

Migratory Fishes as Material and Process Subsidies in Riverine Ecosystems

ALEXANDER S. FLECKER*

*Department of Ecology and Evolutionary Biology, Cornell University
Ithaca, New York 14853, USA*

PETER B. MCINTYRE

*Center for Limnology & Department of Zoology, University of Wisconsin
Madison, Wisconsin 53706, USA*

JONATHAN W. MOORE

*Department of Ecology and Evolutionary Biology, University of California
Santa Cruz, California 95060, USA*

JILL T. ANDERSON¹

*Department of Ecology and Evolutionary Biology, Cornell University
Ithaca, New York 14853, USA*

BRAD W. TAYLOR

*Department of Biological Sciences, Dartmouth College
Hanover, New Hampshire 03755, USA*

ROBERT O. HALL, JR.

*Department of Zoology and Physiology, University of Wyoming
Laramie, Wyoming 82071, USA*

Abstract.—Migratory fishes are common in freshwaters throughout the world and can fundamentally alter recipient ecosystems. We describe different types of fish migrations and consider their importance from the perspective of ecosystem subsidies—that is, landscape-scale flows of energy, materials, and organisms that are important in driving local food web and ecosystem dynamics. We distinguish between two general categories of subsidies, which we term here material subsidies and process subsidies. Material subsidies are the transfer of energy, nutrients, and other resources resulting in direct changes in resource pools within ecosystems. We posit that material subsidies occur under only a subset of life history strategies and ecological settings, and the potential for migratory fish to represent major material subsidies is greatest when (1) the biomass of migrants is high relative to recipient ecosystem size, (2) the availability of nutrients and energy is low in the recipient ecosystem (i.e., oligotrophic), and (3) there are effective mechanisms for both lib-

* Corresponding author: asf3@cornell.edu

¹ Present address: Department of Biology, Duke University,
Durham, North Carolina, 27708, USA

erating nutrients and energy from migratory fishes and retaining those materials within the food web of the recipient ecosystem. Thus, anadromous semelparous Pacific salmon *Oncorhynchus* spp. with en masse programmed senescence in oligotrophic Pacific Northwest streams can be large material subsidies. In contrast, process subsidies arise from feeding or other activities of migratory species that directly affect process rates within recipient ecosystems. For example, the physical and chemical effects of grazing and sediment-feeding fishes such as prochilodontids, as well as seed dispersal by large-bodied frugivorous characins, represent potentially key process subsidies by migratory fishes in some of the great rivers of South America. We speculate that process subsidies are more widespread than material subsidies from migratory stream fishes because they are independent of the type of migration patterns, life history, and distance traveled. Nevertheless, the magnitude of process subsidies is likely to be greatest under a specific subset of ecological conditions, which can differ from those where material subsidies might be most important. In addition to migrant biomass, the potential for migratory fish to represent strong process subsidies is regulated by migrant interaction strength and the degree to which a migratory species is functionally unique in a particular ecological setting. Unlike material subsidies, which require high migrant biomass as conveyor belts of materials, migratory fishes can be crucial process subsidies, even when migrant biomass is low, if they are functionally unique and strong interactors. We provide specific examples of these different types of subsidies and outline key directions of research for furthering our understanding of the functional significance of migratory stream fishes. Our aim is to highlight the diversity of subsidies provided by migratory fishes in order to foster a more comprehensive perspective on fishes as essential components of riverine ecosystems.

Introduction

Migratory fishes are a common component of the ichthyofauna of streams and rivers. Migratory species have received considerable attention among fish biologists and resource managers due to their long-distance movements, which often involve spectacular numbers of individuals (McDowall 1988; Lucas and Baras 2001), as well their importance in many of the largest riverine fisheries around the world (Welcomme 1985; Allan et al. 2005). Although the significance of migratory species to commercial and recreational fisheries has long been realized, over the past two decades there is increasing recognition that migratory species can be major ecological drivers shaping the structure and function of freshwater

ecosystems via a host of direct and indirect mechanisms as consumers, ecosystem engineers, modulators of biogeochemical processes, and transport vectors (e.g., Pringle 1997; Holmlund and Hammer 1999; Freeman et al. 2003; Willson et al. 2004, Greathouse et al. 2006). Appreciation of the fundamental ecological roles of migratory species has, in part, been an outcome of a growing literature linking the role of species and ecosystem function and the notion that the loss of key species can have widespread consequences in ecosystems (e.g., Holmlund and Hammer 1999; Kareiva and Levin 2003; Hooper et al. 2005).

The development of the concept of food-web subsidies (Polis et al. 1997, 2004) offers a useful framework for assessing the ecological influences of migratory species in streams. The

central idea of subsidized food webs is that energy, materials, and organisms are not spatially static in their distribution, but instead move across habitat boundaries with the potential to significantly influence the structure and function of recipient ecosystems. While migratory organisms can be considered subsidies in the context of transporters of energy and materials, they also can act as subsidies by modulating ecosystem processes via their behavior. Streams are particularly appropriate systems for studying ecosystem subsidies due to their unidirectional flows, the juxtaposition of habitats that can differ substantially in productivity, and the tremendous mobility of many stream organisms. Although much of the ecosystem subsidies literature in streams has not focused on stream fishes *per se*, we suggest that understanding the influence of fishes, which are often the most mobile organisms in freshwater systems, is vital for the effective management and conservation of many running waters.

Our goal here is to provide an overview of the types and significance of subsidies to stream ecosystems created by fish movement. We begin by briefly summarizing the major categories of migratory patterns in freshwater fishes, ranging from relatively short-distance movements across habitats to remarkable long-distance migrations of up to thousands of kilometers. We then make the distinction between two fundamentally different types of ecosystem subsidies, material and process subsidies, and provide examples of stream fishes acting as key subsidies crucial for understanding the structure and function of running water ecosystems. Although studies on the role of migratory fishes as ecosystem subsidies is still limited to a relatively small number of species that spend part or all of their lives in streams, this area of research offers great potential for advancing understanding of stream fish ecology. We end by suggesting some future directions ripe for investigation.

Migration in Riverine Fishes

A great deal has been written about migration and movement by fishes (e.g., Meek 1916; Judd et al. 1932; Myers 1949; McDowall 1988, Lucas and Baras 2001), although much of the literature focuses on the topic from a behavioral and bioenergetics perspective (e.g., Harden Jones 1968; Leggett 1977; McCleave et al. 1984; McKeown 1984). Migration has been defined in different ways; for the purposes of this paper, we adopt from Lucas and Baras (2001) a broad definition of migration as an adaptive strategy involving movement between discrete sites that is usually, but not necessarily, predictable or synchronous in time. Many fishes migrate during a limited part of their lifetimes, and for numerous species this takes place annually on a seasonal basis. Migrations occur for a variety of purposes, including feeding, reproduction, and seasonal refuge from severe conditions such as extreme temperatures during winter or low water and dissolved oxygen deficit in floodplains during the dry season. For freshwater fishes, defined here as species that spend part or all of their lifecycle in freshwater, several broad categories of migration have been described (Myers 1949; Lucas and Baras 2001), and these have different implications with regard to subsidies in freshwater ecosystems.

Diadromous migrations occur between freshwater and marine ecosystems, whereas potamodromous fish migrations are confined entirely to freshwaters. Diadromous migrations can be further characterized as anadromous, catadromous, and amphidromous. Anadromous species are born in freshwater and then migrate to sea to grow and mature before returning as adults to freshwater to spawn. Anadromy has been reported in some 110 fish species from 18 families (McDowall 1988) and is most commonly observed in temper-

ate latitudes between 30° and 65° (McDowall 1987; Gross et al. 1988). Some of the best-represented groups of anadromous fishes include lampreys (Petromyzontidae, Geotriidae, and Mordaciidae), sturgeons (Acipenseridae), salmon and trout (Salmonidae), smelts (Osmeridae), and shads and herrings (Clupeidae). In contrast, catadromous fishes are born in marine systems and migrate to freshwaters where they spend most of their lives before returning to the sea to reproduce as fully grown adults. Catadromy is most commonly observed in tropical latitudes and has been reported in at least 56 fish species from 18 families, including freshwater eels (Anguillidae), tarpons (Megalopidae), mullets (Mugilidae), and sculpins (Cottidae) (McDowall 1988). Amphidromy refers to species that migrate to sea as larvae soon after hatching, where they feed and grow for a period of usually a few months before returning to freshwater as juveniles (McDowall 2007). Amphidromous migrations are not motivated by breeding; rather, most growth and all reproduction by these fishes occur in freshwater. Amphidromy is known for some 75 fish species, most of which are sicydiine gobies and galaxiids, and is observed primarily in species on tropical and subtropical islands. Amphidromous species are mostly small in body size (less than 150 mm total length), in contrast to other diadromous fishes such as sturgeons and salmonids (McDowall 2007).

Potamodromous migrations are wholly confined to freshwater ecosystems and are widespread among freshwater fish assemblages. Nevertheless, the significance of potamodromy has received far less attention than diadromy (Northcote 1998). This is, in part, due to the paradigm that long dominated freshwater fish research, suggesting that movement of most riverine species is relatively restricted (Gerking 1959), a view put into question by research indicating that many fish are consid-

erably more mobile than once believed (e.g., Gowan et al. 1994; Gowan and Fausch 1996; Northcote 1997; Lucas and Baras 2001). Unlike diadromy, no global analysis of potamodromous species has been undertaken, and it is not yet possible due to the difficulties in amassing information for inconspicuous and little-studied species of negligible commercial or recreational value, especially in the tropics (but see Lucas and Baras 2001 for a review at the family level). Moreover, for broadly distributed species that migrate relatively short distances, it is often difficult to document movement patterns without intensive field analyses. Nonetheless, in both the tropics and temperate zone, potamodromy is likely the most common form of migration in stream fishes. For example, some 34% of Canadian freshwater fish species are potamodromous compared to 21% diadromous (Lucas and Baras 2001; based on information from Scott and Crossman 1973), and in many large tropical rivers, more than 95% of the migratory fishes are potamodromous (Lucas and Baras 2001). Likewise, Taphorn (1992) estimated that at least 28 of a total of 138 characiform species found in the Apure River basin of the Orinoco are migratory. These are likely underestimates of the extent of potamodromy, as information is largely anecdotal and few studies have quantified shorter and less conspicuous movements in tropical fishes.

Potamodromous migrations occur among different freshwater habitats and take place (1) entirely within the main stem of streams or rivers, (2) between streams and their tributaries, and (3) between lakes and their inlet or outlet tributaries (i.e., adfluvial migrations) (Northcote 1997). In floodplain systems, migrations between river main stems and seasonally inundated floodplains are also well known, particularly in the tropics where a substantial proportion of the ichthyomass is migratory

and includes some of the largest freshwater species in the world (e.g., pangasiid catfish in Asia and pimelodid catfish in South America; e.g., Welcomme 1979, 1985; Goulding 1980; Lowe-McConnell 1987; Barthem and Goulding 1997; Winemiller and Jepsen 1998; Carolsfeld et al. 2003; Hogan et al. 2004; Godinho and Kynard 2008). For example, in South America, large numbers of characins (Characiformes) and catfish (Siluriformes) migrate into flooded forests and savannas as waters rise with the flood pulse (Junk et al. 1989; Bayley 1995). Moreover, migrations for some potamodromous fishes are known to cover great distances, such as pimelodid catfishes of the genus *Brachyplatystoma*, which can migrate more than 5,000 km between the mouth of the Amazon and spawning grounds in the upper parts of the basin (Barthem and Goulding 1997; Batista and Alves-Gomes 2006).

Taxonomically, many fish families exhibit potamodromy, and it is an extremely common phenomenon within some groups. For instance, Lucas and Baras (2001) reported examples of potamodromy from 16 of the 25 families of freshwater fish found in Canada. About half (34 species within nine genera) of the world's 69 species of Salmonidae (trout, salmon, and whitefish) are reportedly potamodromous, and this is likely an underestimate as movement in some salmonid species is poorly known (Northcote 1997). Potamodromy is prevalent in suckers and redhorses (Catostomidae), and some species make enormous spawning migrations from lakes into tributary streams (Raney and Webster 1942; Cooke et al. 2005). Moreover, many species of the highly diverse family Cyprinidae are believed to make potamodromous migrations, although the spatial extent of migrations is largely unknown (Smith 1991; Lucas and Baras 2001; Winter and Fredrich 2003). Collectively, potamodromous species can represent a substantial proportion of fish

biomass even in the largest freshwater ecosystems. For instance, dozens of species from the Laurentian Great Lakes migrate seasonally into tributaries to breed, including native suckers, trout, pike, minnows, walleyes, whitefish, sturgeon, and lampreys as well as exotic lampreys, salmon, and smelt. In South America, potamodromous fishes are dominated by large pimelodid catfish and characins, many of commercial importance, whereas in Africa they include characins, siluroids, cyprinids, and mormyrids that move from lakes to tributaries and up-stream swamps to spawn (Welcomme 1985). In Asia, among the best known potamodromous fishes are pangasiid catfish and cyprinids such as some barbs, as well as members of the genus *Tor* that are known to ascend Himalayan streams (Welcomme 1985).

The migratory strategy of a species should influence its role as a material or process subsidy. Synchronous migrations can enable species to achieve densities and biomass that would otherwise not be possible. Polis et al. (1997) originally hypothesized that subsidies will be most important when the donor ecosystem is much more productive than the recipient ecosystem; migratory strategies that connect high productivity and low productivity habitats may strongly influence aquatic ecosystem structure and functioning. However, these patterns are likely to vary for different types of subsidies. In the following sections, we describe different ways that fishes subsidize streams and how these subsidies are linked to migration type.

Migratory Species as Ecosystem Subsidies: Material Inputs Versus Process Modulating Perspectives

Although stream ecologists have long recognized the importance of allochthonous inputs in fueling lotic ecosystems (e.g., Cummins

1974; Vannote et al. 1980), it is relatively recently that the significance of landscape-scale flows of energy, materials, and organisms in driving local food web and ecosystem dynamics has become broadly appreciated (e.g., Polis et al. 1996, 1997, 2004). The burgeoning literature on ecosystem subsidies shows that substantial subsidies are widespread in nature and often represent important linkages across landscape boundaries among a broad diversity of ecosystems (e.g., Polis and Strong 1996; Menge et al. 1997; Huxel and McCann 1998; Power and Rainey 2000; Polis et al. 2004; Baxter et al. 2005). Despite these advances in the empirical analysis of ecosystem subsidies, there have been few evaluations of the pathways by which migratory animals influence recipient ecosystems. Here, we outline two contrasting ways in which migratory organisms generate ecosystem subsidies, which we refer to as **material subsidies** and **process subsidies**. **Material subsidies** are the input of energy, nutrients, and other resources by migrants that directly augment resource pools within ecosystems. In contrast, **process subsidies** arise from feeding or other behaviors of migrants that affect physical structure or process rates within the recipient ecosystem. The presence of migratory individuals can modulate ecosystem functioning under both types of subsidy; the key difference is that material subsidies involve direct delivery of new material, whereas process subsidies affect the dynamics and cycling of existing material. In some cases, this dichotomy can become blurry, such as when nutrient inputs (materials) enhance ecosystem primary production or respiration rates (processes) via indirect pathways.

Initially, studies of fish subsidizing freshwater ecosystems focused on the contribution of migrants to material flows augmenting resource pools (e.g., Juday et al. 1932). In contrast, relatively little attention was paid to the

modulating effects of migratory organisms on ecosystem processes via their behavior and, in particular, to comparing the relative importance of subsidies from material versus process perspectives. However, the functional influence of migratory fish on ecosystem processes has received increasing recognition (e.g., Freeman et al. 2003; Schindler et al. 2003, Moore 2006; Moore et al. 2007; Tiegs et al. 2008, Janetski et al. 2009). In fact, we surmise that a much broader diversity of migratory fishes are important in connecting ecologically distant ecosystems via this modulation of ecosystem structure and function through the within-system activities of strongly interacting migratory species, rather than as conveyor belts of materials that augment resource pools. This is, in part, because fishes can only represent ecologically significant material fluxes under a restricted set of biological constraints and ecological settings. The parsing out of the relative importance of different types of subsidies has not been well explored among migratory stream fishes (but see Janetski et al. 2009). Below, we will review selected examples of stream fishes as subsidies and provide a framework for the conditions where stream fish subsidies are most likely to be important from material versus process perspectives.

Material Subsidies from Migratory Stream Fishes

We propose that significant material subsidies from migratory species are expected under only a subset of life history strategies and ecological settings. The potential for migratory fish to represent major material subsidies is greatest when (1) the biomass of migrants is high relative to ecosystem size, (2) the availability of nutrients and energy is low in the recipient ecosystem (i.e., oligotrophic), and (3) there is an effective mechanism for liberating nutrients

and energy from migratory fishes and retaining those materials within the food web of the recipient ecosystem (Figure 1). The most efficient mechanisms for liberating nutrients generally involve (1) local mortality of migrants in the recipient ecosystem due to programmed

senescence in semelparous species; (2) local migrant mortality due to predation, parasitism, and disease in iteroparous species; or (3) excretion and gamete deposition by spawning fishes. Regardless of whether nutrients are released via decomposition of carcasses, excre-

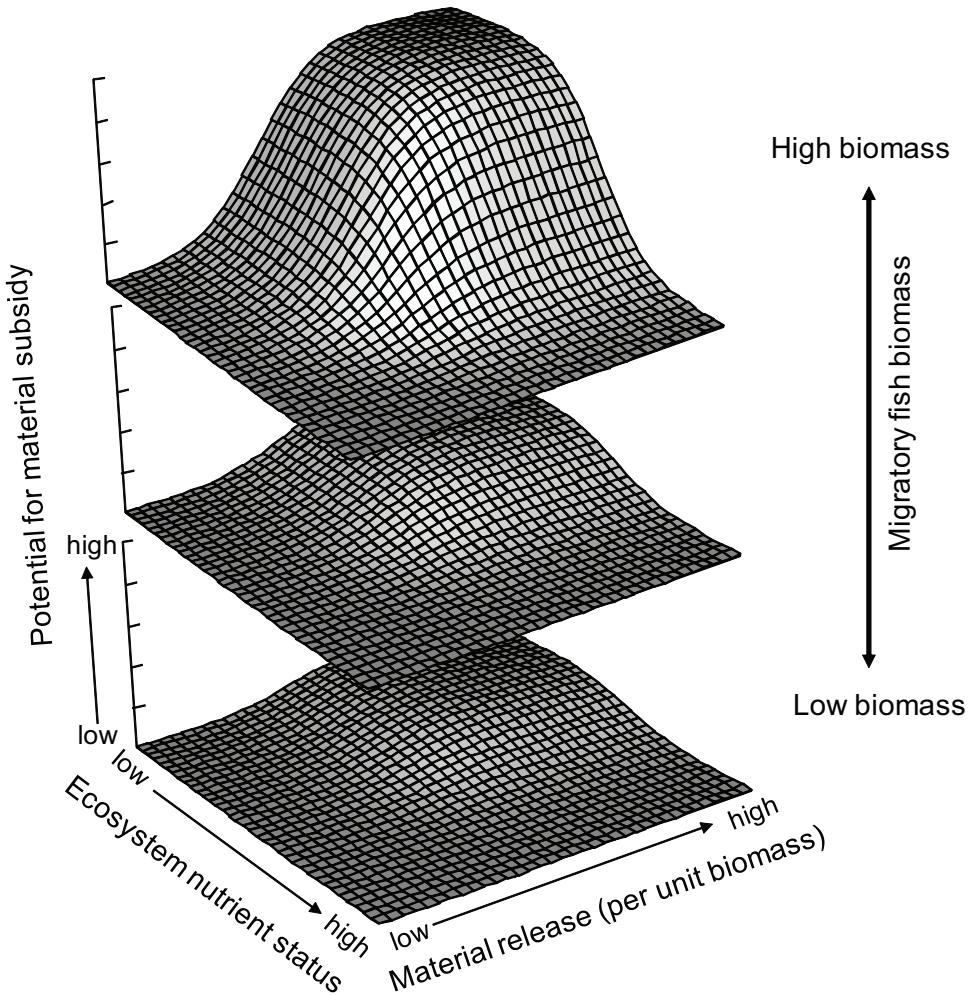


Figure 1. Ecological attributes influencing the potential for migratory fish to act as material subsidies. The potential for material subsidies should be highest when (1) migratory fish biomass is high relative to recipient ecosystem size, (2) the trophic status or availability of nutrients and energy is low in recipient ecosystems (i.e., oligotrophic), and (3) there are effective mechanisms for both liberating nutrients and energy from migratory fishes and retaining those materials within the food web of the recipient ecosystem. Mechanisms for releasing nutrients include local migrant mortality, excretion, and gamete deposition. In general, mortality provides per capita or per unit biomass nutrient input that is much greater than excretion and gamete release. Semelparous life histories can promote the potential for material subsidies because they are often accompanied by synchronized programmed senescence. See text for details.

tion, or gamete release, a mechanism for the liberation and retention of nutrients and energy originating elsewhere is crucial for material subsidies to be significant.

The best examples of material subsidies derived from migratory fishes have emerged from research on anadromous (e.g., Pacific salmon) and potamodromous species that display high biomass of migrants; hence, we focus upon these categories of migrants. The significance of migrations for nutrient and energy dynamics has been assessed for only a modest number of species that currently or historically made spectacular migrations. Catadromous fishes have limited capacity to subsidize freshwaters because they more likely represent an export flux of nutrients and energy to the sea. The significance of amphidromous fishes as material subsidies has not been evaluated (Freeman et al. 2003), but they are often small in body size, live for years after re-entering freshwater, and represent comparatively small net influxes of biomass into streams; thus their importance from a material subsidy perspective is likely to be limited.

Anadromous Fishes

The most well-known instances of fishes as material subsidies involve anadromous species transferring marine-derived nutrients (MDN) to streams and lakes. There is little question that the flagship for anadromous fish subsidies is Pacific salmon *Oncorhynchus* spp; their importance in translocating nutrients between marine and freshwater systems has long been recognized (see Juday et al. 1932) and been the subject of a large number of papers (see reviews of Willson et al. 1998, 2004; Naiman et al. 2002; Schindler et al. 2003; Janetski et al. 2009). Pacific salmon can represent particularly effective subsidies because they accrue more than 95% of their biomass in the marine

environment (Naiman et al. 2002), migrant biomass can be substantial (Gresh et al. 2000), and semelparity results in highly concentrated mortality at the natal sites to which spawners return.

Anadromous Pacific salmon import massive quantities of nutrients when they return to freshwater to spawn and die (Juday et al. 1932; Larkin and Slaney 1997; Gresh et al. 2000). Richey et al. (1975) first explored the importance of the decomposition of salmon carcasses as sources of MDN in streams; however, concerted research on the topic began in earnest in the 1990s (Naiman et al. 2002). Juvenile salmon that migrate out to the ocean can export large quantities of nutrients from freshwater, but this flux is generally of a lower magnitude (Moore and Schindler 2004; Schueerell et al. 2005). Mobile consumers of carcasses further disperse MDN to other habitats (Ben-David et al. 1998; Willson et al. 1998; Gende et al. 2002), including birds (Payne and Moore 2006) and bears (Hilderbrand et al. 1999; Gende et al. 2004; Helfield and Naiman 2006; Holtgrieve et al. 2009). Through a combination of excretion by live fish and decomposition of dead fish, streams with high densities of salmon are characterized by elevated levels of nutrients (Johnston et al. 2004; Moore et al. 2007). Retention of these MDN can be low in flowing waters (Johnston et al. 2004; Mitchell and Lamberti 2005; Moore et al. 2007), and much of the MDN likely accumulates in depositional zones like backwaters or lakes. However, MDN are assimilated into stream and riparian food webs, as evidenced by a host of stable isotope studies (e.g., Bilby et al. 1996). Dissolved MDN are taken up by primary producers and can stimulate their growth—trees along streams with high salmon runs were observed to be larger for their age (Helfield and Naiman 2001) and, in some cases, periphyton increases in the presence of salmon carcasses

(Wipfli et al. 1998; Chaloner et al. 2004; Tiegs et al. 2008). Either through this bottom-up fertilization or via direct consumption of carcasses and/or gametes, salmon can increase production of higher trophic levels such as benthic invertebrates (Lessard and Merritt 2006) and stream fishes (Wipfli et al. 2003). These observations have led to speculation that MDN might drive feedback loops between present and future populations of salmon (Stockner 2003), and have inspired management efforts to try to increase salmon production by increasing MDN loading to streams by adding dead salmon. This is an active and controversial avenue of research (Compton et al. 2006).

Even though there is a large literature documenting the effects of Pacific salmon as material subsidies, the magnitude and biological responses to these subsidies are context-dependent (Moore and Schindler 2008; Tiegs et al. 2008; Janetski et al. 2009). Using a meta-analysis approach based on 37 publications of Pacific salmon effect sizes from 79 streams, Janetski et al. (2009) reported that salmon sometimes increase and sometimes decrease primary and secondary production in streams. The variation among ecosystems was attributable to differences in salmon biomass, stream discharge, and salmon species. Much of this variation is likely because Pacific salmon are not just acting as material subsidies, but also as a process subsidy via bioturbation during their nest digging, which we describe more in the following section.

In contrast to Pacific salmon, the evidence for other salmonids, such as Atlantic salmon *Salmo salar*, acting as material subsidies is much more limited (Nislow et al. 2004; Saunders et al. 2006). Atlantic salmon differ from Pacific salmon in life history; they are generally iteroparous, have extended spawning periods and naturally smaller run sizes, resulting in less concentrated densities of carcasses (Nislow et

al. 2004). In addition, populations of Atlantic salmon are greatly reduced in many of their native streams, and much of their range spans sites with high external nutrient loadings from anthropogenic sources. Several investigators have reported that Atlantic salmon in some European streams can represent a net import of nutrients (e.g., Lyle and Elliott 1998; Jonsson and Jonsson 2003), although in some cases migration out of stocked smolt can result in a net loss of nutrients when returns of adult salmon are minor, as currently observed in North America (Nislow et al. 2004). Moreover, despite the net importation of nutrients by Atlantic salmon, Lyle and Elliott (1998) estimated that it was a very small fraction (<1%) of the total nutrient flux through the eutrophic system where they undertook their study. Similar to Pacific salmon, the importance of Atlantic salmon as material subsidies is likely to vary dramatically as a function of the magnitude of spawning returns, stream nutrient status, and mechanisms of nutrient retention.

Although salmon have received a great deal of attention, other anadromous fishes could potentially be important material subsidies in freshwater ecosystems. Along the East Coast of the United States, the significance of material subsidies by anadromous clupeids (shad and herrings) has been explored to some degree. However there have been few efforts to quantify material loadings by current-day clupeid migrations (but see Post and Walters 2009; Walters et al. 2009), and population declines coupled with anthropogenic eutrophication of rivers might today minimize the relative contribution of what were once significant subsidies to stream food webs. Historically, shad reached great population densities and comprised important fisheries throughout much of their native ranges (Waldman 2003), although many populations around the globe have collapsed due to dams, pollution, and other threats. Lim-

burg et al. (2003) estimated that large runs of 1,000,000 individuals of American shad *Alosa sapidissima*, similar to historic levels once seen in rivers in the southern United States, would have released some 180 metric tons of marine-derived nitrogen following their death. Likewise, Garman (1992) surmised that migratory clupeids once contributed substantial allochthonous inputs of energy and nutrients to Atlantic coastal streams and estimated that before the construction of barriers, the potential annual allochthonous input of a suite of anadromous clupeids (American shad, hickory shad *A. mediocris*, blueback herring *A. aestivalis*, and alewife *A. pseudoharengus*) to the James River as some 155 kg/ha. Interestingly, stream water ammonium concentrations were observed to increase by an order of magnitude in a James River tributary during an *Alosa* spawning migration compared to when few clupeids were present (Browder and Garman 1994). On the basis of ecosystem area and volume, the amount of nutrient inputs from clupeids can be relatively large. In a pioneering study, Durbin et al. (1979) quantified the ecosystem effects of spawning alewife migrations, a clupeid that returns to its natal stream to spawn. Although iteroparous, mortality on spawning grounds is high, amounting to as much as 59% of spawners. Furthermore, they estimated that on their spawning grounds alewives lost from excretion some 38%, 19%, and 17% of body mass for carbon, nitrogen, and phosphorus, respectively. Durbin et al. (1979) concluded that alewives contributed sufficient amounts of nutrients to result in marked changes in primary production and leaf decomposition and suggested that on an areal basis, mortality of spawning alewife added a greater amount of fish carcass biomass to a set of small New England ponds than observed for sockeye salmon *Oncorhynchus nerka* in some lakes in Alaska well known for their large spawning runs (Karluk Lake, Juday et al.

1932; Lake Iliamna, Donaldson 1967). Likewise, recent work on anadromous alewives in Connecticut suggests that nutrient excretion by spawning fish can represent a significant source of material loading that is rapidly incorporated into stream food webs and makes its way into all stream trophic levels (Post and Walters 2009; Walters et al. 2009).

In addition to contributing nutrients that can stimulate primary production and heterotrophic activity, shad can also subsidize higher trophic levels directly as a food resource for piscivorous birds and fishes. Studies showing shifts in stable isotope signatures before and after *Alosa* spp. spawning runs reveal that resident piscivorous fishes, including largemouth bass *Micropterus salmoides*, bowfin *Amia calva*, and longnose gar *Lepisosteus osseus*, derive a measureable proportion of their carbon from migratory shad species (Garman and Macko 1998). Moreover, *Alosa* can subsidize non-indigenous species; for instance, introduced blue catfish *Ictalurus furcatus* similarly show major shifts in isotopic composition that can be attributed to a marine signal from migratory shad (MacAvoy et al. 2000). Birds such as cormorants can also be subsidized by migratory shad (Dalton et al. 2009), potentially acting as mobile vectors that further disperse MDN, although the extent of such material subsidies remains to be quantified. Based on stable isotope signatures of fishes in the Rappahannock River system in Virginia, MacAvoy et al. (2009) concluded that predators were the only fish guild that displayed a marine signal from *Alosa* spp. spawning runs. They found no evidence of MDN at lower trophic levels and suggested that in contrast to Pacific salmon, which import nutrients to the base of stream food webs, marine materials delivered by anadromous shad directly enter the top of riverine food webs via consumption of migrants by piscivorous fish.

Despite the occurrence of anadromy in some 18 fish families, the significance of material subsidies by most taxonomic groups has not been explored. However, like Pacific salmon and shad, some of these species may be of current or historical importance to stream food webs and the cycling of materials. For example, the eulachon *Thaleichthys pacificus*, the largest member of the smelt family (Osmeridae), once made impressive migrations into streams of the Pacific Northwest. These migrations supported commercial-fishing harvests of thousands of kilograms of fish in tributaries of the Columbia River (WDFW and ODFW 2001). While some individuals spawn repeatedly, the vast majority of individuals die after spawning, thereby providing input of MDN. Based on typical body nutrient content of scaled freshwater fishes (%N = 2.54% wet mass, %P = 0.5% wet mass, Schindler and Eby 1997; McIntyre and Flecker 2010, this volume), we estimate that these fisheries alone represented as much as 50 metric tons annually of nitrogen and 10 metric tons annually of phosphorus harvested from the Cowlitz, Lewis, and Sandy rivers in Washington and Oregon. Unfortunately, these fisheries declined precipitously in the 1990s (Figure 2). Before populations of eulachon crashed in Columbia River tributaries, their migrations were accompanied by large numbers of avian predators, including a variety of gulls, mergansers, cormorants, and eagles (WDFW and ODFW 2001). Eulachon migrations are still substantial in some streams in southeastern Alaska and are likely important in subsidizing the diets of predators such as red-breasted mergansers *Mergus serrator* and some gulls (Marston et al. 2002).

Potamodromous Fishes

Potamodromous fishes also have considerable potential to represent major material

subsidies, especially when they display the requisite features of large migrant biomass and high local mortality or nutrient release in streams of comparatively low nutrient status (Figure 1). With few exceptions, potamodromous fishes do not display life histories of highly synchronized spawning accompanied by programmed sudden senescence, in contrast to some anadromous species such as Pacific salmon. Thus, substantial mortality from other means, such as predation, is required for potamodromous species to act as significant material subsidies. For instance, Fittkau (1970) recognized the importance of migratory fishes to the nutrient supply of oligotrophic tributaries and floodplain lagoons of the central Amazon. He posited that black caiman *Melanosuchus niger* act as keystone predators that are vital for intercepting and regenerating nutrients imported by migratory fish. Moreover, he proposed that the extirpation of this once-widespread crocodylian has contributed to the demise of many Amazonian fisheries due to loss of critical nutrient inputs.

Although Fittkau's intriguing hypothesis has not been explicitly tested, there is evidence that migratory fish can indeed be important as food subsidies of higher trophic levels in tropical rivers. In South America, some of the best candidate fish species acting as material subsidies are members of the Prochilodontidae, namely the highly migratory genera *Prochilodus* and *Semaprochilodus*, which make long-distance migrations and are often a dominant component of fish biomass in Neotropical rivers. Winemiller and Jepsen (1998, 2004) used stable isotopes to reveal that energy and nutrients from massive schools of detritivorous/algivorous prochilodontids (*S. kneri*) are delivered to blackwater river systems via predation. These abundant fishes spend the wet season in productive

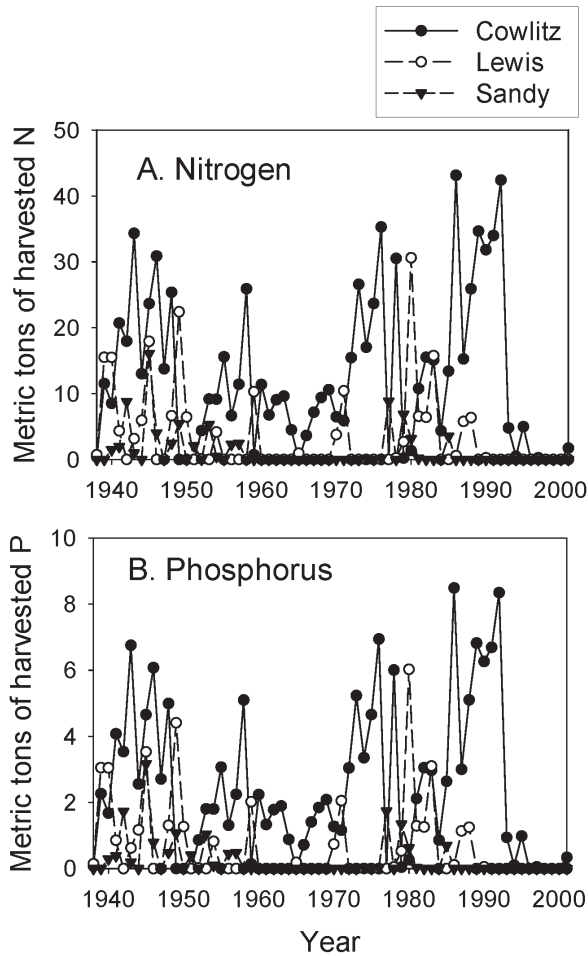


Figure 2. Historical commercial landings (1938–2001) of the migratory eulachon in tributaries of the Columbia River (Cowlitz, Lewis, and Sandy rivers in Washington and Oregon), expressed as metric tons of harvested nitrogen and phosphorus.

whitewater floodplains where they feed and spawn. During the dry season, juveniles migrate hundreds of kilometers into nutrient-poor blackwater rivers where they are subject to high rates of predation by resident piscivorous fish, especially large cichlid predators (speckled pavon *Cichla temensis*). Winemiller and Jepsen estimated that *Semaprochilodus* comprises nearly half of the annual biomass ingested by *Cichla* and provides important nutritional subsidies to this and other piscivores such as piranhas (*Serrasalmus*), payara

(*Hydrolycus*), and pink river dolphin *Inia geoffrensis*. Thus, material subsidies by migratory fishes may help to explain the seeming enigma of highly productive fisheries in nutrient-poor blackwater systems.

In the temperate zone, the ecological significance of material subsidies by potamodromous fishes is a ripe area for research. For example, large spawning runs are often observed from lakes or large rivers into tributary streams, and these adfluvial migrants could be important sources of energy and nutri-

ents in nutrient-poor tributaries. Perhaps the most likely candidates for significant nutrient inputs to North American streams are the suckers and redhorses (Catostomidae). These large and abundant fishes are distributed throughout the continent, and most species migrate into headwater streams to breed. The available data suggest impressively large runs in many regions. For example, runs of longnose suckers *Catostomus catostomus* can rival or exceed those of each of the four Pacific salmon breeding in Alaska's George River during some years (Linderman et al. 2004). Though most catostomids are long-lived and iteroparous, breeding mortality of 25–40% has been reported (Barton 1980), suggesting potential for substantial nutrient inputs. Indeed, current research in oligotrophic tributaries of Lake Michigan indicates that spring migrations of white sucker *C. commersonii* and longnose sucker are closely associated with a

time-lagged increase in dissolved phosphorus concentrations (Figure 3; P. B. McIntyre and J. D. Allan, University of Michigan, unpublished data). Interestingly, this nutrient pulse occurs late in the run, suggesting that it results from decomposition of adult carcasses, gametes, or larval mortality rather than excretion by surviving breeders. Further transfer of lake-derived nutrients from breeding suckers into the terrestrial zone is likely to be mediated by raptors, which derive a considerable portion of their spring diet from suckers (e.g., Dunstan and Harper 1975; Dombek et al. 1984), and potentially otters and black bears, which are anecdotally reported to forage on breeding suckers. Though they have not been studied in the context of material subsidies, substantial inputs of energy and nutrients to streams may also be provided by many other adfluvial North American fishes, including percids, salmonids, esocids, moronids, and osmerids.

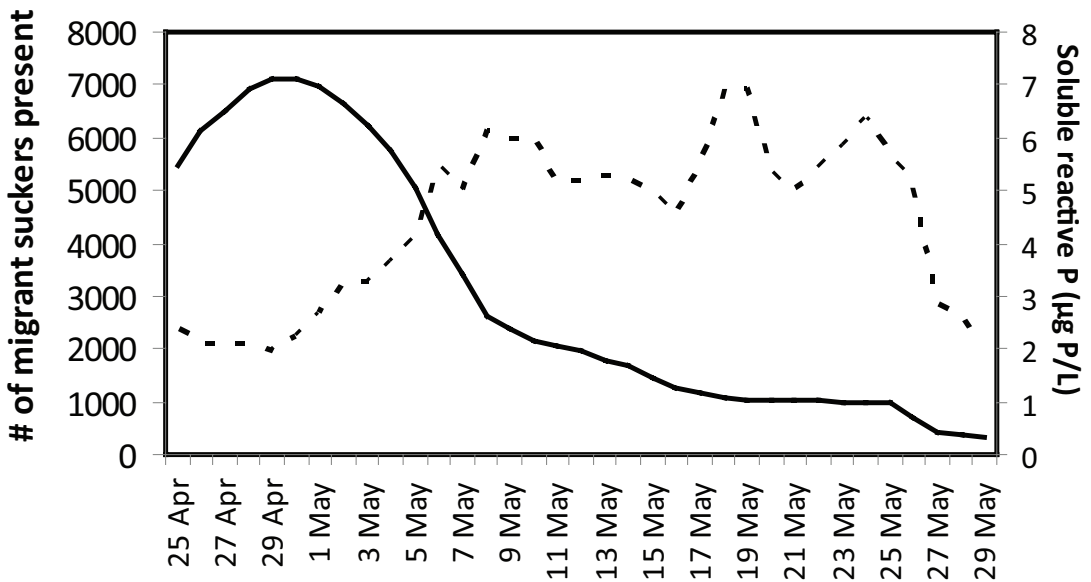


Figure 3. Time series of migrant suckers (white suckers and longnose suckers; solid line) and soluble reactive phosphorus concentrations (dashed line) in a second-order tributary of Lake Michigan. Phosphorus concentrations were low and stable upstream of a barrier ($2.14 \mu\text{g P/L} \pm 0.26 \text{ SD}$), suggesting that nutrient dynamics were driven by suckers.

Process Subsidies from Migratory Fishes

Despite our growing understanding of the importance of material subsidies from migratory fishes, they are more than simply mobile bags of nutrients and energy. In addition to conveying material subsidies, migratory fishes can strongly affect stream ecosystem processes through their feeding and other activities. In fact, we speculate that process subsidies may well be more widespread than material subsidies from migratory stream fishes. The rationale for this hypothesis is that process subsidies are expected regardless of the type of migration patterns (i.e., anadromous, catadromous, amphidromous, and potamodromous), life history (semelparous to iteroparous), and distance traveled (i.e., short- to long-distance movements), though their magnitude is likely to be greatest under a specific subset of ecological conditions. Notably, these conditions can differ from those where material subsidies might be most important. We posit that in addition to migrant biomass, the potential for migratory fish to represent strong process subsidies is influenced by migrant per biomass interaction strength and the degree to which a migratory species is functionally unique in a particular ecological setting (Figure 4). Not surprisingly, strongly interacting migratory species that are abundant and represent a large proportion of total fish biomass (i.e., dominant species, cf Power et al. 1996) will have great capacity to provide process subsidies. However, as migrant biomass declines, the functional uniqueness of a particular migratory species becomes increasingly important in determining whether it plays a strong role in modulating ecosystem structure and function. Thus, even when migrant biomass is low, we posit that functionally unique, strong interactors can be vital process subsidies. By definition, such strong interactors would be keystone species, whereby their impacts on ecosystem structure and function would be

substantial and disproportionately greater than would be predicted based on their relative biomass alone. For example, migratory fishes that are hosts of parasitic stages of mussel larvae are functionally unique, and even small numbers of fishes as hosts could be crucial to the dispersal and demography of mussel populations. In turn, these mussels can be important ecological players that strongly influence ecosystem dynamics (Vaughn and Hakenkamp 2001; Strayer 2008; Vaughn 2010). Consequently, a number of workers have discussed how the construction of dams has caused major disruptions of mussel species that are important ecosystem drivers, in part due to the loss of migratory fishes as key hosts of mussel larvae (e.g., Freeman et al. 2003; Helfman 2007). This is just one of a wide variety of mechanisms by which migratory fish can act as important process subsidies, and we summarize several classes of process subsidies below. Rather than serving as an exhaustive list, our intention is to highlight the diversity of mechanisms by which migratory fishes can act as important process subsidies in stream ecosystems.

Migratory Fishes as Physical Ecosystem Engineers

Over the past decade, the importance of ecosystem engineering by migratory stream fishes has received increasing attention as a structuring mechanism in running water ecosystems (e.g., Flecker 1996; Matthews 1998; Moore 2006; Tiegs et al. 2008; Janetski et al. 2009). The concept of ecosystem engineering originally focused on species that modify their physical environment (Jones et al. 1994, 1997), and engineering effects of migratory stream fishes can be manifested via a variety of mechanisms, such as bioturbation and particulate matter processing (Moore 2006).

In tropical South American streams, flannelmouth characin *Prochilodus mariae* make

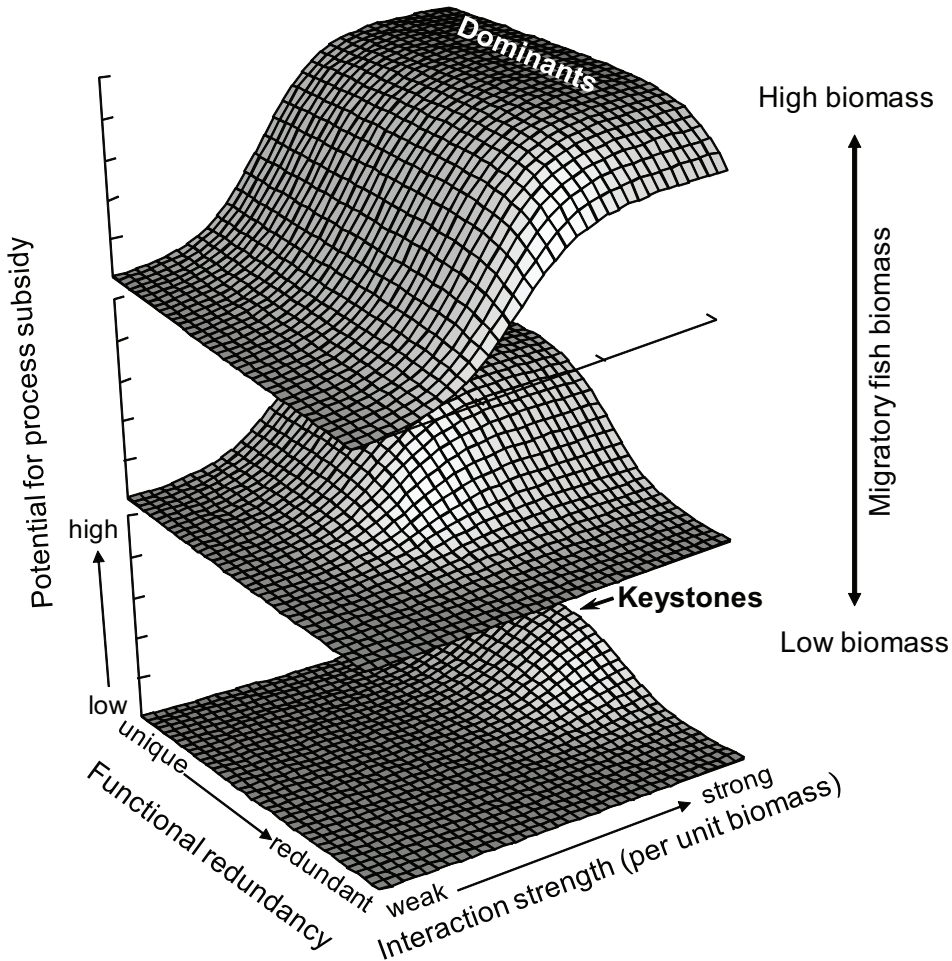


Figure 4. Ecological attributes influencing the potential for migratory fish to act as process subsidies. The potential for process subsidies should be regulated by (1) fish biomass relative to ecosystem size, (2) interaction strength (per unit migrant biomass), and (3) the degree to which a migratory species is functionally unique in a particular ecological setting. Unlike material subsidies, which require high migrant biomass, migratory fishes can be crucial process subsidies even when migrant biomass is low, if they are functionally unique and strong interactors (i.e., keystone species). See text for details.

enormous migrations from extensive seasonal floodplains to the Andean foothills. These fishes play a key role in influencing organic matter dynamics by processing large volumes of organic-rich sediments that accrue on the streambed (Flecker 1992, 1996, 1997; Taylor et al. 2006). As a result, organic matter accrual is greatly reduced by flannelmouth characins via sediment ingestion and resuspension. Moreover, primary producers display a variety of responses to the

experimental exclusion of *Prochilodus*; diatoms generally increase in the absence of *Prochilodus*, whereas other autotrophs such as the cyanobacterium *Calothrix* are facilitated by *Prochilodus*. Presumably, *Prochilodus* prevents the accrual of large volumes of sediments that otherwise bury mats of *Calothrix* filaments in the absence of this important migratory fish species. Taylor et al. (2006) used a large-scale experimental approach coupled with observations of interan-

nual variation in the magnitude of *Prochilodus* migrations to show that these migratory fish exert strong control on carbon cycling during the dry season months. Whole-stream fluxes of suspended particulate organic carbon displayed significant interannual variation and were consistently much greater during years when migrant biomass was high. Likewise, experimental exclusion of *Prochilodus* at a scale of hundreds of meters resulted in decreased transport of organic carbon as well as enhanced ecosystem metabolism (i.e., gross primary production and heterotrophic respiration). In a similar fashion, migratory *Semaprochilodus kneri* strongly influence patterns of benthic matter and algal accrual during their feeding migrations into lowland blackwater rivers of the Orinoco system during the dry season (Winemiller et al. 2006).

Researchers working with Pacific salmon have recognized that strong ecosystem effects of anadromous fishes are a function of both resource subsidies and ecosystem engineering. Migratory salmon dig large nests up to 17 m² and often spawn at high densities, dramatically altering bed surface morphology (Kondolf et al. 1993; Gottesfeld et al. 2004; Moore 2006; Hassan et al. 2008). In some cases, this bioturbation can move more sediments than floods (Gottesfeld et al. 2004; Hassan et al. 2008). The effects of nest digging are varied, including increasing concentrations of suspended particulate matter (Moore 2006), decreasing periphyton biomass (Minakawa and Gara 1999; Peterson and Foote 2000; Moore et al. 2004; Moore and Schindler 2008), and disturbing stream invertebrates, which reduces their densities (Minakawa and Gara 1999; Moore and Schindler 2008; Monaghan and Milner 2009; Honea and Gara 2009) and temporarily increases prey availability for drift-feeding fishes (Peterson and Foote 2000; Scheuerell et al. 2007; Moore et al. 2008, Monaghan and Milner 2009).

There is also increasing appreciation of the context dependence of alternative mechanisms of ecosystem subsidies (Moore 2006; Tiegs et al. 2008; Janetski et al. 2009). Moore (2006) has pointed out that engineering effects are likely to be most important not only where migrant density is high, but also where biotic disturbance is not overshadowed by frequent and intense hydrologic disturbance. Tiegs et al. (2008) found that this disturbance is more important in streams where sediments are small and thus more easily disturbed by the nest-digging salmon. Given that the process subsidy (i.e., bioturbation) and the material subsidy (i.e., marine-derived nutrients) from Pacific salmon have such different ecological consequences, understanding the net impacts of these species necessitates considering both subsidy pathways.

Migratory Fishes as Chemical Ecosystem Engineers or Modulators of Nutrient Cycles

In addition to engineering their physical environment, some migratory fishes can modulate nutrient cycles. As process subsidies, these modulating effects are not a direct consequence of material inputs (i.e., material subsidies), but rather the result of organisms engineering their chemical environment via their activity. Fishes can modify their chemical environment by altering element cycles directly (e.g., fish excretion and egestion) or indirectly (e.g., reduced algal demand caused by fish feeding) (Vanni 2002). A key distinction we consider with regard to direct chemical engineering via excretion is the source where nutrients originate. Migrants that spend little time at a site before leaving or dying will excrete nutrients originating primarily from an external ecosystem and thus provide material subsidies (e.g., Pacific salmon). In contrast, fishes that feed and excrete nutrients mainly from within a local stream site provide process

subsidies. Hence, a large migration of fish that stay and feed within the recipient local stream can constitute both material and process subsidies from an excretion standpoint.

An active area of research has been aimed at exploring the degree to which migratory salmonids in North America and prochilodontids in South America influence nutrient cycles. For example, *Prochilodus* plays a disproportionately great role in contributing to aggregate community excretion and in the generation of biogeochemical hotspots by mineralizing stream nitrogen (McIntyre et al. 2007, 2008). This recycling flux constitutes a process subsidy rather than a material subsidy because the fish are primarily processing existing stream nutrients rather than importing nutrients from downstream. *Prochilodus* also facilitates N-fixing cyanobacteria (Flecker 1996), which represents a further pathway by which migratory fish can act as an important control on nitrogen availability in nutrient impoverished Andean piedmont streams.

Researchers in North America working with migratory Pacific salmon have provided strong evidence that fish are important influences on nutrient cycling (e.g., Mitchell and Lamberti 2005; Moore et al. 2007; Tieggs et al. 2008; Janetski et al. 2009). Here too, anadromous *Oncorhynchus* are a functionally unique component of many Pacific coast streams and historically reached high densities. Janetski et al.'s (2009) meta-analysis reports that live salmon have much greater influence on NH_4 , NO_3 , and soluble reactive phosphorus concentrations than dead salmon, suggesting an important role of live fish on these solutes, presumably due to excretion and mineralization. However, in contrast to potamodromous fish such as *Prochilodus* that actively feed and excrete wastes generated locally, nitrogen excretion from anadromous fishes are likely metabolites from MDN. Ultimately, understanding the origins of excretory products is important for determining whether

migrants are bringing nutrients from elsewhere (i.e., a material subsidy) or recycling local nutrients (i.e., a process subsidy). For instance, in the case of adfluvial suckers, it remains unclear whether increases in nutrients associated with migrations (Figure 3) are derived purely from the lake ecosystem (a material subsidy) or also include stream-derived nutrients mineralized from feeding during the breeding migration.

Migratory Fishes as Seed Dispersers

Migratory fish can also play key functional roles as seed dispersal agents (e.g., Goulding 1980; Kubitzki and Ziburski 1994; Horn 1997; Banack et al. 2002; Correa et al. 2007; Galetti et al. 2008; Anderson et al. 2009). Frugivory is especially prominent in the tropics, where at least 182 species from some 32 families of fish have been recorded eating fruits (Correa et al. 2007). Although frugivorous fishes are known from Asia (e.g., pangasiid catfishes from the Mekong basin), Africa (e.g., alestid characins and the osteoglossid bonytongue *Heterotis*), and even North America (e.g., Chick et al. 2003), most research on ichthyochory (i.e., seed dispersal by fishes) has been conducted in the Neotropics due to the elevated diversity and abundance of fruit-eaters in this region. Some of the most notable examples include large-bodied migratory characins (Characidae: *Colossoma* and *Piaractus*) as well as pimelodid and doradid catfish. These highly mobile species live in floodplain forests of the Amazon, Orinoco, and parts of Central America and have a much longer gut passage time than other vertebrate frugivores such as birds and mammals (Correa et al. 2007; Anderson et al. 2009). Fishes that feed on fruits are seed predators for some plant species but also have the capacity to act as seed dispersal agents. For fishes to act as dispersal agents requires not only that they consume large quantities of fruit, but that seeds are capable of germinating follow-

ing gut passage and are defecated in habitats that are suitable for germination after floodwaters recede. Additionally, fish movement patterns could differ fundamentally from other biotic or abiotic dispersal agents because many species of fruit-eating fishes are highly mobile and can swim long distances upstream (e.g., Goulding 1980; Junk et al. 1997; Makrakis et al. 2007). Research conducted mostly in the Neotropics over the past decade provides evidence for a variety of fish species meeting these requirements (e.g., Agami and Waisel 1988; Kubitzki and Ziburski 1994; Horn 1997; Banack et al. 2002; Chick et al. 2003; Mannheimer et al. 2003; Correa et al. 2007; Galetti et al. 2008; Anderson et al. 2009; Reys et al. 2009). For example, in the Ventuari River of the upper Orinoco in Venezuela, intact seeds of some 32 tree species were found in the guts of the characid *Brycon bicolor* (Figure 5A). Moreover, a large proportion of the intact seeds in *Brycon* guts germinated within a 2-week observation period (Figure 5B). Estimates of frugivorous fish movement rates by radio telemetry (*B. guatamalensis* in Costa Rica [Horn 1997], *Colossoma macropomum* in Peru [J. T. Anderson, Duke University, J. S. Rojas, CODEA, Iquitos, Peru, and A. S. Flecker, Cornell University, unpublished manuscript]) show the potential for substantial long-distance dispersal of ingested seeds to floodplain wetland habitats favorable for plant establishment. Thus, frugivorous fishes likely provide a unique and fundamental role as mutualistic dispersal agents of tropical floodplain trees. Indeed, these frugivores exemplify the potential for migratory fishes to play keystone roles in the functioning of stream ecosystems, even when their biomass is relatively low.

Frontiers in the Study of Migratory Fishes as Subsidies

Clearly, there has been enormous progress made over the past 25 years in increasing our appre-

ciation of the vital ecosystem roles of migratory fishes. While research on salmonid subsidies has ballooned during this period, our knowledge of the roles played by the vast majority of migratory fishes remains limited. A particularly large void exists in our understanding of functionally unique species that do not require high biomass to act as critical process subsidies. In closing, we highlight a number of major shortcomings in knowledge of stream subsidies derived from migratory fishes. We believe that expanding our understanding in these areas represents an important frontier for future research in stream fish ecology.

Direct and Indirect Effects of Migratory Fishes as Consumers

A considerable literature over the past three decades demonstrates the importance of stream fishes as consumers influencing the dynamics of different trophic levels (e.g., Power and Matthews 1983; Power 1990; Flecker 1992; Flecker and Townsend 1994; Huryn 1998; Matthews 1998; Pringle and Hamazaki 1998; Forrester et al. 1999; Nakano et al. 1999; Flecker and Taylor 2004; McIntosh et al. 2004; Power et al. 2008). While there is no question that consumption by fish can drive stream ecosystem structure and function, surprisingly little research has been conducted on the direct consumptive effects of migratory fishes on lower trophic levels (but see Power 1990, Power et al. 2008 for an example of strong top-down effects of juvenile steelhead *Oncorhynchus mykiss*). Although migrations of some fish are focused purely on spawning (e.g., *Oncorhynchus* with programmed senescence), many highly mobile fish feed extensively as they move around the riverscape and have the capacity to exert strong consumptive and trait-mediated effects. Freeman et al. (2003) speculated on the prominent role that some migratory fishes, such as the American

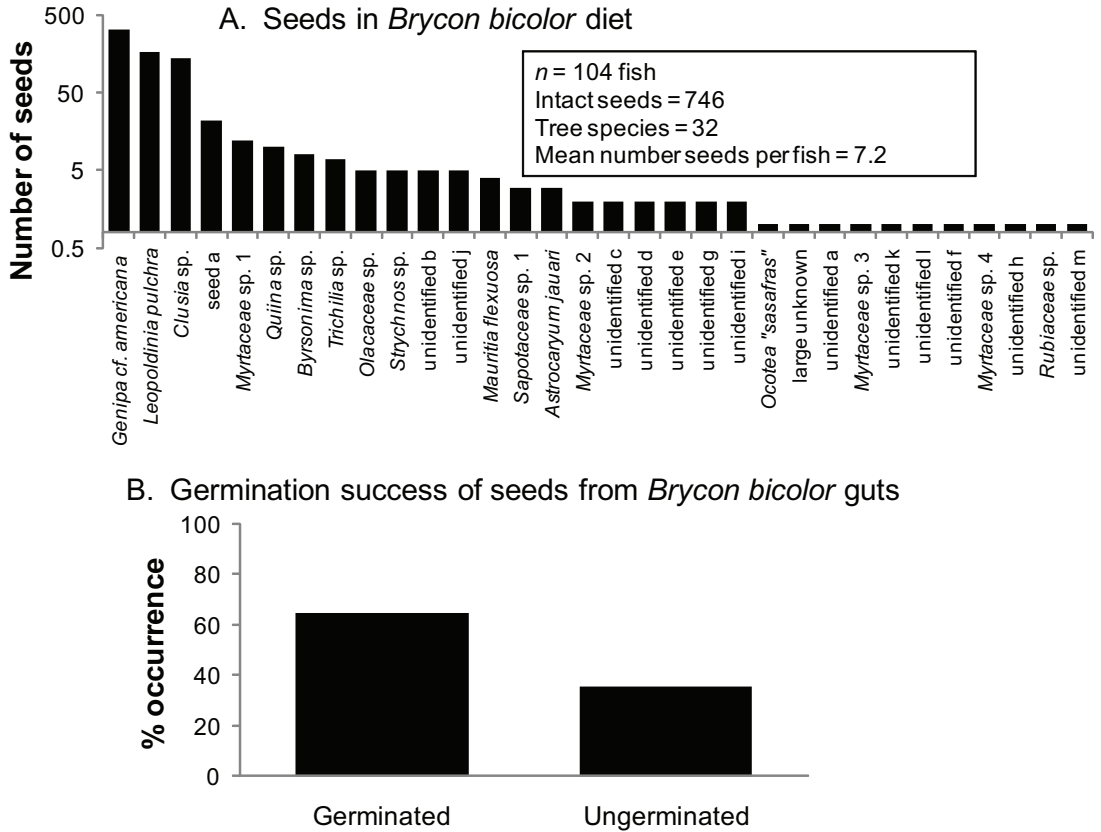


Figure 5. Dispersal of seeds by *Brycon bicolor* (Characidae) in the Rio Ventuari, Venezuela, during the wet season (June 2002). (A) Dominance diversity curve of intact seeds present in the digestive tracts of 104 individuals over 1 month. (B) Germination success of intact seeds monitored over 2 weeks.

eel *Anguilla rostrata* and long-finned eel *A. dieffenbachia*, might have once played as large-bodied predators before dams interfered with migrations. Also, some of the large catfish of South America, and tigerfish in Africa might be important in this regard by acting as effective predators and influencing the lateral migrations of other fishes (see Winemiller and Jepsen 1998; Lucas and Baras 2001; Layman and Winemiller 2004). In North America, large-bodied migratory fish such as northern pikeminnow *Ptychocheilus oregonensis* have long been assumed to be major fish predators, and this has dominated management along the Columbia River where there is a bounty on them. In the Colorado River, Colorado

pikeminnow *P. lucius* are large (>1 m) native predators that can migrate more than 100 km to spawn (Tyus and McAda 1984). Their precipitous decline in population size may have reduced predation rates on fishes in spawning rivers. Much of the literature on large migratory predators is anecdotal; therefore, carefully designed studies to tease apart the functional significance of fishes occupying higher trophic levels are sorely needed.

The Functional Significance of Small-Scale Movement

The literature on fishes as ecosystem subsidies in rivers is dominated by work on species that undertake medium to long-distance migra-

tions. Although there remains debate about whether stream fishes are relatively stationary over the bulk of their lifetime (i.e., the restricted movement paradigm; Gerking 1959; Gowan et al. 1994; Gowan and Fausch 1996; Rodriguez 2002), most stream fishes probably make short-term movements of 10^1 to 10^4 m. While there is a well-developed literature on fish movement (Matthews 1998; Hancock et al. 2000; Lucas and Baras 2001), there have been few attempts to rigorously quantify movement for most species of riverine fishes around the world, and in general, we know very little about the functional significance of fish movement from an ecosystem perspective. Small-distance movement could engender important process subsidies, such as the diel migrations among habitats of some predators. For example, many fishes move from deeper waters during the day to shallower waters at night (Lucas and Baras 2001); nevertheless, we know virtually nothing about the functional consequences of such behavior. Meyer et al. (1983) showed in coral reef systems that diel migrations of schooling grunts *Haemulon* spp. (Haemulidae) between sea grass beds at night where they actively fed and coral reef heads during the day where they rested had important implications for local nutrient transport. Thus, fish were key nutrient transport vectors among habitats, and short-distance movements significantly increased rates of coral growth and tissue condition. For short-distance movement of stream fishes to create similar process subsidies, it is necessary that fish movement distance exceed the travel distance of nutrients. For example, if fish move farther than the average distance that a dissolved-nutrient molecule travels before it is taken up, then fish excretion can potentially concentrate or deplete nutrients in specific areas that are favored or avoided. Such detailed studies of movement and ag-

gregation by stream fishes are scarce but are likely to be insightful for understanding the spatial heterogeneity of stream ecosystem structure and function.

Migratory Fishes as Vectors of Contaminants

Although the food-web subsidies literature has generally focused on exchanges of materials in short supply, such as limiting nutrients, subsidies via migratory fish can also involve the bulk transport of undesirable materials such as industrial pollutants and pesticides (e.g., Lum et al. 1987; Castonguay et al. 1989; Comba et al. 1993; Ewald et al. 1998; Krümmel et al. 2003; Gregory-Eaves et al. 2007). Krümmel et al. (2003) showed how sockeye salmon *O. nerka* can act as biotransport vectors of polychlorinated biphenyls (PCBs), persistent industrial pollutants that are sequestered by salmon at sea and then delivered long distances to natal spawning sites. Contaminants transported by migratory salmon can subsequently accumulate in resident species via the food web, which has been shown for resident grayling and rainbow trout (nonanadromous *O. mykiss*) in the Pacific Northwest (Ewald et al. 1998; Gregory-Eaves et al. 2007). Likewise, the Pacific salmon that have been stocked in the Great Lakes transport a variety of contaminants into tributaries (Sarica et al. 2004; O'Toole et al. 2006). Furthermore, resident fish in streams accessible to migrating salmonids have been found with high concentrations of PCBs and pesticides (Merna 1986; Scudato and McDowell 1989). Conversely, American eel accumulate organic pollutants such as the pesticide mirex in Lake Ontario, which is subsequently transported to the St. Lawrence estuary (Lum et al. 1987) and presumably as far as the Sargasso Sea, where these fish spawn and die. Little comparable work has been conducted in tropical rivers.

For example, it is unclear the degree to which fish migration might transport mercury upstream in the Orinoco and Amazon basins, where mercury loads can be elevated locally from gold mining activities (Araujo-Lima and Ruffino 2003) or natural sources (Barbosa et al. 2003). Thus, a key area of research is to understand the magnitude of contaminant loading from migratory fishes, which ultimately could have tremendous human health implications (Naiman et al. 2002).

Disease and Migratory Species as Ecosystem Subsidies

Migratory species can act as potentially important vectors of pathogens, a topic that has received little attention in the freshwater ecology literature. Willson and Halupka (1995) discussed some cases in which the effects of anadromous fishes are detrimental to individual consumers, and point to disease as one example. Thus, migratory salmon can be intermediate hosts in the complex life cycle of the parasite responsible for salmon poisoning, a disease caused by a rickettsia and fatal to canids. Moreover, there has been concern in the public health community about salmonids from aquaculture contributing to the emergence of new diseases. Salmon aquaculture has been linked to the expanding range of fish tapeworms *Diphyllobothrium latum* in localities such as Chile (Cabello 2007). Furthermore, in the lower Amur watershed of the Russian Far East, epidemics of infections to humans and predatory mammals of tapeworms of marine origin coincide with periods of chum salmon *O. keta* and pink salmon *O. gorbuscha* migrations (Muratov and Posokhov 1989; Muratov 1990).

Disease can also be potentially important in the population biology of migratory species and influence their capacity to serve as ecosystem subsidies. Disease represents one

mechanism to periodically augment material subsidies by migrants. Similar to predators capturing imported nutrients from donor ecosystems, disease resulting in high mortality to weakened migrants could enable the release of materials to recipient ecosystems, although there has been little study of this topic from a subsidies perspective. On the other hand, disease that is particularly virulent should have the opposite effect by greatly reducing population size of migratory species and thereby diminishing their importance as material and process subsidies.

Ecosystem Subsidies Created by Species Introductions

Some migratory species have been introduced to new environments, and understanding their effects from material and process subsidies perspectives is an important and insightful avenue of research. Invasive migratory species can represent both material and process subsidies and, in some cases, are functionally unique. For example, in southern South America, the accidental introduction of Chinook salmon *O. tshawytscha* has occurred as escapees from aquaculture have become established (Becker et al. 2007; Soto et al. 2007). Streams where they are now found in Chile and Argentina are naturally oligotrophic, but it remains unclear the degree to which pulses of nutrients from spawning populations modify the nutrient budgets of these systems. There has been some speculation that nutrient subsidies from spawning salmon increase productivity of other introduced species such as brown trout *Salmo trutta* (Soto et al. 2007), which could result in a host of indirect effects. Moreover, juvenile invasive salmon could both compete for food or serve as prey for native fish species (Correa and Gross 2008). Likewise, Chinook salmon have been introduced to New Zealand and have also potentially facilitated populations of other exotic salmonids (McDowall 1990).

Another well-known example involves nonnative kokanee salmon (lacustrine sockeye salmon), which were introduced to Montana's Flathead Lake in 1914 and once had large populations that moved seasonally to tributaries for spawning. These fish attracted an assemblage of charismatic piscivores, including bears and bald eagles, whose populations were subsidized by spawning fish but crashed following the decline of salmon after the introduction of opossum shrimp *Mysis relicta* to the lake (Spencer et al. 1991). Similarly, nonnative Pacific salmonids fertilize Great Lakes tributaries, resulting in elevated periphyton growth and transfer of lake-derived nutrients and pollutants into stream food webs (Schuldt and Hershey 1995; Sarica et al. 2004). In Yellowstone Lake, native cutthroat trout *O. clarkii* migrate to tributary streams to spawn but have suffered major declines with the introduction of nonnative lake trout and whirling disease (Koel et al. 2005). Spawning density to one tributary stream has declined from 40,000 to fewer than 3000 individuals (Koel et al. 2005). This decline has likely lowered nutrient fluxes to streams because the excretion flux alone was a substantial input of reactive nitrogen during the spawning migration (Tronstad 2008). Interestingly, the effect of the loss of cutthroat trout on nitrogen cycling was much stronger in the spawning streams than on Yellowstone Lake where trout reside for ~90% of the year (Tronstad 2008). Beyond the stream itself, this decline in migrating trout has reduced the nutrient flux to terrestrial food webs via piscivorous otters (Crait and Ben-David 2007).

Overall, we know remarkably little about a host of other invasive migratory fishes as material and process subsidies, and there are many unanswered questions about their ecosystem consequences. Are anadromous American shad, which were introduced to the Columbia River in the 1880s and are today highly abun-

dant (Hinrichsen and Ebbesmeyer 1998), material subsidies of marine-derived nutrients in the same ecosystems where native migratory salmon have declined? Likewise, are American shad significant process subsidies as abundant planktivores that can potentially cause strong cascading effects on lower trophic levels (Petersen et al. 2003)? Many effects of invasive species as material or process subsidies may not be readily apparent. While the consequences of sea lampreys *Petromyzon marinus* (Petromyzontidae) as parasites on other fishes are well known (Mills et al. 1993), more subtle effects are largely unrecognized. For example, sea lampreys alter streambeds through their nest building activities and can modify streambed convective flow patterns and downwelling zones (White 1990). A variety of frugivorous fishes have been introduced around the world, and we know nothing about their importance as novel seed dispersal agents or seed predators in new environments. Will large frugivorous Neotropical characins such as pacus (*Piaractus brachypomus* and *Colossoma macropomum*) become unique seed-dispersal agents in river systems in Asia and other places they have become established (Correa et al. 2007)? These and other questions on the consequences of highly mobile invasive fish species as ecosystem subsidies remain unanswered.

Migratory Species of Little Economic Importance

At present, almost all intensive studies on stream fishes as subsidies involve species of current or historic economic importance, namely those exploited by fisheries (Lucas and Baras 2001). This bias is largely because research on fish as subsidies has concentrated on readily apparent migratory species with exceptionally high biomass, which are also easy targets for exploitation. One of the greatest needs for future research on stream fish subsi-

dies is to expand beyond species that undergo extraordinary migrations in terms of vast numbers and long-distance movement. Research on a broader array of species is especially important for generalizing about the overall importance of subsidies in stream ecosystems. Is the role of fishes as ecosystem subsidies limited to a small subset of species and ecological settings? Or is this a more general feature common to many stream ecosystems? For the case of process effects, in which we have suggested that large biomass is not requisite to ecological influence, we believe that subsidies may be widespread and involve many species, life histories, and scales of movement ranging from short to long. Material subsidies may indeed involve a more limited number of species due to the more restricted set of constraints involving large biomass, and semelparous life history or other mechanisms for liberating nutrients. Determining the ecological importance of a broad variety of fish species from a subsidies perspective will elucidate the general significance of subsidies in stream ecosystems, and it is likely that interesting insights will emerge as a greater number of fish species are studied.

Understanding Subsidies from an Evolutionary Perspective

An exciting frontier of biology is the recent interest in linkages between evolutionary biology and ecosystem ecology (e.g., Hairston et al. 2005; Fussmann et al. 2007; Harmon et al. 2009; Pelletier et al. 2009; Post and Palkovacs 2009; Bassar et al. 2010). Ecosystem subsidies have much potential to contribute to this emerging focus. For example, we have posited here that life histories can be a key determinant of the ability of fishes to act as material subsidies, thereby providing a potentially important mechanistic link for influencing ecosystem structure and function. Further, the evolution

of different migratory strategies has significant implications from an ecosystem subsidies perspective. For instance, there are well-known latitudinal gradients of semelparity among salmon and clupeids along the Atlantic coast of North America. It would be interesting to know whether the selective forces that favored iteroparity at some latitudes and semelparity at others are influenced by latitudinal variation in the importance of material or process subsidies. If so, patterns of ecosystem-level responses to breeder mortality could have helped to drive life history evolution in these anadromous species. Alternatively, unrelated selective pressures might be responsible for such life history differences, in which case these factors have strong indirect ecological consequences through mediation of subsidies.

Biodiversity Loss of Migratory Fishes and Ecosystem Function

Migratory fishes are particularly susceptible to a suite of human activities such as river regulation, habitat degradation, and overharvest. Understanding the ecosystem consequences of their functional loss is a critically important area of future research in stream fish ecology. A large literature addresses the ecosystem impacts of dams on migratory species (e.g., Rosenberg et al. 1997; Pringle et al. 2000; Gregory et al. 2002; Freeman et al. 2003; March et al. 2003; Greathouse et al. 2006). While the deleterious effects of large dams on migratory fishes have received a great deal of attention, small dams are much more numerous and their overall impact may exceed that of large dams (March et al. 2003). Other small barriers are even more widespread such as road culverts, which can constitute barriers that significantly interfere with movement and increase the vulnerability of mobile fishes to predators (Warren and Pardew 1998; Gibson et al. 2005), yet the indirect effects of these disruptions to movement

are largely undocumented at an ecosystem level.

In addition to barriers, other threats have deleterious impacts on migratory fishes (Carolsfeld et al. 2003; Allan and Castillo 2007) and their capacity to act as material and process subsidies. The wide variety of impacts of land use and pollution on running waters can be especially problematic for migratory species that use large areas over the course of their lifetimes. Moreover, the ecosystem consequences of overharvest has been understudied (Allan et al. 2005) and are undocumented for all but a small number of freshwater migratory fishes. As mentioned previously, migratory fishes are targeted in many fisheries due to their historically large population sizes and the relative ease of harvest along migration corridors. Fisheries generally harvest preferentially the largest species, which can play special ecosystem roles, especially because many are apex predators (Allan et al. 2005) or can contribute disproportionately to community-wide nutrient recycling rates (McIntyre et al. 2007). Moreover, large-bodied frugivorous fishes such as pacus (*Piaractus brachipomus* and *Colossoma macropomum*) are important commercial species in the Amazon and Orinoco basins. The largest individuals are most vulnerable to the fisheries, and recent evidence indicates that these are the same individuals with the greatest potential to provide ecosystem services of seed dispersal (Galetti et al. 2008; Anderson et al. 2009).

Finally, in some cases migratory fishes are now so depleted or extinct that we can only conjecture about the historical roles they once may have played as key ecosystem drivers in the rivers they inhabited. The extinct upokoro or New Zealand grayling *Prototroctes oxyrhynchus* (Retropinnidae) provides a case in point (Figure 6). This diadromous fish reportedly ascended New Zealand rivers in immense shoals (Allen 1949) and was once so abundant

that early European settlers described their taking by the cartloads (Rutland 1878). However, soon after European settlement the fish began a precipitous decline, likely due to brown trout *Salmo trutta* introduction and habitat degradation, with the last-known specimen collected in 1930 (McDowall 1990). In addition to its large biomass, *Prototroctes* was apparently a functionally unique species with highly specialized dentition, and unlike other New Zealand freshwater fishes, it fed predominantly on filamentous algae. In fact, their presence was said to be detected by the occurrence of feeding scars left on the rocks where they recently foraged (Allen 1949). By all accounts, we can surmise that *Prototroctes* was a key process subsidy with its loss resulting in profound functional changes in New Zealand rivers in the absence of a functional analog. Unfortunately, the New Zealand grayling and its accompanying functional role as an abundant vertebrate grazer has permanently vanished. Nevertheless, our hope is that recognizing the diversity of subsidies provided by the extinct New Zealand grayling, as well as a host of extant migrants, aids in fostering a more comprehensive perspective on mobile fishes as indispensable components of riverine ecosystems.

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Figure 6. Top panel: The extinct Upokororo or New Zealand grayling. This once-abundant herbivore was last collected in the early 1930s. Reportedly, foraging individuals left distinct feeding scars on stones and the species was likely a highly specialized and functionally unique fish in New Zealand streams. Illustration by J. Buchanan, courtesy of The New Zealand Electronic Text Centre; image URL found at http://www.nzetc.org/tm/scholarly/Bio02Tuat01-fig-Bio02Tuat01_023a.html. Bottom panel: Maori fishermen setting a trap in a fish weir on the Waiapu River, New Zealand, March 1923. This appears to be the last known record of fishing for New Zealand grayling. Photograph by James Ingram McDonald, courtesy of the Alexander Turnbull Library.

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