Benthic macroinvertebrates burrow deeply into layered sediments and accelerate nutrient cycling. Burrowing bivalves, crayfish, tubificid worms, and aquatic insect larvae mix the sediments, aerate deeper layers of sediments, and increase rates of recycling of macronutrients (nitrogen, phosphorus, and organic carbon) and micronutrients (trace elements) by bioturbation and fecal production. Mysid shrimp, amphipods, and gastropods enhance microbial growth and nutrient cycling through their mixing of surface sediments and breakdown of organic detritus.

Diversity of benthic freshwater communities

Freshwater benthic species evolved from many phyla over millions of years and represent a rich fauna. In the fourth and last volume of *A Treatise on Limnology*, G. Evelyn Hutchinson (1993) reevaluated the question he first posed 40 years ago — "Why are there so many kinds of animals?" — but in the context of the zoobenthos. Hutchinson (1993) concluded that "the Diptera are by far the most diverse order of insects in fresh water; they are in fact the most diversified of any major taxon of freshwater organisms." He estimated that more than 20,000 Dipteran species breed in fresh water worldwide, approximately four times the number of Coleoptera. Others estimate that there are large numbers of benthic species of protozoa, crustacea, and other groups (Palmer et al. 1997). Moreover, systematists estimate that only a small percentage of certain taxa (e.g., freshwater nematodes) have been described. Diverse forms are continuously discovered, especially in deep groundwaters, in which regional endemics reflect isolation and evolutionary adaptations

to specific conditions (e.g., Holsinger 1993). Many species still remain undescribed, both taxonomically and ecologically (Hutchinson 1993, Palmer et al. 1997). Protecting diverse benthic communities will require more thorough understanding of long-term functional relationships among these species in an ecosystem context.

Importance of individual species in ecosystem processes

It is evident from studies of terrestrial species that the number of species per se is not necessarily related to rates of ecosystem production (e.g., Chapin et al. 1997, Tilman et al. 1997). Instead, each species is adapted to function under variable conditions, with different species being of different relative importance to particular ecological processes. Changes in distributions and abundances of one species can result in disproportionate and unexpected responses by other species as they attempt to compensate functionally for changes in the associated species (Frost et al. 1995, Naeem 1998).

Recently, Palmer et al. (1997) proposed that particular benthic species

are especially important for determining how organic matter is processed in freshwater ecosystems. They described the diversity and ecological roles of freshwater benthic species and the major processes that these species influence in freshwater ecosystems. In this article, we summarize several recent studies that show how specific zoobenthic species alter ecosystem processes. We emphasize that zoobenthic species, especially crustaceans, influence both energy flow through freshwater food webs and nutrient cycling (Figure 2). We suggest that in some cases, the presence or absence of a single species can dramatically alter ecological processes such as rates of grazing and decomposition.

In benthic communities, even closely related species may obtain their food resources differently. Consequently, species are anticipated to differ in the ways or rates at which they perform a distinct ecosystem service (e.g., acting as primary producers, herbivores, predators, or detritivores). Although we highlight only a few examples, there are numerous food-web linkages in which one species interacts positively or negatively with others or in which the addition or loss of a single species alters food-web dynamics. Based on current information about the separation of niches among benthic species, we conclude that different species of sediment-dwelling macroinvertebrates are unlikely to be interchangeable components in many complex ecosystem processes.

Diversity and species redundancy in ecosystems

Linkage of niche theory to trophic dynamics led to the "rivet hypothesis" (Ehrlich and Ehrlich 1981), which postulates that each species has the potential to perform an essential role in the persistence of the community and the ecosystem and that some species may remain as the sole representatives of a particular functional group (Ehrlich and Walker 1998).

Although it is clear that at some level each species is unique, overlap in resource use among species is not unusual, especially in freshwater food webs. For decades, ecologists have

questioned how much overlap in resource use can persist over time among competing species. Recently, this question has been rephrased to ask if, and under what conditions, the functional roles of each species are necessary for ecosystem processes to persist. This "redundancy hypothesis" predicts that not all species are equally necessary at any one time for ecosystem processes to continue (Lawton and Brown 1994, Ehrlich and Walker 1998). If some species were "redundant" in terms of their functional relations, then their loss would not result in observable changes in energy flow or nutrient cycling. The concept of "parallel redundancy" used in engineering analysis for system reliability is likely to be applicable for comparing species' roles in ecosystem studies (Naeem 1998).

The redundancy hypothesis can be broken down into three subhypotheses. The "functional group hypothesis" predicts that as long as one species from each functional group is present, ecosystem processes will continue. The "trophic-level hypothesis" predicts that as long as the biomass or turnover of organisms at each trophic level remains relatively uniform and is independent of species composition, energy flow and ecosystem processes will persist. Finally, the "keystone species hypothesis" predicts that not all species are of equal functional importance; rather, only a few are truly necessary for ecosystem processes, even through these species may not be abundant.

Species redundancy in freshwater sediments

As mentioned above, essential information on the unique contributions made by individual benthic species is lacking. Moreover, there is insufficient information about how individual zoobenthic species interact with one another under the dynamic range of natural conditions in freshwater sediments. Nevertheless, from detailed field observations it appears that redundancy in many freshwater benthic ecosystems is low. For example, numerous zoobenthic species occupy particular microhabitats along stream channels or at various depths in lakes (e.g., Hutchinson
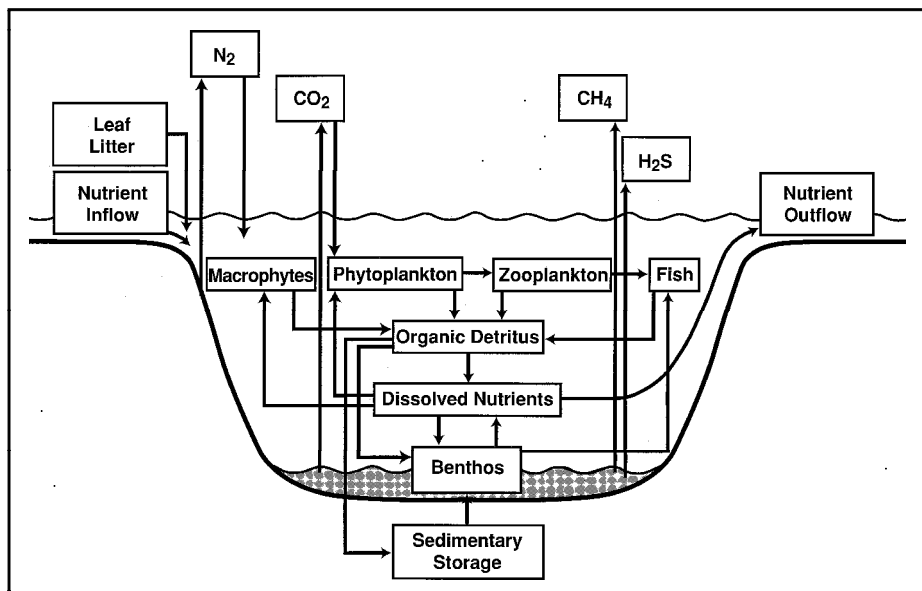

Figure 2. The roles of benthic macroinvertebrates in cycling nutrients and controlling nutrient outflows from ecosystems. The benthos transforms organic detritus from sedimentary storage into dissolved nutrients that can be mixed into overlying waters and used by rooted plants (macrophytes) and algae (phytoplankton) to enhance primary productivity. Some benthic species are omnivores and feed on macrophytes, algae, and zooplankton. Many benthic species are consumed by fishes. Through their mixing of sediments and consumption of diverse resources, benthic invertebrates can, directly and indirectly, influence microbial production and release of greenhouse gases (CO_2 and CH_4), toxic gases (H_2S and NH_4), and nitrogen (N_2).

1993) and at various times of year (e.g., Cummins et al. 1989). These spatial and temporal distributions suggest that benthic species have different preferences for particular ranges of temperature, pH, current velocity, and types of substrata. Colonization studies of streams and rivers also suggest that there are important differences in preferred use of microhabitats (Milner 1987, Malmqvist et al. 1991). These differences in the ability of species to disperse to and live in certain microhabitats become especially important after major disturbances, when species abundances and community structure may shift. From these observations, we infer that rates of ecosystem processing may change after a major disturbance because species composition often changes.

Different spatial patterns of distribution have formed a basis for generalizations about functional relationships of zoobenthic species in different freshwater ecological processes. One example is the River Continuum Concept (Vannote et al. 1980), which relates sources of energy and the dominant ecological mode by which energy is obtained in

headwater and tributary streams to the types of consumers distributed along a drainage network (Cummins et al. 1995). According to this concept, particular groups of benthic consumers use different sources of energy, such as riparian leaf litter or in-stream plant productivity from algae or macrophytes (Wallace and Webster 1996, Parkyn et al. 1997, Wallace et al. 1997). Certain species of aquatic insects that live in small headwater streams use specialized mouthparts or feeding appendages to break up large pieces of organic detritus into smaller fragments. In the process of feeding, some shredded and suspended fragments are transported downstream (along with fecal pellets). Other species are specialized to filter out variously sized particles and are typically located downstream from the shredders. Such specializations suggest that the loss of some pivotal species, such as shredders, would alter food availability for suspension feeders and thereby alter ecosystem processing of detrital carbon. However, experimental studies on the roles of single species are generally lacking for stream ecosystems (Heard and Richardson

1995). An integration of empirical and theoretical studies is essential if the linkages of benthic species' roles to freshwater ecosystem processes are to be better understood.

Roles of benthic species in ecological processes

Benthic species perform a variety of functions in freshwater food webs. First, as already described, benthic invertebrates provide essential ecosystem services by accelerating detrital decomposition (van de Bund et al. 1994, Wallace and Webster 1996). Dead organic matter is one of the main sources of energy for benthic species in shallow-water habitats (Covich 1988, Hutchinson 1993, Wallace and Webster 1996). Benthic invertebrates are estimated to process 20–73% of riparian leaf-litter inputs to headwater streams. Second, benthic invertebrates release bound nutrients into solution by their feeding activities, excretion, and burrowing into sediments (Figures 1 and 2). Bacteria, fungi, algae, and aquatic angiosperms can quickly take up these dissolved nutrients, accelerating microbial and plant growth (van de Bund et al. 1994, Cummins et al. 1995, Pelegri and Blackburn 1996, Wallace et al. 1997). This increased growth of benthic microbes, algae, and rooted macrophytes is in turn consumed by herbivorous and omnivorous benthic invertebrates (Creed 1994, Lodge et al. 1994, Nystrom et al. 1996, Cronin 1998). Third, many benthic invertebrates are predators that control the numbers, locations, and sizes of their prey (Crowl and Covich 1990, 1994). Fourth, benthic invertebrates supply food for both aquatic and terrestrial vertebrate consumers (e.g., fishes, turtles, and birds). Finally, benthic organisms accelerate nutrient transfer to overlying open waters of lakes (e.g., Lindegaard 1994, Threlkeld 1994, Blumenshine et al. 1997, Clarke et al. 1997) as well as to adjacent riparian zones of streams (e.g., Covich et al. 1996, Johnson and Covich 1997, Naiman and Décamps 1997, Wallace et al. 1997).

The extent of understanding of the effects of benthic organisms on freshwater ecosystem processes varies with the type of freshwater system (i.e., streams, lakes, and wetlands). For example, much more is known about how benthic species of aquatic insects and other consumers influence detrital processing in streams than about how they do so in lakes or wetlands (Hutchinson 1993, Wallace and Webster 1996, Rosemond et al. 1998). Species-specific linkages are known to enhance algal growth and productivity (Dodds 1991, Pringle et al. 1993), and field experiments are beginning to show that benthic macroinvertebrates have species-specific roles in processing organic matter. For example, one species of freshwater shrimp can process leaf litter faster than another shrimp species in an insular tropical headwater stream (see discussion below). Although both shrimp are detritivores, they do not substitute completely for one another in leaf-detrital processing and nutrient cycling. In stream reaches where both of these shrimp species co-occur (Covich and McDowell 1996), their interactions and different modes and rates of leaf-litter processing may enhance each other's effectiveness.

Different benthic species alter rates of decomposition

If sufficient dissolved oxygen and appropriate substrata are available, then many species of benthic organisms, especially insects and crustaceans, can accelerate microbial processing of dead organic material. Because many species process organic detritus, most freshwater ecologists have generally categorized these consumers into functional feeding groups (Cummins et al. 1995) or feeding guilds (Hawkins and MacMahon 1989). To simplify data collection and analyses, most investigators "lump" species, making the assumption, for example, that those with similar feeding appendages or mandibular morphology generally perform similar roles in processing leaf litter (Merritt and Cummins 1996).

Although ecologists still disagree about how to best categorize different species (e.g., Wallace and Webster 1996), it is widely agreed that shredders feed by tearing up large pieces of microbially conditioned leaf detritus with specialized mouth parts, whereas scrapers feed on attached algae or "biofilms" of bacteria and algae. However, some species of scrapers also consume bacteria and fungi from fresh and decomposing leaf surfaces (Kornijow et al. 1995). As species scrape and shred coarse plant litter in the process of obtaining their food, they convert coarse litter into fine particulates. Collectors filter suspended organic particulates from flowing waters or from small, water-filled spaces within the sediments. Although these functional classifications are useful for some studies, they can obscure important food-web dynamics that result from differences among individual species and changes in feeding behavior under specific conditions.

Additions of benthic species to food webs. Given the general lack of empirical and theoretical work on the roles of single species in freshwater ecosystems, one way to glean conceptual insights may be to consider range extensions of benthic species into additional habitats as a source of information on the role of particular species in ecological processes. Although we do not advocate moving species around, it is essential to monitor the ecosystem-level consequences of any movements that do occur. The arrival of an additional species is often associated with the loss of one or more resident species (Lodge et al. 1998b). However, it is also important to ask about the effects on ecosystem processes. Because native species are generally well adapted to local conditions, movements of additional species into freshwater assemblages can sometimes alter energy flow and change nutrient cycling.

Although many range extensions and introductions are transient, the spread of some benthic species is persistent. Successful invaders often have biotic attributes that predispose them to have major impacts on highly variable ecosystems. Identifying these invasive characteristics may be useful for better understanding how resident, native benthic species function in an ecosystem context. These attributes include aggressive use of food resources, rapid reproduction, larvae that are well adapted for dispersal, or resistant resting

stages that survive in muds for many years. Intensive monitoring studies are just beginning to reveal the ecological traits that account for some benthic species' abilities to extend their ranges and to alter ecosystem processes. Well-designed field experiments are needed to identify unique roles of both invasive and non-invasive species before the consequences of losing resident, native species can be fully understood.

Losses of benthic species in food webs. Loss of some species will likely alter or degrade critical ecosystem processes because of the unavailability of replacement species. Although the exact consequences of each species' loss cannot be predicted, Wilson (1992) noted that if one species after another were lost from an ecosystem, then at some point the ecosystem would likely change drastically. Once species are lost, the costs for maintaining natural ecosystems with engineering processes would be prohibitively expensive (Postel and Carpenter 1997). If at least one species were to remain in each functional group and the rate of processing by that species were sufficiently high, then, in theory at least, ecosystem processes should continue. However, because environmental conditions change over time, populations of some of these remaining species would most likely become locally extinct, disrupting ecosystem processing. Consequently, ecosystems composed of a bare minimum of species in a fluctuating environment probably could not continue to function over time merely by compensating for the losses of some species with increased densities, biomass, or processing rates of the few remaining species.

Freshwater ecosystem processing by crustaceans

Several studies have shown that crustaceans play important roles in stream and lake food webs. We outline these studies as examples to stimulate additional field studies and to emphasize the need for more effective conceptualization of cross-linkages among different benthic species.

Detritivorous shrimp. An example of how individual species can alter

detrital processing comes from a recent experimental manipulation of decapods in a tropical headwater stream in the Luquillo Experimental Forest in Puerto Rico. This rain forest is one of the sites in the National Science Foundation's Long Term Ecological Research (LTER) Program. The Luquillo LTER is focused on the effects of disturbances such as hurricanes and drought on forest and stream ecosystems (Covich et al. 1996). Leaf litter was manipulated in a series of pools to identify the effects of two shrimp species on leaf-detrital processing. The stream pools at this elevation (550 m) are located above several high waterfalls where no fish predators occur (Todd Crowl and Alan Covich, unpublished data); the food web is relatively simple and is dominated by several decapod species (Covich and McDowell 1996). By clearing pools of all naturally occurring leaf litter and macroinvertebrates, it was possible to measure detrital processing by each decapod species separately in response to additions of leaf litter from a single riparian tree species. Leaf litter from *Cecropia schreveriana* (an early successional tree that often colonizes disturbed riparian habitats after mud slides and hurricanes) was added back to the cleared pools along with either of two naturally co-occurring species of detritivorous shrimp (*Atya lanipes* and *Xiphocaris elongata*). Predatory shrimp (*Macrobrachium carcinus*, *Macrobrachium crenulatum*) were excluded from the pools with in-stream fencing to further reduce the number of species interactions that could affect rates of leaf decomposition.

Although both shrimp species influenced the rates of leaf-litter decomposition, their effects were distinctly different (Todd Crowl and Alan Covich, unpublished data). Over the 23 days of the experiment, *Xiphocaris* shredded the leaf litter as they ingested leaf fragments and the bacteria and fungi that colonized the decomposing leaf. As a result of this shredding, *Xiphocaris* increased the concentration and rate of downstream transport of suspended fine particulate organic matter as well as the concentrations of both total dissolved nitrogen and dissolved organic carbon. *Atya* also increased

the rate of leaf breakdown relative to controls, but because they both shred and scrape leaf surfaces as well as filter out suspended detritus, their processing resulted in less downstream transport of suspended fine organic particulates. Thus, a single functional classification for *Atya* is not as effective as for *Xiphocaris*. Moreover, these species are not complete substitutes for one another in terms of food-web dynamics and ecosystem processing.

Because of their functional differences, these two shrimp species may complement one another wherever they co-occur, resulting in a less "leaky" headwater ecosystem than one containing just a single shrimp species. That is, few leaves are washed downstream out of pools containing both species because *Xiphocaris* breaks leaf material into small size fractions that are then available to filter-feeding *Atya*. Thus, the relative spatial location of these two species within or between pools could alter the effectiveness of overall detrital processing. For example, when *Atya* occur downstream of *Xiphocaris*, growth of the former could be enhanced by the increased availability of suspended fine organic particulates. In addition, the degree of complementarity depends on stream flow and water depth. In a shallow pool or riffle that has sufficient velocity to suspend organic particulates, leaf shredding by *Xiphocaris* could increase concentrations of detrital particulates for filter-feeding *Atya*.

The "processing chain" that results from different species of shrimp interacting as detritivores within and between pools is similar to that hypothesized in the River Continuum Concept, in that aquatic insect shredders occur primarily in upstream reaches and are thought to increase the availability of fine organic particulates for downstream collectors and suspension filter feeders (e.g., Vannote et al. 1980, Heard and Richardson 1995). More field manipulations are needed to determine how various species of aquatic insects, crustaceans, gastropods, and other benthic invertebrates differ in their individual species effects on rates of detrital processing and nutrient cycling.

Grazing crayfish. Herbivorous benthic species have distinct functional morphologies, feeding preferences, and behaviors, resulting in major differences in their grazing rates (Cronin 1998, Lodge et al. 1998a). Grazing crayfish generally do not consume all types of rooted macrophytes as widely as they consume most algae in stream food webs (Nystrom et al. 1996). Rooted angiosperms were derived from terrestrial ancestors and contain indigestible cellulose and secondary compounds, such as glucosinolates (Newman 1991). Such chemical defenses against herbivores appear to be restricted to particular species of grazers. The size and structure of macrophytes are also known to influence consumption by different grazers (Nystrom et al. 1996, Cronin 1998). This combination of chemical and structural defenses may result in uniformly low rates of herbivory among particular assemblages of producer and consumer species.

Because benthic species differ in their abilities to consume rooted macrophytes, the rate of removal of submerged vegetation can be greatly altered if additional herbivorous species extend their range into shallow-water ecosystems. An example of the addition of a new herbivore to a littoral food web occurred when the "rusty" crayfish, *Orconectes rusticus*, moved into northern Wisconsin lakes from Indiana and Ohio. These northern shallow lakes had previously been dominated by another species of crayfish, *Orconectes virilis*, whose abundance had already been decreased by the earlier immigration of another non-native crayfish, *Orconectes propinquus* (Lodge et al. 1994, 1998b). The native crayfish, *O. virilis*, was less aggressive in its diurnal feeding on submerged macrophytes than *O. rusticus*. *O. rusticus* removed entire macrophyte beds in the littoral zones of lakes, from which it displaced *O. virilis* by clipping plant stems. The removal of the macrophyte beds had a major effect on assemblages of other species of benthic invertebrates, such as gastropods (Lodge et al. 1998b). Furthermore, because larval fish require the protective cover of submerged vegetation to avoid predation by larger fishes, recruitment of juvenile fish declined, and within a few years fishermen caught fewer large fish.

Omnivorous crustaceans. Crayfish consume a wide range of both plant and animal foods, and the spread of *O. rusticus* into northern habitats therefore also illustrates how species-specific differences in feeding by omnivores can change energy flows through benthic food webs. In addition to altering the structure of macrophyte beds, *O. rusticus* also altered the gastropod community associated with submerged plants. Before the arrival of *O. rusticus* and the consequent removal of macrophytes, gastropods had access to abundant periphyton growing on the macrophytes and found protection from fish and crayfish predators among the leaf cover. After the macrophytes were removed, the gastropod species' shell thickness and their ability to evade shell-breaking predators (such as crayfish) were important predictors of which species of gastropods persisted (Covich et al. 1994, Lodge et al. 1994). For example, some species of gastropods avoid day-active predators by burrowing into the sediments if macrophytes are unavailable for structural cover (Alan Covich, unpublished data). While finding microbial food in the sediments, these gastropod species actively recycle nutrients and continue their ecological roles as consumers.

There are other examples of omnivorous crustaceans that illustrate some unexpected results because of unanticipated foraging behaviors by non-native benthic species entering fresh waters. For instance, lake managers in the western United States did not anticipate the decline in fisheries caused by intentional introductions of a species of crustacean prey transferred from some deep northern lakes to other lakes to increase fish production (Martinez and Bergersen 1989). These benthic crustaceans, "opossum shrimp" (*Mysis relicta*), consume microorganisms during the day, when they remain in or on the sediments (e.g., Johannsson 1992). At night, however, they move off the bottom and switch to feeding on phytoplankton and zooplankton (which also migrate vertically in the evening). As a result of its varied feeding locations, *Mysis* can be fed on by lake trout and kokanee salmon only under specific light conditions.

In one case, *Mysis* spread downstream (from an initial introduction to a relatively shallow lake) through an outflowing river and into Flathead Lake, Montana. Although movement of *Mysis* along rivers had not been expected (because these crustaceans are usually not found in rivers), it soon disrupted this larger, deeper lake's open-water community of planktonic crustaceans by feeding on juvenile zooplankton. Adult cladoceran zooplankton had previously been prey for lake trout and kokanee salmon, which had also been introduced earlier in this deep lake. The loss of open-water zooplankton prey led to declines in sport fishes in Flathead Lake, and the *Mysis* remained in deeper, darker waters, where they avoided fish predation. After the kokanee declined, fewer bald eagles and bears were observed feeding in the inflowing river because there were fewer fish left to swim upstream to spawn (Spencer et al. 1991).

Mysis were deliberately introduced into many other western lakes and reservoirs on a trial-and-error basis. Often, the results were not as expected: fisheries declined instead of flourishing (Martinez and Bergersen 1989). Dispersal of benthic species from one lake to another as a management tool is now generally recognized as inappropriate, but unintentional introductions of many different species are increasing as recreational and commercial boat traffic expands.

Conclusions and policy implications

These examples illustrate that benthic invertebrate species function in different ways that are important to maintaining ecosystem functions such as energy flow in food webs. Many benthic species convert live plant and dead organic material into prey items for larger consumers in complex food webs. In the process of maintaining energy flow, these benthic species simultaneously provide essential ecosystem services, such as nutrient cycling and aeration of sediments. Different species comprise distinct functional groups that provide ecological integrity. In some

cases, these functional groups may be represented by only a few species, so that any loss of species diversity could be detrimental to continued ecosystem functioning. Thus, it is increasingly important to protect the biodiversity of benthic communities to lower the risk of unexpected and unwanted consequences.

In the past few decades, freshwater habitats have received significant remediation (Norton and Davis 1997) as a result of the Clean Water Act's call for greater ecological integrity; in particular, their biodiversity has increased. For example, the Cuyahoga River in Ohio is no longer so contaminated with petroleum wastes that it catches fire (Olive et al. 1988). Lake Erie's levels of dissolved oxygen are increasing in its bottom waters, and mayflies are beginning to return to sediments in the shallow western basin (e.g., Kolar et al. 1997) that was once thought to be "dead." The return of mayflies means that nutrients are again rapidly converted from long-term storage in lake sediments into prey that are available to many species of fishes and other consumers rather than accumulating in the muds. Without these benthic insects, many nutrients would reach high concentrations in the sediments and not be available to consumer species. However, the ecosystem is being modified now by the spread of invasive non-native species such as the zebra mussels (*Dreissena polymorpha* and *Dreissena bugensis*) that have altered the flow of energy within the benthic community (Stewart et al. 1998). These invasive mussels alter food webs in several ways. First, filter feeding by these mussels removes suspended organic materials in overlying waters and can enrich sediments for use by other benthic species. Second, zebra mussel shells provide hard surfaces for colonization by various benthic invertebrates (Botts et al. 1996). Finally, these shells also serve as structural refugia for prey so that many types of benthic invertebrates may avoid fish predators. From available information it is not possible to predict precisely how the addition and persistence of these invasive mussels will ultimately change energy flow and influence water quality. However, their addition to

North American fresh waters clearly demonstrates that particular species can alter ecosystem productivity.

There is now widespread agreement that the global ecosystem cannot function without an adequate supply of inland waters. As the demand for fresh water increases in response to population growth, climate shifts, and economic development, additional conflicts among competing users (such as drinking water supply for cities or irrigation) will create new challenges to ecological processes in natural and managed inland waters (Naiman et al. 1995, Meyer 1997). In the United States, discussions about reauthorizing the Endangered Species Act and the Clean Water Act will require ecologists to inform policymakers of alternative solutions to complex issues involving large drainage areas and their connections to wetlands, lakes, and rivers. Besides communicating the intrinsic value of individual species, it will be important to explain the functions of diverse benthic communities under different ecological conditions before any additional species are lost.

Freshwater ecologists understand that benthic species provide important ecosystem services, but an adequate model for evaluating these services is lacking. The public generally understands that water is "reused" in the hydrologic cycle: evaporation from surface waters and transpiration by plants provides water vapor for cloud formation and precipitation back to the earth's surface. But there is less public understanding of how water enters the belowground water table and recharges aquifers. Few individuals appreciate that much of flowing water eventually passes through the subsurface zones, where a rich faunal diversity contributes to a wide range of ecological services. The freshwater benthic biota (microbes to macrofauna) mediate biogeochemical transformations and act directly to prevent the buildup of carbon in the sediments and the deoxygenation of bottom waters. They also sequester and move contaminants and excess nutrients from groundwaters and sediments while influencing the flux of greenhouse gases (carbon dioxide and methane).

Although these diverse species may be hidden and "invisible" because they live below the surface, the integrity of the freshwater supply depends on how various benthic species make their living and contribute to complex food webs.

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Biology Reporting Awards

The Awards

The American Institute of Biological Sciences Media Award was established in 1995 to recognize outstanding reporting on research in biology. This year's winners will each receive $1000 and expenses to attend the annual meeting of the American Institute of Biological Sciences, 11–14 November 1999, where the awards will be presented.

The awards are designed to encourage the communication of biology to the public. One award is for print journalism specifically, the other for broadcast journalism. AIBS intends to promote public understanding of how biologists approach their research, collect and interpret their data, and reach conclusions, as well as how the research and its conclusions are relevant to society.

Rules

The awards will be limited to nontechnical journalism. Articles published in newspapers and magazines are elegible for the print award, and stories broadcast on radio and television are eligible for the broadcast award. Both freelancers and staff writers are eligible. Professional scientists writing in their area of research are not eligible. Books and articles in technical journals will not be considered. Articles appearing in *BioScience*, the publication of the American Institute of Biological Sciences, are not eligible.

Biological research is broadly defined to include laboratory and field work, as well as theoretical advances. For the purposes of this award, it does not include testing of medical or veterinary treatments.

Entries will be judged on the basis of clarity, reporting and writing skills, originality, and appeal to the general public.

Applicants may submit a single contribution or a series. Stories must have been published or broadcast betwen 1 January 1998 and 31 December 1998. A series will be accepted if more than half of it appeared between those dates. Applications may be submitted by the journalist or on his or her behalf.

For information and entry form

Send a self-addressed envelope to AIBS Media Award, 1444 Eye St., NW, Suite 200, Washington, DC 20005.

All applications and submissions must be received by 1 April 1999. Submissions will not be returned.

Judges

The award will be judged by a panel of science journalists and scientists chosen by the American Institute of Biological Sciences. The winner will be notified by 1 July 1999.