



## ANALYSIS

## Ecosystem services generated by fish populations

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In this paper, we review the role of fish populations in generating ecosystem services based on documented ecological functions and human demands of fish. The ongoing overexploitation of global fish resources concerns our societies, not only in terms of decreasing fish populations important for consumption and recreational activities. Rather, a number of ecosystem services generated by fish populations are also at risk, with consequences for biodiversity, ecosystem functioning, and ultimately human welfare. Examples are provided from marine and freshwater ecosystems, in various parts of the world, and include all life-stages of fish. Ecosystem services are here defined as fundamental services for maintaining ecosystem functioning and resilience, or demand-derived services based on human values. To secure the generation of ecosystem services from fish populations, management approaches need to address the fact that fish are embedded in ecosystems and that substitutions for declining populations and habitat losses, such as fish stocking and nature reserves, rarely replace losses of all services. © 1999 Elsevier Science B.V. All rights reserved.

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**1. Introduction**

Fish constitute one of the major protein sources for humans around the world. There are to date some 25 000 different known fish species of which

15 000 are marine and nearly 10 000 are freshwater (Nelson, 1994). Global capture fisheries harvested 101 million tonnes of fish including 27 million tonnes of bycatch in 1995, and 11 million tonnes were produced in aquaculture the same year (FAO, 1997). Despite the abundance and variation of fish, most western fisheries focus on a few target species. Approximately 75% of the world's marine fish landings consist of 200 (~

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1%) known existing marine fish species (FAO, 1997). Further, recreational fishing in lakes and along coasts is a major tourism activity (FAO, 1996; Postel and Carpenter, 1997). Estimates of the value of fish populations for human societies have predominantly focused on these goods. The fact that such values are derived from ecosystems with complex interactions, and that both economically and non-economically valuable fish populations play active roles in the maintenance of these ecosystems and in the provision of a range of ecosystem services, is seldom taken into account. Ecosystem services have been defined as “conditions and processes through which natural ecosystems, and the species that make them up, sustain and fulfill human life” (Daily, 1997, p. 3). This includes the life-support functions (Odum, 1989) of ecosystems and nature’s capacity to provide aesthetic and cultural quality to human life (Daily, 1997).

In 1995, almost 70% of the world’s major marine fish resources were fully- to overharvested, or depleted (World Resources Institute, 1996). Capture fisheries not only reduce the abundance of targeted stocks with cascading responses in the food web and with consequences in other ecological and fishery dependent systems, but also impact an array of other species, including mammals, as bycatch (Dayton et al., 1995; Steneck, 1998). In addition, many nearshore ecosystems are substantially altered through the destruction of benthic habitats by detrimental fishing methods (Malakoff, 1997). Indirect effects of fishing can have more important impacts on aquatic ecosystem structure and function than the removal of the fish (Hammer et al., 1993; Hughes, 1994; Botsford et al., 1997; Estes et al., 1998).

In this paper, we review some of the current knowledge about how fish populations provide ecosystem services for human societies, and the relations between these services and functioning ecosystems in different regions of the world. Available literature relating to large-scale marine systems is limited owing to the obvious difficulty of performing ecosystem experiments here. Small-scale freshwater ecosystems, on the other hand, are better understood in terms of influences of fish on ecosystem structure and function (Carpenter et

al., 1995). We also discuss some of the consequences of human impacts on fish populations, such as overfishing in relation to ecosystem resilience. We define resilience here as the amount of change or disruption that is required to transform a system from being maintained by one set of mutually reinforcing processes to a different set of processes (Holling, 1973). Identifying ecosystem services that various fish populations are part of, or generate for human societies, is one step toward holistic, ecosystem-based, resource management with increased understanding of effects on the dynamic, often unpredictable ecosystems by fisheries.

## 2. Ecosystem services

In this paper, we distinguish between two major categories of ecosystem services: fundamental and demand-derived ecosystem services (Table 1). By ‘fundamental ecosystem services’ we mean those that are essential for ecosystem function and resilience, such as nutrient cycling. These are ultimately a prerequisite for human existence, irrespective of whether humans are aware of it or not. Such services are often not linked to any specific economic market value. The ‘demand-derived ecosystem services’, such as recreational values, are formed by human values and demands, and not necessarily fundamental for the survival of human societies. Nevertheless, all demand-derived ecosystem services ultimately depend on natural systems and the fundamental ecosystem services provided by fish, and are not replaceable by technological innovations.

## 3. Fundamental ecosystem services generated by fish populations

### 3.1. Regulating services

Consumption of organisms by fish is a salient feature which can regulate trophic structure and thus influence the stability, resilience, and food web dynamics of aquatic ecosystems; moreover, these regulatory influences change as fish pass

from one life stage to another (Carpenter et al., 1992; Post et al., 1997). A fish larva, feeding on zooplankton, is as distinct ecologically from its adult form as it is from its planktonic prey. Piscivores (fish that eat fish), preying on zooplanktivores (fish that eat zooplankton), can exert a strong top-down control resulting in a cascade of effects down the food chain (Fig. 1). The general mechanism is explained as a decrease in the predation pressure on zooplankton result-

ing in an increase of zooplankton, which in turn increases the predation on phytoplankton (Carpenter et al., 1985). Although most trophic cascade studies have been done in calm freshwater environments such as lakes, some studies have been done in freshwater streams, the brackish Baltic Sea, and coral reefs (Hughes, 1994; Rudstam et al., 1994; Deegan et al., 1997). The degree of regulatory influence on foodchain relationships by fish varies with physical and climatological preconditions, including stream flow, temperature, upwelling fronts, storms, seasonal variability, and also with nutrient content and water depth (Rudstam et al., 1994; MacKenzie et al., 1996; Deegan et al., 1997; Jeppesen et al., 1998a). Also, Carpenter and Kitchell (1993) suggest that regulatory effects on species composition can be strong without affecting the overall function of the ecosystem. We illustrate these general concepts with several examples that follow.

### 3.1.1. Regulating food web dynamics and nutrient balances

Removal of fish with key characteristics and functions from the ecosystem may result in loss of resilience and in the ecosystem changing from one equilibrium state to another (Holling, 1986; Chapin et al., 1997; Grime, 1997; Tilman et al., 1997) (cf. multiple stable states, e.g. Sutherland, 1974; Sheffer, 1990; Levin, 1992; Walker, 1993).

Coral reef ecosystems in shallow coastal waters are exposed to hurricanes, typhoons, or cyclones which are irregularly occurring events. Thus, the regeneration of a healthy reef system is dependent on rapid colonization of larval recruits. Hughes (1994) showed how this recovery mechanism has been hindered in Jamaican coral reefs by human activities. Since the 1950/1960s the Jamaican coral reefs have been chronically overfished, such that sharks, snappers, jacks, triggerfish, groupers, and a number of other target species have declined markedly (Hughes, 1994). The loss of herbivorous and predatory fish species has reduced total fish biomass and altered the taxonomic composition of the fish community.

However, the ecological effects of this decrease in biodiversity were not realized for several decades, as the reefs appeared to be healthy with

Table 1  
Major fundamental and demand-derived ecosystem services generated by marine and freshwater fish populations

Fundamental ecosystem services	
Regulating services	Linking services
Regulation of food web dynamics	Linkage within aquatic ecosystems
Recycling of nutrients	Linkage between aquatic and terrestrial ecosystems
Regulation of ecosystem resilience	Transport of nutrients, carbon and minerals
Redistribution of bottom substrates	Transport of energy
Regulation of carbon fluxes from water to atmosphere	Acting as ecological memory
Maintenance of sediment processes	
Maintenance of genetic, species, ecosystem biodiversity	
Demand-derived ecosystem services	
Cultural services	Information services
Production of food	Assessment of ecosystem stress
Aquaculture production	Assessment of ecosystem resilience
Production of medicine	Revealing evolutionary tracks
Control of hazardous diseases	Provision of historical information
Control of algae and macrophytes	Provision of scientific and educational information
Reduction of waste	
Supply of aesthetic values	
Supply of recreational activities	

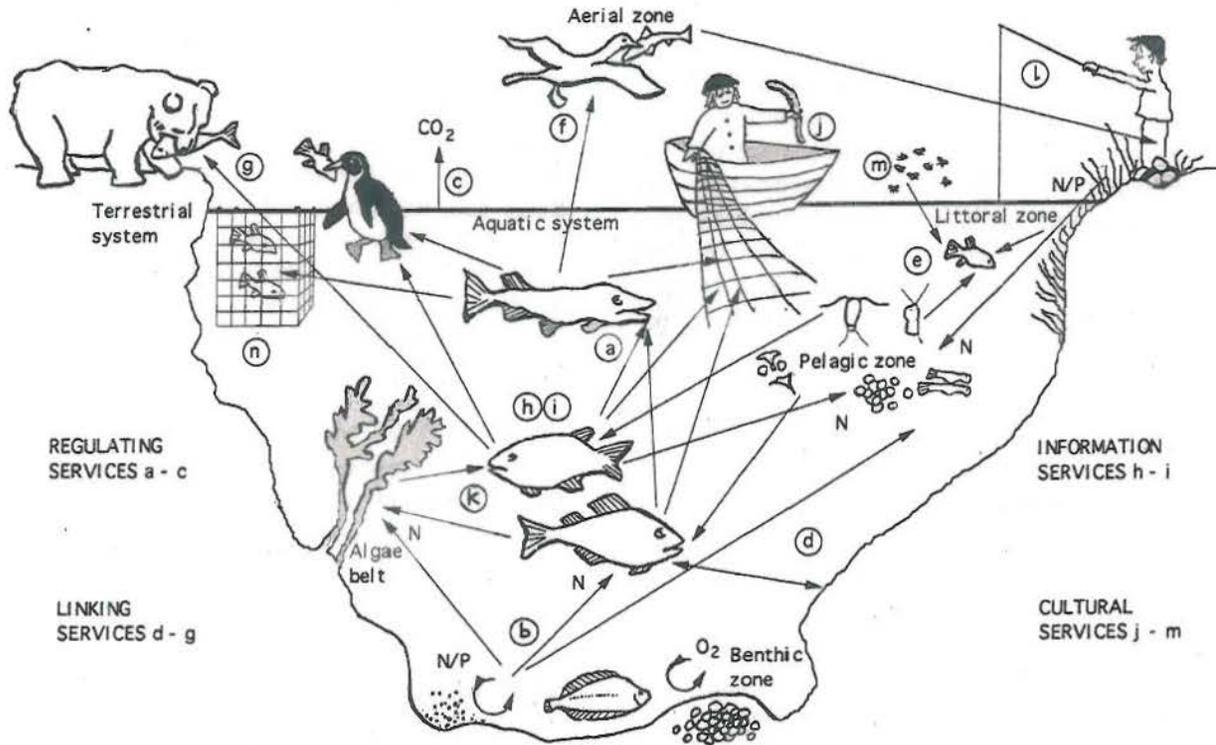


Fig. 1. Illustration of ecosystem services generated by fish populations: Fundamental ecosystem services: Regulating services include (a) top-down effects regulating population dynamics and nutrient availability, (b) bioturbation in or near sediments, and (c) carbon exchange. Linking services include active transport of nutrients, carbon and energy between the pelagic and (d) hard and soft bottoms, and (e) the littoral. Linking services also include passive transport of nutrients between ecosystems when fish eggs, fry, juveniles, adults, and carcasses are preyed on by (f) birds, and (g) mammals. Demand-derived services: Information services include fish as indicators of (h) ecosystem health, recovery and resilience, and (i) environmental recorders. Cultural services include fish as (j) goods, (k) for purifying water, (l) for recreation, (m) for mitigating the spread of diseases, and (n) for aquaculture.

large coral cover and high benthic diversity (Hughes, 1994). This was largely due to the high abundance of one grazing echinoid *Diadema antillarum*, which held in check the growth of algae on the reef. After the decline of fish predators and competitors, *Diadema* increased (Hughes, 1994).

However, after an intensive hurricane at the beginning of the 1980s the coral cover decreased between 1980 and 1993 from 52 to 3%, while the cover of benthic macroalgae increased from 4 to 92%, shifting the system from a coral dominated to an algal dominated ecosystem (Hughes, 1994). Hughes (1994) argues that this shift is partly explained by the fact that in 1983, *Diadema* suffered a mass mortality due to a species-specific pathogen reducing the population by 99%, and partly a result of loss of buffering capacity due to

the previous overfishing of grazing fishes.

In the Baltic Sea, Atlantic cod (*Gadus morhua*) is among the commercially most important species. Cod, although omnivorous, is also most likely the most dominant piscivore in the Baltic Sea (Rudstam et al., 1994). Approximately 70% of the diet of adult cod is fish of which 55% is Atlantic herring (*Clupea harengus*) and sprat (*Sprattus sprattus*) (Sparholt, 1994). Between 1980 and 1992 the biomass of cod in the Baltic Sea decreased from a peak of over 800 000 to less than 80 000 t, owing to overfishing in combination with human-induced eutrophication and natural climatic variations (MacKenzie et al., 1996). The decline is illustrated by the Swedish harvest of cod in the Baltic Sea, which reached a maximum of 59 000 t in 1984, and dropped to 16 000 t in 1993.

The overall decline of cod resulted in a shift in major fish community composition in many parts of the Baltic Sea towards a relatively high abundance of sprat and herring (Bagge et al., 1994; Rudstam et al., 1994; Sparholt, 1994). This has resulted in a shift in Baltic commercial fisheries from cod to an increased industrial fishery for mainly zooplanktivorous herring and sprat, which are used for fish meal production.

In freshwater systems, the feeding behavior of many adult and young fishes has cascading effects on population dynamics down the food web (Carpenter et al., 1985). The feeding pattern of fishes can also influence the temporal availability of nutrients and the potential for algal blooms in nutrient-rich lakes, since fish mineralize nitrogen and phosphorus through excretion and defecation, thereby making these nutrients available for primary production (Schindler, 1992). Further, it has been suggested that in lakes with adult piscivores, large zooplankton are more abundant than small zooplankton, while in lakes dominated by adult zooplanktivores, small-sized zooplankton are more abundant than large-bodied taxa (Brooks and Dodson, 1965; Vanni et al., 1990). Large zooplankton recycle nutrients more slowly and are more efficient grazers on phytoplankton than are small zooplankton. Hence, in a nutrient-rich lake with piscivory and large zooplankton, primary production can be suppressed (Shapiro and Wright, 1984; Vanni and Layne, 1997). This is illustrated by the events in Lake Mendota, WI, USA. Here, the sudden, massive mortalities of the zooplanktivorous cisco (*Coregonus artedii*) during an unusually hot summer resulted in reduced predation pressure on zooplankton, and increased abundance of large zooplankton, and decreased the availability of nutrients in the water column, with resulting decreases in biomass of algae and improved water clarity (Vanni et al., 1990).

Juvenile fish also have the potential to influence the abundance of algae. In Lake Pääjärvi in Finland, juvenile roach (*Rutilus rutilus*) feed on and suppress benthic insects and zooplankton in the littoral zone, and thereby stimulate the growth of algae in the lake (Kairesalo and Seppälä, 1987).

Further, the capacity of top-down control of grazing freshwater fishes has been shown to influ-

ence dynamics of nutrient-rich lakes. Changes of grazing fish community, such as grass carp (*Ctenopharyngodon idella*), can trigger a shift between two alternative stable states of a nutrient-rich lake, one turbid and one clear (Jeppesen et al., 1998b).

### 3.1.2. Regulating sediment processes

A limited number of studies about the relationship between fish, bioturbation (the physical disturbance of sediment associated with foraging or burrowing activities by consumers), and the structuring of bottom conditions has been done in rivers and lakes (Fuller and Cowell, 1985; Flecker, 1992; DeVries, 1997; Gelwick et al., 1997).

Salmonids cause bioturbation in streams while spawning and thereby create and maintain their own habitats (Montgomery et al., 1996). The female salmon deposits her eggs in redds, whereafter the eggs are fertilized, and covered with a layer of gravel. The spawning activities remove aquatic macrophytes, fine sediment particles including organic matter (Field-Dodgson, 1987), and may displace invertebrates from the bottom to the water column, making them more available to the river fish, as suggested by Bilby et al. (1998). Repeated salmon spawning over many years at the same location can modify the bottom contour and may lead to the formation of persistent bedforms with dune heights of over a meter (DeVries, 1997). The stream-bed alteration may provide suitable habitats for juvenile salmonids (Field-Dodgson, 1987), and enhances the survival of salmon embryos as the build-up of coarse gravel protects the embryos from rapid stream current (Montgomery et al., 1996).

Gelwick et al. (1997) describe how benthic algivorous fishes in the Illinois River in OK, USA, primarily *Campostoma anomalum*, *Campostoma oligolepus*, and Ozark minnow (*Notropis nubilus*), resuspend silt, detritus, and other particulate organic matter from the bottom into the current while feeding, and thereby maintain a rapidly growing algal community and enhance food availability for collector-filterers. Flecker (1992) found that feeding activities on algae or detritus associated with sediments by a diverse fauna of grazing fishes, in the stream Rio Las Marias in

Venezuela, modified the distribution and abundance of resources important to insects living in the stream. In the subtropical Lake Thonotosassa, FL, USA, spawning beds of the cichlid fish (*Sarotherodon aurea*) disturbed 11.5% of the littoral zone and modified benthic community organization (Fuller and Cowell, 1985). These studies suggest that riverine and freshwater fishes may play an active role in influencing abiotic and biotic factors during feeding or spawning.

Although no literature was found of the role of marine fish as bioturbators, the authors speculate that marine fish also participate in influencing the organized layers of microbial communities in sediments (Service, 1997), and other life conditions for benthic organisms, including animals living in sediments (Woodin, 1978; Brenchley, 1981), when spawning, hiding, resting or feeding in or close to bottoms. In addition, bioturbation should be of special importance in nutrient-poor environments, since bottom-derived nutrients released into the water can be incorporated into primary production instead of stored in the sediments.

### 3.1.3. Regulating carbon flux

Oceans and lakes can function as either carbon sinks or sources (Kling et al., 1992; Cooper et al., 1996). Carbon fixation increases with high nutrient input and high primary production. Recent whole-lake experiments comparing two nutrient-enriched lakes in WI, USA, have linked the composition of fish communities with ecosystem carbon fixation (Schindler et al., 1997). The first nutrient-rich lake (Peter Lake) with zooplanktivorous fish became a carbon sink because zooplankton were suppressed, and primary producers (carbon fixers) were released from grazing pressure. The second lake (West Long Lake) with piscivores was shown to be a carbon source because the piscivorous fish suppressed the abundance of zooplanktivores. This allowed the zooplankton community to exert a high grazing pressure on phytoplankton. Carbon fixation decreased, the concentration of dissolved carbon dioxide in the water increased due to community respiration, and a net diffusion of carbon from the water surface to the atmosphere followed. The study by Schindler et al. (1997) illustrates that the

structure of fish communities can regulate the carbon-fixing capacity of nutrient-rich lakes, and thus indirectly mediate the flux of carbon between lake and atmosphere.

## 3.2. Linking services

Fish generate a large number of services related to their movement patterns, including daily, seasonal, and yearly migration patterns in lakes, rivers, estuaries, and oceans (Polis et al., 1997). Fish that are consumed also transport nutrients across spatial boundaries and thereby link different ecosystems. The function of fish as active or passive transporters and distributors of energy and materials can enhance primary production in nutrient poor environments (Bilby et al., 1996; Larkin and Slaney, 1997).

### 3.2.1. Fish as active links between ecosystems

Several species of anadromous salmonid fishes migrate from marine environments where they spend most of their lives, to natal rivers to spawn and then die, and thereby transfer nutrients and carbon (Bilby et al., 1996; Larkin and Slaney, 1997). In North American rivers, it has been shown that marine-derived carbon and nutrients are delivered to the river through fish excretion, production of gametes, and fish carcass decomposition, and contribute to the production of algae, insect larvae, microbial decomposers, young salmon, and other fish in the rivers (Kline et al., 1990; Bilby et al., 1996; Larkin and Slaney, 1997). For example, in Snoqualmie River in WA, USA, 20–40% of the nitrogen and carbon in juvenile coho salmon (*Oncorhynchus kistutch*) originated from spawning coho salmon (Bilby et al., 1996). In Lakes Dalnee and Blizhnee, Paratunka River basin, in Kamchatka, northern Russia, between 20 and 40% of the total annual phosphorus input was supplied by anadromous sockeye salmon carcasses (*Oncorhynchus nerka*) (Krokhin, 1975). Further, marine-derived nutrients and organic matter originating from salmon eggs and carcasses have been found to stimulate biomass production up to 50 km downstream (Bilby et al., 1996; Larkin and Slaney, 1997).

The timing of this linking service is important. As shown by Cederholm (1989), and Bilby et al. (1998) carcasses and eggs from migrating salmon add marine-derived nutrients to river systems from late autumn to early spring, a period of the year when other nutrient inputs, like litterfall, are scarce in these streams. Thus migrating salmon provide the nutrients necessary for the spring algal bloom, which in turn drives ecosystem production at other trophic levels.

An example of the vast spatial scale over which fish can link freshwater and marine ecosystems is provided by European eels (*Anguilla anguilla*) in the Baltic Sea. Eel juveniles and adults spend most of their life in fresh or brackish waters where they feed and grow before they return to their spawning grounds in the Sargasso Sea, over 8000 km away, where they reproduce and then die. The eels are not presumed to feed during their migration to the Sargasso as their alimentary tracts virtually disappear with the onset of sexual maturity (Anon., 1994). Consequently, eels in the Baltic Sea is one example of long-distant migrating fish species that transport nutrients, carbon and other substances from one part of the world's seas to another.

There is considerable evidence for the importance of fish as 'mobile links' between ecosystems at short distances, relating to their daily migrating between feeding and resting areas. In lakes, fish transport and redistribute phosphorus and other essential nutrients between the shore, pelagic, and deeper bottom zones (Carpenter et al., 1992). In coral or rocky reefs, juvenile grunts (*Haemulon* spp.), blacksmith (*Chromis punctipinnis*) and other fishes transport substantial amounts of nutrients from their feeding areas (seagrass beds or open water) to their resting areas in the reef in the form of fecal products (Meyer et al., 1983). Bray et al. (1981) calculated that blacksmith feces contribute an average of 23 mg and a maximum of 60 mg of carbon per square meter per night to smaller crevices in the reef. Geesey et al. (1984) showed that migrating blacksmith contribute to an input of phosphorus and trace minerals to coral crevices.

### 3.2.2. Fish acting as ecological memory

By acting as energy and nutrient reservoirs, and as gene pool storage between years and ecosystems, migrating fish link spatial and temporal scales (Kairesalo and Seppälä, 1987; Cederholm, 1989). These active linking qualities of fish (Section 3.2.1) function as 'memory' in the ecosystem. Consider the migratory behavior of fish in connection with a natural break-down or change of an ecological system, for example a glaciation over thousands of years. During the ice period, migratory fish can move into adjacent ecosystems that remain ice-free and stable, and thereby escape the 'destructive' ice period. As the glaciation diminishes, fish can return to the altered ecosystem, provide nutrients, energy, and their genetic material while spawning, and also contribute to the structure and function of the new ecosystem while feeding and moving about. Migratory fish can be seen as an important part of the ecological memory that is necessary for the renewal (build-up) phase of ecosystems (Holling and Sanderson, 1996).

### 3.2.3. Fish as passive links between ecosystems

When fed upon by other organisms, fish, including eggs, fry and carcasses, serve as passive links between aquatic, aerial and terrestrial ecosystems, contributing to other food webs (Fig. 1). Scavengers are important as vectors of this linkage. For example, in three streams on the Olympic Peninsula in WA, USA, carcasses of coho salmon (*O. kisutch*) constituted a food source for 22 species of mammals and birds living near the river (Cederholm, 1989).

In the Baltic Sea, approximately 20 000–25 000 t of fish are eaten by seabirds every year (Sparholt, 1994). The birds produce phosphate-rich feces which are usually deposited at the seabirds' colony sites on islands or in coastal zones and has been shown to stimulate the production of macroalgae in rockpools in the Baltic Sea region (Ganning and Wulff, 1969).

In eastern Florida Bay, many of the seagrass areas are nutrient-limited (Powell et al., 1991). However, nutrients from fishes consumed by seabirds are deposited along shores as feces and stimulate the growth of the seagrass meadows in

Florida Bay up to 200 m away from bird colony sites. Increased seagrass biomass is of economic and ecological importance as seagrass is the primary habitat for larval pink shrimp (*Penaeus duorarum*), an important prey item for fish, birds and humans (Powell et al., 1991).

In the more extreme environment of Marion Island, between South Africa and Antarctica, the excretory products of fish-feeding penguins represent a net subsidy of nitrogen that is crucial for the growth of plants and peat formation (Lindeboom, 1984).

Loss of fish from the diets of avian and terrestrial animals can have direct socio-economic consequences. In the Flathead River-Lake ecosystem, located in Glacier National Park in MT, USA, the population of landlocked kokanee salmon (*O. nerka*) collapsed after the invasion of opossum shrimp (*Mysis relicta*) in 1981 (Spencer et al., 1991). The opossum shrimp was deliberately introduced in order to enhance the fish production. However, both opossum shrimp, and kokanee salmon living in freshwater are zooplanktivores, and Spencer et al. (1991) suggest that opossum shrimp, a voracious predator, outcompeted kokanee salmon in only a few years. The angler harvests, which up until 1985 were around 100 000 kokanee per season, declined to zero in only a few years. Long-range spatial negative effects on the terrestrial and avian fauna, which had depended on salmon eggs, juveniles, adults, or carcasses, resulted as well. The population of bald eagles in the Flathead River-Lake area decreased by 96% between 1981 and 1989, leading to a decrease of visiting bird-watchers from 46 500 to 1000 persons between 1983 and 1989. Other wildlife populations were also negatively affected by the loss of kokanee: coyotes (*Canis latrans*), minks (*Mustela vison*), river otters (*Lutra canadensis*), white-tailed deer (*Odocoileus virginianus*), and grizzly bears (*Ursus arctos*) (Spencer et al., 1991). Hence, the number of recreational activities in Glacier National Park dramatically decreased as a result of altered ecosystem function and loss of ecosystem services owing to loss of a fish population.

A more recent example of the importance of fish functioning as passive links is provided by the economically valuable guano production by

seabirds in Peru (Gootenberg, 1989). In 1998, owing to El Niño, many fish schools occurred at depths beyond the reach of the seabirds, resulting in the death of guano birds and other animals, and loss of income from guano production (Line, 1998).

#### 4. Demand-derived ecosystem services generated by fish populations

##### 4.1. Information services

The features and functions of fish populations provide information to scientists and managers. Due to the size and abundance of fish they are easily sampled research objects. Studies of the genetic make-up of fish, earstones (otoliths) and other features inform about the life history of fishes, including growth rate, age, taxonomic studies, identification of spawning locales, migrating and colonization patterns, as well as environmental history (Campana and Neilson, 1985; Ryman and Utter, 1986). Such information is crucial for management and our understanding of the relative importance of fish for resilient ecosystems, what ecosystem services they influence, how overfished or naturally fluctuating populations should be dealt with, etc. In addition, genetic material of fish populations serves as a source of information for aquaculture production and for biological conservation programs.

##### 4.1.1. Assessing ecosystem stress

Fish are sensitive to many stresses from parasites or diseases to acidification. Further, due to such factors as rapid growth rates, large body sizes, habitat choice, and trophic level, many fish have the capacity to bioaccumulate toxic substances. It has also been suggested that response by fish to stress at the population level can be identified before changes at the ecosystem level (Schindler, 1990). These features make many fishes suitable as early-warning signals of anthropogenic stress on natural ecosystem dynamics, or conversely, as indicators of ecosystem recovery (Harris, 1995; Moyle and Moyle, 1995; Balk et al., 1996), and of resilience (Carpenter and Cotting-

ham, 1997). In addition to the physical condition of fish, fish species richness and composition, trophic composition, and abundance can be used for monitoring human influence on water quality (cf. Index of Biotic Integrity, e.g. Fore and Karr, 1994). For example, the distribution pattern of butterflyfishes (*Chaetodontidae*) in the reefs of Hawaii and Sri Lanka has been suggested to function as indicator of disturbance caused by human activities, since the abundance of butterflyfishes appears to be positively correlated with the distribution of live coral reefs (Reese, 1995; Öhman et al., 1998).

#### 4.1.2. Long-term environmental recorders

The present fish fauna is living witness to climatic changes in the past, a fact that gives us information about past climate. For example, the distribution of Arctic char (*Salvelinus alpinus*) in Scandinavian lakes reveals a climatic pattern of a maximum water temperature of 16°C from the most recent glaciation period 10 000 years ago to today (National Environmental Protection Board, 1989, p. 106). Also, the distribution of 7 000–9 000-year-old bones of the warm-water living bream (*Abramis brama*) found in north of Sweden shows evidence of a climatic temperature maximum here in the past (National Environmental Protection Board, 1989, p. 106).

#### 4.2. Cultural services

Fish are generally valued for their qualities as goods, selected by human preferences, in the form of food protein, fishmeal, fish oil, game fish, and for aquaculture production. Also, in the pharmaceutical industry, certain substances from fish are used in research and might become important in the production of medicines. For example, a new water-soluble, broad-spectrum antibiotic class has been found in stomach extracts from the dogfish shark (*Squalus acanthias*) (Carté, 1996). Another example of pharmaceutical production involving fish concerns the extraction of the substance tetrodotoxin—a potent neurotoxin—from puffer fish (*Tetraodontidae*), which is a valuable tool in the study of the human nerve cell (Higa, 1997). However, because fish are part of ecosystems, fish

as goods depend on ecosystem services such as food web interactions involving fish and other organisms.

Cultural services generated by fish populations are based on our preferences and refer to when knowledge about the ecology of fish is used for producing renewable goods for human societies, for supplying aesthetic and recreational values, and for ameliorating human health.

##### 4.2.1. Food production

In 1995, 139 million tonnes of fish were harvested by capture fisheries and produced in aquaculture, and the average global food fish supply reached a record high level of 14 kg per capita (FAO, 1997). The production of fish in natural systems is strongly influenced by the intricate and alternating prey-predator relationships between the target species and other species. Thus, exploitation of one particular fish species ultimately affects the existence of other organisms including other fishes. Conversely, overexploitation of fish can undermine the life-support systems of other organisms in the same or adjacent ecosystems.

An illustrative example is provided by the rapidly developing intensive shrimp farming localized in or adjacent to mangrove forests. In 1990, approximately 25% of the world's shrimp production came from shrimp farming (Rosenberry, 1996). Deforestation of mangroves for shrimp farming degrades essential habitats for both wild shrimp and several stationary and migratory fish populations in the adjacent coastal zone, resulting in diminished fish and shrimp catches in capture fisheries (e.g. Martosubroto and Naamin, 1977; Sasekumar and Chong, 1987). Moreover, the coastal fishing communities are deprived of their main basis for livelihood based on ecosystem services provided by the mangrove ecosystem, leading to a marginalization of these communities (Primavera, 1991; Flaherty and Karnjanakesorn, 1995; Rönnbäck, this issue).

In contrast, integrated fish cultures exist in several countries with long traditions of using coastal resources (Mitsch and Jørgensen, 1989; Folke and Kautsky, 1992). Based on the principles of ecological engineering, the self-organizing ability of ecosystems is stimulated by profiting

from the natural functions of fish and other species for an efficient and environmentally sound production of fish and other goods. Materials and energy in the system are managed so that little or none go to waste, and goods can be harvested without degrading the resource base or services on which the goods depend (Folke and Kautsky, 1992). One of the most developed systems of ecological engineering is the integrated fish pond culture in China which has existed for more than 3000 years (Jingsong and Honglu, 1989). These managed food webs consist of primary producers (plants and phytoplankton), various levels of consumers including the harvested carp species, and decomposers, that recycle the nutrients.

Fish are also used as a management tool to enhance rice production in rice paddies. For example, in the Philippines several fish species are cultivated in rice fields (Halwart et al., 1996). The exact functional role of fish in rice paddies however is not yet fully understood. Halwart et al. (1996) suggest that juvenile Nile tilapia (*Oreochromis niloticus*) and common carp (*Cyprinus carpio*) act as biological control agents by preying on rice pests, such as damaging arthropods and snails.

#### 4.2.2. *Supplying recreational values*

During this century, sport fishing of wild and stocked game fishes in lakes, rivers, and along coasts has become one of the most popular recreational activities internationally (FAO, 1996). Intimate contact with nature while fishing is claimed to be one of the major incentives for sport fishing (Schramm and Mudrak, 1994). The increasing demand for game fish and suitable fishing- and swimming-areas, is in conflict with the decreasing water quality owing to other human activities. Biomanipulation (Shapiro and Wright, 1984; Jørgensen and Jørgensen, 1989) is a management tool used for improving water quality in nutrient-rich lakes, based on the idea of top-down food web control (Section 3.1), by removing fish or stocking piscivorous fish in order to suppress algal blooms (Benndorf et al., 1988), or stocking herbivorous fish such as grass carp to suppress vegetation (Lodge et al., 1998). However, the actual role of fish in biomanipulation, as well as long

term ecosystem effects of introductions of exotic fish species, has been much disputed and is not yet clear (DeMelo et al., 1992).

#### 4.2.3. *Supplying aesthetic values*

Fish in public aquaria, wild species in tropical reefs, in crowded streams during spawning, or in lakes and along coasts, generate highly valued aesthetic services (Moyle and Moyle, 1995). In economic terms, the global aquarium industry is estimated to generate seven billion US dollars per year (Moyle and Moyle, 1995). In Stockholm, Sweden, annual salmon and trout stockings in the city streams enhance the aesthetic qualities of the city, with the incentive of increasing tourism, as the salmonids splash about and are relatively easily caught (Holmlund, 1996).

In the short term all of these aesthetic services may not seem to depend on functioning ecosystems. However, in the long-term many of these services, such as stocking of hatchery-reared fish, depend on evolving fish populations contributing with their genetic diversity.

#### 4.2.4. *Improving human health*

Besides the obvious improvement of human health in terms of food protein, and medicine supply, fish are used in management to mitigate vector-borne diseases like schistosomiasis and malaria. Mosquitofish (*Gambusia* spp.), for example, feed on and control aquatic disease bearing invertebrates and plants in tropical climates (Marshall and Maes, 1994; Moyle and Moyle, 1995).

## 5. Discussion

Human societies benefit in numerous ways from ecosystem services generated by fish populations. Fish are part of food chain dynamics, nutrient cycling, and ecosystem resilience. Their mobility within the nested set of temporal and spatial cycles of ecological systems enhances the functional importance of fish as ecological memory in the form of energy, nutrients, genetic reserves, and information. Fish also generate employment, function as a genetic library for possible future use in medicine and aquaculture, stimulate human

interest in nature, and provide aesthetic and recreational values. Certain ecosystem services generated by fish populations are also used as management tools, for example, in enhancing rice production (Tilapia, carp), mitigating diseases in tropical zones (mosquitofish), mitigating algal blooms (pike *Esox lucius*, pike-perch *Lucioperca sandra*), mitigating growth of lake vegetation (grass carp), and indicating ecosystem stress (butterflyfishes).

However, increasing fishing pressure, pollution, habitat destruction, introduction of substituting exotic species, and other stress factors continue to exert strong pressure on fish populations around the world (Malakoff, 1997). Capture fisheries appropriate a substantial part (8%) of the global primary production in the sea, and require 24–35% of upwelling and continental shelf production (Vitousek et al., 1986; Pauly and Christensen, 1995). Further, the focus on high yields of a few species at the top of the food web by current fishery management has moved fish communities towards a composition dominated by lower trophic levels and forced fisheries to fish lower down the food web, as in the case of the Baltic Sea fisheries (Hammer et al., 1993; Pauly and Christensen, 1995). The human-induced direct and indirect degradation of common fisheries resources might cause impacts at the ecosystem level, jeopardizing the fundamental and demand-derived ecosystem services generated by fish with consequences for biodiversity, and ecosystem resilience (Naeem et al., 1994; Perrings et al., 1995). Loss of ecosystem services generated by fish populations can have unexpected negative economic consequences for human societies, as in the case of kokanee salmon in Glacier National Park (Spencer et al., 1991). Gradual loss of resilience due to human activities may be dramatically manifested as a rapid change to an alternate stable state, as exemplified in the Jamaican coral reef system, documented by Hughes (1994).

The search for substitutes for declining commercially important fish populations will most likely increase next century. A common practice during the 20th century has been to stock hatchery-produced indigenous or exotic species into lakes and open water systems (Welcomme, 1988).

However, fish stocking as compensation for declining fish resources often creates artificial systems dependent on continuous inputs of reared fish. Further, regular stocking practices may mask natural discontinuities and irregularities, diluting feed-back signals between ecological and social systems. Owing to natural dynamics, and the time lag between stocking and ecological effects, it is difficult to foresee long-term cascading effects of stocking practices in the ecosystem (Mooney et al., 1995; Holling et al., 1998). In many cases, stocking practices that seem to be successful in the short term, have been found to cause dramatic changes in the long term, such as depletion of other economically valuable species, changes in nutrient balances, or biodiversity decline (Krueger and May, 1991; Waples, 1991; McKaye et al., 1995).

Thus, stocking practices often overlook the functional roles of fishes as embedded in natural ecosystems during their life cycle. The stocked individuals rarely compensate for the loss of all ecosystem services. One example is provided by the case of Baltic salmon (*Salmo salar*). Large-scale yearly stocking of reared Baltic salmon since the 1950s to compensate for loss of natural spawning due to hydro-power construction in Baltic rivers has resulted in an overwhelming (90%) dominance of hatchery-reared fish in the Baltic salmon population, seriously eroding the genetic diversity. The reared salmon smolts have further been shown to have a higher mortality rate than wild fish (Lindroth, 1984). Ecosystem services generated by spawning adults and their eggs, larvae and juveniles, and salmon carcasses, have been largely lost, including inputs of marine-derived organic matter and nutrients to streams and adjacent terrestrial ecosystems, with unknown consequences.

The establishment of nature reserves is another common tool used for conservation or restoration purposes. However, isolated reserves cannot replace the multitude of fish populations continuously evolving and generating ecosystem services (Folke et al., 1996; Hughes et al., 1997). Naturally reproducing fish populations in geographically and temporally separated systems evolve under pressures of natural selection. Over large areas

and long time periods, population diversity increases, and thereby enables species better to continuously adapt to changing environments (Myers, 1997). Diversity of fish populations provides a buffer for uncertainty and secure resilience during ecosystem perturbation and safeguards the future health of natural and social systems (Folke et al., 1996; Dayton, 1998). Thus, allowing certain populations to be degraded with the underlying assumption that this is compensated for by conserving other populations in distant ecosystems, or in nature reserves, fails to recognize that fish populations are uniquely adapted to a relatively narrow range of environmental conditions, and are necessary for sustaining the function and resilience of particular lakes or coastal areas, and ultimately the economy of local human communities.

Current western fishery institutions need to recognize the interdependency between human societies and fish populations and develop adaptive resource use patterns (UNEP, 1998). This is of fundamental importance in light of the growing human population, rapid transformation of the Earth's ecosystems, and increasing fishing pressure. Management needs to be directed towards an multi-hierarchical, ecosystem-based approach which links the actions of populations to ecosystem properties, including functional diversity and resilience (Vitousek, 1990; Schultze and Mooney, 1994; Lawton and Jones, 1995; Carpenter and Turner, 1998). Identifying and taking into account what ecosystem services the fish depend on and what services the fish generate, we believe, is one step in that direction. Such ecosystem-based management approaches, relying on both scientific and traditional ecological knowledge, have been identified, and exemplified by a growing body of case studies of sustainable local fisheries, e.g. integrated fish cultures in China (Jingsong and Honglu, 1989; Berkes, 1995; Berkes and Folke, 1998). Less emphasis is put on controlling how much fish that can be harvested. Instead, regulations focus on when, where, and how to fish, taking into account the spatial and temporal life-supporting systems of fish (Johannes, 1981; Wilson et al., 1994; Hammer, 1995; Acheson et al., 1998; Johannes, 1998).

Knowledge about ecosystem services also enhances our comprehension of the non-linear nature of ecosystem behavior, as well as bridges between the temporal and spatial scales of management on the one hand and ecological systems on the other (Hammer et al., 1993; Ludwig et al., 1993; Holling and Sandersson, 1996). This may help us to organize the system of fish resource governance including property rights regimes, decision-making processes, and collaboration between local and central levels, in identifying beneficiaries of ecosystem services, and in dealing with resource conflicts (Ostrom, 1990; Hanna, 1996; Miller et al., 1997; Ostrom, 1998).

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