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Source: BioScience, 55(12) : 1041-1051

Published By: American Institute of Biological Sciences

URL: https://doi.org/10.1641/0006-3568(2005)055[1041:OOIW]2.0.CO;2

Overfishing of Inland Waters

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Inland waters have received only slight consideration in recent discussions of the global fisheries crisis, even though inland fisheries provide much-needed protein, jobs, and income, especially in poor rural communities of developing countries. Systematic overfishing of fresh waters is largely unrecognized because of weak reporting and because fishery declines take place within a complex of other pressures. Moreover, the ecosystem consequences of changes to the species, size, and trophic composition of fish assemblages are poorly understood. These complexities underlie the paradox that overexploitation of a fishery may not be marked by declines in total yield, even when individual species and long-term sustainability are highly threatened. Indeed, one of the symptoms of intense fishing in inland waters is the collapse of particular stocks even as overall fish production rises—a biodiversity crisis more than a fisheries crisis.

Keywords: overfishing, fishing down, freshwater biodiversity, ecosystem function, fish harvest

Overexploitation of the world's fisheries is the subject of much recent concern (FAO 2002, Pauly et al. 2002, Hilborn et al. 2003). Although the global production of fish and fishery products continues to grow, the harvest from capture fisheries has stagnated over the last decade. Today numerous fish stocks and species have declined since their historical peaks, and some have even collapsed, leading to urgent calls for more stringent management and the establishment of protected areas (Roberts et al. 2003). However, the discussion of the current fisheries crisis has focused nearly exclusively on marine resources, and to some extent on associated threats to marine biodiversity, particularly those affecting charismatic animals such as seabirds, marine turtles, dolphins, and whales. The fisheries of inland waters have received only slight consideration within global analyses (FAO 1999, Hilborn et al. 2003, Kura et al. 2004). Here we summarize and evaluate the evidence that overfishing in inland waters is occurring and is a contributing factor to the decline of freshwater biodiversity. We define inland fisheries as the capture of wild stocks of primarily freshwater fish, including migratory species that move between fresh water and the oceans. Although aquaculture significantly augments the supply of certain species and contributes a substantial fraction to the overall harvest, we focus on capture fisheries of natural stocks.

Fishing and the activities surrounding it—processing, packing, transport, and retailing—are important at every scale, from the village level to national and international economies. Fishing is a crucial source of livelihoods in developing nations, particularly for low-income families in rural areas where job options are limited. Small-scale commercial and subsistence fishing often provides the employment of last resort when more lucrative labor opportunities cannot be found (Kura et al. 2004). This is particularly true for inland fisheries. Although there are no global estimates of the number of people engaged in inland fisheries, in China alone, more than 80% of the 12 million reported fishers are engaged in inland capture fishing and aquaculture (Kura et al. 2004).

The contribution of fisheries to the global food supply is also significant. In 2000, fish and fishery products constituted 15.3% of the total animal protein consumed by people (FAO 2003). About 1 billion people—largely in developing countries—rely on fish as their primary animal protein source (calculation based on Laurenti 2002), and this is especially true for poor rural communities. For example, within the lower Mekong basin, the average consumption of fish and other aquatic animals is estimated at 56 kilograms (kg) per capita per year (Hortle and Bush 2003), and may reach 71 kg per capita per year in high-yielding fishing areas such as the floodplains around Tonle Sap Lake in Cambodia (Ahmed et al. 1998). In comparison, the global average is 16 kg per capita per year (FAO 2002).

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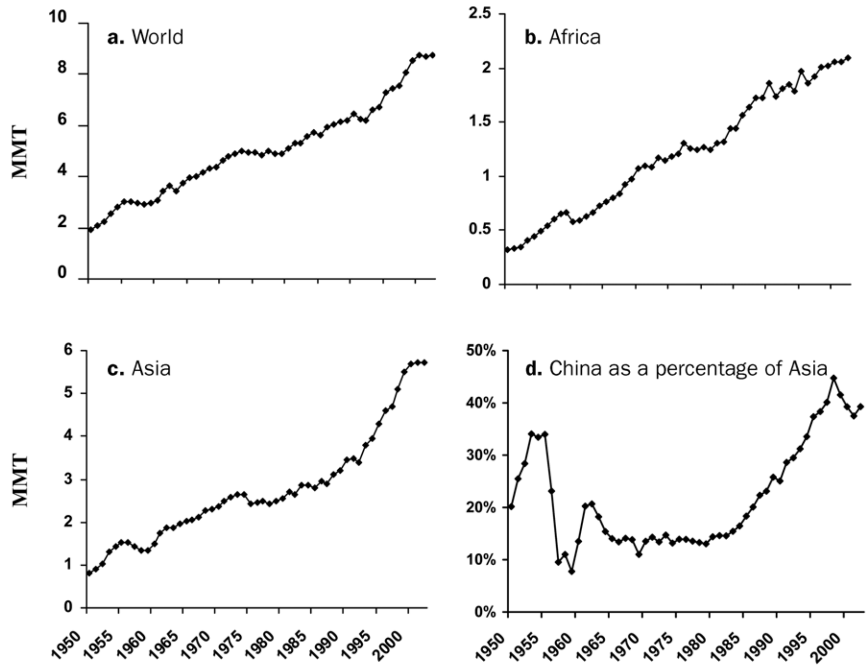

Figure 1. Fisheries landings from inland waters, 1950–2002: (a) world, (b) Africa, (c) Asia, and (d) China as a percentage of Asia. Data are from the Food and Agriculture Organization of the United Nations (FAO 2004). Abbreviation: MMT, million metric tons.

The status of inland fisheries

The total catch from inland waters, exclusive of aquaculture harvest and recreational fishing, was 8.7 million metric tons in 2002, the last year for which statistics are available (FAO 2004). Of this total, Asia accounted for 65% and Africa for 24%, with the remainder landed in South America (4%), Europe and the former USSR (4%), North America (2%), and Oceania (less than 1%). Fisheries landings from inland waters have experienced a more than fourfold increase, roughly 3% annually, since data were first compiled in 1950 (figure 1). China accounts for about one-quarter of the world's inland catch. Other countries with significant inland catches are India, Bangladesh, Cambodia, Indonesia, Egypt, Tanzania, Myanmar, Uganda, and Thailand—all developing or transitional economies where inland fish harvests have rapidly increased over the last 10 to 15 years.

Developed regions of the world have seen the opposite trend. North America, Europe, and the former Soviet Union all show declining trends in inland capture fisheries, as many inland commercial fisheries have been abandoned and replaced by recreational fisheries, which may add substantially to the total fisheries harvest but are not always reported (Cooke and Cowx 2004). The global recreational harvest is poorly documented, but may be on the order of 2 million metric tons (FAO 1999). Even when fish are released, recreational fishing can result in substantial postrelease mortality (Muoneke and Childress 1994) and reduced growth and fitness (Cooke et al. 2002). The extent of decline due to recreational fishing is often unappreciated, even in well-managed regions, because of inadequate records, lack of a historical framework, and subsidies to the fishery through hatchery stocking (Post et al. 2002). In relatively remote areas of the Orinoco, we have observed rapid declines of large peacock bass (*Cichla* spp.) subsequent to the fishery's "discovery" by affluent anglers (K. W., personal observation).

The reporting of global fisheries statistics to the Food and Agriculture Organization of the United Nations (FAO) relies on data provided by member countries, with the potential for distortions. Watson and Pauly (2001) argued that increases in China's reported marine catch, beginning in the 1980s, were consistent neither with a careful examination of other catch statistics nor with a model based on oceanographic conditions, suggesting instead that catches had been exaggerated. In 1998, in response to domestic and foreign criticism, China declared a zero-growth policy in which reported catches were frozen at 1998 levels. Perhaps reflecting similarly questionable reporting for inland waters, China's reported inland catch leveled off after 1998, and its share of Asia's total catch, which had increased strongly since the 1960s, fell (figure 1).

The use of catch statistics to assess stocks, a common practice with marine species, is difficult with inland species because much of the inland catch includes artisanal, recreational, and illegal fisheries; moreover, landings are dispersed, and are underreported by a factor of three or four, according to the FAO (1999). FAO records date back only to 1950, and separate accounting of inland fisheries was introduced only in the 1990s; thus, historical declines of important fish stocks are poorly documented. Finally, catch data are rarely reported at the species level, making stock assessments even more challenging.

Overfishing and freshwater biodiversity

The status of inland waters and their species should be of broad concern, yet threats to freshwater fisheries and associated biodiversity have received scant attention from conservation groups and the media. This imbalance seems particularly dangerous considering evidence that freshwater ecosystems and the species they support are, on average, more threatened than marine ecosystems (Ricciardi and Rasmussen 1999).

Inland waters and their species experience myriad direct and indirect stresses in addition to overfishing, including altered flows and habitat fragmentation due to dams and other infrastructure, pollution, habitat degradation, nonnative species introductions, and detrimental interactions with hatchery-reared fish (Allan and Flecker 1993). Although the importance of other anthropogenic stressors in relation to fishing may appear greater for inland waters than for the seas, the contributions of pollution, species introductions, and other human impacts in the collapse of coastal ecosystems should not be underestimated (Boesch et al. 2001). As Jackson and colleagues (2001) document in the context of marine fisheries, overfishing commonly was the first disturbance in the historical progression, followed by other factors including pollution and eutrophication, mechanical habitat destruction, introduced species, and climate change. Fish stocks are unable to recover from historical overfishing because of a host of current pressures, and in their altered state may be more vulnerable to disturbances, including species invasions and outbreaks of disease. A recent assessment of inland fisheries (FAO 1999) concluded that most inland capture fisheries that rely on natural stock reproduction were overfished or being fished at their biological limit, and that the principal factors threatening inland capture fisheries were habitat loss and environmental degradation. Overfishing, then, may not always be the sole or even the primary threat, but in conjunction with other stresses it can be a serious one.

Characteristics of inland fisheries

Inland fisheries are complex in their multigear and multispecies aspects, in their interannual variability as driven by abiotic factors, and in their social and economic context. Many inland fisheries, particularly those of large tropical river basins, occur within species-rich, ecologically diverse assemblages where population dynamics are difficult to observe and interpret. As in most ecological communities, a few species are highly abundant, more are moderately abundant, and many are rare (Winemiller 1996); this distribution of abundances also applies to the numerical distribution of fish species caught by individual gears (Welcomme 1999). Another widespread trend is for small individuals and species to greatly outnumber large individuals and species (McDowall 1994), a consequence of the low ecological efficiency of food chains, and of the coupling of high reproductive output and high juvenile mortality that characterizes most fish species. About 50% of species present in any system do not grow larger than 15 centimeters (cm) standard length, and 90% of species never grow larger than about 50 cm (figure 2; Welcomme 1999). Wherever larger fish are targeted, their relatively small numbers and lower population growth rates, relative to small species, make them more prone to depletion. In addition, a greater proportion of large species are piscivorous, as illustrated by the trophic composition of the fish species present in the various inland waters of West Africa (figure 3). Although many exceptions can be cited—including the detritus-eating Mekong giant catfish (*Pangasianodon gigas*), the omnivorous major carp of India (e.g., *Catla catla*), and the herbivorous tambaqui of South America (*Colossoma macropomum*)—in many instances removal of the largest fish translates into the removal of apex predators, with the potential for substantial top-down effects on food web dynamics.

To fully exploit the wide diversity of inland fish species, each with its own habits and size range, mankind has developed an equally extensive armory of fishing gears, broadly classified as active and passive (von Brandt 1984). These include gill, cast, seine, lift, and hand nets; traps; lines; poisons; and dynamite. In developing countries, high reliance on fishing, together with the depletion of large high-value stocks, results in the exploitation of a great variety of species and habitats by diverse fishing methods and large concentrations of fishers (figure 4; Welcomme 2001). In affluent societies, in contrast, only a handful of fishing methods (gill nets, hoop nets, longlines) are employed to capture those large species with the highest economic value.

Fishing down in inland waters

As harvest intensity increases over a period of years, the classic model for a fishery predicts a rise in catch with increasing effort until reaching a relatively high level where the maximum sustainable yield may be harvested over the long term. Further increases in effort beyond this maximum are expected to lead ultimately to declining catches and possible collapse. The reality is far more complex. Especially when fishers are able to shift their effort to other members of the fish assemblage, overfishing leads to numerous changes in both the target species and the assemblage, and may not immediately cause declines in total catch.

As in marine systems, intensive, multispecies fishing in inland waters can lead to what is known as "fishing down the food web"—the successive removal of the larger elements of a multispecies fish assemblage and their replacement by

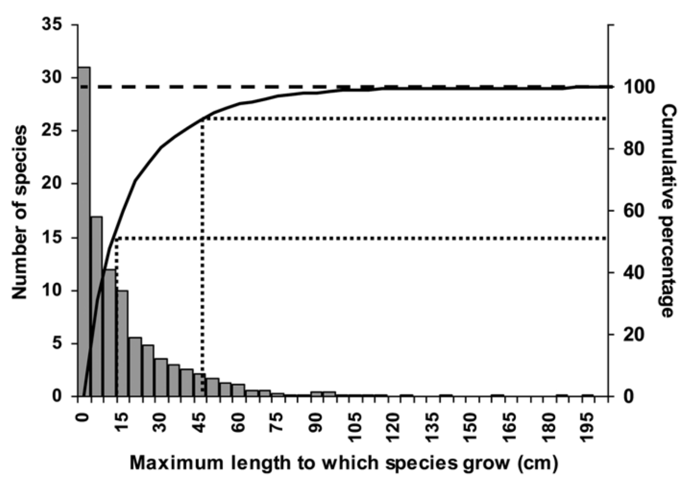

Figure 2. Relationship between the maximum length attained by a species (in centimeters) and the number of species attaining that length, averaged for a number of river systems. Total number of species is expressed as a cumulative percentage, with dotted lines showing approximate maximum size attained by roughly 50% and 90% of the species pool. Data include the Niger, the Mekong, the Magdalena, the São Francisco, North American rivers, and several Indian rivers. Data are from Welcomme (1999).

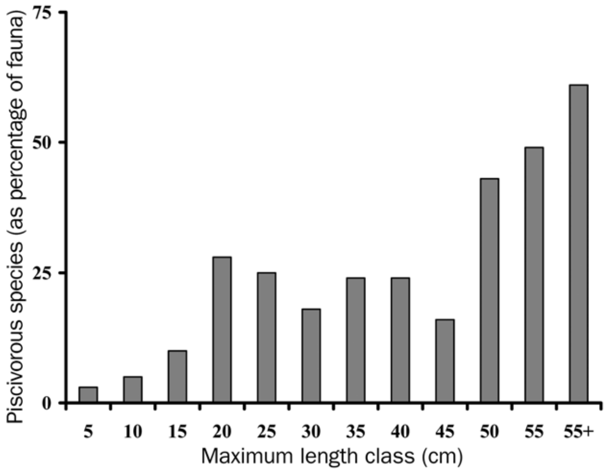

Figure 3. The percentages of fish species in West African rivers that are piscivorous in a given maximum length class (standard length in centimeters). Data are from Lévêque and colleagues (1990, 1992).

smaller elements of the assemblage, which typically are at lower trophic levels (Regier and Loftus 1972, Pauly et al. 1998). Usually this means successive elimination of larger individuals and species, although some fish populations respond to heavy fishing pressure with reductions in mean body size and size at maturation. A synthesis of evidence from inland waters supports the following general model (figure 5; Welcomme 2001). Fishing down initially leads to an increase in the weight of total catch as the number of harvested species and individuals increases, followed by a plateau or slight decline in total catch. As overfishing reduces the mean size of individuals and species in the assemblage, fishers reduce the mesh size of gear they use. Where mesh sizes are universally small, in the 2-cm size range, the assemblage may experience intense selection on size and age at maturity. Even in the absence of data on mean fish length, consistent declines in net mesh sizes may be an indicator of the state of the fishery, as small-meshed nets are expensive and time-consuming to make and usually will be adopted by fishers only out of necessity.

Fisheries based on gill nets will successively concentrate on smaller species and length classes as mesh sizes are reduced, resulting in an increase in the number of species forming the catch (figure 5c). In contrast, multigear fisheries are generally designed to catch all species and ages of the target assemblage, so the total number of species in the catch is high initially and declines as large species are fished out. As the fishing-down process causes larger species with slow life cycles to be replaced by smaller species with more rapid life cycles, remaining populations are expected to exhibit higher growth and mortality rates, higher ratios of productivity to biomass, and possibly population cycles with greater amplitude (Welcomme 2001).

In floodplain river fisheries, catch responds to the intensity of flooding in previous years, and the lag in response indicates the time taken for a year class to enter the fishery. In the 1950s, some river catches were correlated with floods as much as four to five years earlier, indicating that the fishery targeted older fish and exhibited a low level of exploitation relative to potential. More recent catches often are correlated with floods of the same year, indicating that the fish-

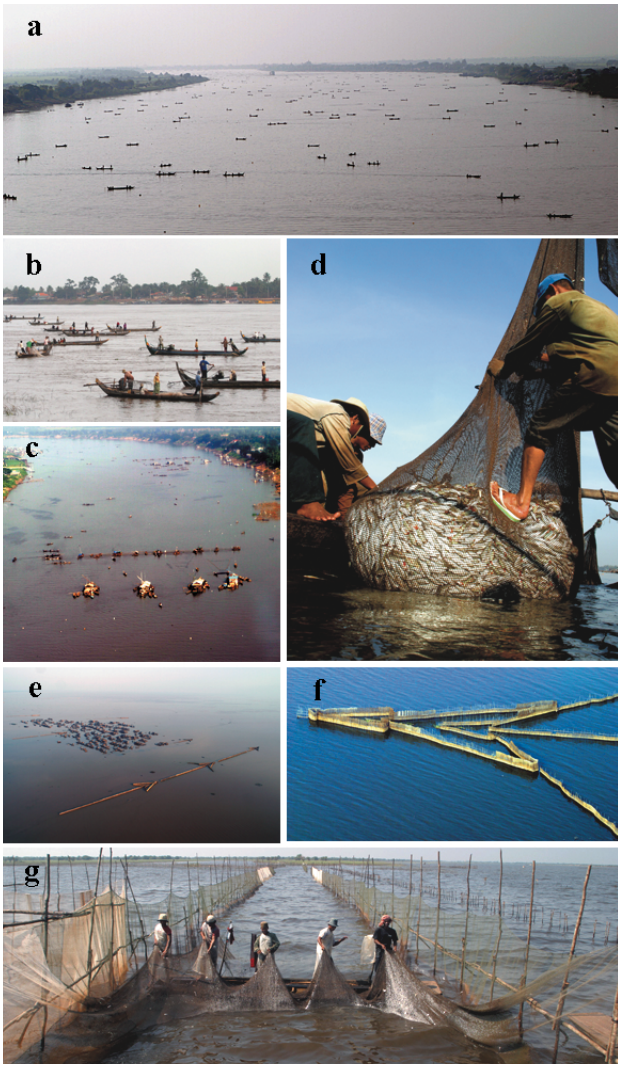

Figure 4. Fishing in the Mekong River basin, Cambodia. (a, b) Cambodian fishermen crowd the river, using gill nets and purse seines. One boat can catch in excess of 500 kilograms of fish over a 1-week period. (c) An aerial view of bag nets, cone-shaped nets 25 meters in diameter and 125 meters long, which can catch up to 10 metric tons of fish per day during the peak season. (d) Close view of a bag net. (e) On the Tonle Sap Lake, local people live in floating villages; they harvest fish using (f) arrow and (g) fence traps. Bamboo fences often block migrating fish, directing fish into traps. Small cyprinids, known collectively as trey riel, make up almost half of the total catch from the Tonle Sap River and are so important that the Cambodian currency (the riel) derives its name from the fish. Photographs: Zeb Hogan.

ery is based mainly on very young fish, and that it is at risk (Welcomme 1979).

Evidence of overfishing

Despite the challenge of evaluating the effects of fishing owing to complex system responses and the presence of other pressures, there is ample evidence that overfishing is a significant factor in the decline of numerous species and fisheries, and is of global importance as a threat to inland water biodiversity. We identify two main types of overfishing and illustrate each type with case studies. In the first type of overfishing, intensive fishing of a targeted species leads to marked declines in catch per unit effort and size of individuals captured. Such overfishing most likely was primarily responsible for the decline of a number of fish species prior to the contributions of dams, habitat alteration, and pollution. In the second type, known as assemblage or ecosystem overfishing (Murawski 2000), overfishing of an assemblage is demonstrated when catches proceed beyond the asymptotic maximum of a plateau-type curve or decline below the asymptotic or plateau level. Symptoms include sequential declines of species and depletion of individuals and species of large size, especially piscivores; declines in the mean trophic level of the assemblage; and changes in the responsiveness of populations to environmental fluctuations (such as shorter time lags). The associated decrease in size of the fish caught is unacceptable in some parts of the world, such as Latin America, but the preference for small fish in many African cuisines and the use of fish pastes and sauces in Asia encourage harvest of extremely small species, thereby allowing the entire assemblage to become depleted.

High-value individual targets

The declines of the Murray cod of the Murray-Darling river system in Australia, some sturgeon stocks of Eurasia, the tilapiine species *Oreochromis esculentus* and *Oreochromis variabilis* of Lake Victoria, and perhaps the Pacific salmon of the Columbia River are examples of the historical influence of overharvest. The Mekong giant catfish and the Nile perch of Lake Victoria provide contemporary cases.

The Murray cod. Native to the vast Murray-Darling river system of southern Australia, the Murray cod (*Maccullochella peelii*) is a large (up to 114 kg), long-lived (estimated at 50 to 100 years), and relatively slow-growing species (Rowland 1989). A large fishery had developed by the 1860s, and government concern for the fishery was expressed as early as 1880. Railroad consignments and sales in urban markets indicate that catches increased to a peak in 1918 and then gradually declined, and fishing became unprofitable for large operators by the 1930s. The Depression and World War II may have contributed to a decline in fishing pressure, and cod populations had recovered somewhat by the early 1950s.

The Murray cod then underwent a second, precipitous decline, which most likely had several causes, illustrating the wider panoply of threats that began to develop during the 20th century. Catch statistics show an increase from 1940 to 1955, and then a steep and rapid decrease to much lower levels by the early 1960s. River regulation and species introductions were probably the primary causes, although pollution and the growth of recreational fishing may also have contributed (Rowland 1989). The major impoundments on the Murray-Darling were constructed mainly after 1936, and their cumulative effect on river regulation was substantial by the 1950s–1960s. Although reproduction in the cod occurs annually regardless of flooding, year-class strength is linked to the occurrence of floods, which now are highly restricted. In addition, Eurasian perch (*Perca fluviatilis*), an exotic, became abundant by the 1940s, resulting in increased competition and predation on young Murray cod.

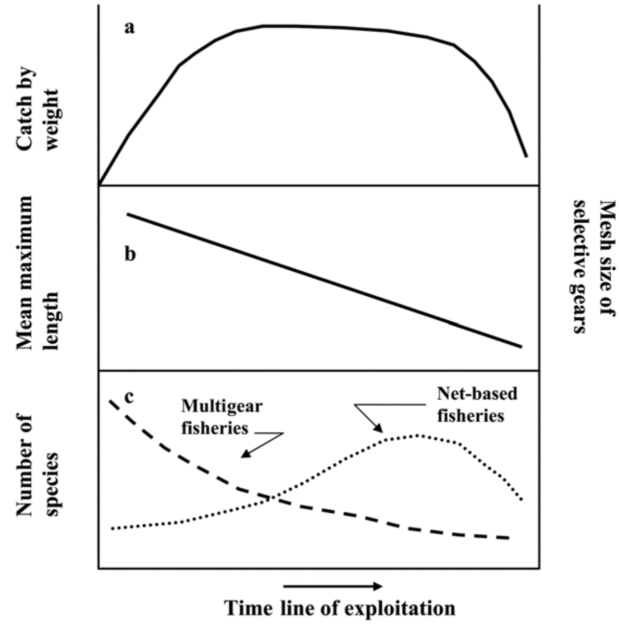

Figure 5. Characteristics of fishing down, including trends in various parameters of a multispecies fish assemblage in response to increasing effort: (a) total catch; (b) mean maximum length of assemblage and catch, and mesh size of nets; (c) number of species accessible to net-based and multigear fisheries.

The history of the Murray cod illustrates several points that may have general application: A large, highly valued fish, selectively targeted during the latter half of the 19th century before diverse human influences were manifest, is reliably known to have been fished beyond the level of commercial profitability. Some recovery appears to have occurred when fishing pressure was relaxed, but then river regulation, exotic species, and pollution became severe. Reduced larval recruitment rather than capture of mature fish has become the primary reason for low abundances, although the increasing recreational fishery after the 1950s may also have contributed, and hatchery stocking has played a substantial role in its recent recovery (Rowland 1989).

Large fish of the lower Mekong. The Mekong, the largest river in Southeast Asia, is home to over 1200 species of fish—the highest level of fish diversity in any river system except the Amazon and the Congo—including some of the largest species of freshwater fish in the world (figure 6). Several species of Mekong fish are now endangered, and the wild population of at least one species, the Mekong giant catfish, is close to extinction (Hogan et al. 2004). This species, a Mekong endemic, reaches a maximum length of 3 meters and a total weight of up to 300 kg. A large fishery had developed for the Mekong giant catfish in Luang Prabang (Laos) as early as 1890, and declines were observed in northeastern Thailand around 1940. Recent data reveal a fishery characterized by a pattern of increasing catch and increasing effort, followed by a declining catch with sustained high fishing effort, typical of an overexploited population (figure 7).

The same trend appears to be taking place with other large Mekong species. Anecdotal and published records (Mattson et al. 2002) point to the steep decline of the catch of large species such as the Sutchi catfish (*Pangasianodon hypophthalmus*), the giant barb (*Catlocarpio siamensis*), and the freshwater whipray (*Himantura chaophraya;* figure 6). Indeed, most of the world's largest freshwater fish are at risk according to the IUCN Red List (table 1), and overexploitation contributes in a number of these cases.

Assemblage overfishing

Overfishing of an entire assemblage may be most common in tropical regions, where fish diversity and the reliance of local people on fish harvests both are high. However, it clearly occurs in temperate latitudes as well, including in the Laurentian Great Lakes, where a number of valued species were overharvested in succession.

Laurentian Great Lakes. The fish assemblage of the Laurentian Great Lakes has undergone continual change since the earliest records, brought about by fishing, nutrient enrichment, and myriad invasive species. However, major changes after the late 1800s and continuing into the first half of the 20th century reflect an intensive and selective fishery targeting a succession of species and resulting in a succession of collapses (Smith 1968). The lake sturgeon (*Acipenser fulvescens*) was intentionally overfished because this large fish frequently damaged gear intended for more valuable species, and by the late 1920s it was so reduced that restrictions were imposed. The cisco (*Coregonus artedi*) experienced a collapse in the mid-1920s attributed to overfishing, and while occasional strong year classes occurred subsequently, their extreme rarity since the mid-20th century is most likely due to the additional pressure of increasingly unfavorable environmental conditions. A trap net introduced in 1928 was a very effective new gear for lake whitefish (*Coregonus clupeaformis*), and its use expanded rapidly through the US (but not the Canadian) waters of the Great Lakes. Although specific areas were rapidly depleted, overall catch increased until the 1930s, when declines in catch led to gear restrictions. Thus, several Great Lakes stocks were successively overfished in the early 20th century, when additional threats emerged, including the establishment of the invasive sea lamprey (*Petromyzon marinus*) after about 1940, the expanding influence of pollution, and a further sequence of invading species. Moreover, despite the loss of sturgeon and the collapse of certain stocks in parts of the Great Lakes, the total production of the fishery was relatively stable until the 1940s, although somewhat reduced from the high values seen before 1920.

Oueme River fisheries. The Oueme River, Republic of Benin, experienced intensive fishing by the 1950s, with the number of fishermen estimated to be 25,000 in 1957 and 29,800 in 1968 (Welcomme 1971). The surrounding environment was still largely undeveloped at that time, although it was used for intensive drawdown agriculture and cattle grazing. Assemblage overfishing was evidenced by changes in the composition and mean length of the fish caught. Large species reaching maximum lengths of around 60 cm, such as *Lates niloticus* (Nile perch), *Heterotis niloticus,* and *Distichodus,* were a significant fraction of the catch in the 1950s, but had disappeared from the lower Oueme or reduced their size at first maturation by the 1970s. They were replaced by smaller species such as *Labeo, Clarias, Heterobranchus, Schilbe, Synodontis,* and larger mormyrids of maximum lengths of about 40 cm. As fishing down continued into the 1990s, the fishery became dominated by numerous small species of cichlids, mormyrids, clariid catfishes, and the bagrid catfish *Chrysichthys auratus,* attaining maximum lengths of 10 to 30 cm.

Tonle Sap fisheries. Overfishing along the Mekong River threatens not only large species but the overall catch as well. The number of fishers in the Tonle Sap River basin has increased from 360,000 in the 1940s to an estimated 1.2 million in 1995 (Hortle et al. 2004). During the same period, catch per fisher has decreased by 50%, but overall catch has nearly doubled. Although large and medium-sized fish dominated the 1940s catch, by 1996 the catch was heavily dominated by small fish, largely because of increased fishing pressure and assemblage overfishing. Small cyprinids now make up more than 40% of the total catch of the Tonle Sap system, and populations of large migratory catfish and carps have declined. Fishers report that catches of river catfish have dropped by 90% in some fishing lots of the Tonle Sap Lake, for example, from about 100 metric tons 20 years ago to just 5 metric tons, or even 1 metric ton, today (Z. H., personal observation). Nonetheless, the shift from large to smaller species is very difficult to demonstrate because of the lack of long-term data. What is clear is that small, low-value cyprinids now dominate the fishery, whereas anecdotal evidence indicates that migratory and larger species—once much more abundant—have declined as a result of fishing pressure.

Ecosystem consequences of overfishing

Loss of apex predators results in a relaxation of top-down control of prey populations and stronger top-down control at the

Table 1. Conservation status of the world's largest freshwater fish species.

Common name	Scientific name	Maximum size	Distribution	IUCN Red List category	Major threats
Mekong giant catfish	*Pangasianodon gigas*	300 cm, 300 kg	Mekong River basin	Critically endangered	Harvest, habitat loss
Giant barb	*Catlocarpio siamensis*	300 cm, 300 kg	Mekong River basin	Not evaluated	
Isok barb	*Probarbus jullieni*	180 cm, 100 kg	Mekong River basin	Endangered	Harvest
Freshwater whipray	*Himantura chaophraya*	500 cm, 600 kg	Mekong River basin	Vulnerable	Harvest, habitat loss
Giant pangasius	*Pangasius sanitwongsei*	300 cm, 300 kg	Mekong River basin	Data deficient	Harvest
Sutchi catfish	*Pangasianodon hypophthalmus*	250 cm	Mekong River basin	Not evaluated	
Goonch	*Bagarius yarrelli*	200 cm	Mekong River basin	Not evaluated	
Largetooth sawfish	*Pristis microdon*	650 cm	Mekong River basin	Endangered	Harvest, habitat loss
Piraíba or valentón (giant catfish)	*Brachyplatystoma filamentosum*	360 cm, 200 kg	Amazon and Orinoco River basins	Not evaluated	
Pirarucu (bonytongue)	*Arapaima gigas*	450 cm, 200 kg	Amazon River basin	Data deficient	Harvest
Huchen	*Hucho hucho*	200 cm	Danube River basin	Endangered	Harvest, habitat loss
Taimen	*Hucho taimen*	200 cm, 100 kg	Selenge River basin (Lake Baikal)	Not evaluated	
Chinese paddlefish	*Psephurus gladius*	300 cm, 300 kg	Yangtze River basin	Critically endangered	Harvest, habitat loss
Yangtze sturgeon	*Acipenser dabryanus*	250 cm	Yangtze River basin	Critically endangered	Harvest, habitat loss
Murray cod	*Maccullochella peelii*	200 cm, 113 kg	Murray River basin (Australia)	Critically endangered	Harvest, habitat loss
Nile perch	*Lates niloticus*	200 cm, 200 kg	Congo, Niger, and Nile River basins	Not evaluated	
Wels catfish	*Silurus glanis*	500 cm, 306 kg	Widespread in Europe and Asia	Not evaluated	
Colorado pikeminnow	*Ptychocheilus lucius*	200 cm	Colorado River basin	Vulnerable	Habitat loss
Alligator gar	*Atractosteus spatula*	305 cm, 137 kg	Mississippi River basin	Not evaluated	
Lake sturgeon	*Acipenser fulvescens*	274 cm, 125 kg	Saint Lawrence, Great Lakes	Vulnerable	Harvest, habitat loss
Tigris River "salmon"	*Barbus esocinus*	230 cm, 136 kg	Tigris River basin	Not evaluated	

Source: IUCN Red List (*www.redlist.org/info/categories_criteria2001.html*).

next trophic level below. Because species richness tends to be lower at higher trophic levels, the likelihood that another species will fill the role of an extirpated apex predator may be diminished (Raffaelli 2004). Although the influence of predator composition and diversity on ecosystem stability remains poorly understood, a synthesis of experimental studies found significant destabilizing effects of predator removals on herbivore biomass (Halpern et al. 2005). Exclusion of top predators also has been found to release smaller predators that control dominant herbivores, thereby altering algal assemblages and their associated invertebrates. Because herbivorous fishes can regulate primary producers through direct grazing on benthic algae (Flecker 1996) and macrophytes (Bain 1993), changes in piscivore density can have a marked influence on primary production and abundance of basal resources via indirect pathways in trophic cascades.

Freshwater fishes also influence nutrient dynamics in freshwater ecosystems, both directly via excretion and indirectly via grazing and bioturbation of algae and detritus. Detritivorous gizzard shad (*Dorosoma cepedianum*) have been shown to affect inorganic nutrient ratios and planktonic primary production in a North American lake (Vanni 1996). Sediment grazing by fishes altered abundances of attached algae and the response of algae to limiting nutrients in an Andean piedmont river in Venezuela (Flecker et al. 2002).

One of the most spectacular and certainly best documented influences of fish on the supply of nutrients is due to the death and decay of great spawning runs of Pacific salmon after entering fresh waters. As salmon populations have decreased because of overfishing and other causes, declines have also occurred in lake productivity and juvenile salmon recruitment, leading to a number of fertilization experiments. Virtually without exception, the addition of nutrients has resulted in greater algal production and increased biomass of zooplankton and salmon smolts, and a few studies report greater survival of smolts and adults as well (Hyatt et al. 2004).

Although artificial fertilization can replicate the nutrient subsidy of formerly large spawning runs, a reduction in the seasonal flux of anadromous fishes into inland waters has serious implications for a diverse assemblage of terrestrial and semiaquatic animals, and terrestrial plant assemblages. In

Figure 6. Large fish species of the Mekong River: (a) Mekong giant catfish, **Pangasianodon gigas;** *(b) Sutchi catfish,* **Pangasianodon hypophthalmus;** *(c) freshwater whipray,* **Himantura chaophraya;** *(d) giant barb,* **Catlocarpio siamensis.** *Photographs: Zeb Hogan.*

North America, spawning salmon and their fry have been shown to be important to a wide variety of mammals, from mink to North American brown bears, as well as to piscivorous birds; furthermore, salmon influence the densities of insectivorous passerine birds in the riparian areas of salmon streams as a result of the indirect effects of salmon on insect prey (Willson and Halupka 1995). Nutrients derived from decaying fish that are transported into terrestrial habitats by subsurface flow, flooding, and consumers fertilize terrestrial ecosystems and enhance the growth and diversity of plants and soil microbes (Gende et al. 2002). Thus, declines in spawning runs of anadromous fishes result in the loss of an important flux of resources into terrestrial systems.

Mass migrations of fishes within fluvial basins are responsible for active transport of nutrients and energy at the landscape scale. Prochilodontid fishes, the major species in commercial fisheries in the large river basins of South America, are renowned for seasonal migrations of hundreds of kilometers, connecting food webs of distant, and sometimes divergent, ecosystems. During the falling-water period, young prochilodontids migrate en masse from productive whitewater floodplains into unproductive blackwater rivers, thus subsidizing apex predators in a species-rich food web (Winemiller and Jepsen 2004). Large pimelodid catfishes of the Amazon and Orinoco Rivers migrate many hundreds of kilometers between nursery areas in the lower river reaches and adult feeding and spawning areas in the upper reaches of the basins. These large piscivores may induce top-down effects on local

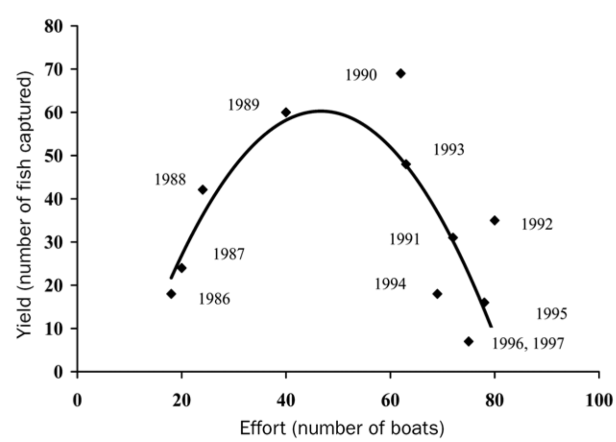

Figure 7. Yield as a function of effort for the Mekong giant catfish fishery in Chiang Khong, Thailand. The initial increase in catch as effort increases, followed by a steep decline in catch but sustained high effort, may indicate a fisheries crash. In the past, increases in fishing effort have resulted in increased catch. This is no longer the case today. Source: Giant Catfish Fishermen's Club of Chiang Khong.

fish populations, particularly when they enter rivers that drain unproductive watersheds (Winemiller and Jepsen 1998). Commercial fisheries have caused declines in at least one of these migratory catfish (*Brachyplatystoma vaillantii*) in the lower reaches of both major South American rivers (Barthem and Goulding 1997).

Finally, overfishing of inland waters has the potential for severe and unexpected impacts on the health of human populations, particularly in developing countries. For example, the trematode parasite responsible for schistosomiasis is vectored by snails of several genera that are consumed by numerous species of cichlid fishes. Substantial increases in recent years in the human incidence of schistosomiasis in freshwater systems, such as Lake Malawi, have been attributed to increases in vector snail populations released from predatory control by cichlid fishes, a likely consequence of overfishing (Stauffer et al. 1997). Investigations of the effects of overfishing on waterborne diseases such as schistosomiasis and cholera are currently in their infancy, but the consequences for human populations of depleting fish assemblages in these systems may be profound.

In sum, the functional or actual elimination of species from the ecosystems of inland waters is likely to have numerous consequences of varying severity. Progressive reductions in assemblage diversity mean that fewer species are available to perform critical functions, and consequences will be greatest when species with disproportionately strong influences on nutrient, habitat, or assemblage dynamics are lost. The ecological correlates of overfishing, although unevenly documented, almost certainly are profound and widespread.

Future directions

Overfishing threatens both the biodiversity of inland waters and the ecosystem goods and services on which people rely. However, its importance as a threat is underappreciated, because intensive fishing frequently acts synergistically with other pressures, and its consequences for inland fisheries and ecosystems are poorly understood and documented. The development community is beginning to appreciate the need to promote sustainable catches instead of increased production (World Bank 2003), but individual countries, municipalities, villages, and even some fisheries managers may not be as farsighted.

Overfishing is being driven by overcapacity and excess effort, which in turn are due to the generally open access regimes of many inland fisheries and to the effective use of fisheries as an occupation of last resort in developing economies. Managing fisheries today is not limited just to satisfying the commercial fishing industry, but must accommodate the wide array of economic and social benefits that people derive from freshwater ecosystems, including food security and economic growth. The practical effect of this is a widening of the group of stakeholders that have legitimate interests in how fisheries are managed. Setting up appropriate institutional structures and legal frameworks that will allow wider stakeholder participation in resource management is essential for the successful implementation of better fishery management strategies. Proposals have been made on many rivers for co-management systems that will substitute for the previously centralized approaches (Hartmann et al. 2004). Such decentralized systems will by definition involve local people to a greater degree in decisionmaking, resulting in more flexible management systems, with greater likelihood of formulating and enforcing regulations that correspond best to the needs of the fishery at the local level.

Fishery science and management is shifting its focus from single species to ecosystem-based fishery management (Pikitch et al. 2004). Assessing the effects of fishing on community-wide interactions and on ecosystem structure and function is a new challenge, and extending this assessment beyond fish populations (e.g., to benthos or producers) will be especially difficult. Harvest reserves and no-take zones, strategies with similar potential for achieving benefits beyond the fishery itself, have attracted impressive attention from the marine conservation and management communities (Hilborn et al. 2004) and also merit greater attention in inland waters (Hoggarth et al. 1999). Owing to the high degree of impact that freshwater systems experience from upstream and upland environmental threats, reserves in inland waters should be designed within a framework of integrated river basin management.

Until knowledge of ecosystem processes and their response to human actions is better developed, we suggest that four core principles should guide the management of inland fisheries for the long-term benefit of the widest range of stakeholders, including the environment: sustainability of yields, maintenance of biodiversity, protection from other anthropogenic stressors (habitat degradation, invasive species, pollution, etc.), and provision of socioeconomic benefits to a broad spectrum of resource consumers. Fishery management should be guided by a precautionary approach in setting management targets and limits (Pikitch et al. 2004). Managing inland fisheries, in most cases, will require developing plans that consider pressures occurring across multiple scales, through a process that includes both fishers and other stakeholders who have an interest in how a basin's resources are used. Biodiversity conservation and fishery management should be undertaken together, as the two constituencies ultimately have many shared goals.

Acknowledgments

We thank those who provided us with case studies and documentation, including Stuart Rowland, Jean Jackson, Alistair Richardson, and Ronald Bjorkland. Helpful comments on earlier drafts of the manuscript were provided by Brian Allan, Jim Diana, Peter Esselman, Ben Halpern, Ed Houde, Michael Nussman, Margaret Palmer, and three anonymous reviewers. J. D. A. thanks the David H. Smith Program of The Nature Conservancy for support during the initial development of this manuscript.

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