

Ecosystem-Level Consequences of Migratory Faunal Depletion Caused by Dams

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Abstract.—Humans have been damming rivers for millennia, and our more ambitious efforts over the past century have arguably altered river ecosystems more extensively than any other anthropogenic activity. Effects of damming on river biota include decimation of migratory fauna (e.g., diadromous and potamodromous fishes and crustaceans), lost fisheries, and imperilment of obligate riverine taxa. Although effects of dams on biota have been widely documented, ecosystem-level consequences of faunal depletion caused by dams are only beginning to be appreciated. We discuss consequences to river ecosystems of altering distributions and abundances of migratory fauna, which often provide trophic subsidies and may strongly influence the structure of local habitats and communities. It is well documented that anadromous fishes can provide a major input of nutrients and energy to freshwater systems when spawning adults return from the sea. Other less-studied taxa that migrate between distinct portions of riverine systems (e.g., acipenserids, catostomids, and prochilodontids) may similarly provide trophic transfers within undammed river systems in addition to modifying local communities and habitats through feeding and spawning activities. Experimental faunal exclusions have demonstrated strong potential effects of some amphidromous shrimps and potamodromous fishes on benthic organic matter and algal and invertebrate communities. Depletion of these animals above dams is likely to significantly affect ecosystem processes such as primary production and detrital processing. The decline of freshwater mussels isolated by dams from their migratory fish hosts has likely lowered stream productivity, nutrient retention, and benthic stability. Greater focus on effects of dams on ecosystem processes, as mediated by faunal change, would improve our ability to assess the costs and benefits of future river management strategies.

Introduction

Dams form a pervasive feature of present-day river systems worldwide. The International Commission on Large Dams estimates that 42,000 large dams (>15 m high) existed in 1996 (Rosenberg et al. 2000); there are at least 800,000 small dams globally (McCully 1996). These estimates omit many uncounted dams that impound low-order streams; NRC (1992) cites an estimate of more than 2.5 million dams in the United States alone. Dams have transformed the main stems of many large rivers into stair-stepped chains of reservoirs connected by highly regulated flow regimes. Dams have facilitated water diversions to the extent that some major rivers, such as the Colorado in North America and the Nile in northern Africa, no longer

reach the sea in most years (Postel 1996). Societies around the globe continue to dam rivers, including largely intact systems such as the Brazilian Amazon (where 75 dams are planned or proposed; Fearnside 1995) and the Mekong (slated for 12 main-stem dams and >100 in the region; Dudgeon 2000; IRN 2001). Dams are constructed to meet a variety of social needs (e.g., hydropower generation, municipal and agricultural water supply, and navigation), but damming also incurs social and environmental costs (McCully 1996; Rosenberg et al. 1997). Included among these costs are effects of dams on the supply of goods (e.g., fisheries) and services (e.g., nutrient assimilation) provided by riverine ecosystems.

Dams and associated reservoirs influence environments at global (e.g., increased rates of greenhouse gas emissions to the atmosphere) to local (e.g., replacement of lotic by lentic habitat) scales (Rosenberg et al. 1997). Effects of damming on river

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biota similarly occur at different scales, including local losses of species that are intolerant of reservoir and dam-tailwater habitats, basin-wide decimation of migratory fauna, regional losses of fisheries, and imperilment of obligate riverine taxa (reviewed by Dudgeon 2000; Pringle et al. 2000). Although many stream-dependent species may persist in dam-altered basins, populations are often reduced in local abundances and are restricted to fragments of their former ranges.

In this paper, we discuss consequences to river ecosystems of altering distributions and abundances of migratory fauna (i.e., diadromous and potamodromous fishes and crustaceans) brought about by dams. Ecosystem-level effects include changes in productivity, community structure, and fluxes of nutrients and carbon. Migratory fauna often provide spatial nutrient and energy subsidies and may strongly influence the structure of local habitats and communities (Polis et al. 1997). Dams fragment stream systems, restricting flows of biota as well as materials between headwaters and downstream water bodies, rivers and floodplains, and uplands and estuarine systems. The direct effects of this fragmentation on populations of migratory fauna are widely recognized, but reciprocal effects of faunal changes on other components of stream and riparian systems are less widely appreciated. Understanding potential consequences of faunal decline and loss for the productivity and community structure of stream ecosystems affected by dams is essential for holistic management.

Our objectives are to summarize evidence that shows strong ecosystem effects of depleting migratory fauna and to discuss effects that have generally gone unrecognized but that merit consideration. Our discussion is based on data from New World temperate and tropical streams, but we speculate that these principles apply globally. We have divided effects of migratory stream fauna into two general categories: (1) fauna as sources of trophic subsidies (i.e., as prey and in the form of carcasses, eggs, and excretory products) and (2) fauna which are strong interactants (i.e., through feeding and bioturbation; Paine 1992) within stream communities. For each faunal category, we discuss how dams have affected these taxa and consequences for ecosystem processes. We conclude by discussing implications for river management.

Migratory Fauna as Nutrient and Energy Subsidies

Anadromous Fauna

The deleterious effects of dams on migratory taxa are widely documented, particularly declines in commercially important diadromous fishes. Pacific salmon (seven *Oncorhynchus* spp.) have been severely diminished by extensive damming of North American coastal rivers, contributing to extirpation of more than 100 native stocks and imperilment of over twice as many more (Nehlsen et al. 1991). Salmon runs that once totaled more than 50 million fish are reduced to less than 4 million in Washington, Oregon, Idaho, and California, where returning fish are blocked from about 40% of their native range (Gresh et al. 2000). Other anadromous fishes have similarly declined, in large part because dams have blocked spawning runs. The Atlantic salmon *Salmo salar* has been extirpated from North American rivers south of Maine to Connecticut, and the remnant wild runs in the USA are protected under the Endangered Species Act. Historically large runs of anadromous shads and herrings (including six North American *Alosa* spp.) have declined sharply in numbers and distance traveled inland (Garman 1992; Jenkins and Burkhead 1994). American shad *A. sapidissima* once ascended rivers along the East Coast of North America from Canada to Florida in spawning runs that numbered at least in the hundreds of thousands; runs have been reduced to less than 10% of historic sizes and have been extirpated from more than 4,000 km of river habitat (Limburg et al. 2003, this volume). Anadromous alosines have been similarly restricted by dams in Europe (Baglinière et al. 2003, this volume) and Asia (Dudgeon 2000).

The loss of anadromous fish populations extends beyond lost fisheries to effects on ecosystem function. The best studied example is the loss of marine-derived nutrients (MDN) and biomass supplied by anadromous salmonids in the Pacific Northwest, where the importance of returning adult salmon has been well documented over the past several decades (reviewed by Ben-David et al. 1998 and Gresh et al. 2000). Large runs of spawning salmon provide a pulsed input of prey and nutrients to coastal and inland streams. In south-eastern Alaska, more than 40 spp. of birds and mammals congregate to prey on large runs of anadromous fish including salmon and smelt (e.g., eulachon *Thaleichthys pacificus*; Willson and Halupka 1995; Willson et al. 1998). Floods and terrestrial predators transfer some portion of the bio-

mass of anadromous spawners to terrestrial systems in the form of carcasses and excretory products, with subsequent fertilization effects on riparian vegetation (Bilby et al. 1996; Ben-David et al. 1998; Willson et al. 1998). Growth rates of riparian trees may be significantly enhanced by marine-derived nitrogen delivered by spawning salmon, with a positive feedback in the form of increased input of habitat-forming large woody debris to the stream (Helfield and Naiman 2001).

Nutrients released from carcasses of postspawning fish can provide a substantial subsidy to aquatic foodwebs by stimulating periphyton and bacterial productivity (Richey et al. 1975; Kline et al. 1993) and by sorption onto streambed gravels and subsequent incorporation into epilithic organic matter, invertebrates, and fish (Bilby et al. 1996). Carcasses, salmon eggs, and fry are also directly consumed by aquatic invertebrates and fish (Bilby et al. 1996). The significance of MDN to freshwater systems may depend on whether nutrient availability limits stream productivity and whether the survival rate of juveniles to returning adult fish is sufficient to outweigh the biomass exported by outmigrating juveniles (Gross et al. 1998), but the potential significance is clear. The 92–95% decrease in annual biomass of salmon returning to Washington, Idaho, Oregon, and California streams means that “just 5–7% of marine-derived nitrogen and marine-derived phosphorus once delivered annually to rivers of the Pacific Northwest is currently reaching those streams” (Gresh et al. 2000).

Anadromous shads likely provide, or provided, similarly large subsidies of nutrients and carbon to riparian systems. Garman (1992) estimates that the nontidal James River, Virginia, may have received annual biomass input from anadromous alosines of 155 kg/ha (assuming 3.6 million fish with 70% postspawning mortality) before dams blocked shad passage above the fall line (the geographic transition from Piedmont to Coastal Plain) in the 1870s. The density of biomass contributed to small New England ponds by postspawning mortality of anadromous alewife *A. pseudoharengus* can exceed that of some Alaskan salmon runs (Durbin et al. 1979). The fishing pressure on the run studied by Durbin et al. (1979) had diminished the nutrient and carbon influx from alewives by about 80%. Even at reduced abundances, Durbin et al. could detect accelerated detrital decomposition in streams with migrating alewife, attributed primarily to fertilization from carcasses and secondarily to fish excretion. Anadromous shad also subsidize upper trophic levels. Juvenile anadromous alewife and

blueback herring *A. aestivalis* are high-quality prey for resident largemouth bass *Micropterus salmoides* in coastal headwater lakes, boosting growth of younger bass in lakes where herring consumption is high (Yako et al. 2000). Samples of predatory fish taken from tidal freshwaters after the residence of migrating alosines had greater than 35% (Garman and Macko 1998) and up to 84% (MacAvoy et al. 2000) of their biomass carbon derived from marine sources, based on stable isotope analyses. Garman and Macko (1998), citing a 90% reduction in *Alosa* abundances in the Chesapeake Bay landscape over the last 30 years, conclude, “the ecological roles hypothesized for anadromous *Alosa* spp. may now be greatly diminished compared to historical conditions.”

Amphidromous Fauna

Amphidromous taxa migrate between freshwater and marine habitats at a particular life stage for reasons other than breeding (Myers 1949). Amphidromous freshwater shrimps (e.g., *Atya* spp., long-faced shrimp *Xiphocaris elongata*) and gobiid fishes (Gobiidae, e.g., *Sicydium* spp.) have declined in response to damming in tropical streams. The life cycle of amphidromous shrimp taxa (March et al. 1998; Benstead et al. 2000) and gobies (Erdman 1961) is characterized by adults living and spawning in upland streams; larvae passively drift downstream to estuaries, and juveniles migrate back upstream (Figure 1). In Puerto Rico, all native fishes, including the green stream goby *Sicydium plumieri* and freshwater shrimps, are extirpated upstream from large (>20 m) dams with no spillway discharge (Holmquist et al. 1998). Low-head dams in Puerto Rico may also be causing declines in shrimp populations. Water diversions at low-head dams for municipal use cause direct mortality to migrating shrimp larvae (e.g., 34–62% of drifting first-stage larvae), and the concrete barrier and low water flows behind the dams may impact the upstream migration of juvenile shrimp (Benstead et al. 1999). Amphidromous freshwater shrimps and fishes are also reported to be affected by dams in Guadeloupe (Fièvet 1999), Japan (Miya and Hamano 1988), Guam (Concepcion and Nelson 1999), New Zealand (McDowall 2000), and the United States (Bowles et al. 2000).

The nutrient subsidy and trophic consequences of larval amphidromous shrimps and fishes to estuarine and coastal areas have yet to be evaluated. Dams and associated water withdrawals can potentially have cascading trophic effects by removing this important food source for estuarine and

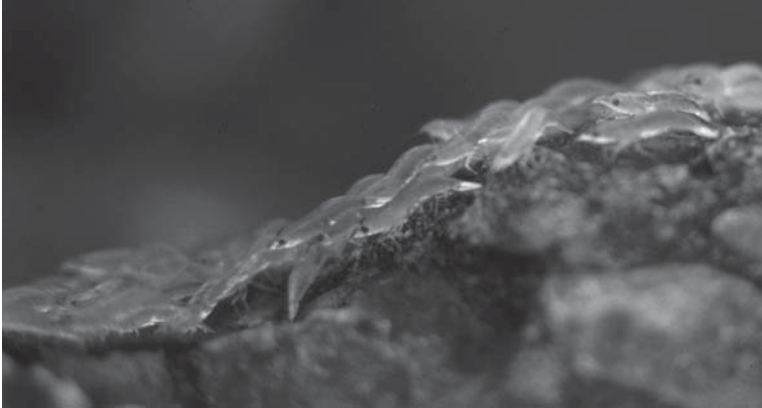


Figure 1.—Juvenile amphidromous freshwater shrimp migrating upstream at a low-head dam on the Culebrinas River, Puerto Rico. At migratory bottlenecks (e.g., waterfalls and low-head dams), juveniles can be seen crawling up splash zones in large numbers. Photograph by J. March (University of Georgia).

coastal fishes. March et al. (1998) conservatively estimate losses of 377 g dry mass/d of larval shrimp biomass (15.3 million larvae/d) for the entire Caribbean National Forest (113 km²) given that 50% of the water leaving the forest is currently withdrawn on an average day (Naumann 1994). This translates to 137.6 kg dry mass of larvae lost per year (5.5 billion larvae) to water withdrawals. Further research will be required to determine the significance of drifting amphidromous larvae to downstream consumers (i.e., relative to other prey sources), but this example illustrates a potential effect of depleting amphidromous taxa. Declines in adult populations upstream of dams (resulting from decreasing recruitment; Holmquist et al. 1998; Benstead et al. 2000) may also have cascading trophic effects, which are discussed later in this paper (See *Migratory Fauna as Strong Interactors*).

Potamodromous Fauna

Dams have directly (by blocking migrations) and indirectly (e.g., through effects on floodplains and flood regimes) reduced abundances and ranges of long-lived fishes that historically migrated among river habitats to spawn. Examples of potamodromous fishes that have declined in response to hydrologic alteration include sturgeons (Acipenseridae) in the northern hemisphere (Birstein 1993), suckers (Catostomidae) and minnows (Cyprinidae) in North America and Asia (Dudgeon 2000; Pringle et al. 2000), and prochilodontid (*Prochilodus* and *Semiprochilodus* spp.) fishes in South America (Duque et al. 1998). Similarly, future dam development is expected to deleteriously affect migratory catfishes in Asia

(Pangasiidae; Dudgeon 2000) and South America (Pimelodidae and Doradidae; Barthem et al. 1991). Dams have also been found to disrupt migrations of the Amazon River dolphin *Inia geoffrensis* and the gray dolphin *Sotalia fluviatilis* and to affect the food source of dolphins by severing migrations of fish prey (Reeves and Leatherwood 1994).

Distances traveled by most potamodromous fishes are poorly understood, but animals may migrate considerable distances and between geomorphically distinct portions of river systems. Amazonian catfishes such as piramutaba *Brachyplatystoma vaillanti* and dourada *B. flavicans* (also known as gilded catfish) traverse thousands of km and ecologically connect a large part of the Amazon basin, from estuaries to headwaters, through their reproductive cycles and food web relationships (Barthem and Goulding 1997). Sturgeon species migrate from marine or estuarine habitats, or from lakes or lower portions of rivers, to upriver sites to spawn in fast-flowing water (Auer 1996). The lakesuckers *Chasmistes* spp. and Lost River sucker *Deltistes luxatus* (Scoppettone and Vinyard 1991) of western North America also migrate between distinct freshwater habitats to spawn (e.g., from lakes into tributaries). The southeastern blue sucker *Cycleptus meridionalis* migrates some 200 km between spawning and overwintering habitats in the lower Alabama River, Alabama (Mettee et al. 1996), and might travel farther were its upstream movements not blocked by a dam. The Colorado pikeminnow *Ptychocheilus lucius*, now restricted to about 20% of its former range in the Colorado River basin, may migrate more than 300 km to distinct spawning sites (Tyus 1990). Similar

long-range movements may have been common among large-bodied riverine fishes prior to widespread river fragmentation by dams.

Migratory riverine fishes presently support large fisheries in Asia and South America; for example, piramutaba and dourada are among the five most important food fishes for human populations in the Amazon (Barthem and Goulding 1997). Migratory riverine fishes were also substantially more abundant in North America prior to widespread damming. Hesse et al. (1993) documented large fishery declines following main-stem damming of the Missouri River; however, the historic abundances of many migratory fishes are less well documented. A mid-19th century account hints at the bounty provided by fishes gathered to spawn in river shoals near Montgomery, Alabama: "One visitor recalled meeting 'several persons coming up from the river with many fine large fish, called buffaloes, of which it was said upwards of 500 were caught, at a single haul'... Locals would not have given that catch a second look" (Jackson 1995). E. D. Cope, in his 1870 report on fishes of North Carolina, noted the abundances of a number of redhorse suckers (*Moxostoma* spp.) in spring and autumn catches at weir traps and decried the use of baited spring traps to take "cart loads" of robust redhorses *M. robustum* (Cope 1870). The case of robust redhorse exemplifies what we do not know about fish movements and the significance of lost migratory fishes to stream ecosystems. This species has declined to the point of apparent extirpation from all except three river systems in its native range on the south Atlantic Slope, nearly all of which have been dammed at the fall line. Extant populations in the Altamaha and Savannah rivers (Georgia and South Carolina) migrate unknown distances upstream to spawn in the only riffle habitats remaining downstream from fall line dams. Data recently obtained through attempts to establish an experimental population in a Savannah River tributary show that immature fish will travel downstream at least 80 km (where they encounter a reservoir) and that mature adults may make the return trip upstream to riverine habitats (B. J. Freeman, unpublished data). To the extent that robust redhorses and other historically abundant riverine fish migrate between distinct portions of river systems to complete their life cycles, these populations could transfer significant amounts of nutrients and carbon between river habitats, especially if spawning-related mortality is high.

The significance of declines and local extirpations of sturgeons, suckers, Amazonian catfishes,

and other migratory riverine fishes to nutrient dynamics of stream ecosystems is largely unexplored. Because individuals typically spawn in multiple years, postspawning mortality presumably is not a concentrated source of nutrient addition to stream habitats, as in the case of semelparous salmonids and alosines. However, results from one attempt to quantify total fish migrations in a small heterotrophic stream show a net upstream displacement of biomass with more large individuals moving upstream during spring spawning runs than returning downstream (Hall 1972). Mortality associated with spawning could be high relative to mortality associated with other adult activities given the energetic demands of spawning and increased vulnerability of spawning fish to predation. Willson and Halupka (1995) report bald eagles *Haliaeetus leucocephalus* preying on spring runs of suckers in midwestern streams. Catostomids often spawn in large aggregations in shallow-water riffles where they could be relatively vulnerable to terrestrial predators. Additionally, dense aggregations of large-bodied spawning fish certainly could contribute a seasonal subsidy in the form of gametes and juveniles to local food webs. In southeastern U.S. streams, minnows aggregate downstream from spawning suckers, and captured individuals have guts packed with eggs (B. J. Freeman and M. C. Freeman, personal observations), conceivably reflecting an important subsidy to small fish, themselves in the process of reproductive maturation.

Migratory Fauna as Strong Interactors

Detritivores and Algivores

Many of the migratory taxa that have declined in response to damming in neotropical streams feed on benthic detritus and algae. Examples include amphidromous freshwater shrimps and gobies (discussed above) as well as a potamodromous fish, the flannelmouth characin *Prochilodus mariae*. The flannelmouth characin undergoes extensive migrations within river systems in the neotropics. Adult flannelmouth characin forage in upland streams and rivers during the dry season, migrating downstream to feed and reproduce in floodplains during the wet season; juveniles and adults migrate back upstream as the floodplain dries (Duque et al. 1998). Flannelmouth characin migrations are blocked by dams on at least nine rivers in Venezuela; individuals trapped upstream of the Bocono Dam appear unable to reproduce, and the population down-river of the dam is diminished by re-

duced wet-season flooding and effects of hydro-power generation (Duque et al. 1998).

Experimental studies provide strong evidence of the importance of these migratory species to the structure of stream communities. Studies of shrimp in montane Puerto Rico indicate that they can structure benthic stream ecosystems on a variety of scales. In low-order streams dominated by atyid shrimp (Decapoda: Atyidae), shrimp alter benthic community structure and algal species composition and reduce algal standing crop and fine benthic organic matter (Pringle et al. 1993; Pringle and Blake 1994; Pringle 1996; March et al. 2002). Shrimp also increase leaf litter processing in low-order streams (Crowl et al. 2001; March et al. 2001). Shrimp effects depend on their location along the stream continuum, with strong effects on algal communities in middle and upper reaches and on detrital processing only in upper reaches (March et al. 2001, 2002). Shrimp also influence interstream differences in algal communities and the quantity and quality of fine particulate organic matter (FPOM). Low-order streams with abundant atyid shrimp have low levels of algae, FPOM, and a lower carbon to nitrogen ratio, compared to low-order streams with low densities of atyids (Pringle et al. 1999). Migratory freshwater shrimp in Costa Rica *Macrobrachium* spp. also affect benthic organic matter, sediments, algae, and insects (Pringle and Hamazaki 1998). Preliminary observations in Puerto Rico show measurable benthic algal and organic matter differences in rivers upstream from large dams where shrimp and gobies are extirpated compared to rivers with no large dams (Figure 2; E. A. Greathouse, unpublished data).

Flannelmouth characin (and likely other migratory, floodplain-dependent fishes) represents an upstream flux of nutrients and carbon as well as a direct modifier of local stream communities and possibly of production and decomposition rates. Flecker (1996) has characterized the detritivore-*algivore* flannelmouth characin as an "ecosystem engineer" because instream enclosure-exclosure experiments showed that it decreased accrual of fine inorganic and organic matter and altered algal and invertebrate assemblages in Venezuelan streams. Similarly, *algivorous* gobies *Sicydium salvini* reduced benthic sediment accumulation and periphyton biomass and increased densities of glossosomatid caddisflies (order Trichoptera, family Glossosomatidae) in a Costa Rican stream (Barbee 2002).

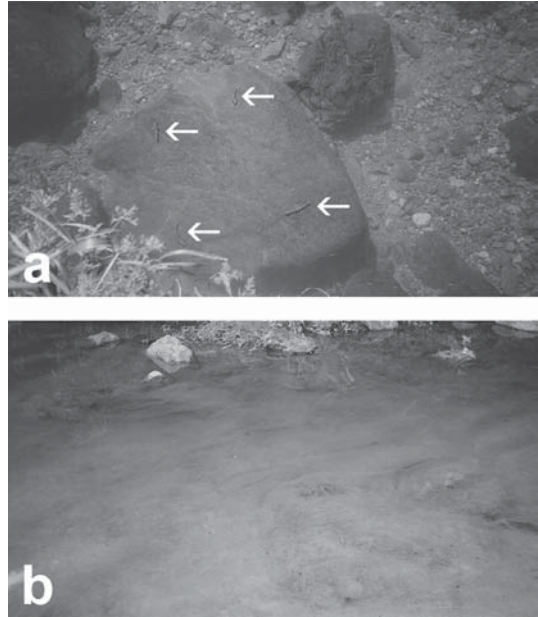


Figure 2.—Algal biomass, benthic organic matter, and fine sediments in rivers in Puerto Rico may be affected by extirpation of native fauna due to dams. Substrate in the Guayanilla River (a) is "clean," with low amounts of benthic algae, fine particulate organic matter, and fine sediments. The Guayanilla River has no large dams and an abundance of native bottom-feeding fishes (the green stream goby) and freshwater shrimps. Arrows point to four stream gobies (images enhanced). Algal bloom in the Toa Vaca River (b), approximately 2.5 km upstream from the Toa Vaca Reservoir, is shown. All native fishes and shrimps have been extirpated from this river because the 61-m-high Toa Vaca dam blocks their migration (Holmquist et al. 1998). Photographs by E. Greathouse.

Predators and Competitors

Many migratory organisms diminished by dams, including most of the anadromous and potamodromous fishes discussed above and diadromous taxa such as anguillid eels *Anguilla* spp. (Allibone 1999; Haro et al. 2000), mountain mullet *Agonostomus monticola*, and sleepers (Eleotridae; e.g., bigmouth sleeper *Gobiomorus dormitor*; Holmquist et al. 1998), prey on invertebrates and other fishes. The extirpation or diminished abundances of predators is likely to alter food web dynamics. For example, predatory fishes, including an anadromous species (rainbow trout *O. mykiss*) in a California river, depress smaller-bodied predators of herbivorous midges (Chironomidae) that indirectly leads to reduced algal standing stocks (Power 1990). Elimination of top predators or changes in the physical regimes that mediate spe-

cies interactions (e.g., by dams and hydrologic alteration) are likely to affect food web dynamics (Power et al. 1996). Losses of competitors may also alter communities and food webs. For example, extirpation of long-finned eels *Anguilla dieffenbachi* (also known as New Zealand longfin eels) above dams in New Zealand may allow the threatened koaro *Galaxias brevipinnis* to become competitively dominant over and displace other threatened galaxiid species (Allibone 1999).

Effects of predator or competitor loss may be difficult to predict (Power et al. 1996) or to identify in systems that have already been faunistically altered. For example, the effects of eliminating the American eel *Anguilla rostrata*, an often abundant, large-bodied omnivore, on aquatic food webs are unquantified but could be substantial. Similarly, what has been the effect of eliminating seasonal occurrences of large fishes such as sturgeons (Figure 3) from upper portions of river systems? Likewise, if damming proceeds as planned in the Amazon basin, how will the migratory patterns of large predatory fishes such as dourada and piramutaba be altered and how might this affect ecosystem processes?

Bioturbators

Some fishes diminished by dams, including salmonid and catostomid species, form dense spawning aggregations and bury their eggs in streambed sediments. These taxa have the potential for physically

modifying benthic habitats and communities during and for some period subsequent to spawning. Salmonids displace finer particles from bed sediments though the action of redd construction (Kondolf et al. 1993). Peterson and Foote (2000) reported temporary increases in surface gravel size, the abundance of drifting insects, and drift feeding by juvenile salmon in response to spawning activities of sockeye salmon *O. nerka* in two small Alaskan streams. Effects of benthic stream spawners other than salmonids are, to our knowledge, largely uninvestigated. What was the effect of historically large spawning aggregations of redhorse suckers on bed sediments and benthic community composition in river shoals? Robust redhorses bury eggs in gravel and cobble substrates to a depth of at least 0.18 m, and the spawning trio of two males flanking a female creates a plume of displaced sediment (B. J. Freeman and M. C. Freeman, personal observations). We have similar observations for four other sucker species (river redhorse *Moxostoma carinatum*, golden redhorse *M. erythrurum*, v-lip redhorse *M. collapsum*, and spotted sucker *Minytrema melanops*), and we hypothesize that spawning aggregations could temporarily alter substrate particle composition and periphyton and invertebrate communities and provide a pulsed increase in prey availability to drift feeders. Co-occurring sucker species frequently spawn sequentially from early to late spring. Thus, historical abundances of spawning suckers may have significantly affected food webs in river



Figure 3.—Atlantic sturgeon *Acipenser oxyrinchus* captured from the Oconee River near the fall line (>300 km upriver from the Atlantic Ocean) at Milledgeville, Georgia, around 1900. *Acipenser* spp. now rarely occur this far inland in Atlantic and Gulf Slope river systems, in part because dams block upstream migrations. Photograph from University of Georgia archives.

shoals, through bioturbation and trophic subsidies in the form of eggs and perhaps carcasses, over a protracted period.

Fauna Dependent on Migratory Species

Freshwater mussels (Unionoidea) provide prime examples of fauna that have declined in part because of their dependence on migratory species. Mussels historically formed a widespread and often abundant component of the benthic fauna in streams of eastern North America (Strayer et al. 1994). Some large river mussel assemblages were legendary for their size and diversity, such as at Muscle Shoals in the Tennessee River (Ortmann 1924). Mussels are presently among the most imperiled of freshwater faunal groups and have declined in large part because of habitat and flow alteration by dams and impoundments (Layzer et al. 1993; Williams et al. 1993; Neves et al. 1997; Vaughn and Taylor 1999). Dams have also indirectly caused mussel extirpations by blocking migrations of host fish required by the parasitic larval stage of mussels (Williams et al. 1993; Watters 1996). For example, the ebonyshell *Fusconaia ebena*, historically one of the most abundant mussels in the upper Mississippi River, was extirpated from the upper Mississippi following construction of a dam at Keokuk, Iowa, which blocked migration of the mussel's host, skipjack herring *Alosa chrysochloris* (Theler 1987). Conversely, the alewife floater *Anodonta implicata* expanded its upstream range at least 200 km in the Connecticut River following the provision of passage for anadromous alosines at each of four dams on the river (Smith 1985). Williams et al. (1993) consider elimination of host fish the largest effect of dams on freshwater mussels.

The effects on stream systems of eliminating mussels from river systems are not well studied but could be substantial (Strayer et al. 1994, 1999). Mussel species vary but can be large (i.e., >30 cm; Williams et al. 1993) and long-lived (e.g., >100 years; Vaughn and Taylor 1999). The elimination of dense populations of these relatively sedentary filter feeders likely includes substantial losses in system productivity, decreased local retention of nutrients, and alterations in the structure and stability of the benthic stream environment (Strayer et al. 1994, 1999).

Implications

Despite the enormous number of dams worldwide, many river basins still retain a substantial length of unimpounded habitat that supports stream-dependent biota and provides other ecosystem benefits (e.g.,

water supply, runoff absorption, nutrient processing, recreation, and wildlife habitat; Postel and Carpenter 1997). However, even when streams retain good physical integrity, they are likely to be biologically altered if they are isolated by structures that impede faunal movements. The growing evidence for effects on stream function of losing migratory fauna implies that these effects should be explicitly considered in decisions of whether and where to build dams or how to manage regulated river systems. In contrast, faunal losses associated with dam construction or operation most often become an issue only if the species involved support fisheries or are legally protected under endangered species laws such as the U.S. Endangered Species Act. In either case, if the species can be sustained through alternative means (e.g., hatchery propagation or population relocation), the issue is typically considered addressed. This species-centered approach overlooks the importance of those species to ecosystem processes, including stream productivity and nutrient retention.

In parts of the world where rivers have been extensively fragmented by dams, including the continental United States (Benke 1990) and Europe (Dynesius and Nilsson 1994), even seemingly high-quality streams likely function much differently than they did when they were parts of interconnected river systems. Clearly, it is difficult to separate effects of fragmentation from those of channel modification (including large-scale removal of large woody debris; Maser and Sedell 1994), pollution, changes in land cover, and faunal changes such as loss of beavers *Castor canadensis* (Naiman et al. 1986). However, increasing evidence for effects of migratory fauna on nutrient and carbon processing suggests that fragmentation has altered stream ecosystems apart from effects of other physical changes. We hypothesize that streams draining much of our landscape are substantially less productive than when they were open to migratory aquatic fauna. These streams likely have fewer trophic pathways and reduced biotic capacity for processing detrital and algal resources and have lost seasonal imports of biomass, nutrients, and/or consumers. Lowered productivity and lost trophic subsidies are not necessarily restricted to headwater streams; downstream habitats may lose populations of consumers dependent on upstream habitats (e.g., for spawning) as well as inputs provided by pulsed fluxes of migrants (e.g., drifting larvae). For humans, the most obvious consequences are lost fisheries; all of the migratory taxa discussed above have at some time provided significant fisheries. However, other consequences

may include: noxious algal blooms (e.g., with the loss of benthic algivores), reduced capacity to process and retain nutrients (e.g., with the loss of trophic pathways and productivity), and detrimental effects on riparian (Helfield and Naiman 2001) and wildlife (Willson and Halupka 1995; Willson et al. 1998) populations.

We have focused on effects of stream fragmentation and accompanying losses of migratory fauna because societies are currently making decisions about developing future water supply and hydroelectric capacity. Developing regions of Latin America, such as Brazil, propose to meet over half of future electricity needs from large dams on the Amazon (Best and daSilva 1989). In contrast, in developed regions, water supply alternatives may include building many small or fewer large dams, reducing demand (e.g., through conservation) rather than expanding supply, or protecting portions of river systems to provide for uniquely river-derived goods and services. In highly altered basins, societal values may be best served by removing dams or investing resources in constructing passage past dams for migratory fauna. Ideally, these decisions will be built on a holistic understanding of the ability of stream systems to provide irreplaceable services such as self-sustaining fish and wildlife populations under alternative development scenarios. Ecologists and fisheries biologists could probably predict many of the effects of a particular scenario of dam construction on river fauna and particularly on migratory fauna. We need a better understanding of the ecosystem consequences of those faunal changes.

At least three approaches are likely to provide insight and enhance understanding of the consequences of altering stream faunal assemblages. Modeling processes and pathways including species interaction webs (Power et al. 1996) and nutrient fluxes based on best available knowledge will help in identifying potential effects of faunal alteration. Testing for faunal effects through field experiments in streams with relatively intact fauna (Flecker 1996; Pringle et al. 1999; Crowl et al. 2001) has and will continue to provide valuable insights on mechanisms. Finally, comparisons of dammed and undammed rivers could give insights on the extent to which effects of migratory fauna on ecosystem properties evident at experimental scales operate at large scales. In summary, providing stakeholders a better understanding of ecological consequences of dams, faunal extirpations, or restoring migratory populations is a critical component of improving management of stream resources.

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