

Preface: When and Where Do Fish Have Strong Effects on Stream Ecosystem Processes?

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The notion that fishes, or for that matter animals in general, can have strong effects on stream ecosystems is a relatively new idea. This is evident when comparing the composition of this volume with that of the Matthews and Heins (1987) book. The latter contains only two chapters explicitly focused on how fish affect other biota, and the effects of fish on bona fide “ecosystem processes” (e.g., primary production, nutrient cycling) were discussed in only one of these chapters (Matthews et al. 1987). In contrast, this volume has an entire section, consisting of four chapters, focused on the importance of fishes in stream ecosystems.

The evolution of the idea that fish can be important at the ecosystem scale is also mirrored in trends in general stream ecology books over the past several decades. The Hynes (1970) classic text on stream ecology contains no mention of the idea that fishes can mediate stream ecosystem processes; interspecific competition is the only biotic interaction involving fish that is discussed. More generally, there is essentially no discussion of community- or ecosystem-level impacts of predation by fish or other animals. There is also very little discussion of nutrient cycling, whether by fish or other animals, or of biotic regulation of nutrients in general. In essence, the prevailing idea was that the influence of physical factors, namely flow regime, overwhelmed biotic interactions in structuring communities and regu-

lating ecosystem processes. In contrast, Allan and Castillo’s (2007) book on stream ecology has two entire chapters dedicated to species interactions and communities (plus a chapter on energy flow through food webs), and these include sections on community-level effects of grazers and predators, trophic cascades, and food web interactions. Additionally, Allan and Castillo’s (2007) chapter on nutrient dynamics includes a significant section on consumer (animal) effects on nutrient dynamics.

Clearly then, the idea that fishes and other animals can play important roles in stream ecosystem processes is relatively new but has become more or less mainstream (pun intended) among lotic ecologists. Indeed, since the publication of Matthews and Heins (1987), there has been an explosion of studies examining the role of consumers—including fish—in stream ecosystem function. Studies on this topic have also become increasingly complex and sophisticated. As Gido et al. (2010, this volume) point out, early studies on fish effects focused on direct predator–prey interactions. Subsequent research incorporated indirect effects of fish (e.g., trophic cascades) but, as with earlier studies, focused mostly on effects mediated via consumption. With some notable exceptions (e.g., studies on the effects of migrating salmon; reviewed by Janetski et al. 2009), only recently have studies explicitly and experimentally investigated fish effects on ecosystem processes

such as nutrient cycling, sediment accrual and export, and ecosystem metabolism.

So, what have we learned about the effects of fish on stream ecosystems? I would argue that we know that stream fish can have large and pervasive effects on stream ecosystems... except that sometimes they do not. In other words, there is much variability in fish effects and we do not understand how to predict when and where stream fish have strong effects. This context dependency is, unfortunately, common for many ecological interactions and processes, even well-established interactions such as keystone predation in rocky intertidal zones (Paine 1966; Menge et al. 1994) and fish-mediated trophic cascades in lakes (Carpenter et al. 1985; Borer et al. 2005). Because studies on fish effects on stream ecosystem processes have only recently become common, we are just beginning to quantify and understand variability across time and space. In this introductory chapter, I will highlight how the chapters in this section contribute to our understanding of the ecosystem effects of stream fishes. I will focus on how effects may vary across some important ecological dimensions and suggest some future directions for research.

The role of fishes in stream ecosystems probably varies along many ecological dimensions (e.g., stream size, productivity, successional status, etc.). Rather than consider all possible dimensions, I will focus on three that I feel are especially important and that are addressed by the chapters in this section: time, space, and biodiversity. "Time" refers to the idea that fish effects may vary temporally or seasonally (e.g., with time elapsed since a disturbance event). "Space" alludes to variation in fish effects among ecosystems and along environmental gradients and also incorporates the idea that spatial connectivity can mediate the role of fishes. "Biodiversity" here means that different fish taxa (e.g., different species or

functional groups) have contrasting effects on stream ecosystems. Obviously, these dimensions do not vary in isolation, so I also consider interactions among these dimensions.

Time

Fish effects vary over many temporal scales. One important aspect is the time elapsed following a disturbance event. Long-term studies on a California stream show that trophic cascade effects of fish vary with time since flooding and among different flood events (Power et al. 2008). Experiments by Gido et al. (2010) illustrate the striking context-dependency of fish effects in relation to disturbance dynamics, as revealed by the pronounced variation across 10 experiments designed to assess effects of fish on postdisturbance ecosystem dynamics. Fish effects depend on the magnitude of disturbance as well as time since disturbance. Small floods wash away algae and perhaps invertebrates, but not fish; thus fish can strongly mediate postdisturbance trajectories of ecosystem processes. In contrast, large floods displace fish, and because they take longer than algae or invertebrates to recolonize, fish have relatively weak effects on succession following these large storms. Effects of fish via nutrient cycling are hypothesized to diminish with time, following a disturbance, because algae will become increasingly dependent on internal cycling within the algal mat (Gido et al. 2010). However, one could also argue that algae will become more nutrient-limited with increasing time since disturbance, as their biomass accumulates and dissolved nutrients are depleted. If so, nutrient excretion by fishes may have greater impacts during these periods of strong nutrient limitation. Thus, the relative importance of consumptive and nutrient-mediated effects of fish as a function of disturbance history is not well known and should be pursued further.

More generally, fish effects on ecosystem processes should be more important during low flow periods. For example, fish can mediate ecosystem processes such as nutrient cycling, sediment accrual, and ecosystem metabolism in tropical streams, as discussed by McIntyre and Flecker (2010, this volume) and Flecker et al. (2010, this volume), but these effects have been demonstrated only during the dry season. During the wet season, flow is much higher and fish effects are likely to be overwhelmed by the effects of flow on nutrients and sediment. However, owing to the difficulties of studying ecosystem processes during the high flows of the wet season, this hypothesis has not been adequately tested.

Space

Spatial variation encompasses variation both among stream ecosystems and among habitats within a stream, as well as the spatial connectivity of habitats for mobile fish. Because lotic systems are spatially heterogeneous and display varying degrees of connectivity, quantifying how fish effects on ecosystem processes vary spatially is a major challenge. Effects of fish on periphyton (Gido et al. 2010) and nutrient supply (McIntyre et al. 2008; McIntyre and Flecker 2010) can vary greatly even at small scales (e.g. in pools versus riffles). In addition, predatory fish often induce potential prey species to move into different microhabitats (e.g., to shallower areas where they are less vulnerable to predators; Hoenighaus and Pelicice 2010, this volume). This can induce spatial variation in the ecosystem effects of fishes, for example, trophic cascades emanating from predator-induced movements of herbivores (Power et al. 1985; McIntosh et al. 2004). Effects at the reach scale will also vary, partly because of varying physical characteristics of streams, but also because of the variability

of fish movements and how these sources of variation impact ecosystem processes. For example, the speed at which fish can recolonize a particular stream reach after disturbance may depend on habitat connectivity (e.g., whether pools are isolated or connected). As mentioned above, recolonization rates of fish following disturbance plays a large role in determining the extent to which fish mediate successional trajectories (Gido et al. 2010).

Movements of fish across larger spatial scales can also be important to ecosystem processes. The importance of anadromous salmon in transporting nutrients between marine and freshwater ecosystems has long been appreciated (reviewed in Janetski et al. 2009). But, as Flecker et al. (2010) point out, the general importance of fish movements for ecosystem processes is poorly understood, in part because we know little about the movement patterns of most fish species. Because the impressive effects of anadromous salmon, a charismatic and economically important taxon, have shaped our view of how fish movements can mediate ecosystem processes, the emphasis has been on “material subsidies” (Flecker et al. 2010; i.e., the physical transport of materials, such as nutrients and carbon, when a large biomass of fish moves among ecosystems). However, fish can also provide “process subsidies” (Flecker et al. 2010), whereby the activities of fish (e.g., feeding and bioturbation) affect process rates in ecosystems into which they migrate. In the case of process subsidies, fish may have strong effects even when they are not very abundant and if they have strong per-capita effects on other taxa or on habitat structure. In contrast, material subsidies are more likely to be important when the fish is abundant because it is more likely to provide a resource that is relatively scarce in the recipient habitat. Because process subsidies can occur when fish are relatively scarce, they will be harder to detect than

material subsidies. As Flecker et al. (2010) point out, an important question is how these two subsidy types vary in importance among different fish species and ecosystems, and how movement patterns of fish mediate their importance.

Biodiversity

Ecosystem effects of fishes vary greatly among species and functional groups. A considerable amount of this variation is associated with three traits: feeding guild, body size, and ecological stoichiometry. (Also note that migratory behavior and other movements are important traits but were discussed above.) The importance of feeding guild (diet) in mediating ecosystem effects is touched upon in all four chapters of this section. Gido et al. (2010) show that grazing (benthivorous) and water column feeding minnows have contrasting effects on ecosystem processes in prairie streams. Sediment-feeding characids (e.g., *Prochilodus*) have disproportionately strong effects on sediment accrual, nutrient cycling, and ecosystem metabolism, compared to other fish, in neotropical streams (Flecker 1996; Taylor et al. 2006; McIntyre et al. 2007; McIntyre and Flecker 2010; Flecker et al. 2010). More generally, Hoeninghaus and Pelicice (2010) point out that predator effects vary with physical factors such as depth and flow but that the mediating effects of these factors depend on which predator and prey species are present.

Body size mediates many ecological interactions. This trait is particularly relevant for many fish species because diet varies greatly ontogenetically. Thus, an individual fish may shift among several feeding guilds throughout its life, and these ontogenetic shifts can cause variation in predator-prey interactions and subsequent indirect effects. Body size is also related to movement patterns; for example,

anadromous fish will inhabit streams only when they are very young and then again when they spawn; as a consequence, the prey of very small and large, but not intermediate-sized, individuals may be most affected in streams. The role of body size in mediating metabolic rates is also well known and forms the basis of some central ecological theories (Gillooly et al. 2001; Brown et al. 2004). In terms of ecosystem effects, nutrient excretion is a metabolic rate of great relevance. McIntyre and Flecker (2010) show that, among species, both N and P excretion rates are strongly related to body size more or less in accordance with allometric predictions. However, important differences emerge between nutrients; P excretion is more closely tied to body size than is N excretion, but P excretion increases more slowly with body size. As a consequence, the N:P ratio of excretion increases with body size (McIntyre and Flecker 2010).

Ecological stoichiometry refers to the relative amounts of multiple elements required by organisms versus the availability of these elements in their food resources (Sterner and Elser 2002). The relative imbalance between organism demand and availability has many consequences for ecosystem processes, namely for the rates and ratios at which consumers store and recycle nutrients. Ecological stoichiometry relates elemental imbalances from the molecular to ecosystem scale and is underlain by the principle of mass balance. Thus, it can serve as a unifying framework for predicting nutrient-cycling effects of stream fish (McIntyre and Flecker 2010). Indeed, evidence suggests that elemental composition of fish species (e.g., body P content and N:P ratio) can predict the N:P ratio at which nutrients are excreted (Vanni et al. 2002; McIntyre and Flecker 2010). Because of this relationship, different fish species can have greatly contrasting effects on whole-stream nutrient cycling

(McIntyre et al. 2007). Interestingly, it appears that variation among families is much greater than variation among species within a family, suggesting a link between phylogeny and ecosystem function (Vanni et al. 2002; McIntyre and Flecker 2010).

Interactions Among Time, Space, and Biodiversity

These three dimensions obviously can interact in mediating the role of fishes in stream ecosystems. Rather than discussing the various means by which they might interact, I will instead focus on a specific example of interactions among all three dimensions, deriving from work on nutrient cycling in Rio Las Marchías (RLM), Venezuela (as discussed in the chapters by McIntyre and Flecker and Flecker et al. in this section). As is typical of tropical systems, RLM has a diverse fish fauna in terms of the number of species, families, and feeding guilds. However, as mentioned, different fish species vary greatly in terms of their contributions to nutrient cycling, and this interspecific variation manifests differently for N versus P cycling. Several species of armored catfish (Loricariidae) inhabit the stream and have very low P excretion rates; thus, they excrete nutrients at a high N:P ratio, presumably because they need to sequester much P to build their P-rich bony armor (Vanni et al. 2002). At the ecosystem scale, the detritivore *Prochilodus* contributes disproportionately to nutrient cycling compared to other fishes in RLM, but its contribution compared to other species is much greater for N than for P. The contrasting effects on N and P cycling exhibited by loricariids, *Prochilodus*, and other taxa nicely illustrate the importance of biodiversity to ecosystem function (McIntyre et al. 2007). Furthermore, because *Prochilodus* is harvested by humans as a food source, its population in

RLM is being shifted to smaller sizes, with potentially strong effects on nutrient excretion rates and the N:P ratio excreted, via the body size effects discussed above. *Prochilodus* is also migratory, arriving in the RLM every dry season but in varying numbers. Thus, its migratory behavior and the connectivity between downstream and upstream areas (time and space effects) play critical roles in mediating its importance. Finally, the importance of fish in N and P cycling in RLM varies greatly among pools and riffles (McIntyre et al. 2008), illustrating spatial variability at small scales.

Moving Forward

Each of the four chapters in this section presents ideas for future research directions, and there is no need to rehash those here. Rather, I will suggest some pathways for designing studies that will help stream ecologists generalize about where and when fish have large effects on ecosystem processes.

The emergent ecosystem effects of a consumer usually reflect the balance of several interactions, and experiments that quantify the relative importance of these interactions are needed. For example, fish can affect other species via direct consumption, by inducing changes in the behavior of their prey, through ecosystem-engineering impacts (e.g., bioturbation), and via nutrient cycling. Furthermore, all of these interactions can generate additional indirect effects. Very few studies have quantified the relative importance of the various interactions, but such studies are needed for a mechanistic understanding of consumer effects on ecosystem processes. For example, grazing fish can have effects on periphytic algae by direct herbivory, excreting nutrients, reducing nutrient availability by sequestering nutrients in their bodies, and removing sediment that may otherwise reduce light intensity. Yet, only a few

studies have tried to quantify how these different mechanisms interactively affect periphyton (e.g., Power et al. 1985; Flecker 1996; Knoll et al. 2009). Embedded in these complex interactions are compensatory responses of species that are differentially affected by fish; however, the role that compensatory interactions play in determining ecosystem responses is not clear (Hoeinghaus and Pelicice 2010).

Ecosystem effects of fish (and other consumers) should more explicitly include an evolutionary perspective because phylogenetic history may help predict interactions. Studies relating phylogenetic identity, ecological stoichiometry and nutrient-cycling effects may illustrate these interactions (McIntyre and Flecker 2010). Specifically, the pronounced variation in nutrient excretion rates among neotropical fish families (Vanni et al. 2002; McIntyre et al. 2007) suggests that evolutionary history may exert a strong influence. However, the generality of this relationship is not clear. As mentioned above, in RLM, interspecific variation in ecological stoichiometry is largely driven by armored catfish (Loricariidae), whose bodies are covered with P-rich bony plates that presumably evolved as an antipredation defense. Are such relationships found in other regions (i.e., is there a group of fish equivalent to loricariids on other continents)? Also, identifying the selective pressures accounting for variation in body stoichiometry will facilitate understanding. The growth-rate hypothesis (Elser et al. 2000) predicts that species with high growth rates need high concentrations of P-rich RNA and thus an overall high body P content. However, the prevalence of bony structures may or may not be correlated with growth rate. If high body P evolved in tight association with growth (i.e., selection favors high growth rate, and thus high RNA and body P), this suggests strong selection to optimize P acquisition to achieve

a growth rate that will maximize fitness. However, if body P evolved mostly in isolation from selection on growth rates (e.g., selection for P-rich anti-predation structures), this suggests that a particular body stoichiometry is the by-product of selection pressures that are somewhat unrelated to growth rate. Thus, more phylogenetically explicit studies are needed, linking P limitation of growth, body P content, and nutrient cycling rates across a range of taxa (McIntyre and Flecker 2010). More generally, stream ecologists should explore functional traits that relate to body stoichiometry, and relate these to ecosystem effects (Hoeinghaus and Pelicice 2010). Such traits should include not only growth rate and the allocation of P to various body structures, but also traits such as selective foraging for stoichiometrically balanced prey, nutrient assimilation efficiencies, and postassimilation allocation of nutrients. As pointed out by Flecker et al. (2010) and McIntyre and Flecker (2010), studies linking evolutionary biology and ecosystem ecology as manifested in nutrient cycling are being carried out with guppies in Trinidadian streams (Palkovacs et al. 2009), as well as sticklebacks in lakes in Canada (Harmon et al. 2009). Hopefully, these studies will provide insights into the feedbacks between evolution and ecosystem processes.

Finally, we need studies on the effects of fish on stream ecosystems that are large in scale and scope (i.e., that adopt a more realistic ecosystem-scale perspective). For example, despite the recent interest in consumer-mediated nutrient cycling, only two published studies have compared nutrient supply by fish to nutrient demand in a stream ecosystem (Grimm 1988; McIntyre et al. 2008). These two studies were done 20 years apart in drastically different environments, a desert stream and a neotropical stream, and yielded very different results. Grimm (1988) found that nutrient cycling

by fish supported only 5–10% of N demand, whereas McIntyre et al. (2008) found that fish supplied about 75% of N demand. Clearly, we cannot make any conclusions about the importance of fish based on two such disparate studies. In addition, few studies have quantified the effects of fish on whole-stream metabolism (i.e., the balance of autotrophy versus heterotrophy). Gido et al. (2010) hypothesize that fish in prairie streams have stronger effects on algae than on heterotrophic microbes and will thus affect metabolism mainly through effects on primary production rather than heterotrophic respiration. More hypotheses like this one need to be generated and of course tested.

Elucidating the effects of fishes at ecosystem scales will require experiments at large scales and must include manipulation of whole-stream fish assemblages or, at least, of the dominant species (e.g., Taylor et al. 2006). Perhaps we need a “LINX-style” approach (Mulholland et al. 2008) in which the effects of fish on stream ecosystems are assessed using coordinated, controlled experiments in many different geographical locations. Such an approach would require tremendous effort, but the history of collaborative research among stream ecologists suggests that it can be done.

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