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Scales in Stream Ecology

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Linking Scales in Stream Ecology

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The hierarchical structure of natural systems can be useful in designing ecological studies that are informative at multiple spatial scales. Although stream systems have long been recognized as having a hierarchical spatial structure, there is a need for more empirical research that exploits this structure to generate an understanding of population biology, community ecology, and species–ecosystem linkages across spatial scales. We review studies that link pattern and process across multiple scales of stream-habitat organization, highlighting the insight derived from this multiscale approach and the role that mechanistic hypotheses play in its successful application. We also describe a frontier in stream research that relies on this multiscale approach: assessing the consequences and mechanisms of ecological processes occurring at the network scale. Broader use of this approach will advance many goals in applied stream ecology, including the design of reserves to protect stream biodiversity and the conservation of freshwater resources and services.

Keywords: dispersal, networks, resiliency, rivers, streams

Ecologists are challenged to understand natural systems linked by processes acting at multiple spatial scales, from the microscopic to the global. They must identify both critical processes and the scale at which those processes are acting. Recognizing and capitalizing on the hierarchical structure of natural systems (e.g., food webs, animal societies, weather) can be helpful in designing ecological studies that are informative at multiple scales of organization. Stream systems have long been recognized as having a hierarchical spatial structure (Strahler 1964): Stream habitats, characterized by differences in gradient and flow, make up reaches, which link together to form larger stream networks (figure 1). While there are outstanding examples of empirical research exploiting this hierarchical structure to generate an understanding of stream ecology that applies across multiple spatial scales, we believe there is also a need for broader application of this multiscale approach to solidify understanding in established areas of research and to address important emerging questions.

The Hubbard Brook Ecosystem Study, initiated in 1963, pioneered the integration of studies across multiple spatial scales to understand the dynamics of nutrients, sediment, and water in streams. Early research at the Hubbard Brook Experimental Forest set a standard for comprehensive assessment of the ecosystem ecology of small watersheds (Bormann and Likens 1979, Likens and Bormann 1995). The streams draining these watersheds were used to sample integrated biogeochemical processes (e.g., net watershed-export values). This approach took a deliberate "black box" approach to habitat-scale processes, in that the identification of large-scale patterns was given initial priority over the investigation of localized mechanisms. Mechanistic hypotheses and research testing these hypotheses grew out of emergent patterns, resulting in a strong link between experimental work at fine spatial scales (i.e., within pool or riffle habitats), where specific mechanisms were investigated, and at the reach scale, where the consequences of these mechanisms were observed.

This approach, which capitalizes on the hierarchical organization of stream systems to link ecological patterns and mechanisms across multiple scales, is clearly an efficient strategy for quantifying and clarifying pattern–process linkages in a complicated natural system. To date, hierarchical spatial scale has been addressed more explicitly in investigations of physical and chemical processes in streams (e.g., hydrology, sediment dynamics, nutrient pathways) than in biological research (Dietrich et al. 1982, Gomi et al. 2002, Benda et al. 2004). Here we briefly review selected research investigating population- and community-level patterns and processes across multiple spatial scales. Our goal is to highlight the insight gained from this multiscale approach, and the critical role that testable, mechanistic hypotheses play in its successful application. Few empirical studies have yet applied this multiscale approach to assessing the consequences and mechanisms of ecological processes occurring at the network scale (figure 1), but progress on this frontier is crucial for the management and conservation of stream systems and the resources they provide.

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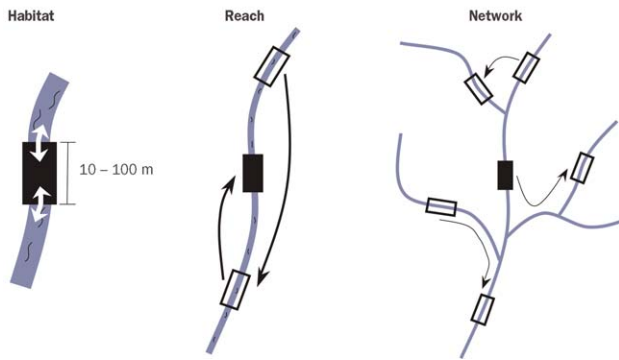
Figure 1. Diagram illustrating three hierarchical scales of organization in stream systems: the habitat, the reach, and the network. Arrows represent pathways of active or passive movement by individuals, biotic material (e.g., leaf litter, propagules, particulate organic material), or abiotic material (e.g., nutrients, sediment, pollutants) observable at each scale of organization.

Multiscale approaches to population biology in streams

Local population dynamics are driven by births, deaths, immigration, and emigration. The potential importance of movement to local population dynamics, particularly in open systems such as streams, requires the explicit consideration of spatial scale in population-level research. There is a growing body of direct, empirical data on the dispersal patterns of stream organisms (Skalski and Gilliam 2000, Lowe 2003, Macneale et al. 2005), existing theory supports the demographic importance of dispersal in streams (Speirs and Gurney 2001), and reach-scale studies have shown that immigration can contribute to local population persistence (Fonseca and Hart 2001). However, our understanding of population dynamics in streams is currently limited by a lack of information about whether a given patch of habitat is a source or sink for dispersing individuals, and about how sources and sinks are distributed within the larger reach.

Schlosser (1998) found that creek chub (*Semotilus atromaculatus*) moved upstream from in-channel beaver ponds into feeder streams. The density of age-0 chub in stream reaches was strongly related to the presence of downstream beaver ponds, suggesting that ponds were sources for colonization of the stream. Population persistence in streams depended on seasonal and flow-mediated restrictions on resources, and on density-dependent overwinter survival. By addressing specific, spatially explicit hypotheses on how population dynamics in local habitats are linked to movements at the reach scale, such studies offer a model for a multiscale approach to the investigation of stream populations.

Alligator (Kushlan and Kushlan 1980) and catfish (Glodek 1978) burrows may also serve as refuges and sources for repopulation of aquatic habitat after drought. In a shallow (maximum depth of 10 centimeters), warm, drying stream pool in western Ecuador, only one poeciliid species occurred. However, Glodek (1978) recovered 192 individuals in 8 families, 12 genera, and 13 species from a catfish burrow that extended least 1 meter (m) below the streambed. Survival of prey species in this dry-season refuge was enhanced because hypoxia caused predators to cease feeding to conserve oxygen.

The persistence of *Poecilia gillii* along a steep-gradient, intermittent stream reach in Costa Rica depended on the availability of hydrologically stable pools and the ability of fish to detect and disperse into these pools during floods (Chapman and Kramer 1991). In an intermittent Colorado stream reach, a nonnative predator (northern pike, *Esox lucius*) reduced dispersal among pools by the endangered Arkansas darter (*Etheostoma cragini*) and survival of darters within pools (Labbe and Fausch 2000). To persist, darters required specific hydroperiod and temperature regimes in pool refugia, as well as flow variation among seasons and years that regulated pool connectivity and restricted movements of the pike.

Power (1984) studied the distribution, grazing and social behavior, growth, and survivorship of 1308 individually marked armored (loricariid) catfish in 16 pools distributed over a 3-kilometer reach in central Panama. Movements of marked individuals out of home pools were detected only infrequently. Nevertheless, the algae-grazing catfish tracked light-driven variation among pools in algal productivity so closely that their reach-scale population closely approximated an ideal free distribution (Fretwell and Lucas 1972) in which the growth and survival of prereproductive individuals were similar in dark (uncrowded), half-shaded, and sunlit (crowded) pools. Dispersal did occur within several months of disturbance events that formed new pools (during scouring floods) or changed the productivity or grazeable surface areas in others. The initial colonists of new or improved pools were smaller individuals that were less at risk while crossing shallow riffle habitats between pools (Oksanen et al. 1995). Therefore, a combination of dispersal and compensatory growth could account for the close tracking of pool-to-pool algal productivity by the loricariids over three years of observation.

These studies and others that link local demographic processes with spatial processes provide insight into fundamental controls on the dynamics and persistence of populations in streams. By elucidating processes in specific, spatially defined units of habitat that recur throughout stream reaches (e.g., deeper pools and intervening shallow habitats), such studies allow the testing of more general hypotheses on the interaction of pattern (e.g., habitat distribution) and dynamics (e.g., survival, recruitment, dispersal) across spatial scales. Making this link should be a central goal of population-level research in streams.

Multiscale approaches to community ecology in streams

Many potential controls on species interactions and community composition in streams operate across a range of spatial scales. These controls include well-known longitudinal (downstream) gradients in abiotic and biotic conditions associated with downstream changes in channel morphology

and discharge (Leopold et al. 1964). In addition, human activities affect stream communities over a range of scales. We focus on studies that have tested scale-explicit, a priori hypotheses to elucidate the mechanisms underlying community-level consequences of both longitudinal gradients and human activities.

Two salmonid fishes, *Salvelinus malma* and *Salvelinus leucomaenis,* have largely nonoverlapping longitudinal distributions in streams on Hokkaido Island, Japan, with *S. malma* occurring in upper reaches and *S. leucomaenis* occurring in the lower reaches. In laboratory experiments, Taniguchi and Nakano (2000) found evidence for temperature-mediated competition, with *S. leucomaenis* aggressively dominating *S. malma* at higher temperatures typical of downstream reaches, but *S. malma* growing more rapidly at lower temperatures typical of upstream reaches. Demographic processes regulated by differences between these species in behavioral and physiological responses to temperature therefore accounted for the longitudinal patterns of species distributions over larger scales.

In many river drainages, fish are excluded from the upper reaches of stream networks by dispersal barriers such as waterfalls or organic debris dams. Storfer and Sih (1998) found that the drift of salamanders (*Ambystoma barbouri*) from upstream, fishless reaches and the resulting gene flow prevented the evolution of effective antipredator behavior in salamanders occupying downstream reaches with predatory fish. They linked the outcome of salamander–fish interactions in stream reaches to the position of the reach within the larger stream continuum.

Human-built dams affect streams in both upstream and downstream directions. Of these impacts, changes in the discharge regime lead to especially widespread habitat alteration. By reducing the frequency of bed-scouring floods in rivers of northern California, dams or diversions favored later successional predator-resistant (armored or sessile) grazing insects, while early successional, more susceptible (soft-bodied, mobile) species dominated invertebrate assemblages in unregulated reaches subject to more frequent disturbance (Power 1992). The artificial stabilization of discharge diverted energy from longer, predator-supporting chains in food webs to shorter chains capped by invulnerable primary consumers.

Human activities have also spread invasive nonnative species in rivers. Zebra mussels (*Dreissena polymorpha*) first appeared in the Hudson River, New York, in 1991, and the population grew and spread rapidly in the following 17 months (Strayer et al. 1999). Invading zebra mussels filtered out small phytoplankton, increasing light and nutrients for the primary producers not eaten by the mussels (e.g., inedible phytoplankton, submersed macrophytes, attached algae). Following zebra mussel invasion, macrophytes and attached algae proliferated in the shallow reach margins, increasing food and shelter for benthic animals in these areas, including the zebra mussels themselves. The larger-scale effect of zebra mussel invasion was a diversion of resources from the pelagic zone and deep-water sediments to the vegetated shallows and associated zebra mussel beds.

A study by Meffe (1984) links community dynamics at multiple scales both to species invasions and to longitudinal gradients in streams. Meffe investigated mechanisms for the coexistence of the native Sonoran topminnow (*Poeciliopsis occidentalis*) and the introduced mosquitofish (*Gambusia affinis*) in Arizona streams. Mosquitofish extirpated the topminnow rapidly in lowland streams that rarely flood, but the two species coexisted in upland streams prone to flash floods. Meffe (1984) combined preflood and postflood population surveys with behavioral studies in the laboratory under simulated flood conditions. He found that the topminnow had innate behaviors (e.g., a tendency to seek lateral shelter as levels of discharge rose) that allowed it to persist under flash flood conditions. The mosquitofish lacked this flood-adapted behavior. Flood-mediated outcomes of behavioral differences between the two species produced larger-scale, longitudinal patterns in community composition.

By connecting experimental and molecular data to large-scale variability in community composition, these studies expand mechanistic understanding of spatial controls on community ecology in streams. They also address the broader importance of environmental gradients and gene flow in regulating the outcome of interspecific interactions and the resulting distributions of strongly interacting species (Case and Taper 2000).

Multiscale approaches to species–ecosystem linkages in streams

Progress made at the Hubbard Brook Experimental Forest and other long-term research sites (e.g., H. J. Andrews Experimental Forest, Coweeta Hydrologic Laboratory, Bonanza Creek) toward linking research on stream biogeochemistry across scales also creates an opportunity to extend multiscale understanding across the species–ecosystem divide. An overarching question in this area of investigation is how the distributions and dynamics of nutrients (e.g., carbon, nitrogen, phosphorus) are influenced by local populations and communities of stream organisms. Current research at the Hubbard Brook Experimental Forest is investigating whether populations of stream organisms recovering from the extensive timber harvesting that occurred throughout New England at the start of the last century may serve as nitrogen sinks in headwater streams, contributing to long-term declines in nitrate export observed in watersheds of the northeastern United States (Goodale et al. 2003, Bernhardt et al. 2005).

In addition to regulating nutrient fluxes, mobile stream organisms—including stream invertebrates, amphibians, and fish—redistribute nutrients in streams, resulting in nutrient hotspots and elevational trends along reaches (Likens and Buso 2006). On the basis of direct measurements of fish migration, total watershed metabolism, and phosphorus flux into and out of the watershed, Hall (1972) concluded that upstream-migrating fish were important in maintaining phosphorus reserves in the upper reaches of New Hope Creek, North

Carolina. Isotope analyses of primary producers, macroinvertebrates, and fish in the South Fork Eel River, California, indicated that algae in shallow pools were a major source of carbon for steelhead trout (*Oncorhynchus mykiss*) during the summer (Finlay et al. 2002). Even fish collected in riffles and much deeper pools had isotopic signatures derived from shallow-pool, algal carbon, indicating that either the fish or their invertebrate prey moved among these habitats.

Aerial and terrestrial consumers that forage or scavenge on river biota (e.g., bats, bears, eagles) also redistribute river-derived nutrients, sometimes far upslope of traditional riparian zones (Spencer et al. 1991, Rainey et al. 1992, Ben-David et al. 1998). Likewise, our studies conducted with Brian T. Greene have shown that stream-associated amphibians can make nightly migrations of up to 15 m from the stream to forage for terrestrial prey, and interstitial metazoans move between the stream channel and groundwaters that extend far into terrestrial habitat (Ward et al. 1998). These observations reinforce earlier findings concerning the interconnectedness of stream and terrestrial food webs and associated nutrient cycles (Likens and Bormann 1974, Wallace et al. 1997, Nakano and Murakami 2001, Power et al. 2004, Baxter et al. 2005), and add an explicit spatial dimension to this interconnection. Specifically, these studies lead to the broader question of how movement patterns of specific organisms mediate the scale at which nutrients and energy are exchanged between stream and terrestrial habitats. Ideally, quantifying stream–terrestrial linkages will lead to studies of what regulates the movements of key organisms and the resulting scale of exchange between terrestrial and stream habitats. A major contribution of this work would be to provide information on the scale and types of land protection needed to maintain these movements and the associated pathways of nutrient and energy exchange (Iwata et al. 2002).

Scaling up to the stream network

At the landscape scale, stream systems exhibit a fractal network structure, in which smaller, lower-order reaches join to form larger, higher-order reaches in a pattern similar to the branching of a tree (Strahler 1964, Benda et al. 2004). How do network patterns (e.g., highly branched networks or simpler "fishbone" patterns) and the spatial configuration of habitats within the network affect fluxes of individuals and materials? Network structure may affect populations and communities of stream organisms by influencing (a) the movement of individuals among hydrologically independent reaches (Lowe and Bolger 2002), (b) the concentrative transfer of physicochemical fluxes (heat, sediment, solutes) from upstream to downstream reaches (Dietrich et al. 1982, Gomi et al. 2002), and (c) the dispersive transfer of these fluxes from downstream to upstream sites in networks (Pringle 1997).

Several studies address potential implications of the network structure for populations and communities in streams. Using metapopulation modeling, Fagan (2002) found that fragmentation in stream networks is likely to have

more severe effects on fragment size than in linear or two-dimensional systems, producing smaller fragments and higher variance in fragment size. He also concluded that stream networks are prone to mismatches between the scales of dispersal and disturbance, and that these mismatches can strongly influence population persistence. For example, populations that are far apart as measured by stream distance, and therefore unlikely to be linked by demographically important rates of dispersal, may be close in terms of overland distance, and therefore likely to be affected by the same disturbance.

A modeling study of the headwater stream salamander *Gyrinophilus porphyriticus* underscores the vulnerability of headwater specialist taxa in human-impacted stream networks, the importance of identifying and protecting source populations and dispersal routes, and the strong positive effect that habitat rehabilitation can have on population resilience when recolonization from undisturbed sites in the network is possible (Lowe 2002). In an empirical study of the same species, it was shown that although *G. porphyriticus* is negatively affected by logging-associated sedimentation in headwater streams, the presence of a confluent occupied stream that serves as a source of immigrants can mitigate this effect (figure 2; Lowe and Bolger 2002). In addition, mark–recapture modeling has shown that dispersal along the stream corridor can stabilize local population dynamics in this species (Lowe 2003), and population genetic data indicate that dispersal occurs primarily along stream corridors, rather than by overland movement between streams (Lowe et al. 2006). Overall, these studies suggest that by understanding how species move within stream networks and capitalizing on the connectivity of these networks, it is possible to manage the spatial pattern of logging and other human activities to increase the resiliency of stream biota.

Power and Dietrich (2002) discussed potential mechanisms by which the network structure may affect stream food webs, including the juxtaposition of contrasting habitat types at confluence nodes; the locally elevated delivery of sediments, nutrients, water, organic matter, or organisms to these sites; and the downstream concentrative versus upstream dispersive consequence of movements of materials or organisms through the network. They hypothesized that although diversity and biomass densities tend to increase downstream, organisms in headwaters may have stronger impacts (per unit biomass) on energy flow and on interspecific interactions, due to smaller habitat volumes; longer individual residence times; slower biomass turnover; and the higher probability that the species may, by chance, be released from competitors, predators, or parasites.

Features of local populations and communities have been related to attributes of stream networks (Dunham and Rieman 1999, Rice et al. 2001, Fernandes et al. 2004), and conceptual and analytical tools for describing and predicting network patterns are becoming more widely available (Pringle 1997, Fausch et al. 2002, Benda et al. 2004, Ganio et al. 2005). Data revealing the specific mechanisms that underlie "network effects" on stream ecology, however, are very rare. Studies by
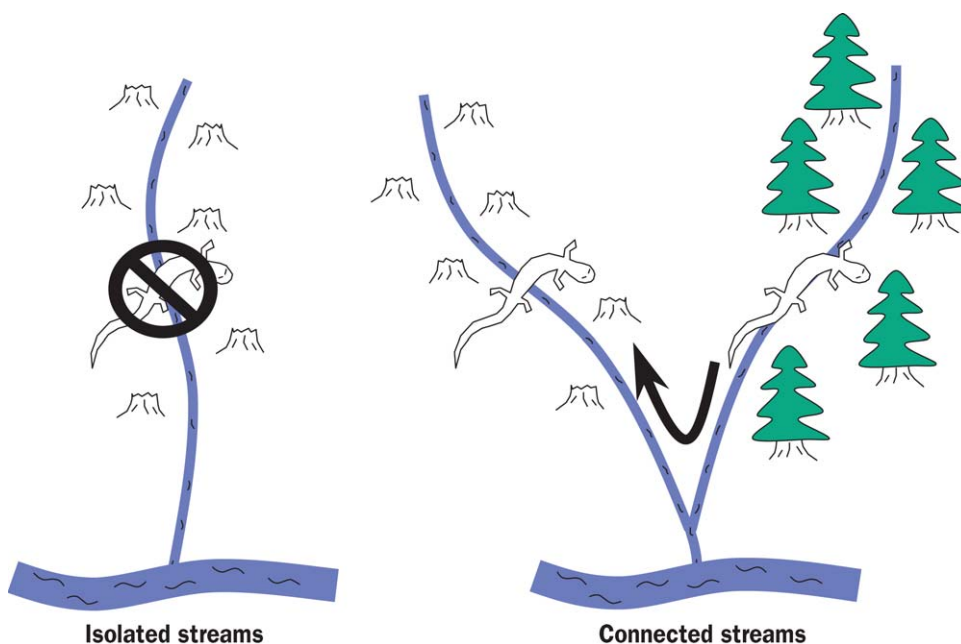
Figure 2. Diagram illustrating the relative effects of logging-associated sedimentation on the salamander Gyrinophilus **porphyriticus** *in headwater streams exhibiting different levels of connectivity within the larger stream network. Isolated streams flow directly into larger streams that are unoccupied by* G. porphyriticus. *Connected streams join other headwater streams occupied by* G. porphyriticus *before flowing into larger streams.*

Fraser and Gilliam (Fraser et al. 2001, Gilliam and Fraser 2001) have shown that in a stream network in Trinidad, a strong piscivore in the main stem of the river fragments populations of prey fish in tributaries. One prey species, *Rivulus hartii,* moved more rapidly through predator-occupied zones than through areas where the predator was excluded (Gilliam and Fraser 2001). Intrapopulation variability in movement behavior mediates both the rate at which individual fish move through predator-occupied reaches and the fitness of those fish that successfully disperse through these zones (Fraser et al. 2001).

In reach- and network-scale surveys of the Eel River in California, Harvey and colleagues (2004) found that the downstream limit of nonindigenous speckled dace (*Rhinichthys osculus*) corresponded to the upstream limits of predators including sculpins (*Cottus aleuticus* and *Cottus asper*) and the nonindigenous Sacramento pikeminnow (*Ptychocheilus grandis*). Pikeminnows occupy the water column, while native sculpins occupy benthic habitat. In laboratory streams, sculpins and pikeminnows together caused greater mortality of speckled dace than was predicted on the basis of their separate impacts, probably because of their complementary hunting habitats. Illustrating a priority effect on ecological invasion (i.e., the order of species' arrival determines the extent of invasion), pikeminnows with native predators appear to have limited the invasion of the speckled dace at the network scale by preventing its dispersal through main stems to basins in the upper Eel River drainage.

Stream ecologists are starting to link individual behavior to population and community ecology, and thereby helping to explain the distribution and abundance of species at scales ranging from local habitats to entire stream networks. Clearly, more empirical examination is needed of network-scale processes that affect the resiliency of stream biota following disturbance. The potential for recolonization from undisturbed sites can be a strong determinant of population resilience (Brown and Kodric-Brown 1977). Past studies document local effects of disturbance and recolonization dynamics on populations of stream organisms (Fonseca and Hart 2001), but do not explicitly relate these findings to the location of source populations. Because disturbances such as floods or pollution pass down streams, undisturbed sources are most likely to be located in adjacent, unaffected tributaries, requiring that colonizers move among branches within the network (figure 2). Documenting the pathways along which network-scale dispersal takes place (e.g., overland movement or movement along stream corridors) may, therefore, be critical to maintaining recolonization potential (Lowe et al. 2006).

A second question that needs more empirical examination is how network-scale processes affect stream community dynamics, and therefore spatial patterns of species diversity. Analyses of species diversity patterns in streams have been largely restricted to longitudinal reach scales (Horwitz 1978). Theoretical and experimental studies have shown that habitat complexity and the potential for dispersal among habitat

patches tend to stabilize interspecific interactions, increasing the likelihood of species persistence and leading to higher overall levels of species diversity (Huffaker 1958). Cuddington and Yodzis (2002) examined this relationship in simulated fractal environments resembling stream networks. In their models, the complexity of the environment, represented by the fractal dimension, was negatively related to interspecific interaction rates. This relationship resulted from the combined effects of individual mobility and spatial architecture on interaction rates, and tended to reduce fluctuations in population densities and to increase persistence of both predator and prey species in more complex environments. These findings lead to the prediction that the complexity of stream networks (i.e., the number of confluences or nodes) may be positively related to the stability of interspecific interactions within those networks, and to overall species diversity. A recent study showing that the diversity of electric fishes in the main stem of the Amazon River is enhanced by the presence of tributaries provides preliminary support for this prediction (Fernandes et al. 2004). In addition to effects on local aquatic conditions, these tributaries add network-scale complexity (e.g., refuges) to main-stem sites.

Applying multiscale research to conservation and management in streams

Broader use of multiscale approaches to explore population and community dynamics and species–ecosystem linkages in streams will produce research results that are applicable to management and conservation challenges, which typically extend beyond local habitats to entire watersheds. Better understanding of ecological scaling in stream systems should also lead to efficient strategies for management by revealing "keystone sites" where localized actions (e.g., removing or adding a culvert, restoring local marsh habitat) will have large-scale benefits, or, alternatively, where local impacts will have widespread consequences. This multiscale approach can inform both the design of stream-based ecological reserves and strategies to protect downstream resources (Saunders et al. 2002). Functional ecological reserves can be designed only when the spatial population structure and dispersal patterns of key resident species are understood. To estimate the minimum area required to prevent local extinction, scientists and managers need to know the spatial requirements of populations through all life history stages. Maintaining population connectivity enhances ecological resilience by increasing the likelihood of recolonization if local extinctions occur. The issue of spatial scaling is of central importance in both of these areas of investigation.

Multiscale research is also crucial for the protection of water quality, fisheries, and other resources that humans draw from freshwater systems. Regardless of where in the freshwater continuum they are exploited (i.e., streams, rivers, lakes, wetlands), these resources depend on integrated upstream networks of flowing water. Recent US Supreme Court hearings on the scope of the Clean Water Act (33 USC, chapter 26) underscore the great regulatory challenge that this con- tinuity poses. Protecting all upstream sources of the water in US wetlands, rivers, and lakes is not possible, but imagining that we can continue to benefit from the myriad services of freshwater ecosystems while disregarding their dependence on upstream tributaries is equally unreasonable. Empirical understanding of the effects of cumulative upstream impacts is critical to determining the levels of protection that must be applied to source areas to sustain freshwater resources. Policymakers and managers are charged with protecting freshwater resources for present and future generations. Given the expanding human footprint on the landscape, they will rely on scale-conscious research that reveals how degraded and undegraded reaches interact to affect downstream and upstream resources, and that identifies thresholds in the intensity, spatial extent, and distribution of watershed impacts beyond which resource degradation is likely.

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