

Landscapes to Riverscapes: Bridging the Gap between Research and Conservation of Stream Fishes

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Rivers and streams, by their very nature long ribbons of aquatic habitat, are inherently difficult to study. Approaching the banks of a flowing-water (lotic) system, one can see only a short fragment of the entire stream, from one bend to another, and can gain little appreciation for important features that lie beyond view. Moreover, materials transported downstream by the flow, and organisms traveling up or down the hydraulic highway, are soon gone from the reach and the opportunity to study them is often lost. Lakes present their own challenges for study, but by contrast to streams, one can usually see large expanses from shore that encompass all major habitats needed for aquatic organisms to complete their life history, such as gravel shoals, beds of aquatic vegetation, and open water habitats. Much of our knowledge of the ecology of rivers and streams is based on observations and experiments on organisms and habitat in the short fragments we can view or quickly traverse on foot, and this limited understanding underpins our efforts at conservation of stream fishes. Here, we argue that this understanding is incomplete, like viewing only disjunct parts of a landscape painting through small holes in a curtain draping it. We propose that a continuous view of rivers is essential for effective research and conservation of their fishes and other aquatic biota—a view not just of disjunct reaches but of the entire spatially heterogeneous scene of the river environment, the *riverscape*, unfolding through time.

One symptom of our incomplete understanding is the alarming rate of decline over the last 50 years of fishes that inhabit rivers and streams of North America. The public is aware that salmon are disappearing from the Pacific Northwest, with about a quarter of the 214 stocks of anadromous salmon and trout imperiled a decade ago (Nehlsen et al. 1991). Even little-known small fishes native to Great Plains and southwestern desert streams have suffered drastic declines

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(Minckley and Douglas 1991, Fausch and Bestgen 1997), and many are now either protected by federal or state listing as endangered or threatened species or are being considered for such protection. North America harbored the greatest diversity worldwide of temperate freshwater fishes (Warren and Burr 1994), crayfishes (Taylor et al. 1996), and mussels (Williams et al. 1993), but about 30% to 75% of the taxa in each group are at increased risk of extinction (i.e., categorized as rare, threatened, or endangered species). Fishes are also the most imperiled vertebrates worldwide (Allan and Flecker 1993, Leidy and Moyle 1998) and a large proportion spend at least part of their lives in streams.

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Fisheries ecologists have attempted to aid managers charged with conserving stream fish populations and assemblages by conducting research, primarily at small spatial scales. Typical studies have consisted of observations or experiments on a sample of 50 to 500 meter (m) reaches, often widely spaced along stream courses or among watersheds in a logical statistical design (e.g., stratified random). After 2 to 4 years of study the scientists draw inferences from their sample to the larger population of such sites about relationships between stream fish and their habitat and provide the information to managers in hopes of enhancing the flagging populations. However, fisheries managers often do not find this new information very useful for ameliorating the large-scale, human-caused disturbances that they are asked to address (Wiens et al. forthcoming), and in the end stream fishes continue to decline.

Although our failure as a society to conserve stream fishes is tied to complex economic, cultural, and philosophical issues (Lackey 1999), we contend that there is also a fundamental problem plaguing the scientific basis for much stream fish conservation biology and management. Simply put, researchers have often answered questions that are relevant over small spatial and short temporal scales, but these may be only weakly linked to the problems at larger spatial and longer temporal scales that managers must address (figure 1). As a result, fisheries ecologists have been largely ineffective at providing

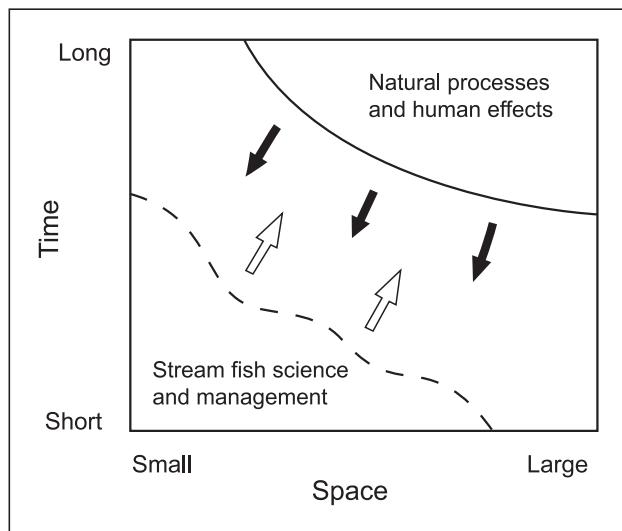


Figure 1. The gap in spatial and temporal scales between the scientific understanding and management of lotic fishes and the natural processes and human disturbances that affect the creation and maintenance of suitable habitat. The black arrows indicate that large-scale natural and anthropogenic effects interact in a hierarchical fashion with processes operating at smaller scales to influence habitat for declining stream fishes. The white arrows point toward the intermediate spatial and temporal scales at which stream fishes complete their life history, and at which fisheries ecologists and managers must begin working to effectively conserve them.

managers with information and tools at the scales needed to conserve stream fish populations and communities, and we believe that this gap in information has contributed to their continued demise.

Meanwhile, in the broad discipline of ecology, research in landscape ecology and metapopulation biology has advanced rapidly during the last decade (Hanski 1999, Klopatek and Gardner 1999), placing a new emphasis on the importance of habitat heterogeneity and providing new theory and methods for conservation biologists to apply to problems at larger spatial and temporal scales. Drawing on these new subdisciplines, Isaac Schlosser and his colleagues (Schlosser 1991, 1995a, 1995b, Schlosser and Angermeier 1995) pioneered a new paradigm in stream fish ecology—a dynamic landscape model of stream fish life history. In this model, fish movement plays a pivotal role in transporting different life stages across landscape scales to occupy patches of critical habitat required to fulfill their life cycle. The model provides a conceptual advance potentially important to managers, because it links important physical and biotic processes in streams and their riparian zones at scales relevant to human perturbations of watersheds (Schlosser 1991).

In this article we draw together threads of recent theoretical and empirical results to argue for studying and managing lotic fishes and their habitats in the context of riverscapes (a term coined by Ward 1998 for riverine landscapes). We first explore the interface between landscape ecology and stream ecology and incorporate it with ideas from Schlosser (1991, 1995a) to propose a new approach for stream fish ecology that explicitly embraces the continuous, hierarchical, and heterogeneous nature of these linear aquatic habitats. Second, we consider what new empirical data support this view, focusing on the heterogeneous nature of stream habitat at intermediate spatial and temporal scales and the role of fish movement in linking the habitat patches together through time. We then use these ideas to advance five principles for more effective research and conservation of stream fishes. We conclude by identifying emerging challenges in stream fish management that will require integrating information across scales using the riverscape approach that we advocate.

Landscapes to riverscapes: The advent of a landscape ecology for stream fishes

Landscape ecology provides a perspective for integrating ecological processes and spatial complexity. The general theory in landscape ecology holds that heterogeneous spatial patterns matter, because they set the context for ecological processes such as fluxes of organisms, materials, and energy among landscape elements (Pickett and Cadenasso 1995, Wiens 1999). Studies of distribution and abundance of organisms have a long history in ecology, because the patterns are presumed to suggest underlying mechanisms at the scale studied, but only recently have researchers specifically addressed the reciprocal effects of spatial pattern on ecological processes at landscape scales (Turner 1989). A landscape approach is particularly important in natural resource

management because humans alter landscapes at multiple scales, so ecological consequences must also be identified and predicted at these scales (figure 1; Risser 1999, Wiens et al. forthcoming).

Three key concepts in terrestrial landscape ecology about the effects of pattern and scale are also particularly applicable in aquatic ecosystems. First, the interplay between the finest spatial or temporal resolution studied (grain) and the size of the entire study area or study duration (extent) dictates the scale of processes that can be understood (Wiens 1989). Second, spatial heterogeneity and patchiness are scale dependent, and the response of organisms to patches also depends on the scale at which they perceive differences in habitat structure (Kotliar and Wiens 1990). Third, many important ecological processes operate primarily at landscape scales (Dunning et al. 1992, Taylor et al. 1993). These include movement of organisms among habitats to complement nonsubstitutable resources or supplement substitutable resources (termed habitat complementation and supplementation); colonization from source areas to “sink” habitats that cannot support reproduction (source–sink dynamics); connections among habitat patches that allow animal movements (connectivity); and boundaries of habitat patches that facilitate or limit animal movements (neighborhood effects). All three concepts are keys to understanding the importance of spatial heterogeneity to populations and communities at larger scales in aquatic systems as well as terrestrial ones.

Landscape perspectives and the canon of stream ecology. Ideas from landscape ecology have begun to influence theory in stream ecology, though many are not entirely new to the discipline. Ecologists have long recognized that streams are strongly influenced by the landscapes through which they flow (e.g., Cummins 1974, Hynes 1975). For example, the “river continuum concept” (RCC; Vannote et al. 1980), arguably the most important conceptual tool developed by stream ecologists to date, explicitly identified the role of organic matter contributions from the surrounding landscape to instream ecosystem structure and function. However, although the RCC provided a clear conceptual model, it included no real visualization of the river itself as a “landscape.” Rather, much of the heterogeneity in stream systems was thought of as “noise” around a simple underlying theme—that physical and biological attributes of streams change predictably from source to mouth. This view fostered an approach to studying streams and their biota based on sampling discrete points along the continuum and extrapolating between them.

During the past two decades, the RCC has proven a valuable heuristic foil, providing a conceptual framework from which researchers could investigate river ecosystems and propose amendments to the theory or complementary concepts. For example, Ward and Stanford’s (1983) “serial discontinuity concept” described departures from RCC predictions expected in rivers regulated by dams, whereas the “flood pulse concept” (Junk et al. 1989) and ecosystem views of riparian zones (Gregory et al. 1991) complemented the theory by

including variation in the lateral dimension onto the floodplain. Recognition of groundwater–surface water interactions led to the “hyporheic corridor” concept (Stanford and Ward 1993), which incorporated heterogeneity in both lateral and vertical dimensions. With each conceptual and empirical step, ecologists embraced more of the complexity of stream ecosystems across more dimensions (Ward 1989).

Some stream ecologists also began to use concepts from terrestrial landscape ecology in developing theories for lotic systems (e.g., Ward 1998, Ward et al. 1999). Frissell and others (1986) proposed a hierarchical framework that explicitly incorporated the role of scale and context, giving researchers a valuable lexicon and tool for organizing their thinking about heterogeneity in stream habitat. With the development of the “patch dynamics concept” of stream ecosystems (Pringle et al. 1988, Townsend 1989), heterogeneity that previously had been perceived as noise was recognized as important ecological information. However, although these ideas have influenced theory, relatively few have been incorporated into practice. For example, many researchers sought to measure patchiness by sampling at disparate points along streams without actually mapping the heterogeneity of the system. Others aimed for a “landscape perspective” or “landscape scale” by sampling more reaches over a larger spatial extent and relating attributes of their biota to basin-scale variables (cf. Allan et al. 1997, Wiley et al. 1997). Although many of these studies have provided important insights, we perceive a need to conceptualize rivers not as sampling points, lines, or gradients, but as spatially continuous longitudinal and lateral mosaics. As such, heterogeneity in the river landscape, or riverscape, becomes the focus of study (e.g., Malard et al. 2000, Wiens 2002).

A new model for stream fish ecology. Schlosser’s dynamic landscape model of stream fish population ecology and life history (Schlosser 1991) blended the new ideas from landscape ecology with those from stream and fish ecology, and comes closest to addressing the heterogeneity in riverscapes. What sets this model apart from others is the importance of the spatial arrangement of habitats for spawning, feeding and rearing, and refugia for different life stages, and the critical role of movement among them by fish to complete their life history (figure 2). Schlosser (1995a) linked the model to landscapes more explicitly by including the concepts of habitat complementation and supplementation, source–sink dynamics, and neighborhood effects (Dunning et al. 1992) and addressed how the spatial arrangement and connectivity of habitats that provide critical resources affect population vital rates. Schlosser and Angermeier (1995) extended the model by incorporating the hierarchical nature of lotic habitats, the role of key ecosystem processes that create and maintain the mixture of habitat patches needed, and the potential for stream fish populations to display metapopulation dynamics driven by movement among the patches. In recent years, Schlosser and his colleagues (Schlosser 1995b, 1998, Schlosser and Kallemyr 2000) have assembled

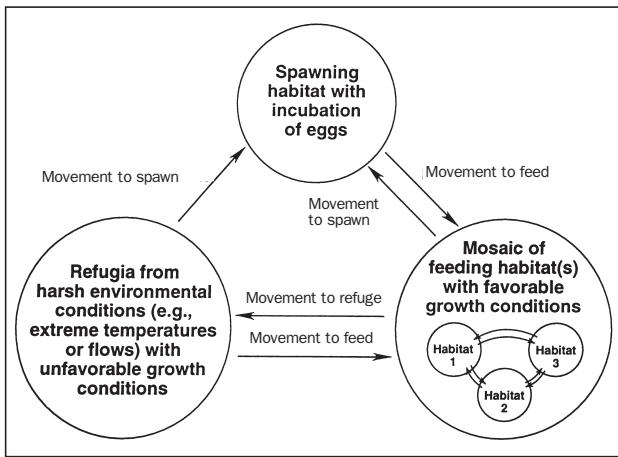


Figure 2. Schlosser's dynamic landscape model of stream fish life history. Movements of different life stages of fish among spatially separated habitats for spawning, feeding, and to find refugia are a key feature of this conceptual model. (From Schlosser and Angermeier 1995, with permission.)

empirical data to demonstrate the importance of several of these key elements and processes.

Schlosser's model provided an important conceptual breakthrough, but testing and applying it in real lotic systems will prove challenging. Overall, fisheries ecologists have not fully appreciated either the complexity of relationships between lotic habitat and the life histories of stream fishes or the implications of those relationships for conservation of stream fishes. Moreover, the traditional sampling schemes and methods used by stream fish ecologists are largely inadequate for gathering appropriate data because of the large scales involved, the hierarchical and heterogeneous nature of stream habitats, and the movement displayed by many stream fishes. Given this, we believe a new approach is needed that considers three important points.

First, our approach to streams and stream fishes will need to be spatially explicit and our data georeferenced (i.e., include map coordinates) if we want to solve real conservation problems. We reiterate Schlosser's (1995a, 1995b) view that the context in which stream habitat features are set will matter at many different scales (cf. Wiens 1999). Because habitats in streams are inherently heterogeneous, with different elements that are critical for stream fish life history often widely separated, knowledge of the spatial and temporal arrangement of these habitat patches will be essential for predicting population and community changes (Kareiva and Wennergren 1995, Moberg et al. 1997). How can we hope to address pressing issues in stream fish management if we abstract ecological patterns and processes from the context that gives them meaning in the first place?

Second, the gap we must bridge between research and conservation is at an *intermediate* scale in both space and time that we have missed, a scale at which many processes critical to populations and communities occur. Although stream ecologists have attempted to gather data at disjunct locations that span large spatial scales, their sampling units are most often at small spatial and temporal scales (e.g., stream reaches ≤ 200 m over periods ≤ 2 years), which are then placed in a framework at very large scales set by geopolitical boundaries ($> 10^5$ m) and evolutionary processes ($> 10^4$ years) (Angermeier et al. 2001). In contrast, populations and communities of stream fishes generally carry out important aspects of their entire life histories at intermediate spatial scales of approximately 1 to 100 km stream segments (figure 3) and respond to habitat changes that often occur at intermediate temporal scales on the order of 5 to 50 years (Reeves et al. 1995, Mantua et al. 1997). The crux of the problem is that these scales are the most difficult for biologists to appreciate, sample, and visualize. For example, standing on a stream bank usually reveals < 100 m of the continuous habitat, often only a fraction of that required for fish life cycles. Conversely, maps or satellite images show watershed scales where stream habitat is represented only as thin, one-dimensional channels that do not reveal features required by fish. It is at the scale intermediate to these, which humans must view by walking or low-altitude flight in an aircraft, that stream habitat features become most important to fish (figure 4).

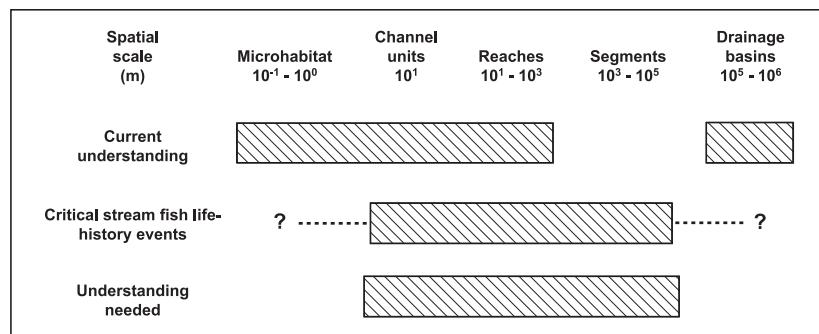


Figure 3. The spatial scales of our current understanding about lotic fishes, the probable range of scales spanned by critical life history events for many species, and the scales of understanding needed to adequately sample and predict attributes of fish populations and communities along riverscapes.

Third, our premises that context and an intermediate scale are important for understanding stream fishes and their habitat lead to a logical syllogism—we must take a top-down approach that is capable of integrating information from the bottom up (figure 5). Streams are hierarchical systems in which climate, geology, and topography at large scales set the context for geomorphic processes that create and maintain habitat at smaller scales (Allen and Starr 1982, Frissell et al. 1986, Montgomery 1999). At the same time, streams are linear systems in which unique habitats or disturbance events at specific locations or nodes can have profound effects that influence properties of the entire system at great distances in either direction. Therefore, the challenge for stream ecologists,



Figure 4. A riverscape perspective of the upper Middle Fork John Day River in northeastern Oregon. Stream habitat features most important to fish, such as channel morphology, habitat complexity, and barriers to fish movement, are best viewed at intermediate spatial scales by walking or low-altitude flight in an aircraft. Photograph by Christian Torgersen.

especially those who study fish, is to understand how these continuous, hierarchical, and heterogeneous habitats are arrayed in space and time and are linked by fish movement to influence the persistence, abundance, and productivity of fish populations and communities along the riverscape (Schlosser and Angermeier 1995). This will require more than just a large-scale definition of ecoregions or watersheds and point sampling of small stream reaches in many strata within them (cf. Angermeier et al. 2001).

Empirical data that support the riverscape approach

What empirical data support Schlosser's model and our view that a riverscape approach is needed in stream fish ecology? Two main research thrusts during the last decade are germane, one showing the patchy nature of stream habitat features at intermediate spatial scales and another demonstrating that stream fishes often move long distances to reach habitat patches required to complete their life history. We address each in turn, using examples from work by ourselves and others.

One body of recent research shows that stream habitat is heterogeneous at intermediate scales different from those traditionally sampled and that the context in which these patches are set has important consequences for stream fish life histories. For example, Baxter and Hauer (2000) reported that in relatively steep mountain tributaries of a Montana river, fall-spawning bull charr (*Salvelinus confluentus*; figure 6)

constructed redds (nests) in low-gradient bounded alluvial valley segments (BAVS), which occurred at long (approximately 5 to 10 km) intervals. Their multiscale study showed that BAVS had upwelling groundwater that created favorable thermal conditions for egg incubation during winter, and that at a finer scale within the segments, the fish chose sites with localized downwelling, presumably to ensure adequate oxygenation of eggs. A traditional sampling scheme that focused on shorter reaches chosen randomly throughout the basin, or only on those reaches where bull charr spawned, would never have revealed the larger-scale patterns of geomorphology that set the context for the smaller-scale patterns of local redd site selection. Such relatively uncommon features like BAVS would have appeared simply as unexplained variation.

In many cases, collecting continuous data at a coarser spatial resolution (grain) will be required to reveal patterns in habitat and fish distribution that suggest mechanisms of population regulation. For example, Torgersen et al. (1999) showed that distribution of spring-run chinook salmon (*Oncorhynchus tshawytscha*) in the North and Middle Forks of the John Day River, Oregon (figure 4), was related to large-scale patterns of stream temperature and pool frequency (figure 7), and that most spawners selected only a few favorable locations along the entire 50 to 70 km length of each river. These locations combined colder temperatures, a few degrees below the upper incipient lethal temperature for the salmon (about

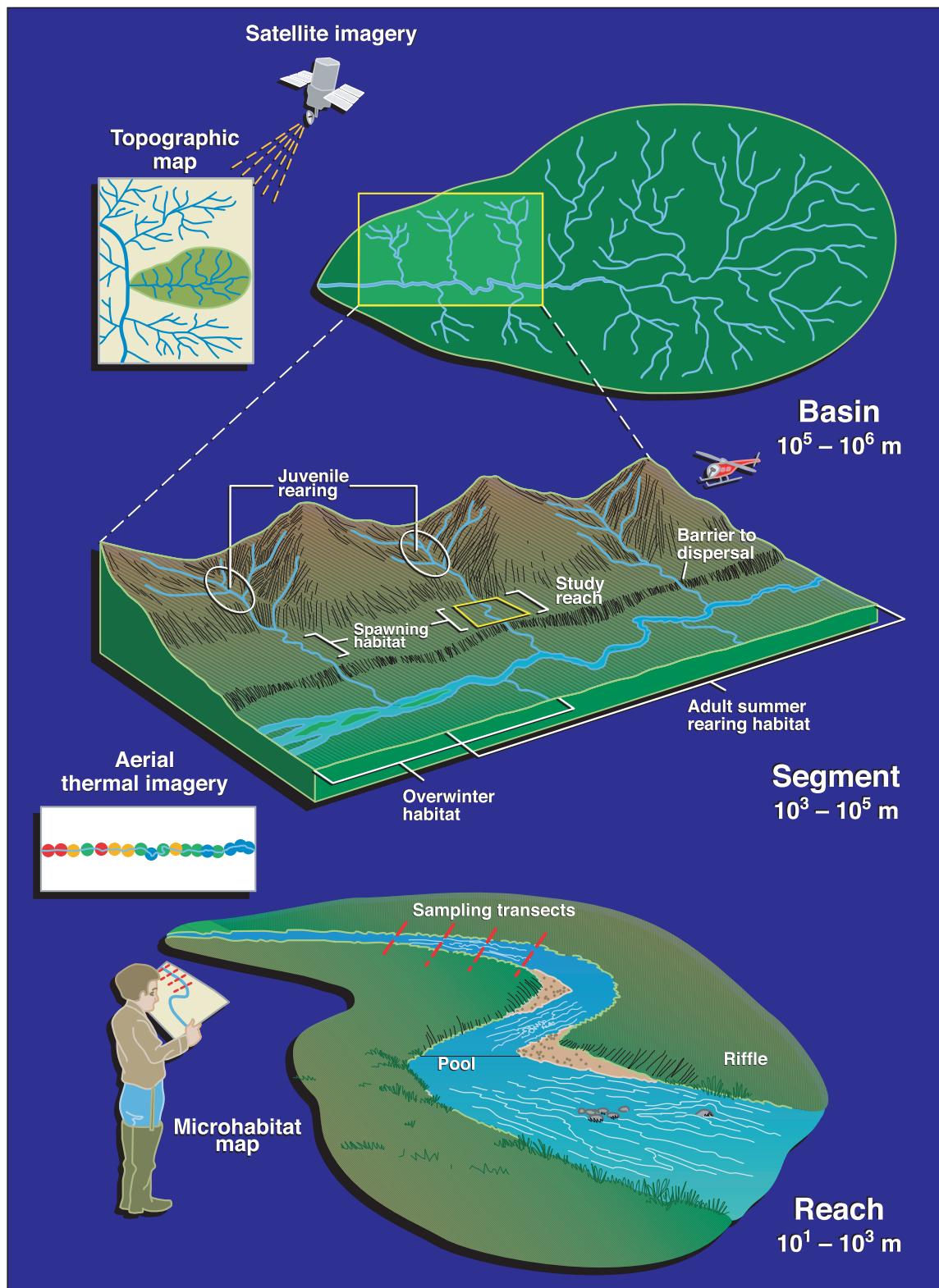


Figure 5. A diagram representing the multiscale approach needed for understanding fish and their habitat in riverscapes, which integrates information from reach scales into the context set by landscapes at basin scales—that is, a top-down approach from the bottom up. The nexus where information is lacking is at the intermediate segment scale, where there is a gap in conceptual models and technology. Although much technology is available for mapping habitats in study reaches and at basin scales, new approaches such as aerial thermal imagery are needed to make continuous surveys of habitat attributes at the intermediate scales over which many stream fishes carry out their life history.



Figure 6. A female bull charr on a redd in a northwestern Montana stream. Understanding the spawning habitat needs of bull charr requires knowledge of habitat heterogeneity at multiple scales, especially intermediate spatial scales different from those traditionally sampled. Species like bull charr use habitat patches distributed over long distances in the riverscape to complete their life history.

25°C), with abundant pools. Continuous data on stream temperature were measured using helicopter-mounted, forward-looking infrared (FLIR) videography (TorgerSEN et al. 2001). Spatially continuous data on fish abundance and pool frequency were gathered by extensive snorkeling and habitat surveys of every pool and riffle throughout each river. Again, random sampling designs, even those stratified a priori based on other geomorphic features, may well have missed these critical peaks in salmon abundance and the habitat and thermal features associated with them.

Heterogeneity of habitat patches, and the boundaries between them that constrain movement, can also occur in time and thereby influence extinction and recolonization. For example, Labbe and Fausch (2000) reported that habitat for a small fish, the Arkansas darter (*Etheostoma cragini*), ebbed seasonally in an intermittent Colorado plains stream, but was also dynamic at intermediate decadal time scales. Sets of pools and entire intervening reaches in a 15 km segment dried from spring through fall of two years, causing high mortality and severing connections among subpopulations (figure 8). Many of the remaining pools monitored during the intervening winter froze completely, extirpating darters from all but groundwater-fed refuge pools. Huge flash floods at 5- to 10-year intervals, driven by thunderstorms in scattered locations throughout the basin, dug new refuge pools and filled others, indicating that relatively long distance dispersal to

colonize the pools was necessary for darter populations to have persisted at the landscape scale. Overall, understanding the complex interactions between natural disturbances that create and destroy habitats and fish movement to colonize new habitats will be required to sustain viable populations of stream fishes (Reeves et al. 1995).

A second main body of research that supports the need for a riverscape approach has been on fish dispersal. Dispersal, more correctly termed ranging behavior (Dingle 1996), is the movement of organisms throughout their lifelong home range and is an important component of the theory of landscape ecology and metapopulation biology. Ranging behavior is the “glue” that links spatially subdivided populations together, allowing fish to colonize patches of newly created habitat and recolonize patches where they were extirpated by drying or other disturbance. The main characteristic is not undirected movement, as the term dispersal implies, but long-distance movement that ceases when patches with suitable resources are encountered (Dingle 1996).

One reason fish ecologists and managers previously focused efforts at small scales was that most members of resident (i.e., nonmigratory) stream fish populations were assumed to complete their life cycle in short stream reaches (e.g., < 100 m) (Gerking 1959, Gatz and Adams 1994). However, Gowan and others (1994) argued that the conclusion by many investigators of restricted movement was unwarranted, be-

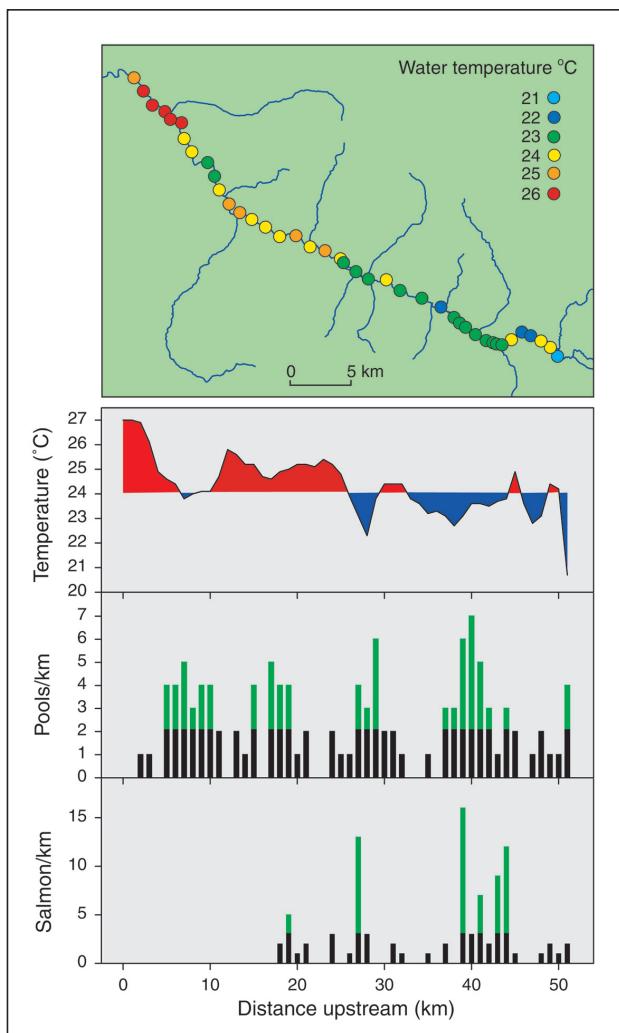


Figure 7. An example of continuous data on stream surface temperature (based on forward-looking infrared videography) and habitat (pool density from snorkeling surveys) related to chinook salmon distribution in the Middle Fork John Day River, Oregon. Red shading in the middle panel shows temperatures that exceeded the median for the segment, and green portions of bars in the lower panels show pool and fish densities that exceeded the means for the segment. (Modified from Torgersen et al. 1999, with permission.)

cause study reaches were too short to encompass the home ranges of most fish. Thus, even though in most studies the majority of fish *recaptured* were found in their “home” sections, the majority of fish originally marked were *never recaptured* (Fausch and Young 1995). This apparent paradox is explained by the leptokurtotic distribution (highly peaked with long tails) of stream fish movements (Skalski and Gilliam 2000). Typically, less than half of the fish marked are recaptured within the study reach (the central peak), apparently having made only short-distance movements, whereas the rest move to many different locations along the channel up to long distances away (the long tails), and thus are never recaptured. However,

because movement to any particular outlying location is a rare event, sampling short reaches outside the study reach typically produces few or no fish, falsely leading investigators to believe they had encompassed the home range of their species. Empirical data collected by more extensive mark–recapture methods (Skalski and Gilliam 2000), in some cases combined with fish weirs (Gowan and Fausch 1996b, Schmutz and Jungwirth 1999) and telemetry (Young 1994), have provided strong support in several systems for this new model of stream fish movement. Overall, these data show the heterogeneous nature of stream fish movement at intermediate spatial scales and indicate how difficult it will be to measure and predict.

Movement by stream fishes may also be highly variable in time, making it doubly difficult to study. Schlosser (1995b) showed that species abundances in a fish assemblage of a small Minnesota stream were unrelated to changes in local stream habitat and were instead driven by immigration of juvenile fishes from adjacent beaver ponds that were created and destroyed on a decadal time scale. Moreover, during four summers of trapping fish moving through a weir just downstream of a beaver pond, Schlosser (1995b) found that nearly all the movement of several fish species occurred in a single pulse during only a few days over the entire four summers! Strong temporal dynamics in stream fish movement also have been reported by others (e.g., Gowan and Fausch 1996b).

Despite the temptation to conclude that some fish are “movers” and others “stayers” (Grant and Noakes 1987, Hughes 2000), it is likely that ranging movements are most often a facultative response to resource abundance and distribution along the riverscape (Behnke 1992). For example, in some populations of rainbow trout (*O. mykiss*), anadromous life history types (i.e., steelhead) produce offspring that are residents, and resident fish produce anadromous offspring, although in other cases anadromy is apparently genetically fixed (Zimmerman and Reeves 2000). Among resident fishes we should also expect to find the full range of movement behaviors, serving to transfer life history stages across riverscapes to take advantage of spatially separated and temporally dynamic resources (Näslund et al. 1993).

The importance of movement in driving metapopulation dynamics is illustrated by recolonization of habitat patches where fish were extirpated by drying or flooding in arid-land streams of the Great Plains (Fausch and Bestgen 1997). Even small fishes may move long distances to repopulate rewetted habitats (Lohr and Fausch 1997) or those decimated by flash flooding (Fausch and Bramblett 1991). Moreover, an entire guild of Great Plains stream fishes spawn semibuoyant eggs that develop as they drift downstream (Platania and Altenbach 1998), ultimately requiring juveniles or adults to move back upstream tens of kilometers to maintain populations (Winston et al. 1991). Therefore, attempting to predict distribution or abundance of plains stream fishes by sampling habitat in only 100 m reaches will miss low barriers that prevent upstream movements of fishes with this unique life history strategy, as well as source

populations along the riverscape from which the drying sink habitats can be recolonized.

Toward principles for effective research and management of lotic fishes

Given the apparent need for a broader approach to stream fish ecology that considers responses of fish to habitat heterogeneity at multiple spatial and temporal scales, what can we offer to help fisheries ecologists generate more useful information for managers? Five principles appear most important to advance research (table 1).

First, research must be conducted at appropriate scales for the questions of interest (Wiens 1989). This will require that scientists maintain flexibility to think about and gather information at multiple scales, to identify those at which work should be focused. Matching study objectives to organism life history will often require continuous sampling at intermediate scales (figures 3, 5) where information is missing. Given that many fishes range farther than originally thought, systematic censuses of coarse-grain habitat features along entire lotic segments (e.g., figures 7, 8) are likely to be much more revealing of important factors influencing fish assemblages than detailed data at the wrong scale (see Fausch et al. 1988 for many examples). New technology for continuous sampling of streams at intermediate scales (e.g., FLIR videography for stream temperatures, side-scanning sonar for fish longitudinal distributions; Duncan and Kubecka 1996) and geographic information systems for visualizing the data at multiple scales will help, but “old” technology, such as walking or snorkeling entire segments, can be used to good advantage (e.g., Hankin and Reeves 1988, Torgersen et al. 1999, Harig and Fausch 2002). New, multiscale nested sampling designs are needed to surpass the limits imposed by spatial scale (Poizat and Pont 1996, Roth et al. 1996, Baxter and Hauer 2000, Labbe and Fausch 2000).

The need to measure habitat and stream fish at high resolution over large spatial and temporal scales may seem logically impossible. Addressing the tradeoff between gathering information at high spatial resolution and high temporal resolution requires developing complementary sampling approaches. For example, Torgersen (2002) combined spatially continuous temperature data using FLIR videography (Torgersen et al. 2001) with continuous monitoring using thermal data loggers at sites selected from the FLIR survey to detect patterns of temperature important to fishes in northeast Oregon streams. Similarly, Baxter (2002) used spatially extensive fish surveys in the same streams to select reaches for seasonal monitoring and subsequently used information on seasonal dynamics and movement to fine-tune the timing of the surveys.

We caution that taking a riverscape approach means more than increasing the spatial extent of study boundaries. Many researchers have developed models that predict the abundance of stream fishes in individual reaches from landscape characteristics. Including landscape structure in stream fish

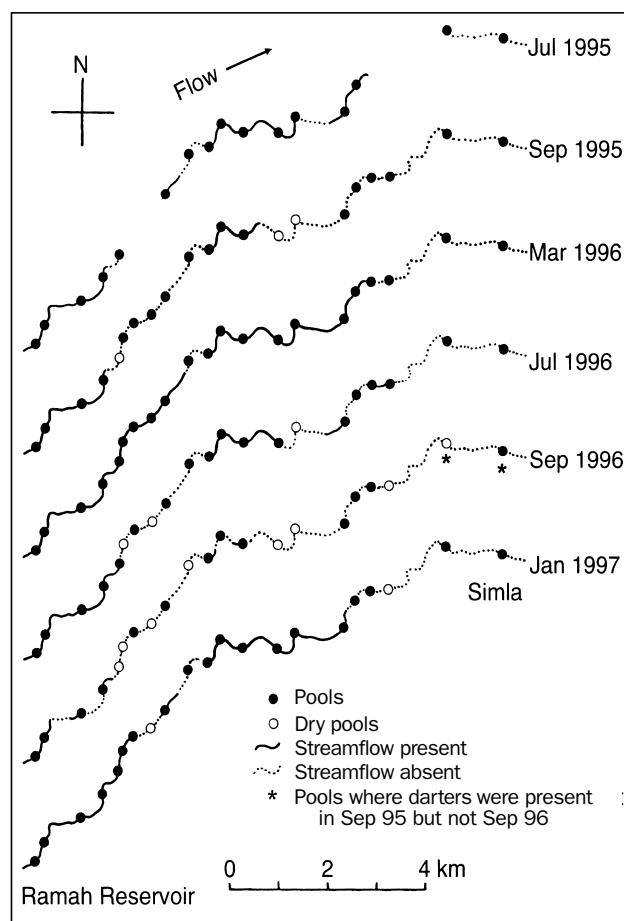


Figure 8. Temporal change in Great Plains stream habitat for Arkansas darter in a 14.6 km segment of Big Sandy Creek, Colorado. Symbols represent pools or sets of pools with similar fates. A barrier prevented upstream movement into the segment, indicating that the two pools farthest downstream where darters were extirpated during the dry 1996 summer were apparently recolonized periodically from source populations at least 2.5 to 3.3 km upstream. Gaps shown during July 1995 were not surveyed. (Modified from Labbe and Fausch 2000, with permission.)

studies represents a major improvement over reach-based approaches that consider only local habitat. However, studies based on multiple reaches distributed across segments or watersheds will most likely miss important variability in fish assemblages and habitat that occur between the sampling locations in a given stream (Torgersen et al. 1999) and assume that reach-level habitat relationships represent stream-level variability (Poizat and Pont 1996, Dunham and Vinyard 1997, Angermeier et al. 2001). Unfortunately, without coarse-grain continuous sampling, there is no way of knowing a priori which scales are relevant to questions of interest (cf. Addicott et al. 1987). Thus, predicting distributions of fishes in local reaches based on basin characteristics may be no more useful for evaluating multiscale relationships than relying solely on local habitat features.

A second principle is that the importance of different physical and ecological processes will be revealed at different spatiotemporal scales, and processes will interact among scales. For example, based on the research described above, Labbe and Fausch (2000) developed a conceptual model showing how physical and biotic processes interact with each other across four spatial scales from pools (0.1 km) to whole watersheds (100 km) to influence the persistence of Arkansas darters in a western Great Plains basin (figure 9). Localized summer thunderstorms at the segment scale caused floods that created refuge pools. Spring rains triggered darter reproduction across large scales, and increased groundwater levels which connected stream reaches and reduced summer drying and winter freezing of pools. The resulting flow connectivity allowed recolonization of rewetted habitats via dispersal from source (donor) populations, promoting persistence of a metapopulation at the landscape scale. Northern pike (*Esox lucius*), a nonnative predator that decimated darters in pools throughout an entire segment, also depended on refuge pools for persistence. Sophisticated management of declining stream fishes like this darter will require understanding the multiscale

processes that create and destroy habitat (Stanley et al. 1997, Montgomery 1999), and in turn set the context for fish reproduction, dispersal, and survival (Sedell et al. 1990, Montgomery et al. 1999, Baxter and Hauer 2000). It is clear that to provide useful information for managers, stream fish ecologists will need to embrace the complexity of these ecological systems at multiple scales, not force simplicity upon them (cf. Wiens 1999).

A third principle is that rare or unique features in the riverscape, either in space or time, can have overriding effects on stream fishes. For example, unique habitat features at critical nodes along the hierarchy of stream channels, such as barriers to dispersal and high-gradient reaches that hamper upstream movement (figure 5), are more important in linear habitats like streams than in lakes, because all fish moving along segments encounter them. Alluvial reaches with groundwater suitable for spawning (Baxter and Hauer 2000) and floodplains and beaver ponds that provide productive rearing environments (Naiman et al. 1986, Hartman and Brown 1987, Schmutz and Jungwirth 1999) create “hotspots” for fish recruitment that supply ad-

Table 1. Proposed riverscape principles for effective research and management of lotic fishes.

Principles	Premises	Recommendations for application
1. Choose appropriate scales—maintain flexibility to think and work at multiple scales	Reach-based, random sampling designs employed over large scales can miss unique habitat features important to the life cycles of stream fish Systematic sampling of coarse habitat attributes at appropriate scales is better than detailed data at the wrong scale Continuous censuses at intermediate spatial scales are needed to set the context for future sampling through time or at smaller scales	New sampling approaches are needed for censusing habitat and fish in rivers and streams at intermediate scales Multiscale, nested sampling designs will prove useful for expanding knowledge beyond limits imposed by spatial and temporal scales
2. Processes will interact across scales—embrace the ecological complexity of lotic systems rather than try to force simplicity upon them	The importance of different physical and ecological processes will be revealed at different scales Sophisticated management will require understanding the complexity of multiscale processes that create and destroy habitat and set the context for fish reproduction, dispersal, and survival	Avoid inappropriate sampling schemes that mask important complexity Use complementary sampling methods at multiple scales to assess spatial and temporal heterogeneity in habitat elements and fish distributions
3. Unique features can have overriding effects—discrete habitat features in space or rare events in time can have important effects on fishes in lotic systems	In linear, hierarchical systems like rivers, unique habitat elements (e.g., barriers to dispersal, beaver ponds) or disturbance or life-history events that are highly heterogeneous in space or time (e.g., floods, pulsed recruitment) will have strong effects on fish assemblages Rare, long-distance fish movement can drive colonization or recolonization of habitats and invasions of nonnative species	Collect spatially continuous data on habitat and fish distributions to ensure that critical elements in linear hierarchical lotic systems are measured Monitor habitat and fish populations at appropriate intervals to record important physical disturbances and life-history events Prevent constraints to fish movement (e.g., barriers) that may hamper colonization or recolonization
4. Unintended consequences of habitat degradation will occur in all directions, including upstream—anthropogenic disturbances may have strong effects at long distances from their source	Long-distance fish movements may intercept habitat disturbances and barriers that fragment habitat, even those far downstream from the center of fish distribution, resulting in unexplained population declines	Consider unintended consequences of habitat degradation and loss of connectivity on fish populations at long distances from the localized disturbance Measure ranging movements of fish at appropriate scales to estimate “ecological neighborhoods” in which degradation will have strong effects
5. Match observations and predictions to the scales at which managers effect change	Information useful to managers making decisions often will be at intermediate scales at which stream fish carry out critical life-history events	Consider changing the focus of research to larger scales and adopting sampling strategies that include continuous spatial censuses followed by long-term temporal sampling at strategic locations

adjacent reaches with colonists. For example, Schlosser (1995b, 1998) reported that beaver ponds created in a northern Minnesota stream harbored source populations of most minnow species and supplied juveniles that colonized sink habitats in adjacent stream reaches where most minnows never reproduced. Schlosser and Kallemyn (2000) found that species richness and abundance of fishes in tributaries to a very large lake were often related less to local stream habitat than to the proximity, direction, successional state, and landscape context of adjacent beaver pond habitats. These studies also highlight the importance of rare, long-distance, “jump dispersal” events that drive recolonization of suitable habitats far from source populations (e.g., Gowan and Fausch 1996a, Schlosser et al. 2000) and invasions by nonnative species (Kot et al. 1996, Lewis 1997).

Many unique spatial characteristics in streams are produced by rare events in time. For example, stand-replacing wildfires at 250- to 350-year intervals in Pacific Northwest coastal streams supply pulses of sediment and large woody debris to stream channels via debris flows that create a heterogeneous mosaic of habitat patches required by different species of anadromous salmonids (Reeves et al. 1995, Montgomery et al. 1999). These pulses cascade through systems in “propagation waves” (Montgomery and Buffington 1998), eliminating habitat in parts of systems and creating it in others as materials are gradually transported downstream. At smaller temporal scales, intermittent events that may be missed during routine sampling can have ecological effects that far exceed their proportional areal extent. For example, over a 4-year period 39% to 47% of all rainbow trout recruits in the Sagehen Creek, California, watershed were emigrants from a small ephemeral tributary that flowed only about 4 months each year (Erman and Hawthorne 1976). The fact that rare or unique features in riverscapes can be disproportionately important to stream fish emphasizes the need for judicious use of continuous sampling in space and time.

A fourth principle for effective research and management of fish in riverscapes is that unintended consequences of habitat degradation will occur in all directions, including upstream. Anthropogenic insults like sediment and water pollution may not only flow downstream to affect fishes and other aquatic biota, but disturbances to downstream habitats may also leave “legacies” of degradation because upstream biota move downstream to intercept them (Pringle 1997). This may cause unanticipated declines in fish populations at long distances from the source of the disturbance. For example, Meyers and others (1992) reported that brown trout (*Salmo trutta*) in a Wisconsin watershed moved downstream more than 16 km to overwinter in reaches that during summer were not even classified as trout habitat because they were too warm. If unwitting managers were to allow water quality or habitat to be degraded in these reaches below that tolerable to overwintering brown trout, populations far upstream from this location could be reduced for unknown reasons. Populations of plains stream

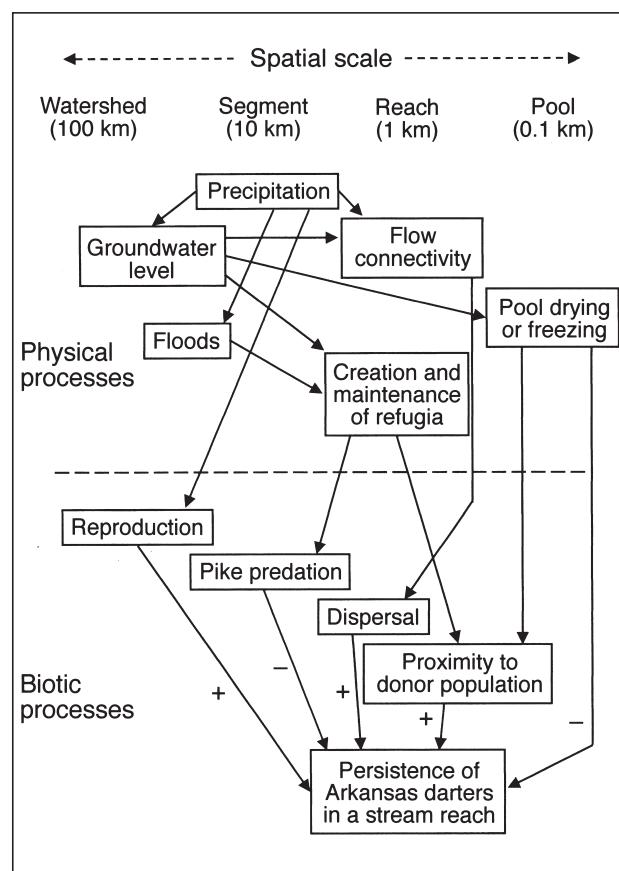


Figure 9. A conceptual model of physical processes that interact across multiple spatial scales to influence biotic processes and, ultimately, persistence of Arkansas darters in a western Great Plains basin. (From Labbe and Fausch 2000, with permission.)

minnows in the guild that spawns semibuoyant eggs are frequently reduced or extirpated from entire watersheds even by low barriers that fragment lotic habitat and prevent upstream recolonization by juveniles (Winston et al. 1991, Bestgen and Platania 1991). Pringle and others (2000) chronicled the extirpation of many obligate riverine fishes, and taxa that migrate within freshwater (i.e., potamodromous), by large dams in both the temperate and tropical New World. Only 10% of the 5500 large dams in the United States, and very few dams in the tropics, have facilities to pass fish both upstream and downstream, despite potamodromous taxa in every major basin. In European rivers like the Danube, annual passage of 35,000 to 100,000 fish have been recorded past hydropower stations, including all life stages of nearly every species, many of which were previously considered nonmigratory (Schmutz and Jungwirth 1999). Therefore, we argue that managers must become aware of potential unintended consequences of habitat degradation and loss of connectivity (Poiani et al. 2000) for lotic fish populations, which can be caused by fish movement from many different locations throughout the watershed to intercept these disturbances.

Finally, a fifth principle is that fisheries ecologists who study stream fishes must strive to make observations and test predictions at the scale at which managers effect change. We conclude that this nexus for theory and application is likely to be at an intermediate spatial and temporal scale over which these organisms carry out critical aspects of their life history (figures 1, 3, 5). For example, Torgersen and others (1999) reported striking differences in the distribution of water temperatures along the North Fork versus Middle Fork John Day Rivers in the mountains of eastern Oregon (cf. figures 4, 7). The patchy distributions of cold, cool, and warm water guilds of the fish assemblages in these basins were related to the heterogeneous patches of cold, cool, and warm temperatures, overlain on the general increase in water temperatures from source to mouth in each basin (Torgersen 2002). The two basins are under different land management regimes (wilderness recreation vs. season-long grazing), and many of the fishes have both anadromous (or potamodromous) and resident life histories. Together these constraints defined each entire basin as the appropriate scale at which observations and predictions must be made to match management of the habitat needed to sustain fish life histories. Measuring relationships of fish to water temperature at smaller scales using traditional reach-based methods would have yielded little information relevant to the scales at which land managers operate.

Application to current and emerging challenges in lotic fish conservation

A measure of the usefulness of the riverscape approach is the extent to which it fosters research to meet pressing challenges in lotic fish conservation and thereby helps stem the tide of rapid decline. Four areas where this more comprehensive approach is needed are managing habitat for threatened and endangered species, counteracting invasions of nonnative species, managing ecosystems to sustain fish populations for sport and commercial fishing, and addressing intermediate and long-term climate change.

Managers of habitat for threatened and endangered species face a double challenge. By definition, populations of these rare species are already fragmented and their habitat is restricted by anthropogenic degradation. However, the critical habitats they require are often created only by streams interacting with intact landscapes (Gregory et al. 1991, Montgomery et al. 1999), and important life history processes often occur over intermediate or large scales (Schlosser 1995a). Human land use truncates the domain over which these physical and biotic processes must occur, leaving managers the task of creating the processes by hand (e.g., building habitat, transporting fish), or worse, failing to conserve species because the processes were not understood or considered. For example, the unique winter run of chinook salmon that enters the Sacramento River, California, in winter and originally spawned far upstream in cold meltwaters of mountain tributaries in early summer was blocked access by Shasta Dam, closed in 1949. These fish now must spawn in a restricted reach down-

stream from the dam where reservoir operations manipulate temperature to favor their reproduction (Yoshiyama et al. 1998). In fact, fishes in most large river basins were adapted to move to use habitats in disparate locations during their life cycle, so barriers to movement or degradation of key elements of habitat or flow regimes have had strong effects on populations over large areas (Schmutz and Jungwirth 1999, Pringle et al. 2000). The demise of bull charr in the Columbia River basin (Rieman and McIntyre 1995), paddlefish in the Mississippi (*Polyodon*; Graham 1997) and Yangtze (*Psephurus*; Wei et al. 1997) River basins, endemic large-bodied minnows (cyprinids) in the Colorado River basin (Carlson and Muth 1989), and Rio Grande silvery minnow (*Hybognathus amarus*) in the Rio Grande River basin (Bestgen and Platania 1991) are a few of the many examples.

Invasions of nonnative species are second in importance only to habitat degradation in causing species declines worldwide (Vitousek et al. 1996, Schmitz and Simberloff 1997), but are also frequently addressed at too small a scale. Nonnative fish and invertebrates released into reservoirs to provide forage for sport fishes have frequently escaped downstream, colonized upstream, or created unintended consequences far from the target site. A well-known example is the opossum shrimp (*Mysis relicta*) released into a lake in the Flathead River basin, Montana. Instead of providing food for sport fish as intended, the shrimp colonized Flathead Lake downstream and fed on the same zooplankton that supported the kokanee salmon (*O. nerka*) population (Spencer et al. 1991). This greatly reduced salmon runs upstream into Glacier National Park, which in turn eliminated an important food source for foraging bald eagles (*Haliaeetus leucocephalus*) and grizzly bears (*Ursus arctos*). Most studies of mechanisms of non-native invasions have been on individual behavior in the laboratory or small field enclosures (Hearn 1987, Fausch 1988, 1998), yet we argue that knowledge of population biology and community interactions that occur throughout riverscapes will be needed to predict the outcome and effects of stream fish invasions (Sakai et al. 2001). Results from small-scale studies may lead investigators to interpret experimental artifacts as important effects (Carpenter 1996) or downplay the importance of disturbances or regional factors that constrain the expression of small-scale behaviors (Peckarsky et al. 1997). For example, changes to landscapes can enhance invasions by increasing sediment supply, which reduces spawning habitat for native species (Jones et al. 1999), or by making conditions more suitable for competitors or pathogens (Holmes 1982, Reeves et al. 1987). Moreover, invasions driven by climatic or hydrologic variables that operate at intermediate or large scales may be predictable only at those scales (Moyle and Light 1996, Fausch et al. 2001). We conclude that prediction of stream fish invasions and their effects stands to gain much from an approach that considers entire riverscapes.

Managing ecosystems to sustain populations for sport or commercial fishing will also require a broader approach to be successful, as aquatic habitats suffer further decline. Recent research indicates that the scale at which habitat is created

naturally, and at which fish use it, may be much greater than the scale at which habitat management has been attempted (e.g., Frissell and Nawa 1992). Cooper and Mangel (1999) modeled a salmonid metapopulation using a simple source-sink model of 10 subpopulations having different degrees of habitat degradation and environmental variation. They reported that managers could be seriously misled by seeking local causes for declines of a subpopulation that is actually supplied from a source subpopulation elsewhere, where habitat degradation is the root cause of decline. Gowan and Fausch (1996a) reported that adding logs to create pools in six small Rocky Mountain streams more than doubled trout abundance during a long-term experiment. However, they found that movement from adjacent stream reaches up to several kilometers away was the main mechanism for the increase, not greater trout recruitment or survival in the reaches where habitat was manipulated. Although fisheries biologists have long attempted to predict local fish abundance from local microhabitat (Fausch et al. 1988), such as by using instream flow assessments (cf. Bovee et al. 1998), recent work indicates that movement of fish, prey, or nutrients across ecosystem boundaries can decouple fish populations from local environments (Polis et al. 1997, Nakano et al. 1999, Nakano and Murakami 2001). Similarly, Orth (1995) used a food-web model to show that flow fluctuations in the highly regulated New River, West Virginia, influenced smallmouth bass (*Micropterus dolomieu*) production more by indirect effects on production of their invertebrate prey than by direct effects on habitat for the smallmouth bass themselves.

Finally, our attempts to manage fishes in the face of intermediate and long-term climate change will perhaps require the broadest view of any conservation challenge. For example, recent evidence indicates that a Pacific Interdecadal Climate Oscillation occurring at 20- to 30-year intervals in the North Pacific Ocean not only affects sea temperatures and drives salmon production but also changes climate over large areas of the North American continent and streamflow in major river basins from Alaska to California (Mantua et al. 1997). Over longer time scales, much habitat will already have been lost due to direct human degradation, perhaps too much to allow recovery of many species, and this problem will be compounded by climate warming, which is predicted to alter the timing and magnitude of both flow and water temperature regimes (Magnuson et al. 2000, Poff et al. 2001). Biota living in the hierarchical habitats of lotic ecosystems, especially those at the headwaters, will be unable in many cases to transport themselves to more suitable habitats at the headwaters of other basins, leaving managers the task of predicting where suitable habitats will be located and moving the biota there. It is evident that researchers will need to provide managers with the tools to make robust predictions over large areas under different climate scenarios to have hope of conserving much of the lotic biodiversity that remains (cf. Meyer et al. 1999).

In conclusion, to be effective in conserving populations and assemblages of stream fishes, researchers, conservation

biologists, and managers will need to address questions and design management strategies at scales that match the life histories of the species involved. This will require a shift in thinking (Wiens 1999), a different way of sampling riverscapes, and creative ways of planning landscapes (Moyle and Yoshiyama 1994) to ensure that a modicum of stream fish biodiversity is sustained for future generations.

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