Community Ecology of Stream Fishes: Synthesis and Future Direction

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Synthesis
The broad range of subjects represented in this symposium highlight exciting new advances in the field of stream fish community ecology. Some of the chapters expand on themes (e.g., community stability, species interactions) that were represented in the 1987 publication Community and Evolutionary Ecology of North American Stream Fishes edited by W. J. Matthews and D. C. Heins. Others present research that was just developing in the late 1980s or represents new lines of research (e.g., landscape ecology, molecular ecology, ecological stoichiometry, and riverscape perspectives). Many contemporary conservation challenges are similar to those facing authors of the 1987 symposium, but some of these challenges have escalated because of increasing human population sizes and associated demands on water resources. The extent to which stream fishes have been affected by these issues is well documented in recent literature (e.g., Dudgeon et al. 2006; Jelks et al. 2008), and it is clear that quality research and innovative conservation actions are necessary to halt the rapid deterioration of stream ecosystems worldwide (Angermeier 2010, this volume). In light of these major conservation challenges, the goal of this symposium was to bring together leaders in the field of stream fish community ecology to highlight current advances in the field and pave a way for future researchers. Prefaces for the five main themes of the book provide excellent syntheses of those focal areas. Our review of the chapters and those theme prefaces yield some consensus on important advances and future directions for the field of stream fish community ecology. In particular, the continuing importance of linking patterns and processes was highlighted as a critical objective for understanding and conserving stream fishes. In this synthesis, we will use the framework of describing patterns and process and make recommendations for future direction. We start with a synthesis of advances in understanding patterns and process in stream fish community ecology over the past 20+ years and follow this overview with recommendations for future research.

Revealing Pattern and Process in Stream Fish Community Ecology
Describing patterns in the distribution and abundance of organisms is central to the field of ecology and is important in developing and testing hypothesized factors structuring stream fish communities. Large-scale patterns of fish species distributions over space and time described in the 1987 symposium were
instrumental in identifying important linkages between fish community structure and human perturbations to the landscape (Cross and Moss 1987; Li et al. 1987; Pfieger and Grace 1987). Papers in the 1987 symposium also linked species distributions to historical biogeography (e.g., Boschung 1987; Mayden 1987). Over the past 20+ years, survey information has accumulated, computing power has increased, and analytical methods for processing those data have been developed and refined (Matthews 2010, this volume). As a result, we are more aware of the complexity of factors that regulate stream fish communities and how scale of observation influences our interpretation of those factors (Hugueny et al. 2010, this volume; Matthews 2010). Some analytical methods present in the 1980s remain valid and have new modifications to improve our understanding of stream fish communities (Jackson et al. 2010, this volume). New methods related to ecological niche modeling (Buisson et al. 2010, this volume), autoregressive regression models (Grossman and Sabo 2010, this volume), and structural equation modeling (Infante and Allen 2010; Zorn and Wiley 2010; both this volume) illustrate recent advances in analytical approaches. A major advancement associated with more extensive data and analytical tools has been the generation and evaluation of conceptual models describing drivers of community structure, many of which are based to a large extent on empirical data collected across larger spatial and temporal scales (e.g., Hugueny et al. 2010; Roberts and Hitt 2010, this volume). Because of the breadth of spatial and temporal scales, these large data sets are also critical for developing predictive models that forecast potential changes in stream fish communities in response to global change (e.g., Buisson et al. 2010).

Authors in the current symposium generally placed less emphasis on describing species compositional changes and more emphasis on describing functional organization of assemblages (e.g., Frimpong and Angermeier 2010; Olden and Kennard 2010; Rahel 2010; all this volume). Matching patterns of functional organization or species composition with environmental variables (e.g., flows) has been particularly helpful in testing main drivers of fish community composition (Grossman et al. 1982; Grossman and Sabo 2010; Taylor 2010, this volume). Indeed, papers published in the past two decades by Poff and Allan (1995) and more recently by Bunn and Arthington (2002) have provided important conceptual frameworks to test linkages between hydrology and dynamics of stream fish communities and to develop effective approaches for managing flow regimes to benefit native species (e.g., Tharme 2003; Annear et al. 2004). Although tracking changes in species over space and time, particularly over long periods of time, remains critical to truly understanding community dynamics or drivers thereof (e.g., Grossman et al. 2010, this volume; Taylor 2010; Turner et al. 2010, this volume), this additional focus on functional organization has helped extrapolate across regions.

In the 1987 symposium, there were a number of small-scale mechanistic studies characterizing resource use, physiology, and responses of stream fishes to disturbance. Many of those papers evaluated resource use of species at relatively small spatial scales (e.g., habitat selection or resource partitioning studies by Angermeier 1987; Felley and Felley 1987; Fisher and Pearson 1987; Gorman 1987; Ross et al. 1987) and invoked species interactions as a mechanism driving those patterns of resource use. Within these studies, the focus on patterns of resource use among stream fishes was aimed at identifying potential competitive interactions. Studies of physiological tolerances (Hlohowskyj and Wissing 1987; Matthews 1987) and responses to disturbance identified abiotic factors that
constrained species distributions in space and time. Small-scale mechanistic studies continue today and can provide important insight into processes that elicit a response to harsh conditions such as drought (Marsh-Matthews and Matthews 2010, this volume) and interactions among species (Copp et al. 2010, this volume). These studies are critical for understanding factors limiting species occurrence within and across streams.

**Linking Patterns with Process**

The same year the 1987 symposium was published, Ricklefs (1987) noted that biological communities failed to converge in similar physical environments (but see Winemiller 1991; Winemiller et al. 1995) and put forth that both regional and historical processes were important drivers of community structure. The field of landscape ecology also has developed rapidly since 1987, providing a framework in which to link local and regional processes (Ward et al. 2002a; Wiens 2002). Fausch (2010, this volume) notes the importance of this “renaissance” in the field of stream fish community ecology, and chapters by Hugueny et al. (2010, this volume), Infante and Allen (2010, this volume), and Zorn et al. (2010) provide examples of research linking local and regional processes. Winemiller (2010, this volume) points out that metapopulation and metacommunity theories provide a framework to link local and regional processes through dispersal (Falke and Fausch 2010; Peres-Neto and Cumming 2010; both this volume). However, quantifying dispersal of individuals across the landscape is still a major challenge for stream fish ecologists, particularly for early life stages or smaller-bodied taxa. Douglas and Douglas (2010, this volume) show how modern molecular techniques can be used to infer dispersal across large spatial and temporal scales, and Rodriguez (2010, this volume) developed a model to account for variable movement behaviors of fish within a population.

A major step towards linking pattern and process in stream fish community ecology stemmed from the work by Winemiller and Rose (1992), who emphasized how life history traits affect population response to patterns of environmental variation, which paves the way for studying the functional organization of communities. By analyzing communities based on functional traits, we can more easily generalize results across systems and link changes in community structure to environmental factors driving those patterns. For example, the widely held view that stream flow is a “master” variable influencing stream fish community structure was influenced early on by Grossman et al. (1982) and later by Poff and Allan (1995), who have linked flows to functional traits of stream fishes. Frimpong and Angermeier (2010) evaluate this trait-based approach and others provide examples of how functional compositions of communities relate to abiotic conditions (Jones et al. 2010; Olden and Kennard 2010; both this volume).

Linking biodiversity to ecosystem function has emerged as a major subdiscipline of ecology and has been central to the study and conservation of stream fishes over the past two decades. In regards to stream fishes, authors have illustrated the importance of fishes from a diverse array of functional groups (e.g., grazers, detritivores, invertivores, and piscivores) on stream ecosystem structure and function (Power and Matthews 1983; Dahl and Greenburg 1987; Power 1990; Gelwick and Matthews 1992; Flecker 1996; Gido and Matthews 2001). Stream fishes also can elicit trophic cascades (Power et al. 1985), alter nutrient dynamics (e.g., Vanni 2002), or stream ecosystem function (Taylor et al. 2006). Papers in this symposium synthesize the important roles fishes play in stream ecosystems (Gido...
et al. 2010; Hoeinghaus and Pelicice 2010; both this volume), while also outlining novel approaches for identifying those roles (e.g., through altering element ratios [McIntyre and Flecker 2010, this volume] or the flow of energy within and across habitats [Flecker et al. 2010, this volume]).

A Path for the Future

Over the past two decades, the amount of information has increased exponentially and new concepts, approaches, and techniques have been applied to stream fish community ecology. The rapid expansion of this field has increased our basic understanding of these systems and informed managers on effective conservation strategies. Unfortunately, the conservation challenges facing stream fishes has expanded and surely will accelerate in the foreseeable future—human population is predicted to reach 9 billion by 2050 (Population Reference Bureau, www.prb.org). Major shifts in climate, land use, and distributions of biota, including exotic species, are projected. To confront these challenges, stream fish ecologists will need to focus their research in areas that will maximize information necessary to appropriately conserve this diverse, beautiful, and functionally important group of animals. At the same time, there are still many species and systems for which we have little basic ecological understanding. Thus, there is still a critical need for descriptive information on the resource use, physiology, reproduction, and population dynamics of many species.

This symposium provided an opportunity to look at the current trajectories of research and speculate on potentially productive areas for future research. Below, we outline several research foci that have provided useful insights for understanding processes structuring stream fish assemblages and make recommendations for future research in the fields. We compiled this list from discussions with participants from this symposium, colleagues, and students. Our intention is not to present an exhaustive list of potentially useful areas of research—that list would be too large. Rather, we present major areas that could be developed to address pressing questions that have not been adequately answered in the past. We refer to theme prefaces and individual chapters of this book for more focused descriptions of major advances and future directions in those areas of research.

Macroecology: Comparative Studies

In his synthesis of the 1987 symposium, Clark Hubbs (1987) identified the need to generalize results from studies conducted at limited spatial and temporal scales. This continues to be an important area of research and there are new approaches to address this issue. The future will likely make more data available for such comparative studies through programs like the U.S. Geological Survey (USGS) hydrologic gauging stations, gap analysis programs of the USGS and Department of Fisheries and Oceans Canada, national and local monitoring programs (e.g., U.S. Environmental Protection Agency Environmental Monitoring and Assessment Program, Environment Canada’s Ecological Monitoring and Assessment Network), and museum databases. The use of meta-analysis (Rosenberg et al. 2000) has been refined as a tool to uncover generalities from multiple studies. Given the breadth and quantity of data that will be available, we suggest several key actions that would facilitate comparative studies among stream fish ecologists: (1) making data available to multiple investigators, (2) building collaborations among scientists, (3) measuring community metrics (e.g., functional traits such as trophic or reproductive guilds or functional groups [Matthews 1998:69]) that enable comparisons, and (4)
developing tools and statistical approaches to rigorously test generalities across regions. Such studies will not only validate the generality of local experiments, but will help evaluate the context dependency of those results across major ecological gradients (see section on scaling below).

Methods of linking functional organization of fish assemblages with environmental conditions (e.g., disturbance regimes) will more explicitly link patterns and process. A major limitation to this line of work is a lack of information on the reproduction, feeding ecology, physiology, and behavior of many species. If such data are available (e.g., Frimpong and Angermeier 2009), promising new statistical approaches are available to evaluate these linkages (e.g., RLQ analysis, Dolédec et al. 1996; and fourth-corner analysis, Dray and Legendre 2008).

Technology: Major Advances in the Field Will Be Facilitated by Technology

While accumulation of research over space and time can incrementally advance the field of community ecology, technological advancement can lead to punctuated steps towards answering key questions. For example, molecular ecology has expanded at a rapid pace, and we now have methods to quantify historical relationships among species using routine procedures (see Douglas and Douglas 2010, this volume). Using this approach and new technologies to simultaneously evaluate genetic differences among populations and the functions of genes responsible for those differences (i.e., functional genomics, Turner et al. 2010, this volume) should provide valuable insight in to the evolutionary processes responsible for structuring stream communities. An example of the use of molecular ecology in regards to conservation is the ability to detect the presence of invasive species in a water body based on the occurrence of its DNA extracted from a water sample (e.g., Mahon et al. 2009); this approach was recently used to detect the invasion of Asian silver carp Hypophthalmichthys molitrix in Lake Michigan.

Rapid advances in molecular methods and efficient cataloging of genetic information have expanded our understanding of the phylogenetic relationship of fishes and has allowed for stronger inferences in community ecology (e.g., Felsenstein 1985). For example, DNA sequence data for many stream fishes are easily accessed through the National Center for Biotechnology Information (GenBank), and these data can be readily used to construct phylogenetic hypotheses. Webb et al. (2002) pointed out that improved phylogenetic hypotheses will inform studies of community organization by (1) examining the phylogenetic structure of community assemblages, (2) exploring the phylogenetic basis of community niche structure, and (3) adding a community context to studies of trait evolution and biogeography. Several studies have incorporated phylogenies into stream fish community studies (e.g., Gotelli and Taylor 1999; Peres-Neto 2004; Alcaraz et al. 2005), but as data from new species accumulates and methods of analysis improve, inferences into the importance of evolutionary constraints relative to other factors (e.g., biotic interactions and abiotic forcing) will become more robust.

Another example of technology that will continue to improve is through ecoinformatic approaches incorporating precise locality and physiological measurements of fishes as well as environmental sensors into geographic information systems. These databases will allow synchronized linkages between environmental conditions and individual fishes, populations and communities. Such methods will allow a higher resolution of data capture than before, so it will be necessary to evaluate the
consequence of these fine-resolution data and potential for error propagation in uncovering large-scale patterns and processes. Other new technologies such as remote sensing, stable isotopes, fatty acids assays, and microchemistry will all likely yield new information on movements and will allow us to integrate resource use over larger spatial and temporal scales. Some challenges still remain. For example, in contrast to fine-resolution sensor technology, will remotely sensed and biochemical data be of sufficiently fine resolution to capture relevant ecological processes at smaller scales?

Connectivity: Spatial and Temporal Connectivity of Stream Fish Communities

Understanding spatial and temporal dependencies of stream fishes is critical in linking local and regional processes. Although the science and technology we use allows us to measure dispersal of fishes over space and time, the complexity of species life histories has limited comprehensive investigations of dispersal dynamics for many fish communities. We need innovative approaches to monitor movements of fishes across intermediate spatial scales. Metacommunity theory (sensu Leibold et al. 2004) has provided a framework for understanding these dependencies, but the theory is well beyond existing empirical research. A major hurdle, as mentioned above, is quantifying dispersal patterns of fishes. Recent advances in telemetry and biomarkers allow us to tag very small fishes, but their numbers are often too great and individuals too fragile to mark enough fish to gain a comprehensive assessment of movement across large spatial and temporal scales. Understanding the consequences of connectivity across habitats will be critical to future conservation of stream fishes. Fausch et al. (2010) highlight the conundrum of wanting to encourage movement of native fishes while limiting the movement of nonnatives. Fragmentation of stream networks by impoundments is central to this challenge, and innovative methods of selectively allowing dispersal will greatly assist conservation issues.

Scaling: Linking Process to Pattern

A major obstacle in linking large-scale patterns to ecological processes is the scale at which experiments are conducted (Hewitt et al. 2007; Sandel and Smith 2009). The link between small-scale mechanistic experiments and observations and large-scale patterns still presents a major challenge to the general field of ecology (Ricklefs 2008). Several recent reviews (e.g., Jackson et al. 2001) have identified approaches that would help link these processes. For example, mechanistic experiments conducted along major environmental gradients (e.g., stream size and latitude) can be used to infer the contingencies of local processes on these larger gradients (Sandel and Smith 2009). In streams, some of the most consistent patterns in diversity and community structure are along gradients of stream size, productivity, and latitude (e.g., Oberdorff et al. 1995). Experiments embedded along those gradients are likely to provide insight into scaling local processes.

Model Development and Validation: Validation of Mathematical Models with Empirical Data

The number of large-scale models (i.e., based on satellite or climatic data) predicting distribution and abundance of stream fishes has expanded rapidly over the past few decades. This work has been facilitated by the availability of large data sets of both biological and environmental factors. In many cases, it is not clear if these models are missing influential constraints such as water chemistry or biotic interactions. Advances in statistical modeling will occur if
these models are able to incorporate processes. To incorporate process, models must be based on plausible mechanistic hypotheses and validated with empirical data. For example, a temperature model predicting species distribution could be coupled with laboratory experiments defining thermal tolerance of species or using insight about habitat use derived from integrated telemetry biosensors. Or the observation of a parapatric distribution of species could be coupled with a competition experiment. Although this sounds straightforward, there are virtually an infinite number of experiments necessary to test all species interactions or physiological responses of fish communities across large spatial scales. A first step is to test mechanisms in an appropriate venue. This may require small mesocosms up to large, unreplicated experiments of the kind that have proven valuable in furthering ecological understanding and influencing policy (e.g., Schindler 1998). Capitalizing on natural experiments also might allow testing of mechanisms hypothesized to be associated with large-scale processes, such as species invasions (e.g., Smith et al. 2004).

**What Role Can Stream Fish Community Ecology Play in Advancing General Ecological Theory?**

We conclude this synthesis with a discussion of how stream fish ecology can contribute to general ecological theory. In particular, characteristics of streams and stream fishes make them ideal for testing a number of general ecological theories (e.g., Ward et al. 2002b; Huugeny et al. 2010). At the largest scale, stream catchments are “islands” and freshwater fishes are separated from other catchments by land or sea. These islands are often replicated across the landscape and are useful in conducting “natural” experiments that test patterns of fish community structure along key environmental gradients. Thus, stream fishes continue to be useful models for describing and testing biogeographic theory (e.g., island biography theory and community convergence of functional traits). At finer spatial scales, streams are dendritic networks (Campbell-Grant et al. 2007) with a hierarchical organization of habitats (Frissell et al. 1986). Limited dispersal among network branches or unidirectional movement of materials (Vannote et al. 1980) also provides a backdrop for testing metapopulation and metacommunity theory (Fausch 2010). Metapopulation and metacommunity theory has advanced rapidly, but often without empirical support with which to calibrate models, let alone test the theory. Stream fish ecologists are well positioned to advance this area, especially when rigorous movement data are able to be collected from fish communities. Landscape ecology is often considered in a terrestrial setting with interest in the movement of individuals among patches and across habitats, often assuming simple but unrealistic straight-line movements between patches. The sharp aquatic-terrestrial boundary and strong longitudinal gradients make stream systems excellent models for measuring species movements and their affinities to particular habitats. These basic properties of streams are also useful in testing genetic models (i.e., effective population size) because it is feasible to obtain information on the dimensions of fish movement, dispersal barriers, and turnover rates of local populations (Douglas and Douglas 2010).

Research on stream fishes and their prey have advanced food-web theory (e.g., Power 1990; Nakano et al. 1999), due in part to compartmentalization of biota and resources in streams, but also because the importance of reciprocal connections between terrestrial and aquatic systems has become increasingly apparent (e.g., Malison and Baxter 2010; Wesner, in press). Moreover, rapid turnover rates of aquatic taxa (primarily lower trophic levels)
allow us to conduct food-web manipulations and observe responses over relatively short intervals. Small-scale experiments of stream organisms, but rarely with fish (e.g., Hargrave 2009), have provided information on the relationship between biodiversity and ecosystem function (e.g., Cardinale and Palmer 2002). However, we still have little understanding of how stream fish diversity is associated with ecosystem function and future research should evaluate these associations (e.g., McIntyre et al. 2008). A particular challenge, as highlighted in recent studies (Power et al. 2008; Murdock et al., in press), is that results are often confounded by the complexity within major food-web compartments (i.e., algal and macroinvertebrate taxonomic composition). Further resolution of these interactions might be necessary to predict the context dependency of fish effects in ecosystems.

Stream fish communities are ideal systems for testing disturbance theory (e.g., Stanley et al. 2010) because many streams are frequently disturbed by flooding, drought or ice scouring (e.g., Fisher et al. 1982; Townsend 1989; Poff and Allan 1995; Mitchell and Cunjak 2007). This nonequilibrium aspect of stream ecology provides a platform to evaluate community assembly rules (i.e., priority effects, niche packing, e.g., Roberts and Hitt 2010, this volume). Studies that couple disturbance with a landscape perspective (e.g., Fausch et al. 2002) at intermediate scales should help to reveal key trade-offs between species interactions and spatial distribution of refugia. Moreover, continuing work in this area will help conservation efforts by giving managers better understanding of how stream fishes will respond to changes in climate, hydrology, land use, and biota.

Research on stream fish communities over the past two decades has shifted away from a predominant focus on competition and resource partitioning (Matthews 2010). Nevertheless, stream fish communities continue to offer important opportunities to evaluate various niche concepts. For example, stream fishes have been used to test community saturation and invasibility (e.g., Ross 1991; Moyle and Light 1996) or for the importance of density-dependent population regulation (Grossman et al. 1998; Lobón-Cerviá 2009). Despite previous experiments testing species interactions (e.g., competition and predation), we still only have a weak grasp on the role of species interactions in regulating stream fish community structure due to the complexity associated with factors such as ontogenetic shifts, plasticity, spatial heterogeneity, indirect food-web interactions, migration, and time-lagged effects. Continuing long-term studies, and studies conducted at larger spatial scales, may reveal new insights into the importance of biotic interactions and role of abiotic features. In particular, small-scale mechanistic studies combined with evaluation of large-scale patterns might be necessary to predict the causes and consequences of species invasions.

In conclusion, we have noted that research highlighted in this symposium and in the broader literature shows a considerable change in its focus relative to the various foci in the previous symposium. Ideally, this change means that we have been addressing some of the prominent issues from 20+ years ago and that our field, and the broader field of ecology, is seeing considerable progress. Alternatively, it may represent the sometimes cyclical nature of research questions presented in the literature (i.e., various themes repeatedly appearing at various times—sometimes under different names). However, the enthusiasm and optimism expressed by the participants in this symposium suggests that we are making considerable progress, especially given the many new conceptual and technical approaches now available. We both found that the symposium
chapters published in Matthews and Heins (1987) provided much stimulus for discussions and helped in the development of ideas during our graduate work. We hope this current work also may serve to initiate and continue debate and discussion among existing and future generations of stream fish ecologists. Given the many challenges facing us, both in basic and applied stream fish ecology, such symposia and syntheses provide valuable insight into the progress made, our current state of knowledge, and setting priorities and goals for future studies.

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