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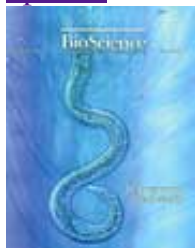
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The Role of Benthic Invertebrate Species in Freshwater Ecosystems: Zoobenthic species influence energy flows and nutrient cycling

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The Role of Benthic Invertebrate Species in Freshwater Ecosystems

Zoobenthic species influence energy flows and nutrient cycling

Alan P. Covich, Margaret A. Palmer, and Todd A. Crowl

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.

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