Historical Impacts on River Fauna, Shifting Baselines, and Challenges for Restoration

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The decimation of aquatic wildlife through overexploitation is usually perceived as a marine phenomenon, yet it has also been common in freshwater ecosystems. Fish and other aquatic animals were superabundant when Europeans first arrived in North America and Australia, and were intensively exploited soon after. Contemporaneously, the construction of barriers in rivers increasingly prevented many species from migrating. Populations usually crashed as a result. Natural resource managers have not fully considered the ecological impacts of the devastation of these species to the environmental degradation that we see today, yet these impacts are likely to be pervasive. Nor have resource managers embedded the role of these species in river restoration. We argue that the functions of these depleted stocks need to be considered and perhaps reestablished if river restoration efforts are to be successful. The establishment of freshwater protected areas may be the most effective way to do this.

Keywords: overharvesting, freshwater, fish, North America, Australia

All human populations modify the landscapes and ecosystems they inhabit, whether by direct exploitation of natural resources or through activities such as damming rivers or introducing alien species (Reynolds et al. 2001, Olden et al. 2008). Although less technologically advanced societies can affect their environments profoundly over time (Pinnegar and Engelhard 2008), especially when colonizing islands, it is typically postindustrial societies that have made the biggest impact on the natural environments of continents (e.g., Crosby 2000).

The process of large-scale, dramatic, anthropogenic environmental change had been occurring in western Europe since medieval times, but the major emigration of Europeans during the 17th and 18th centuries to parts of the world that had hitherto been influenced only by indigenous peoples with relatively low population sizes produced rapid and dramatic environmental changes (Crosby 2000). Those colonizers who formed coastal communities looked to the sea for subsistence and, later, for wealth. The environmental cost was huge. Indeed, historical overharvesting of marine animals, including fishes, whales, and oysters, has been implicated in the collapse of coastal ecosystems (Jackson et al. 2001, Saenz-Arroyo et al. 2006). In each case, a species or stock, such as Atlantic cod or Chesapeake Bay oysters, was harvested to the point of ecological extinction, and the wide-ranging effects of their decimation on food webs are still evident today. Overharvesting, it has been argued, was typically the first environmental disturbance in coastal and estuarine ecosystems colonized by postindustrial societies, occurring before severe habitat alteration, pollution, or introduction of alien species (Jackson et al. 2001).

But many coastal communities also looked to freshwaters to supplement food from the sea (Vickers 2004), and settlement was by no means limited to coastal regions. European colonists in North America and Australia, in particular, made their way inland relatively early in the colonization process, usually settling near lakes or along rivers (Crosby 2000). Exploitation of freshwater animals began right away: People took advantage of abundant aquatic wildlife, typically moving through a series of steps from subsistence, artisanal, and semicommercial fishing to, finally, fully commercial fisheries (see, e.g., Trautman 1981, Vickers 2004). The largest fish species were targeted most intensely (see, e.g., Rowland 1989, Meengs and Lackey 2005), but other animals became commercially important soon after (Naiman et al. 1988, Anthony and Downing 2001). In virtually every case, overharvesting rapidly devastated stocks of the most economically valuable species.

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Unlike the situation in coastal and estuarine ecosystems, however, early exploitation of freshwater wildlife came only shortly before another major environmental disturbance: weir and mill construction (Walter and Merrits 2008). Weirs were built to store water and to power water mills to grind grain crops (Walter and Merrits 2008). This further affected fishes that migrated upstream and downstream at different times in their life cycles and exacerbated the effects of overharvesting (Vickers 2004, Meengs and Lackey 2005). There are myriad accounts of the devastation that these combined disturbances caused to a large number of riverine species (see below).

With overexploitation of the fauna and disruption to freshwater ecosystems typically occurring many decades before the first quantitative stock assessments, one can only imagine what historic numbers were like. Thus, ecologists and managers may be deceived by "shifting baselines"—that is, they may accept that environmental conditions of the immediate past reflect conditions in the intermediate and distant past (Pauly 1995, Sheppard 1995, Pinnegar and Engelhard 2008). This is extremely worrisome for modern efforts aimed at ecosystem restoration (Palmer et al. 2005, Choi 2007, Seddon et al. 2007). River restoration requires targets, which depend on either knowledge of historical conditions or a reference system that is relatively free from human impacts and can serve as a model of what the river and its biota ought to look like (Palmer et al. 2005). With an inadequate or false impression of past conditions, our ability to set targets and to achieve them is flawed and subject to failure. If, as more and more ecologists believe, restoring aquatic ecosystems requires more than restoring the physical and chemical environment (e.g., Holmlund and Hammer 1999, Jackson et al. 2001, Pitcher 2001), then the effects of historical loss of species, and how this in turn affects food webs, must be recognized and integrated in these activities.

Here we aim to demonstrate that overharvesting of freshwater animals (especially, but not exclusively, of large, valuable fishes)—a common occurrence in regions of the world newly colonized by pre- and postindustrialized settlers—and other anthropogenic disturbances (damming of rivers, erosion, and agricultural practices, e.g.) reduced stocks rapidly, resulting in the potential for far-reaching effects on food webs. We argue that, as with marine fisheries, the passage of time and the lack of data about conditions before these disturbances commenced obscure our perception of historic conditions, making it difficult to establish accurate restoration targets. Although we contend that there is no going back to historic conditions—growing pressures on freshwater systems and watersheds prevent this—we nonetheless need to learn from the past, determine which components of the biota contributed to the structure and function of ecosystems, and attempt to mimic these conditions when restoration efforts are made. We also argue that establishing freshwater protected areas and identifying and addressing key environmental stressors, together with reintroductions of extirpated species, provide the best opportunity for reestablishing key ecosystem functions.

Historical abundance of freshwater wildlife

During the early part of the 17th century, settlers quickly exploited the vast freshwater resources they encountered in eastern North America (Vickers 2004). In New England, for example, sturgeon, eels, salmon, shad, and alewives were seen in enormous numbers, with the anadromous species being the most conspicuous because of their massive upstream migrations during spring and summer. Around 1620, Captain John Smith recorded that pilgrims had caught more than 12 hogsheads of fish in one night's fishing (a colonial American hogshead was 48 × 30 inches [122 × 76 centimeters] and could hold about 1000 pounds [454 kilograms] of tobacco) (Vickers 2004). Salmon runs were breathtaking in their size, and at times took up the whole width of the river. In 1637 Thomas Morton observed: "Every man in New England may catch what he will [of sturgeon], there are multitudes of them" (Dempsey 2000, p. 85), and, "There is a fish by some called Shad, by some called Alewives, that at the spring of the year pass up the rivers to spawn in the ponds; and are taken in such multitudes in every river that hath a pond at the end, that the Inhabitants dung their ground with them. You may see in one township a hundred acres together set with these fish, every acre taking 1000 of them" (Dempsey 2000, p. 86).

The Ohio River valley had a similar superabundance of fish. Eighteenth-century travelers and settlers described the huge numbers of pike, walleye, catfish, buffalofish, suckers, drum, and sturgeon, as well as small fish such as sand darters, chub, riffle darters, and minnows (Trautman 1981). Fish were described as being so numerous that a spear thrown into the water only rarely missed one. On the other side of the continent, Lewis and Clarke recorded in 1804 the enormous abundance of salmon in the Columbia River and local people's exploitation of them (Meengs and Lackey 2005). Numbers were so high that the people of that region were able to live in large, permanent groups and had time to develop sophisticated culture, art, and technology (Carson 1996).

Before and during the early years of European settlement, many Aboriginal people in Australia also relied heavily on aquatic wildlife—including fish, crayfish, waterfowl, and their eggs—especially during periods of flooding (Humphries 2007). Fish are central figures in Aboriginal creation myths associated with the Murray River, and some rivers, such as the Paroo, were named after their dominant fish species ("paroo" means bony herring). Explorer George Evans, after crossing the Blue Mountains west of Sydney, observed that "if we want a Fish it is caught immediately; they seem to bite at any time; had I brought a quantity of salt we could cure some 100 [pounds] of them, I am quite astonished at the number the Men catch every Evening" (Evans 1814, p. 24); the cattleman Joseph Hawdon noted that in the evening on the Goulburn River, in southern Australia, "We caught, with hooks and lines, as many cod [presumably Murray cod, *Maccullochella peelii peelii*] as would have supplied a hearty meal for five times our number"—and there were nine in his party (Hawdon 1952, p. 16.). Another explorer, Charles Sturt, described the large numbers of fish caught by the local Aboriginal people wherever his party traveled; he observed that when the Murrumbidgee River, in New South Wales, was rising, "the fish were rolling about on the surface of the water with a noise like porpoises" (Sturt 1982, p. 42). Fish were so plentiful in some places that they were used as pig feed (Rowland 1989).

Indeed, accounts of the superabundance of wildlife encountered by explorers, frontiersmen, soldiers, and early settlers in the newly colonized regions of North America and Australia are the norm (see Trautman 1981, Finney 1984). Most of those people expressed awe at the novel fauna and flora, and are compelling in their descriptions of the enormous abundance of life in freshwater systems. Populations of animals do naturally fluctuate as a result of stochastic and density-dependent influences, but the many descriptions of the incredible bounty of fish and other aquatic animals suggest that this situation was typical of faunas unaffected by postindustrial colonization. This does not imply that indigenous peoples did not harvest animals (and plants). In many cases, components of the freshwater fauna would have been reduced (e.g., Butler and Campbell 2004), but no evidence suggests that freshwater species were extirpated because of overharvesting by indigenous people. The displacement and death of indigenous peoples as a result of European settlement may have freed, for a time, the aquatic fauna from the harvesting pressure it had experienced previously (Humphries 2007), and thus may have allowed wildlife and fish populations to expand. Accounts that predate the reduction of indigenous hunting and fishing pressure, however, suggest that this explanation is not entirely valid. Given the dearth of records of faunal population sizes before and after Europeans arrived, there will probably always be a great deal of uncertainty about how faunal populations responded to European settlement.

Although uncertainty about historical abundances of wildlife cannot be resolved, some river systems in the world are relatively unaffected by human disturbance, and these may give some insight into the abundances of fishes where fishing occurs at only a low intensity. Two such systems are those of Lake Eyre, in central Australia, and the Casiquiare River, in southern Venezuela. The Lake Eyre basin is more arid than the heavily exploited and degraded Murray-Darling basin, but the two systems share many hydrological and geomorphological features and species. A survey of 15 newly disconnected Lake Eyre basin water holes in April 2001 (Arthington et al. 2005) revealed that between 84 and 46,591 (mean ± 1 standard error [SE] = 493 ± 160.9) individuals from 12 indigenous and 2 alien species were collected in three fyke nets and one pull of a 15-meter seine. Five months later, when water holes had shrunk, the catch had declined to between 32 and 1028 fish (mean ± 1 SE = 335 ± 11.4) (Stephen Balcombe, Griffith University, Queensland, Australia, personal communication, 26 February 2009), but the numbers still demonstrate the existence of a large abundance of fish in each water hole. The Casiquiare River basin, in southern Venezuela, is one of the few remaining regions where fish populations are nearly unexploited. Lying within the Guyana Shield formation, this landscape contains pristine rainforest and rivers supporting what is perhaps the most diverse fluvial fish fauna on Earth (Winemiller et al. 2008). In spite of its biological riches, the region has extremely nutrient-poor soils, and consequently human population density is extremely low, with vast areas completely uninhabited. Surveys conducted in the 1990s (Winemiller et al. 1997, Jepsen et al. 1999) show that the size structure of the peacock bass (*Cichla temensis*) population of the Casiquiare basin was very different than the size distributions of populations from the Llanos region of Venezuela, where fishing pressure was moderate (Cinaruco River; see figure 1) or heavy (Aguaro River). Apparently, moderate fishing pressure almost completely eliminates the largest individuals from populations of these predatory fish in just a few years.

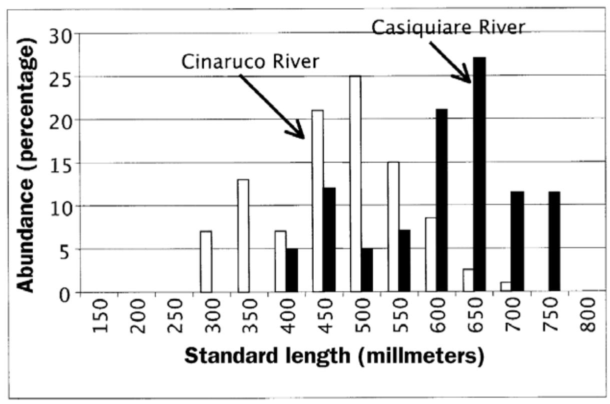

Figure 1. Relative size distributions of peacock cichlids (*Cichla temensis*) captured by angling from moderately exploited (Cinaruco River) and very weakly exploited (Casiquiare River basin) populations in Venezuela. Source: Data from Jepsen and colleagues (1999).

Overexploitation and anthropogenic disturbance in freshwater

Early European settlers in New England soon learned the habits of the fish that they encountered. In spring, settlers set nets, used seines, or made weirs at the base of falls where fish congregated, catching many fish each day, salting them, and sending them back to town (Vickers [2004] is the source of descriptions below). There were reports of constructed weirs allowing the capture of tens to hundreds of thousands of shad, alewives, and salmon per tide. As early as 1645, people of the town of Sandwich on Cape Cod complained of the netting of alewives by bass fishermen, and in 1668 several towns expressed concern about the effects of milldams on upstream fish movement. In 1710, legislation was passed in Massachusetts limiting the number of days per week that fish could be taken, restricting the gear that could be used, and banning fishing during the spawning season. Similar legislation was passed in Connecticut in 1715 and in Rhode Island in 1735.

Overfishing also had a major role in the collapse of the Atlantic sturgeon (*Acispenser oxyrynchus oxyrynchus*) and the short-nosed sturgeon (*Acispenser brevirostris*) in New England (Lichter et al. 2006). Fishing began in the early 1600s in the Merrymeeting Bay area, and by 1720, 20 schooners were operating to catch sturgeon commercially. But sturgeon catches were unreliable and the fishery became sporadic. The mid-1800s and the last quarter of that century saw two revivals in the fishery, but in each case it was discontinued after a few years because overfishing severely reduced stocks. A similar fate befell salmon and shad (*Clupea sapidissima*) in the region (Lichter et al. 2006).

The lake sturgeon (*Acispenser fulvescens*) supported an important fishery from the 1860s in the Great Lakes; this followed the collapse of riverine fisheries of Atlantic sturgeon that caused a shortage of caviar (Petersen et al. 2007). Until that time, there had been little interest in the lake sturgeon. By 1925, this species formed the most important commercial fishery in the Great Lakes, despite the fact that stocks were already collapsing (Petersen et al. 2007). Three years later, commercial sturgeon fishing was banned in US waters; a restricted fishery continues in some parts of Canada. Today, virtually all sturgeon (and paddlefish) species throughout the world have suffered fates similar to those mentioned above—19 of the 27 species of sturgeon and paddlefish stocks are currently listed as threatened (Pikitch et al. 2005).

Pacific salmon were fished extensively by Native Americans before European settlement (Meengs and Lackey 2005). In Oregon, salmon were harvested by indigenous people in numbers comparable to those of the post-European settlement period, and thus it is likely that salmon populations had already been significantly affected by exploitation (Meengs and Lackey 2005). Effects on salmon by European colonizers began slowly, with trade between Native Americans and ships starting in the late 18th century, then extension of the Hudson Bay Company into salmon fishing and trading in the early 1800s. The first impacts on salmon stocks, however, were likely to have been a by-product of beaver harvesting (see below), and the resultant changes to river morphology. Then came gold mining in the mid-1800s, followed by logging and farming, all of which affected salmon habitat. Salmon harvesting in Oregon greatly expanded in 1865 with the establishment of a cannery on the Columbia River at Eagle Point. Although salmon catches fluctuated annually, by 1880 there were 29 canneries employing 4000 people on the Columbia River (Meengs and Lackey 2005). Pacific salmon suffered dramatically from this intense harvesting and from human modifications to rivers (Gustaffson et al. 2006). Since the time when Europeans first colonized the Pacific Northwest of North America, 29% of the 1400 salmon populations that once existed have become extinct (Nehlsen et al. 1991, Gustaffson et al. 2006).The major factor causing local population extinctions was impediments to salmon migration, but overfishing also clearly contributed to this dire situation (Lichter et al. 2006, Jelks et al. 2008). A recent report by IUCN, the International Union for Conservation of Nature, on the status of sockeye salmon (*Oncorhynchus nerka*) indicated that of the 80 known subpopulations, 26 could not be evaluated because of lack of data, 5 were extinct, 17 were threatened, and 2 were nearly threatened (Rand 2008). The top reason given for their decline was overfishing of small populations.

The overall picture is bleak for those North American freshwater fish stocks that have been commercially harvested. A 2008 analysis of the conservation status of all North American freshwater fishes concluded that nearly 40% of the region's fauna is imperiled (Jelks et al. 2008). Overall, habitat degradation and nonindigenous species were considered the main threats. However, a total of 123 North American species were considered as affected by overharvesting. Indeed, for recreationally or commercially important species, overexploitation was considered a major factor contributing to their imperiled status: This was the case for 100% of sturgeon, 81% of salmonid, 67% of silverside, and 12% of ictalurid catfish species.

In southeastern Australia, the Murray Fishing Company commenced commercial fishing in 1855 on the Murray River near Echuca, primarily targeting Murray cod, the biggest and longest-lived fish in the river (figure 2). Six European and some local Aboriginal fishermen were employed, catching 2000 to 3000 kilograms (kg) of fish each week (Argus 1863). At the same time, just north in the Murrumbidgee River, three to four fishermen were catching about 1000 kg per week, within an 8-kilometer stretch of river. Within a few years, the Murray Fishing Company had expanded its activities rapidly and had begun supplying fish to nearby cities. Within eight years, with fishing activity spanning hundreds of miles of river, the sustainability of the Murray Fishing Company's practices came into question: "The fishing operations of the company on Lake Moira are vigorously carried on, and their coach is regularly despatched twice a week with pretty heavy loads. Some steps should be taken for the protection of the fisheries, and the destruction of the fish at all seasons prevented. Already, we understand, they have become very scarce in this neighborhood" (Argus 1863). With increasing fishing effort in the late 1880s and early 1890s, between 40,000 and 150,000 kg of mostly Murray cod (between 7500 and 27,000 fish, at an average weight of 5.5 kg) were caught near Echuca (Thompson 1893). Because of the concerns for the viability of the fishery, government commissions were established between 1880 and 1896, and evidence was given that numbers of fishes, and large fish in particular, were declining rapidly (Dannevig 1903). Regulations followed, but fishing pressure was still intense. By 1900, 200 professional fishermen plied the Murray River in South Australia. Interviews by fisheries scientists at the time revealed that the majority of fishers who had been fishing longer than 10 years considered the fishery to be declining (figure 3). Commercial fishing records indicated that a decline in catches was already under way by the early 1880s, although the easing of fishing pressure during World War I led to resurgences (Dakin and Kesteven 1938). Large-scale commercial fishing became unviable in the mid-1930s, and commercial fishing for Murray cod is now banned

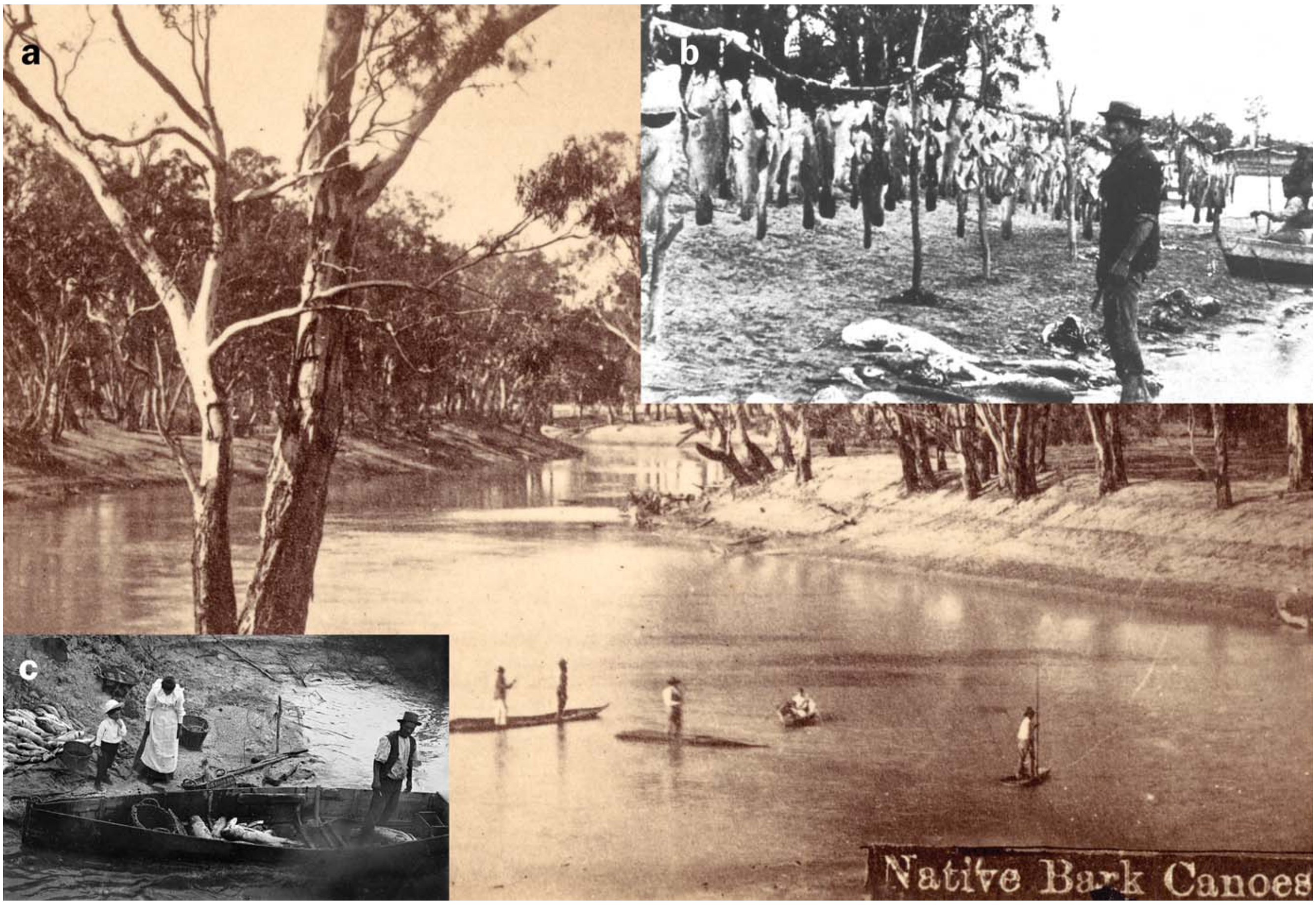

*Figure 2. Fishing for Murray cod (***Maccullochella peelii peelii***) in the Murray River, Australia. (a) Aboriginal men fish in bark canoes in the Murray River, Moira, in 1884; (b) a professional fisherman with his catch of Murray cod in South Australia in 1908; (c) a family unloads a catch of Murray cod in the late 1800s. Indigenous people made extensive use of Murray cod and other aquatic animals before European settlement, after which an intensive fishing industry developed in the Murray River and its larger tributaries from the mid-1800s. Photographs: (a) Courtesy of the National Library of Australia (NLA.PIC-AN3096938-3, NJ Caire); (b) courtesy of the State Library of South Australia (SLSA: PRG 1258/2/2056), and (c) reproduced courtesy of Museum Victoria (MM 5048).*

in all states of Australia. The species is listed as "vulnerable" under national legislation and as "threatened" under regional legislation, despite the fish being a popular angling species. Some Murray cod remain in the Murray-Darling basin, but their numbers are very low—indeed, a comprehensive, two-year, scientifically rigorous survey of fish in New South Wales in the mid-1990s collected no Murray cod from all 20 sites sampled on the Murray River (Schiller et al. 1997).

Fish were not the only freshwater animals harvested in commercial operations. The beaver (*Castor canadensis*), for example, constituted a huge industry in North America, one that began soon after Europeans first colonized that continent (Naiman et al. 1988). Although Native Americans had hunted beavers for millennia, *C. canadensis* numbers at the time of European arrival were estimated at between 60 million and 400 million. Hunting by Europeans began in the early part of the 17th century, and between 1630 and 1640, 80,000 beavers were harvested per year. The hunting intensity was such that by 1900, the North American beaver was economically and ecologically extinct. Hunting continued in Canada until recently. With active conservation and reintroductions occurring in many regions of North America, beaver populations are rebounding (Naiman et al. 1988); the total population is currently estimated to be between 10 million and 15 million.

During the 19th and 20th centuries, freshwater mussels were harvested in enormous numbers to support two huge North American industries (Anthony and Downing 2001). The first was the freshwater pearl industry, beginning in the 1850s and ending in the early 1900s. As mussels declined to very low levels, the low incidence of pearls rendered this industry uneconomical. Although many species were harvested, about 10 dominated the fishery and thus suffered declines more than others. The harvest was very wasteful, with typically less than one pearl per thousand mussels killed. As mussels became more scarce, rivers hitherto untouched were targeted and then depleted. After 1890, mussels were harvested primarily for the pearl button industry. This involved many more species, which meant that impacts were more widespread.

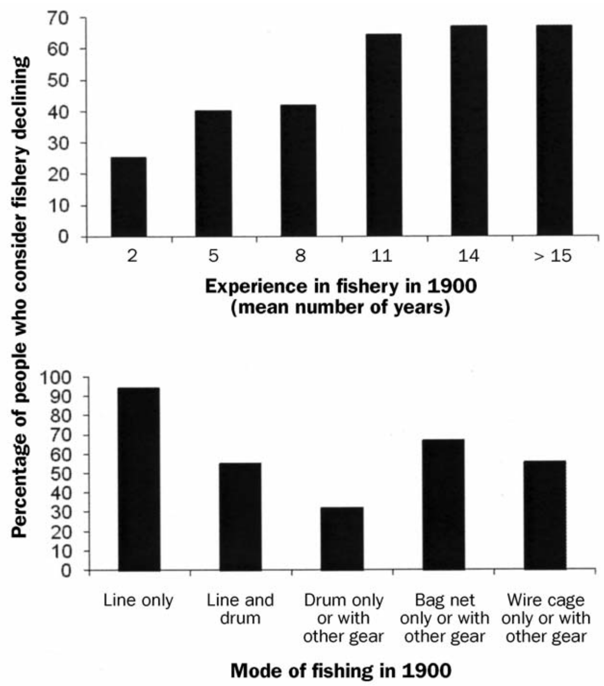

Figure 3. South Australian Murray cod fishers interviewed in 1900 expressed their view of the condition of the fishery: Pessimism about the state of the fishery increased (a) with the length of time in the fishery and (b) with the method of capture (line fishers had the greatest longevity and experience, whereas those using other methods typically changed gear when fish became scarce). Source: Dannevig (1903).

By 1909, 70 button factories depended on freshwater mussels, although the abundance of suitable mussels had begun to decline a decade earlier. As large mussels became rare, smaller ones were targeted. Mussel species were devastated, and many still have not recovered. In 2001, 20 mussel species were considered endangered, threatened, or of concern in the United States, and there has been little recovery of populations since the end of the fishery (Anthony and Downing 2001).

In many instances, it is difficult to determine the primary source of the impact on stocks of aquatic organisms that were formerly abundant. In a review of overfishing in inland waters, Allan and colleagues (2005) summarized the main sources of impacts on the world's largest freshwater fishes. For the 12 species for which a source could be identified, overharvest was cited for 11 species, habitat loss for 9. Commercial and subsistence harvest clearly produces the main impact on fish stocks in many regions of Africa, South America, and Southeast Asia where fishing is intense and dams have not been constructed. In lowland rivers in the vast Amazon basin, the giant pirarucu (*Arapaima gigas*) and piraiba (*Brachyplatystoma filamentosum*) have shown major reductions in size and abundance, mainly because of fishing. In other regions, such as the Upper Paraná River in southern Brazil or the Colorado River in the western United States, dam construction has produced the major impact on native fishes. Giant carps and catfishes of the Mekong River have been severely affected by commercial fishing, including the construction of wooden dams that funnel migrating fishes into pens (Allan et al. 2005). Tigerfish (*Hydrocynus vittatus*) in the Upper Zambezi River in Africa are harvested by huge drift gillnets deployed in the main channel. Undeniably, commercial and subsistence fishing in inland waters have a major impact on fish stocks, and even recreational angling can significantly reduce stocks (Cooke and Cowx 2004).

Ecological effects from reduced populations of aquatic species

In setting restoration goals for freshwater fauna and ecosystems, historic losses of species or reductions of local stocks are seldom considered, and thus the functional consequences of these losses are seldom appreciated and never estimated. We have presented evidence from historical accounts that fish, beaver, and mussel populations in North America and Australia were diminished early in the process of natural resource exploitation and land development by colonists. We must ask, then, what functional roles these animals perform within communities and ecosystems, and what are the consequences of losing these functions in modern freshwater ecosystems?

Many large fishes in natural freshwater fish communities are predators that almost always rank among the most palatable, easily caught, and valuable species in regional fisheries. Given their position in food webs, a potential effect of large predators is top-down regulation of populations of their prey. Recent studies of terrestrial (Sergio et al. 2008) and marine (Myers et al. 2007) ecosystems have confirmed that biodiversity may be influenced by the presence of top predators, and this is likely to be the case also for freshwater systems. Predators can influence prey populations in two fundamental ways: (1) by directly affecting population abundance or size and age structure by influencing mortality, or (2) by indirectly influencing the behavior of prey through the threat of mortality. Top-down effects of fishes on ecosystems have been demonstrated experimentally in northern temperate lakes (e.g., Carpenter and Kitchell 1993) as well as in fluvial ecosystems (e.g., Power et al. 2008).

The loss of biodiversity and changes to food-web structure that the introduction of exotic top predators has wrought on aquatic ecosystems (e.g. peacock cichlids, *Cichla ocellaris,* in Panama's Lake Gatun, and Nile perch, *Lates niloticus,* in Lake Victoria) testify to the major effects of apex predators on food-web structure and ecosystem processes. Ecological functions of healthy populations of native apex predators may never be understood for the regions of the world where historic accounts are lacking. Indeed, there are very few wilderness regions whose freshwater fish populations remain unexploited (figure 4). Peacock cichlids and other large generalist predators in species-rich fish communities of the Orinoco and Amazon basins of South America possess attributes of keystone predators (Winemiller 2007)—that is, they

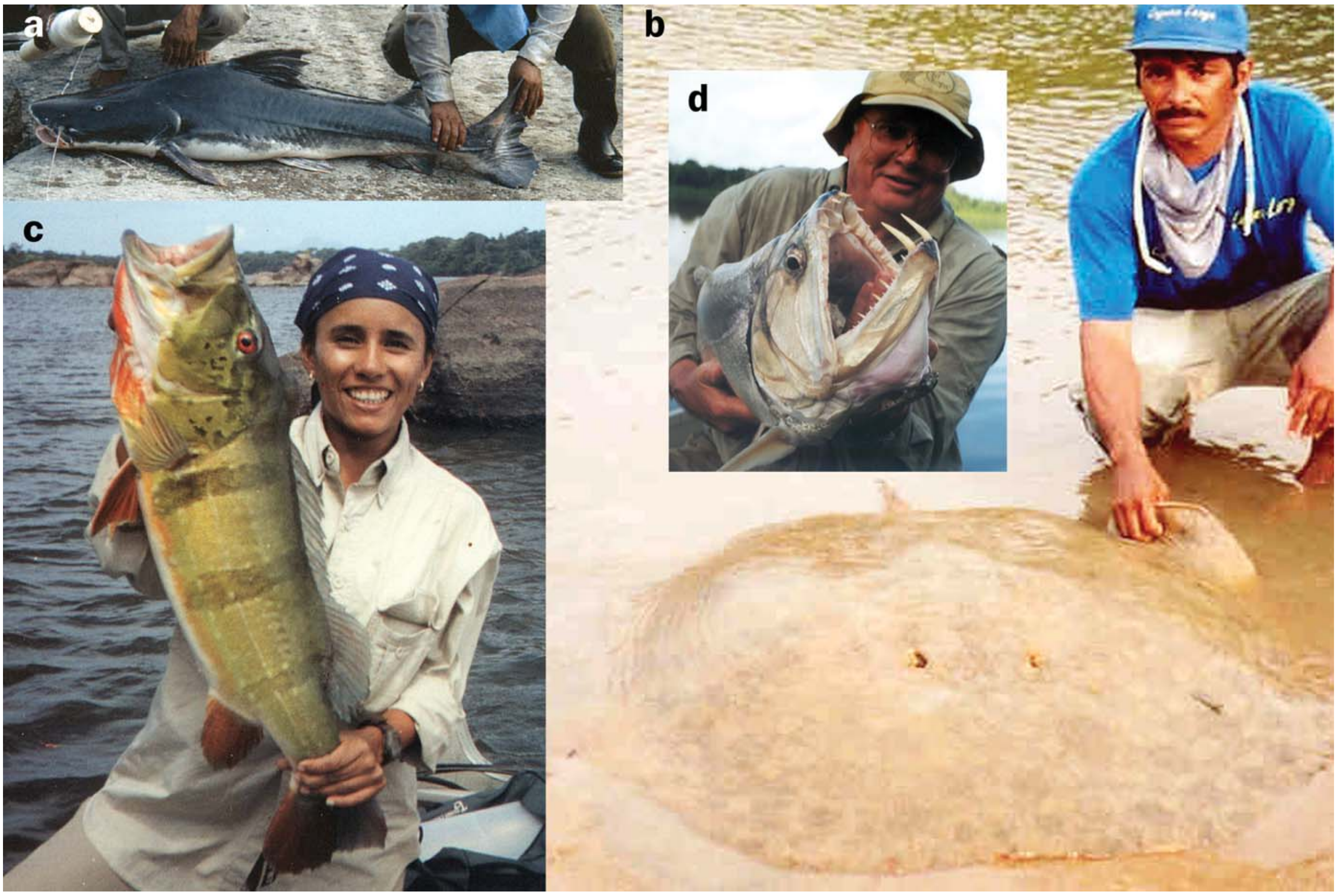

Figure 4. Examples of large predatory fishes from lightly fished regions of southern Venezuela: (a) lau lau, Brachyplatystoma filamentosum, *Rio Siapa; (b) freshwater stingray,* Paratrygon aiereba, *Rio Cinaruco; (c) pavón,* Cichla temensis, *Ventuari River in southern Venezuela; and (d) payara,* Hydrolycus armatus, *Rio Paragua. In most of Earth's freshwater ecosystems, the largest size classes of large predatory fishes were eliminated long ago, making it difficult to estimate the former ecological influences of these populations: a consequence of the shifting baseline syndrome. Photographs: Courtesy of Kirk O. Winemiller (a); Lennie Kouba (b); Carmen Montaña (c); and Richard Ashley, FishQuest (d).*

promote coexistence among prey populations by disproportionately cropping the most abundant species, which otherwise might attain even greater densities and displace competitively inferior species (Paine 1966).

The loss of large predatory fishes and other dominant species also has the potential to affect nutrient dynamics in aquatic ecosystems, either directly, through reduced organic or inorganic inputs, nutrient recycling rates, or inorganic nutrient ratios; or indirectly, through effects on other species, such as detritivores or herbivores, that have strong, direct effects on nutrient cycles (figure 5). For example, through their migrations and subsequent deaths, anadromous salmon import marine-derived nutrients into freshwater; enhance primary and secondary productivity; and afford food for otters, bears, wolves, foxes, and eagles; they are therefore considered keystone species in the Pacific Northwest (Willson and Halupka 1995). Similarly, diadromous fishes entering rivers along the Atlantic coast of North America, such as blueback herring (*Alosa aestivalis*), influence ecosystem dynamics as importers of marine nutrients and as a resource subsidy for top predators (MacAvoy et al. 2000). Examples of fish effects on nutrient recycling, provided by model simulations for a river in Venezuela and for Lake Tanganyika in Africa, demonstrated how the largest negative effects on nutrient recycling were for scenarios that mimicked observed patterns of fishing pressure in these systems (McIntyre et al. 2007). One of the most important functional groups affecting nutrient recycling was benthivorous fish, especially in the Venezuelan river. It has been shown through field experiments that a single species, the detritivorous characiform *Prochilodus mariae,* exerts a strong influence on the rate of carbon cycling in the Rio Las Marias in Venezuela (Taylor et al. 2006). This migratory species has been heavily affected by netting and dams (Barbarino-Duque et al. 1998, Taylor et al. 2006). A growing number of studies reveal the effects of fishes on nutrient cycling and primary production in freshwater ecosystems (Vanni 2002, Vanni et al. 2005, Taylor et al. 2006).

While large fishes usually are the principal targets of freshwater fisheries, other aquatic animals that influence ecosystem processes also have been severely affected by over-

Figure 5. Ecosystem engineers that change the features of aquatic habitats: (a) Salmon that migrate en masse into oligotrophic streams of the Pacific coast of North America import marine-derived nutrients that support aquatic and terrestrial primary and secondary production. (b) Before settlement by people of European descent, North America contained extensive inland ponds and wetlands created by the actions of beavers damming streams. (c) Before decimation of their populations by direct harvest and disturbance of watershed habitats, mussels had a tremendous capacity to filter organic matter from water flowing in North American streams and rivers. (d) In South America, migratory fishes of the family Prochilodontidae, such as **Semaprochilus kneri**, were abundant in major rivers and supported large fisheries. The large effects that these benthic detritivores have on benthic ecology and sediments vary in accordance with fish density. Photographs: Courtesy of Kirk O. Winemiller (a), Guillermo Martínez Pastur (b), Chris Barnhart (c), and Carmen Montaña (d).

harvest. We have already described commercial harvesting and decimation of freshwater mussels and beavers in North America. These animals play important roles in ecosystems, and their diminution or loss profoundly affects food webs and habitat features. Freshwater mussels, for example, make up the bulk of the biomass of macroinvertebrates in lotic and lentic waters in certain regions of the world (Strayer et al. 1999). Depending on the species, abundance, and habitat, mussels can filter between 0.01 and 10 cubic meters per square meter of water per day (Strayer et al. 1999). It has been proposed that consumption of phytoplankton, bacteria, and other organic particles by bivalves may exceed advective losses in shallow aquatic ecosystems (Strayer et al. 1999). Thus, the ability of mussels to affect food webs in rivers is substantial. In addition to filtration, mussels affect ecosystems through excretion, bioturbation, and creation of hard substrates that can be colonized by other organisms (Vaughn et al. 2004).

Beavers are major modifiers of stream habitat, and thus alter the physical and chemical characteristics of flowing water, which in turn influence the fauna and flora (Naiman et al. 1988). There can be as many as three colonies of beavers per square kilometer in the northern United States and eastern Canada. This can result in as many as 16 dams per river kilometer, with 10 being the norm. Beaver dams slow the water current, create pool-run sequences, increase lateral flooding, and enhance retention of sediment and organic matter. Dam building by beavers can increase the abundance and biomass of macroinvertebrates fivefold, and it alters community composition toward lentic-adapted forms. Furthermore, carbon budgets are dramatically altered as a consequence of beaver activities (Naiman et al. 1988). By felling trees and creating space for colonizing plant species, including species beavers find unpalatable, beavers also have a major direct effect on the riparian zone.

Shifting baselines

Pauly (1995) outlined the danger of shifting baselines in marine fisheries management: Scientists may perceive the faunal composition and stock characteristics that existed when they began their careers to be the unaffected reference condition. The inexorable movement of this baseline means that degraded and nonsustainable conditions tend to be accepted as management targets. There is an underlying assumption that only recent data on composition and abundance exist, and that historical data are either nonexistent or not good enough to use in rigorous assessments (Pinnegar and Engelhard 2008). Furthermore, if it is assumed that historical data do not exist, the only option when assessing changes in degraded systems is to make comparisons with reference systems that are considered "natural" or "less degraded'" (Sheppard 1995). This approach is fraught with problems, since these reference systems will have been disturbed in many different ways and often for centuries. While the shifting baselines syndrome has been well outlined for marine systems (e.g., Pinnegar and Engelhard 2008), we believe it applies strongly to freshwater ecosystems as well.

A major problem is that stock and harvest records typically postdate, sometimes by more than a century, the onset of the sorts of impacts we have documented here. For example, commercial salmon and sturgeon fishing near Merrymeeting Bay commenced in the early 1600s, well before dams were built and well before the size of stocks had been quantified (Lichter et al. 2006); and commercial fishing of Murray cod began 30 years before any catches were recorded (Dannevig 1903, Dakin and Kesteven 1938) and almost 100 years before the first comprehensive survey of fish in the Murray River (Rowland 1989).

As generations pass, opinions about the former "natural" abundance of stocks and the causes of their decline inevitably change (see, e.g., figure 3). Fishery declines in 18th- and 19th-century New England were undoubtedly caused by industrialization and impediments to migration. But Vickers (2004) argued that fishing practices even before industrialization had set these stocks on a path to annihilation, and that the changes to rivers that came later were merely the final nails in the coffin. Over the decades following industrialization, past fishing pressures and past abundances of fish were forgotten, and as environmental attitudes changed, the blame for declining fish stocks turned more and more to obstruction of migration paths. The baseline set in the 19th century—which ignored 200 years of fishing pressure—is the one from which further declines were measured.

The shifting baseline syndrome challenges us to acquire evidence of past abundances, distributions, and assemblage compositions of freshwater faunas. For example, Anthony and Downing (2001) outlined the devastating effects of decades of overharvesting mussels in the United States for pearls and buttons, beginning in the 1800s. Yet a recent review of the status of unionid mussels in the United States (Lydeard et al. 2004) identified changes to river habitats, such as damming and flow alteration, as the primary cause for decline; it failed to mention historical overharvesting as a factor.

Unless historical records are very good—a rare circumstance—we must seek other sources of data. Some obvious sources are subfossils and archaeological remains (Lyman 2006, Frazier 2007). The former should give a good estimate of composition and relative abundances in previous centuries, but will be restricted largely to habitats where preservation is favored, such as in oxbow lakes and other ephemeral water bodies where anoxic conditions are common. There are obvious problems with estimating composition and abundances from archaeological remains, because harvesting by indigenous peoples is selective. However, methodologies are improving all the time, and future applications seem promising (Lyman 2006, Frazier 2007).

River restoration

As we have outlined, historical decimation of aquatic wildlife has been as much of a problem in freshwaters as in marine ecosystems, yet its potential effects and the longevity of its impact have been largely ignored. The shifting baseline syndrome has contributed to this unfortunate state of affairs. Fishes have borne the brunt of overharvesting, but other taxa such as beavers and mussels also have suffered. Indeed, the impacts of overexploitation in freshwaters may have been more severe and more rapid than in marine systems, mainly because of the constrained nature of freshwater environments: fishes and other targeted taxa have comparatively limited scope for withstanding intensive harvest. Coincident with overfishing has been the construction of dams, weirs, and mills that prevent movement by migratory species. Moreover, the use of rivers and lakes near growing human populations for irrigation, transportation, discharge of waste, and water extraction or storage imposes further negative impacts on freshwater biota.

These stressors on freshwater ecosystems are not likely to disappear in the foreseeable future (Palmer et al. 2005). If anything, human populations are expanding and demands for water will only increase. Yet commercial fishing of freshwater species is probably at an all-time low in many industrialized countries. In many cases, commercial fishing has been banned altogether as a result of recent conservation efforts and fishing regulations. Widespread recreational fishing, however, continues to place considerable pressure on many stocks (Cooke and Cowx 2004) that may have suffered previously from commercial fishing, and commercial and subsistence fishing in most developing countries is intensive (Allan et al. 2005). Management programs have been established for many of the species mentioned in this article, but it is rare that the role played by these species in ecosystems provides a rationale for their conservation (Lipsey and Child 2007). The critical ecological roles of environmental modifiers, such as beavers and mussels; energy and nutrient transporters, such as salmon and shad; and top predators, such as Murray cod and peacock cichlids, as we have outlined briefly, are becoming clearer and afford opportunities as well as challenges for conservation.

Opportunities exist because this understanding offers added incentive and justification for reintroducing extirpated species to freshwater ecosystems or enhancing populations of functionally extirpated species, and because the chances of success are greater for restoring ecosystems with functionally important species in them than they are for restoring ecosystems without those species. The approaches we are advocating may require habitat restoration *and* species reintroductions if species have become extirpated, so it follows that coordination of these efforts will be needed. We endorse Lipsey and Child's (2007) call for the integration of reintroduction and restoration ecology, and concur that reintroducing extirpated top predators and keystone species without attention to the key community elements with which they interact runs a high risk of failure. We also agree that in some instances, simply providing flow regimes, primary production, or other habitat-related conditions will prove inadequate for maintaining native biodiversity. Thus, a more interventionist approach is called for—one that includes restoration of both habitat and functionally significant species, along with rigorous hypothesis testing (Seddon et al. 2007), but within a context of future environmental conditions, not those of the recent past (Choi 2007). This will require some forecasting, taking into account climate change and resource-use predictions, and an adaptive management approach. We believe it is vital to consider that (a) the degradation of freshwater ecosystems evident today is not solely a result of abiotic—typically bottom-up—effects, and (b) restoring ecosystem function is likely to be unsuccessful without also taking into account critical biotic components, some of which may have been lost. In some cases, there may be no going back, since environmental conditions are so degraded that anything short of wholesale ecosystem restoration would be ineffective. Ultimately, restoration goals are driven by societal values and sociopolitical trade-offs, but specific actions should be based on sound scientific principles (Bernhardt et al. 2005, Palmer et al. 2005).

Freshwater protected areas should, we believe, receive the fullest attention from scientists, managers, and the broader community. The concept of freshwater protected areas is rapidly gaining momentum in scientific circles (Saunders et al. 2002, Kingsford and Nevill 2005, Suski and Cooke 2007), but it is also becoming clear that using terrestrial and marine systems as models for freshwater reserves is inappropriate—new approaches and terminology are needed (Moilanen et al. 2008). There are calls for the establishment of freshwater protected areas for functionally intact systems, partly because such opportunities are diminishing rapidly and many may soon be lost (Revenga et al. 2005), and partly because they represent the most gain per unit effort and monetary expenditure (see, e.g., Abell et al. 2007). We recognize the importance of intact ecosystems and support the notion of their protection, but we also believe that the concept of freshwater protected areas should be broadened to include degraded systems that have potential for rehabilitation through amelioration of degrading factors, as well as fishing regulations, species reintroductions if needed, and removal of barriers to migration (see, e.g., Baird and Flaherty 2005). Furthermore, freshwater protected areas should be established using experimental and adaptive management frameworks, incorporating established restoration protocols (such as those of the International Society for Ecological Restoration) to test for effects within the reserves and outside them (Bernhardt et al. 2005, Palmer et al. 2005).

Ideally, it would be most informative to conduct a series of large, river-scale restoration experiments in systems that have historically suffered the loss of keystone or other influential species through overexploitation but are possible candidates for restoration for other reasons, such as flow alteration, poor water quality, presence of alien species, or barriers to movement. Such experiments would provide opportunities to quantify the community and ecosystem functions (e.g., habitat quality, elemental cycling, productivity, maintenance of native biodiversity) of formerly abundant apex predators and other influential species such as mussels and beavers. Finding multiple, comparable control and treatment rivers is in many cases impracticable. But restoration of a single system using an adaptive management approach with a before-and-after design, which includes addressing stock size and the role of key species in a restoration program, would still be useful. Nonetheless, the first step in the type of restoration program that we advocate is to determine whether species have been lost or effectively extirpated from the system, and to estimate the effects they might have had on the community or ecosystem. A modeling approach would be useful here. If modeling indicates that the species played a significant role in the system, the next step is to identify the most likely stressors that eliminated or severely reduced these stocks and attempt to ameliorate them. Eliminating or greatly reducing fishing mortality, perhaps by establishing no-take zones (Baird and Flaherty 2005, Cooke and Schramm 2007), could be a key component of such efforts. Removing barriers to movement would also be an important step. Monitoring the effects of amelioration efforts on the target species and ecosystem functions would be the next critical step for evaluation. This process would necessarily be iterative: stock rehabilitation efforts would follow amelioration of the most apparent stressors, and other potential stressors and species functions would be revealed as the system changes.

In conclusion, we believe that the effects on freshwater ecosystems of the loss or decimation of freshwater populations more than a century ago were just as profound as those that have been proposed for coastal marine ecosystems. Yet these effects have gone largely unrecognized by freshwater scientists. Furthermore, the insidious nature of the shifting baseline syndrome has affected perceptions of the extent and causes of this degradation, and thus has influenced the targets set for river restoration and rehabilitation. These false impressions result in the underestimation of ecosystem functions that these freshwater populations historically performed. We propose that these missing or degraded populations and their former functions should be addressed in future rehabilitation efforts; in most cases, establishing freshwater protected areas will be the most effective way to achieve this.

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