FISH BIODIVERSITY IN FLOODPLAINS AND THEIR ASSOCIATED RIVERS

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Abstract

Floodplains are major, seasonal wetlands that are formed by overspill of floodwaters from the rivers with which they are associated. Rivers are old features of the landscape inhabited by complex fish communities. The greater the size of the river basin the greater the number of species to be found there. Apart from Arctic systems this relationship is not greatly affected by latitude. Fish assemblages consist of many more small species than large ones. A great range of reproductive, feeding and physical adaptation to low dissolved oxygen and fast current exists linked to morphological features of the river system. Fish biodiversity is influenced by fishing and by other anthropogenic effects on the river. These tend to suppress large species in favour of smaller ones. At the same time specific elements of the assemblage can be forced to local extinction by the removal of its habitat or by blocking migratory pathways. River fish are currently among the most threatened life forms. To conserve the considerable biodiversity whilst at the same time continuing to exploit its constituent species for food and recreation will require considerable effort. Improved management of wild fisheries, where the users of the resource have a greater say in its disposal, establishment of parks and reserves for in-situ conservation and rehabilitation of damaged environments are all valuable tools in this process. For river conservation to be truly effective a national consensus is necessary whereby all users of the resource are committed to its sustainability.

Introduction

Floodplains are major, seasonal wetlands that are formed by overspill of flood waters from the rivers with which they are associated. Biodiversity in these systems is extremely high and riverine faunas depend on the intimate linkage between the flowing water (riverine) component and the static water (floodplain) component. As such no ecological separation can be made between the two phases of the system. Rivers are generally very old features of a landscape as well as being one of the major contributing factors to landforms. They are apparently extremely diverse but geomorphological studies show that they follow simple physical rules relating form to flow and gradient (Calow and Petts 1992). Rivers are generally classified according to stream order (Strahler 1957). In a typical river lower order streams are generally high gradient, torrential and narrow. They are succeeded by streams of intermediate order which still maintain a high gradient, but take on a characteristic sequence of pools and riffles. Higher orders still are braided with numerous small anastomosing channels usually with relatively coarse substrates. Finally the highest order rivers are of

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very shallow gradient, meander across broad floodplains and have bottoms of fine sand and mud. Many rivers do not follow this pattern exactly as accidents of geography can locally alter the gradient. In this way many rivers have a low gradient middle course which is associated with extensive swamp and floodplain wetlands.

This diversity of form and function result in systems that are extremely diverse and which present a wide range of habitats. Lower order streams (rhithron) are usually well oxygenated, relatively cold and nutrient poor. The pool-riffle structure gives an alternation of rocky rapids like sections alternating with deeper and slower flowing pools. The lack of autochthonous primary production results in food chains that rely much on material falling or swept into the water from the land. Higher order rivers are warmer, usually nutrient rich and often poorly oxygenated. The floodplains that are associated with them are broad areas of seasonal wetland, which are often completely flooded during high water. At low water they dry out except for marshes and residual lakes which retain water for at least part of the dry period and often through the whole season. Floodplains may be open and covered with grasslands, which are often maintained by human activities such as deforestation and burning, or they may be forested. Fish species have evolved to take advantage of the characteristics of these various habitats many of which act like island communities in that they can be separated from one another over long geographical periods. In a river such as the Amazon, for example, the many tributaries and small streams are separated one from another by the deep and swift flowing mainstem.

Living aquatic resource in floodplain rivers are extremely robust in their response to natural climatic variability and respond readily to year-to-year variations in flood strength. They can even survive, prolonged periods of drought. They are, however, sensitive to long term disruptions in the flood regime which attack, particularly, the wetland component of the system. Because their is great pressure on such wetlands for human occupation, for agriculture and for other uses such systems are among the most vulnerable natural resources in the world and are disappearing at an increasing rate. This chapter examines the principles underlying the ichthyological diversity of floodplains and their associated rivers and suggests measures for their conservation.

Numbers of species

A variety of indices have been developed as indicative of the diversity of faunas and floras. These usually combine some measure of the number of species present with their relative abundance. However, number of species, or species richness (N) remains one of the primary measures of biodiversity. The number of species inhabiting rivers is related to the size of the river as indicated by main channel length or basin area. For example, a sample of 292 rivers from around the world (Oberdorff et al. 1995) gives a relationship

$$\text{Log}_{10} \text{ Number of species} = 0.478 + 0.266 \log \text{ drainage basin area (km}^2\text{)}$$

with an r^2 of 0.439. The low coefficient of determination of this relationship is caused by differences between continents. Relationships calculated for rivers in each continent give higher values of r^2 (See for example Africa, Fig. 1) (Welcomme 1985). The effect of latitude is relatively slight although temperate rivers do tend to have slightly fewer species than tropical systems of the same size. Species richness in rivers and temperate rivers such as the Danube or Mississippi fit within the scatter for tropical systems although they lie below the mean. The only exception to this occurs in rivers from previously glaciated areas where repopulation of the rivers is still incomplete and species numbers are extremely low. Thus even large arctic rivers may only have a few resident species although diadromous migrants supplement their numbers.

Diadromous fish occupy the inland water system for only part of their life cycle. Anadromous species such as the salmonids and sturgeons spawn and pass their early life stages in freshwaters. Catadromous species such as eels pass their adult stages in rivers and lakes and return to specific areas in the sea to breed. Both these behaviours require long migrations and highly specific physiological adaptations to enable the fish to return to their natal waters for breeding. In general anadromy is commoner in the Arctic and Temperate zones where the seas are richer than rivers and catadromy predominates in the tropics where the rivers are richer than the marine environments.

Species are still being discovered in remote parts of some large river systems. For instance, entire deep-water assemblages have recently been found in the Amazon and Orinoco rivers and a new species are constantly being was described from the Mekong.

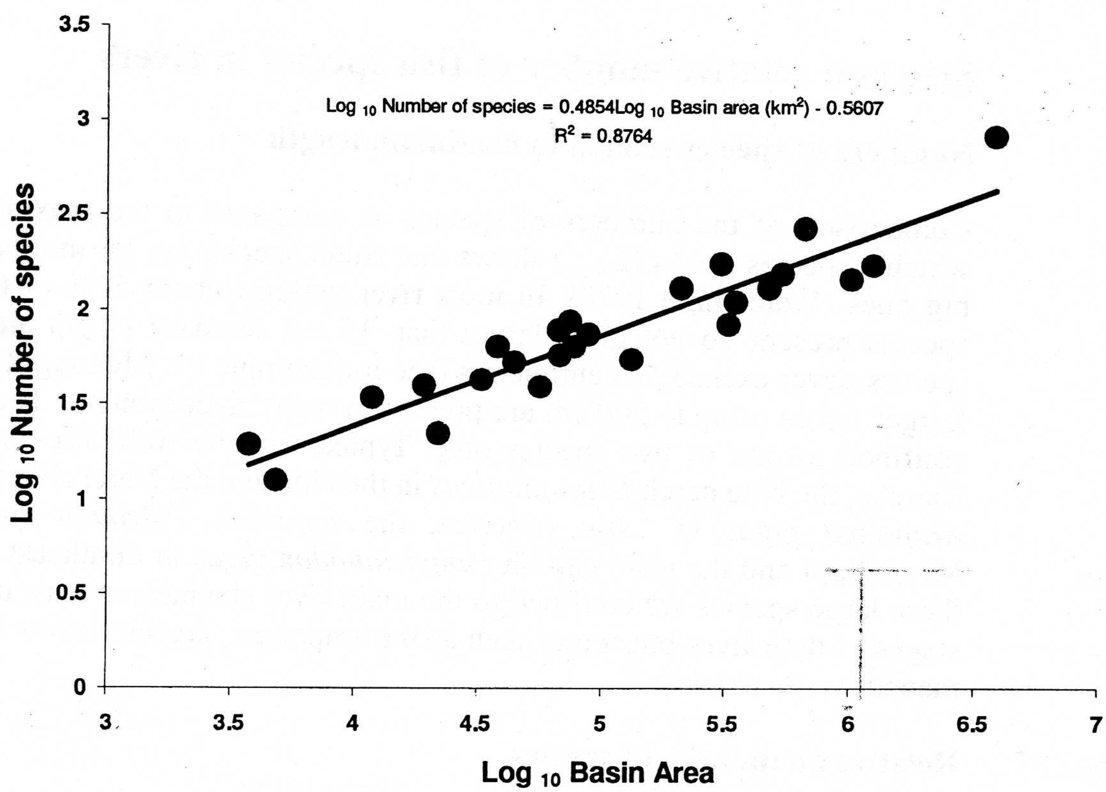

Fig. 1. Number of species as a function of river basin area for 24 African rivers.

The number of species in larger systems, where it is commonplace to catch many tens of species in any one net haul, raises the question of species redundancy (Baskin 1995). Clearly in systems with few species efficiency of resource use, stability and resilience are all increased by the addition of extra species. In systems where several species of apparently identical ecology co-exist the value of the extra species is questionable. In part of course the apparent similarities may be due to lack of knowledge of the fine details of their ecology (Chapin et al. 1997). Furthermore some apparent duplication may be due to community responses to climatic variability. Many rivers in climatically unstable areas have faunas that are adapted to different climatic regimes. In general there is a dry period fauna adapted to periods of drought, which spawns and lives within the main channel of the river, and a wet period fauna adapted to more normal flood regimes, which spawns on the floodplain. In some rivers, such as the Niger, the two faunas are represented by species homologues one of which prefers main channels and the other the floodplain (Welcomme 1984). In other areas different behavioural groups within the same species assure the diversity. The persistence of large numbers of species in rivers appears to contravene the principal of competitive exclusion. The abundance of food during the flood and the relatively low densities of fish relative to the volume of water at this time probably mean that there is no shortage of food and thus there is little cause for species to be eliminated on competitive grounds alone.

Size and relative number of fish species in rivers

Numbers of species related to maximum length

Comparison of the numbers of species as compared to the maximum length to which a species grows (L_{max}) shows that small species are far more abundant than big ones (Welcomme 1998). In most river systems about 50% of the number of species present do not grow larger than 15 cm standard length and 90% of the species never exceed 50 centimetres (see for example the Mekong River Figure 2). Larger fishes of up to 300 cm are present in many river systems. These are usually confined to one or two species only. Typical are the wels *Silurus glanis* in the Danube, the Nile perch *Lates niloticus* in the Nile and the Niger rivers, the arapaima *Arapaima gigas* in Latin America, the spoonbill *Polyodon spathula* in the Mississippi and the giant catfish *Pangasianodon gigas* in Southeast Asia. Many of these large species are confined to the main river channels at least during the later stages of their lives but some, such as the arapaima., are specialists occupying permanent wetland lakes.

Relative abundance of species

The relative abundance of species in any environment has been shown to be lognormal (Preston 1962a and 1962b). This distribution has been found to apply to fish assemblages in the Benue River by Daget (1966), Lake Chad by Loubens (1970) and to total assemblages or to catches by individual gear in other rivers in Africa (personal observations). This type of relationship may be simplified into a simple exponential:

$N = ab^R$

between species ranked in order of abundance where R = rank and N = number. The canonical distribution suggests that fish assemblages are always dominated by very few species. A large number of species will be moderately abundant and a few other species will be rare. Disturbances to species abundance by natural events such as the Sahelian drought and global warming, or by human interventions such as eutrophication or fishing means that different species will assume dominance without the underlying numerical relationship being effected.

Diversity of river fishes

This section illustrates the diversity of river fish species, which has evolved in response to the challenges of the environment along different parts of the river's course.

Zonation

As we have seen gradient is one of the major factors influencing the morphology of a river segment and hence the type of fish assemblage to be found there. Rivers may be divided into zones depending on the fish species present. Zonation is more readily demonstrated in temperate rivers where successions are established by substitution of species (Roux and Copp 1993), than in the tropics where successions tend more to be by accretion of species (see for example Boujard 1992). However, some examples of zonation in tropical rivers have been found by Ibarra and Stewart (1989) (see also Welcomme 1984 for review).

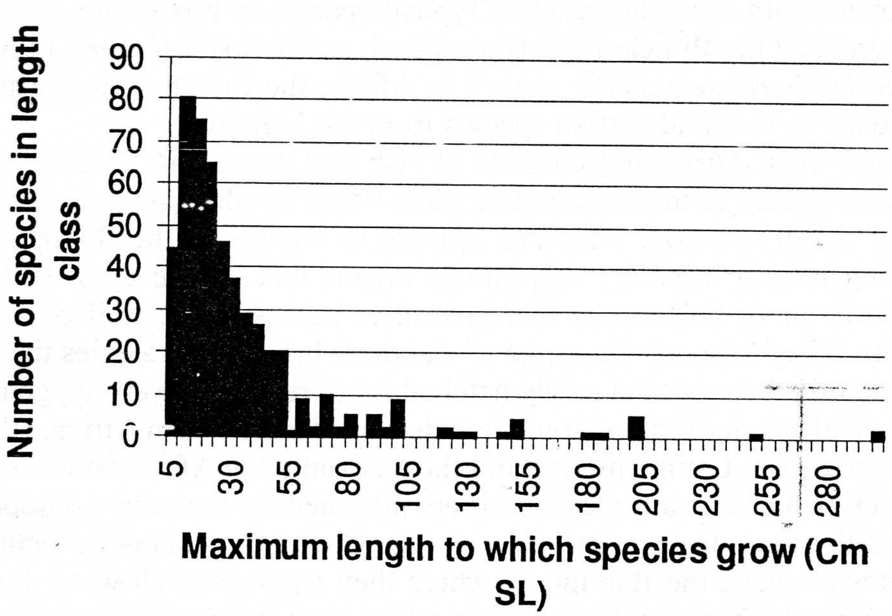

Fig. 2. Number of species classified according to maximum length attained in the Mekong River.

High gradient streams are usually segmented into pool and riffle reaches, each of which attracts specific species complexes. Riffles are rich in invertebrate food organisms and their waters are well aerated. They are occupied by flow-loving species that show a variety of adaptations that enable them to survive in strong currents. Small species or juveniles of larger ones are common which live among the rocks. The quieter waters of the pools are inhabited by less energetic swimmers that can take refuge in areas of slack flow as well as by larger fish which feed on the drift of organisms dislodged from the riffles. Some large, migratory species move upstream to the headwater tributaries from the lower reaches of the river for spawning and to place their young on the food rich riffles. Fish in this zone may bury their eggs in pockets in the gravel of the riffles or may attach their eggs to rocks or submersed vegetation. Some species of up-river spawner scatter their semi-pelagic eggs, which drift downstream with the current until they reach sufficient size to migrate laterally onto suitable nursery sites on the floodplain.

Fish assemblages from the downstream regions are much more complex as a function of the increased complexity and extent of the environment. They fall into four principal behavioural guilds, which are often categorised according to a nomenclature originally developed by traditional peoples in the Mekong River.

- White fish: This guild groups large, strongly migratory fishes from several families that move large distances within the river channels between feeding and breeding habitats. The fish may pass their whole life history in the main channel or may move onto the floodplains to feed at high water. They are generally intolerant of low dissolved oxygen concentrations preferring migration as a means to escape the adverse condition downstream during the dry season. Whitefish are generally one shot spawners, scattering numerous eggs, which may remain to hatch in situ or may be pelagic or semi-pelagic being swept downstream with the current. Typical species in this group are *Salminus maxilosus* and the Pimelodid catfishes such as *Brachyplatystoma* in South America, *Alestes baremoze* and *A. dentex* in Africa, the Indian major carps in India and most cyprinid and catfish species from the Mekong.
- Black fish: This guild consists of fish that move only locally from floodplain water bodies to the surrounding plain when flooded and return to the pools during the dry season. They are adapted to remain on the floodplain at all times often having auxiliary respiratory organs that enable them to breathe atmospheric air or behaviours that give them access to the well oxygenated surface film. They have a wide range of elaborate breeding strategies that allow them to maintain the eggs and newly hatched fry in relatively well-oxygenated localities. Typical species in this group include clariid catfishes in Africa, *Plecostomus* and *Loricaria* in Latin America and the anabantids in Africa and Asia.
- Grey fish: These are species that are intermediate between the floodplain resident and the long distance migrants guilds. Grey fish generally execute short migrations between the floodplain, where they reside at high water for breeding and feeding, to the main river channel where they shelter in marginal vegetation or in the deeper pools of the channel over the dry season. These species are less capable in surviving extremely low oxygen levels but do have elaborate reproductive behaviours, which enable them to use the floodplain for breeding. Species such as the tilapias, many small characins and cyprinids belong to this group.

- River residents that inhabit local areas of the main channel and migrate little. These are relatively uncommon and are usually confined to the larger rivers where deeps in the main channel are sufficiently hospitable. The mormyrid communities in African rivers and the recently discovered deep-water gymnotid fauna of the Amazon provide an example of this group.

Both grey and black fish guilds can show lateral zonation according to the degree to which they penetrate the floodplain. This is largely linked to the resistance of individual species to low dissolved oxygen concentrations.

Adaptations to adverse conditions

Low Dissolved Oxygen

Many environments within the river-floodplain system develop anoxic conditions especially during the dry season. Such oxygen deficiencies may occur in main river channels but are more usual in the permanent marsh and lake habitats of the floodplain wetlands. There is a advantage to be gained by occupying difficult habitats of this type as they are generally free of predators, or, where predators exist the oxygen penalty for the capture and digestion of prey can exceed that which is available. Many fish in the potamon, therefore have adaptations to breathing oxygen from the air, from the surface layers of water or by more efficient utilisation of the small amounts of oxygen that are present.

Several species have lungs for example the lung fishes or lung like organs often modified from the swim bladder, *Arapiama gigas, Lepisosteus, Gymnarchus*, or a modified branchial chamber as in the catfish *Heterpneustes.* Others have auxiliary breathing organs such as the labyrinth organs of the Anabantidae, or the arborescent organ of the Clariidae. Some species have vascularised areas in the gut, the stomach in *Ancistrus, Corydoras, Plecostomus,* the intestine, *Hoplosternum*, or the rectum, *Misgurnus fossilis*.

Many small species, particularly the cyprinodonts are adapted to sip water from the topmost few millimetres, which are better oxygenated. Some larger fishes such as *Oreochromis, Colossoma* and *Brycon* may breath at the surface during anoxic periods and even develop special prolongations of the mouthparts to let them do so.

Current

Species living in areas of high flow have a range of adaptations to enable them to maintain their position and to survive. The simplest of these is the ability to swim fast enough to combat the current, although such behaviour can not be sustained indefinitely and is usually associated with resting in slack current refugia. Physical adaptations are abundant. Hooks, spines or suckers that enable a fish to fasten itself to rocks and vegetation are common in many torrent living species. Such adaptations are usually accompanied by humped shape that keeps the fish on the bottom hydrodynamically. Small size or elongated shapes that allow the fish to live among the crevices of the rock riffles or to entwine themselves in rooted vegetation are also common.

Table 1. (Continued).

Rock and gravel spawners (lithophils)	Zygotes buried in gravel depressions called redds or in rock interstices, large and dense yolk, extensive respiratory plexuses for exogenous and carotenoids for endogenous respiration, early hatched free embryos photophobic, large emerging alevins	Many salmonid species
Spawners in live invertebrates (ostracophils)	Zygotes deposited via female ovipositor in body cavities of mussels, crabs, ascidians or sponges, large dense yolk, lobes or spines and photophobia to prevent expulsion of free embryos, large embryonic respiratory plexuses and carotenoids, probable biochemical mechanism for immunosuppression.	*Rhodeus sericeus.*
	Guarders	
	Substrate choosers	
Pelagic spawners (pelagophils)	Nonadhesive, positively buoyant eggs, guarded at the surface of hypoxic waters, extensive embryonic respiratory structures	Some *Ophicephalus* and *Anabas* spp
Above water spawners (aerophils)	Adhesive eggs, embryos with cement glands, male in water splashes the clutch periodically	*Copeina arnoldi.*
Rock spawners (lithophils)	Strongly adhesive eggs, oval or cylindrical, attached at one pole by fibres in clusters, most have pelagic free embryos and larvae	*Loricaria parva*, *L. macrops* and some small cichlids
Plant spawners (phytophils)	Adhesive eggs attach to variety of aquatic plants, free embryos without cement glands swim instantly after prolonged embryonic period	*Polypterus* spp
	Nest spawners	
Froth nesters (aphrophils)	Eggs deposited in a cluster of mucous bubbles, embryos with cement glands and well developed respiratory structures	*Hepsetus odoe*, *Hoplosternum*, some anabantids
Miscellaneous substrate and material nesters (polyphils)	Adhesive eggs attached singly or in clusters on any available substratum, dense yolk with high carotenoid contents, embryonic respiratory structures well developed feeding of young on parental mucus common	*Notopterus chitala*, *Hoplias malabaricus*
Rock and gravel nesters (lithophils)	Eggs in spherical or elliptical envelopes always adhesive, free embryos photophobic or with cement glands swing tail-up in respiratory motions, moderate to well developed embryonic respiratory structures, many young feed first on the mucus of parents.	*Aequidens* and other cichlids, some characins, e.g., *Leporinus*.

Table 1. (Continued).

Gluemaking nesters (ariadnophils)	Male guards intensively eggs deposited in next bind together by a viscid thread spinned from a kidney secretion, eggs and embryos ventilated by male in spite of well developed respiratory structures	*Gasterosteus aculeatus*
Plant material nesters (phytophils)	Adhesive eggs attached to plants, free embryos hang on plants by cement glands, respiratory structure well developed in embryos assisted by fanning parents.	*Clarias batrachus*
Sand nesters (psammophils)	Thick adhesive chorion with sand grains gradually washed off or bouncing buoyant eggs, free embryo leans on large pectorals, embryonic respiratory structures feebly developed	*Tilapia* spp.
Hole nesters (speleophils)	At least two modes prevail. in this guild: cavity roof top nesters have moderately developed embryonic respiratory structures, while bottom burrow nesters have such structures developed strongly	Several cichlids
	Bearers	
	External bearers	
Transfer brooders	Eggs carried for some time before deposition, in cupped pelvic fins, in a cluster hanging from genital pore, inside the body cavity (earlier ovi-ovoviviparous), after deposition most similar to nonguarding phytophils	*Callichthys*, *Corydoras*
Auxiliary brooders	Adhesive eggs carried in clusters or tails on the spongy skin of ventrum, back, under pectoral fins or on a hook in the superoccipital region, or encircled within coils of female's body, embryonic respiratory circulation and pigments well developed.	*Loricaria* spp.
Mouth brooders	Eggs incubated in buccal cavity after internal, external synchronous or asynchronous, or buccal fertilization assisted by egg dummies, large spherical or oval eggs with dense yolk are rotated (churning) in the cavity or densely packed when well developed embryonic respiratory structures had to he assisted by endogenous oxydative metabolism of carotenoids, large young released	Many cichlids e.g. *Oreochromis*, *Haplochromis*, *Osteoglossum*
Pouch brooders	Eggs incubated in an external marsupium: an enlarged and everted lower lip, fin pouch, or membraneous or toy plate covered ventral pouch, well developed embryonic respiratory structures and pigments, low number of zygotes	*Loricaria vetula* and *L. anus*

Table 1. (Continued).

	Internal bearers	
Facultative internal bearers	Eggs are sometimes fertilized internally by accident via close apposition of gonopores in normally oviparous fishes, and 'nay he retained within the female's reproductive system to complete some of the early stages of embryonic development, rarely beyond the cleavage phase; weight decreases during embryonic development.	*Rivulus marmoratus, Oryzias latipes, Pantodon buchholzi*
Obligate lecithotrophic livebearers	Eggs fertilized internally, incubate in the reproductive system of female until the end of embryonic phase or beyond, no maternal-embryonic nutrient transfer; as in oviparous fishes yolk is the sole source of nourishment and most of the respiratory needs; sane specialization for intrauterine respiration, excretion and osmoregulation; decrease in weight during embryonic development	*Poeciliopsis monacha, Poecilia reticulata, Xenopoecilus poptae*
Matrotrophous oophages and adelphophages	Of many eggs released from an ovary only one or at most a few embryos develop into alevins and juveniles, feeding on other less developed yolked ova present and/or periodically ovulated (oophagy), and in more specialized forms, preying on less developed sibling embryos (adeiphophagy); specialization for intrauterine respiration, secretion and osmo-regulation similar to the previous guild; large gain in weight during intrauterine development.	
Viviparous trophoderms	Internally fertilized eggs develop into embryos, alevins or juveniles whose partial or entire nutrition and gaseous exchange is supplied by the mother via secretory histotrophes ingested or absorbed by the fetus via epithelial absorptive structures (placental analogues) or a yolksac placenta; small to moderate gain in weight during embryonic development.	*Poeciliopsis turneri, Heterandria formosa, Anableps dowi*

Feeding

In small streams food items are limited to insects, small amounts of vegetation and to allochthonous material falling into the water from the land. Food is relatively scarce, specialisations to benefit from specific food types are common and resource partitioning is very high (see for example, McNeely 1987).

In floodplain rivers food does not appear to be limiting during the flood period. Most fish concentrate on the floodplain for feeding during the flood and as such the wetlands become the motor which drives the exceptional productivity of most large river systems. A large number of specialised forms exist (Table 2). Predators are very common and often take strange forms such as fin nippers or scale eaters. Equally specialised categories such as the illiophages (mud-eaters) (Bowen 1984.) are apparently confined to the lower reaches of large river systems. At the same time most species show considerable flexibility in their diet and there are a large number of generalised feeders in floodplain rivers. At low water food becomes scarce, as fish are crowded into an increasingly small area of residual water. However, at this time oxygen levels tend to fall in the permanent waters of the floodplain and even in the main river channels. As a result most fish stop feeding, an effect termed the physiological winter by Lowe-McConnell (1975).

Fish in the increasing number of regulated rivers have to cope with extreme change in their feeding patterns. The apparent lack of competition for food in unregulated systems and the consequent abiotically determined population dynamic is replaced by a more lacustrine situation where food becomes limiting, and population composition and size become density dependent. The elimination of the wetland accompanying rivers therefore becomes critical to the sustainability of the fish communities.

Table 2. Feeding guilds of river fish.

	Bottom feeders	
Mud feeders	Finely divided silt and attached organic molecules	*Prochilodus, Citharinus, Phractolaemus Pterigoplichthys*
Detritus feeders	Coarse decaying plant and animal matter, small crustacea, fungi, diatoms and other microrganisms	Many cyprinids e.g. *Cyprinus carpio, Labeo sp.* Siluroids e.g. *Clarias bathupogon, Plecostomus* Catastomids
	Herbivores	
Phytoplankton filterers	Filter floating or decanted phytoplankton from the water column, usually diatoms and green algae, more rarely blue-greens	Heterotis niloticus Cichlids e.g. *Oreochromis niloticus*,
Phytoplankton grazers	Graze over rocks and plants for attached algae and fungi, and associated 'Aufwuchs' communities (rotifers, micro-crustacea and other micro-organisms)	Many cyprinids, cichlids, siluroids, catastomids,
Higher plant feeders	Graze and eat higher plants	*Tilapia zillii, Ctenopharyngodon, Leporinus maculatus, Cichlasoma, Distichodus*
Fruit, seed and nut eaters	Penetrate flooded forest and floodplains to eat seeds, falling fruit etc.	*Colossoma bidens, Puntius, Leptobarbus, Brycinus*

Table 2. (Continued).

	Omnivores	
Omnivores	Unspecialized feeders that eat insects, zooplankton, detritus, plant matter according to abundance	Many species, even highly specialised forms will occasionally eat other foods when their main food item is scarce
	Micro-predators	
Zooplankton feeders	Pelagic species feeding on zooplankton	*Sierrathrissa leonensis, Astyanax, Hypopthalmus*
Insectivores	Surface feeders taking insects falling on surface of water	*Toxotes chatareus,*
	Bottom feeders feeding over rock, mud or sandy bottoms	Many species of characin, cyprinids, siluroids, cichlids, *Synodontis,*
	Meso-predators	
Crustacean and large insect feeders	Feed on large bottom living	Young of many fish-eating predators, Siluroids, *Schilbe*
Molluscivores	Pickers – remove bivalve and gastropods from their shells with special pick like teeth	Some cichlids
	Crushers – crush whole gasteropods	Astatoreochromis, Siluroids, haplochromine cichlids
	Macro-predators	
Fish eaters	Lurking predators, hide in vegetation or adopt disguise	*Esox, Channa, Lates, Hoplias,*
	Pursuing predators, rapidly pursue prey	*Salminus, Hydrocynus, Hepsetus odoe*
	"Parasites"	
Fin nippers	Some fin nippers are found in most fish assemblages in the tropics. They tend to be lurking predators that creep up on other fish to remove part of their fins	Phago, Serasalmus
Flesh biters	Predators that bite lumps out of prey species. Thes are often relatively small fishes	Piranhas
Blood suckers	Small species that attach themselves to the gills of other species to suck blood	Candiru

Responses of river fish populations to stress

Understanding the way in which fish populations react to externally imposed stresses is important for management as a diagnostic tool, as a basis for developing strategies for management, as a criterion for monitoring and as a means of predicting impacts on biodiversity.

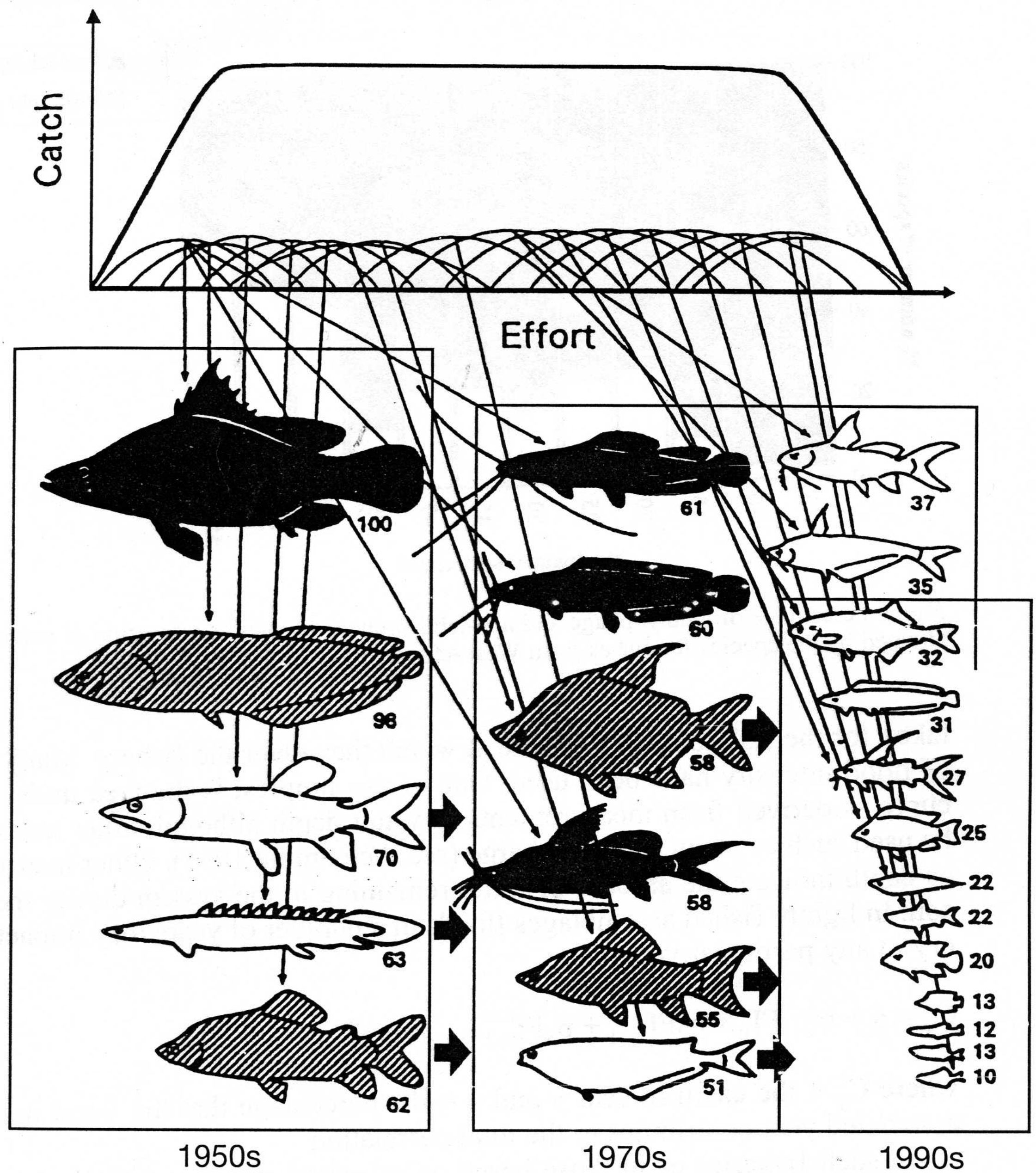

Fig. 3. Illustration of the fishing-down process using the historical condition of the Queme river fishery (West Africa) illustrated with representative species.
Black = species that disappeared from the fishery before 1965; Hatched = species whose numbers were seriously reduced. Black Arrows = species that reduced their breeding size. Peak yearly yields in the 1950-60s were around 10 000t.

species, which are better adapted to life in the main channels benefit from poorer floods but the majority of the species are floodplain dependent. Strong correlations have been attained between some measure of flood intensity (FI) and catches in subsequent years (Welcomme 1995 for partial review). Here the lag time between the year of flooding (y) and the reaction by the fishery (y + t) depends on the time (t)

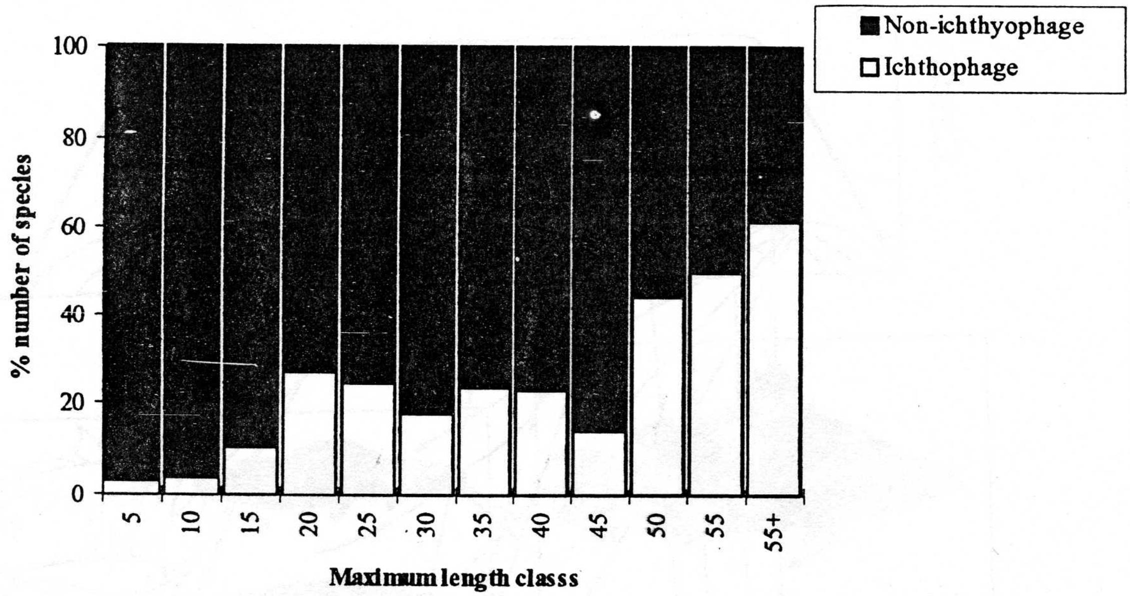

Fig. 4. Percentage of ichthyophage and non-ichthyophage species as a function of maximum length attained by the species for fishes from West Africa.

taken for the fish to grow to a size at which they enter the fishery. Many measures of flood intensity have been used. One of the simplest is the area under the flood curve as derived from measurements of water depth although other measures may be used such as mean daily discharge (see Welcomme 1995). Other measures, such as depth indicate the amount of water remaining in the system during the dry season. In lightly fished assemblages floods in a number of years may impact the fishery in any particular year, thus:

$$C_y = a + b(p_1FI_y + p_2FI_{y-1} + p_3FI_{y-2}........+p_xFI_{y-x})$$

where C_y = the catch in year y and p = the percentage that the flood index of the associated year contributes to the total correlation

In such fisheries or in those based on migratory species with long maturation times it may take several years for the fish to enter the fishery and best correlations are with y-3 and y-4. In these cases the mean size of fish in the catch is relatively large. In moderately fished systems the best correlations are with y-1 and y-2 were obtained. In heavily fished tropical systems lag times are much shorter (y or y-1) and the fish in the catch are correspondingly smaller. In systems such as the extensive Gran Lac/Tonle Sap wetlands of the Mekong the fishing down process is already well advanced (Van Zalinge et al. 1999)

In extremely heavily fished systems the best correlations are obtained with young-of-the-year as they move from the floodplain to the main channel at the end of the floods. For example, 69% of the fish caught in the central Delta of the Niger (Lae 1992) and 95% of the fish caught from the Bangladesh floodplains (Halls et al. 1999) are less than 1 year old.

In regulated rivers the effect of the flood is much reduced and such systems tend to behave more like lakes in that year-to-year variations are much reduced. Nevertheless, fish populations in major temperate rivers such as the Danube (Holcik and Kmet 1986) or the Mississippi (Risotto and Turner 1985), which are partially regulated and whose wetlands are much reduced, still respond to annual variations in flood intensity.

Impacts of Other Users

Control of biodiversity in rivers does not rest solely with the fishery. In fact in most rivers fisheries are the least significant activity economically. Much of the control of the river lies with other users. It has been estimated, for example, that over seventy five percent of temperate waters are severely impacted by dam building (Dynesius and Nilsson 1994). Most tropical rivers have cascades of dams and large scale water abstractions for agriculture and in emergent countries, such as China, nearly all the waterways are severely degraded by pollution and environmental modification (Dudgeon 1992, Lu 1994). The divers activities of other users impact rivers and their fish populations by affecting the quality of the water, the quantity and timing of discharges and the connectivity of the system (Table 3).

Table 3. Summary of the impacts of human interventions in river and lake basins on fish.

Changes in flow	
Temporal changes	
Disruption of spawning patterns through inappropriate stimuli or unnatural short-term flows	Changes in community structure away from seasonal spawners to species with more flexible spawning
In rivers shift from pulse regulated to stable system dynamics	Diminished productivity at community level
Changes in velocity	
Increases in flow rate (usually due to channelization)	Young fish in drift swept past appropriate sites for colonization Local shifts in species composition in tail race with accumulation of predators
Decreased flow rate	Shifts from rheophilic to lentic communities in reservoir upstream and in controlled reaches downstream Changes in flushing rate resulting in accumulation or low dilution of toxic wastes or anoxic conditions leading to fish mortalities
Loss of habitat diversity through river straightening and bank reinforcement	Loss of species Changes in relative abundance of species
Prevention of flooding by dams and levees	Loss of floodplain area available for spawning growth; loss of habitat diversity; change in species composition with loss of obligate floodplain spawners General diminution in productivity of whole system
Drowning of spawning substrates upstream of dams, in channelized reaches of rivers or in lakes	Variable effects usually involving decline of lithophils or psammophils although new wave washed shore or rock riprap may simulate rhithronic habitats
Overly rapid filling or drawdown in reservoirs	Flooding of nesting sites Stranding of nests and eggs Drowning of developing vegetation and prevention of development of food organisms

Table 3. (Continued).

Blocking of channels	
Reservoir creation	Changes in faunal structure with shifts from rheophilic species to limnophilic ones Development of pelagic fish community
Interruption of migratory pathways by dam walls or by the creation of unsuitable conditions for passage	Elimination of diadromous or obligate migrants by preventing movement to upstream breeding sites by adults and slowing down-stream movements of juveniles
Changes in silt loading	
Changes in channel form (due to channelization or to changes in deposit ion/erosion process) Increased rate of silt deposition in lakes, reservoirs and in floodplain structures	Reduction of habitat and community diversity: Loss of species Choking of substrates for reproduction, leading to failure to reproduce in lithophils/ psammophils Changes in density of vegetation usually in favour of pbytophllis Changes in quantity and type of food available and in the benthos leading to restructuring of the fish community toward illiophages
Decrease in suspended silt load	Changes in fish community reduction in number of non-yisual predators and carnivores
Lack of sediment (downstream of dams)	Changes in nutrient cycle and in the nature of the benthos leading to loss of illiophages and increase in benthic limnivores
Changes in plankton abundance	
Increases in phytoplankton in reservoir or downstream due to slower flow and higher water transparency	Increase in abundance of planktivorous fish
Changes in temperature	
Stratification in reservoirs	Difficulties of passage for migrant species Elimination of fish in deoxygenated hypolimnion Mortalities downstream of dams due to emission of anoxic waters and H_2S Mortalities within the lake or reservoir through deoxygenation of the bottom water
Changes in mean temperature caused by low flow regimes or discharge of thermal effluents	Increasing temperature variation can cause shifts in success of spawning due to adverse temperatures either for cold or warm water spawners
Uptake of water	
Induction of water into power stations or through pumips or irrigation canals	Entrainment of fish into currents diverting them; impingement of fish on turbines and pumps resulting in loss of fish particularly juveniles
Water transfers between river systems	Transfer of species and disease organism from one system to another
Eutrophication	
Increased nutrients	Increase in phytoplankton Increase in phytoplankton feeders Increase in overall productivity up to a critical point

Table 3. (Continued).

	Change in nature of phytoplankton from diatom/green algae dominated communities towards blue green dominated communities and corresponding changes in fish species composition.
Lowered transparency	Disappearance of bottom vegetation with resulting disappearance of phytophyllic species
Deoxygenation	Shift from species with high oxygen requirements to those supporting lower levels of dissolved oxygen.
	Trend to increase deoxygenation of bottom waters of lakes and floodplain water bodies with mortality of bottom faunas
Acidification	
Acid waters	Disappearance of living organisms

Water Quality

Eutrophication

Eutrophication is the enrichment of water through inputs of nutrients, principally of nitrogen and phosphorus. Major sources of eutrophication are agro-chemicals and sewage effluents. Most agricultural sources are diffuse making their control difficult. Discharges from urban areas may be as point sources but the increasing disposal of sludge on agricultural land is making this diffuse as well. In rivers natural eutrophication occurs as the river flows towards the sea and accrues organic loads. Flowing water also has a considerable capacity for self-purification. However, this can be exceeded, in which case river channels and permanent wetland features such as marshes and lakes become anoxic. Eutrophication affects fish populations in a similar manner to excess fishing mortality with a tendency to eliminate larger, diadromous and rheophilic species and favour smaller ones that are resistant to low oxygen concentrations.

Pollution

Pollution occurs when toxic substances are discharged into water from industry, mining and agriculture. At their most extreme toxic discharges can produce mass mortalities and prolonged exposure can render systems fishless. Even where discharges have no immediately apparent impact long term effects through the accumulation of pesticides and heavy metals in the food chain can produce grave consequences for fish, wildlife and humans dependent on the system. As toxic discharges from industry and mines are generally point source they are relatively easy to identify and control. Agricultural discharges, mostly of pesticides, are more diffuse.

Sediment

The amount of sediment in water rises when the terrain in the basin is disturbed and soil is washed into rivers and transferred to channels and floodplains lower in the system. Sediments of this type can arise naturally through landslides and storm events although forest cover normally minimises such effects. Logging, agriculture and mining accelerate the process, however, through deforestation that removes the stabilising effects of large vegetation.

As flowing water is able to carry a load of sediment proportional to the flow, any excess is deposited in river beds, lakes, and reservoirs and in the wetland floodplains shortening the life of the waterbodies. Sediment deposits can also raise river channels above the surrounding plains increasing the risk of flooding. The deposition of fine sediment also suffocates bottom living organisms, chokes nesting sites and provides anchor points for invasive vegetation.

Conversely, where sediment has been deposited in reservoirs and other areas of low flow the water downstream has the capacity to pick up sediment often excavating the bed of the river to a point where it can no longer over-bank and flood the surrounding floodplain.

Apart from its impact on morphology, sediment affects the living components of the system. It chokes benthic fauna. It also increases the turbidity, hindering the development of submersed vegetation and phytoplankton. Both of these effects reduce the amount of food available to fish. Excessive sediment can also choke sand, gravels and bottom vegetation normally used by psammophyllic, lithophyllic and phytophyllic species for spawning.

Acidification

Recently, water in many rivers in the Northern Hemisphere has become acid. This process has been traced to rain which dissolves the sulphur dioxide, nitrogen dioxide, and nitrogen oxide released into the air when fossil fuels are burned and transforms it into sulphuric and nitric acids. Increased acidity has also been traced to excessive plantations of conifers in areas where the buffering capacity of the water is low. Low Ph frees large amounts of aluminium from the soil. Acidity of water combined with high concentrations of aluminium kills fish eggs and fry, and also kills adult fish. It also eliminates most aquatic plant and animal life depriving fish of food. Countries affected such as Scandinavia and Canada have to spend considerable sums on liming programs to combat this process in lakes but the efficiency of such activities in rivers is less obvious.

Water Quantity and Timing

Changes in Discharge

Dams and levees are primarily devices for managing flow. Dams retain large quantities of water to be released when needed or to be diverted into other river systems. Levees prevent floodplains from acting as natural dampers by absorbing floodwater and releasing it slowly over time. In modified systems both the quantity and timing of discharge can be drastically altered from the pre-modified condition. River fish are closely adapted to certain flow regimes. Not only do the adults need adequate quantities of oxygen to maintain them but they also require specific flow characteristics to act as triggers for maturation, breeding and migration. Low water conditions can also pose physical barriers to movement in the main channel and between the channel and the flood plain by disrupting the connectivity of the system. These problems became apparent early on with abstractions from temperate trout streams, and minimum flow requirements were established as a basis for management of the water regime. With the extension of water management to large rivers through damming and water transfers inadequate flow can suppress flood peaks so the floodplain is no longer seasonally flooded. In such cases it may be necessary to plan for releases of water to create artificial floods.

In many species, especially those laying eggs on or in the bottom, well-oxygenated water is needed for their development. Acceleration of flow in rivers during the time when semi-pelagic eggs and drifting juveniles are in the system can mean that these will be swept past nursery area, and in the case of heavily channelized systems, even out to sea. Ill-considered changes in discharge can, therefore, disrupt breeding success of vulnerable fishes.

Drawdown

Drawdown is classically defined as the difference between maximum and minimum levels in lakes and reservoirs but can also be used to describe the difference between the total flooded and minimum level in rivers. In rivers the over rapid withdrawal of water can cause stranding of fish, breeding sites and eggs attached to marginal bottom substrates reducing survival and reproductive success. Equally accelerated flooding destroys rooted aquatic vegetation and will not allow enough time for the development of the rich supply of food organisms at the edge of the advancing water and on the bottom. It will also prevent nesting species from breeding by drowning nesting sites. For this reason the shape of the flood is as important as its quantity.

Timing

In many species markers during the hydrological cycle serve as physiological signals as to when to start maturation or migration. This is particularly evident with long distance migrants, many of which commence migration at low water in order to arrive upstream in time to breed on the rising flood. Less conspicuous examples are present among most floodplain species that have to be in breeding condition as the rising water passes bankfull and spreads out over the plain. Suppression or inappropriate timing of the flood can disturb these signals and thus reduce breeding success. Within a species disturbances to the water regime can favour one race over another leading to suppression of some genetic variants. Other sturgeon species have been completely eliminated from several of the rivers.

Interruptions to Connectivity

Dam Building

Most river systems throughout the world have been dammed at some point. Dams have several effects.

Firstly, by impounding water they create a reservoir, which replaces the flowing river with a more static lacustrine waterbody. In extreme cases, such as the Parana River in Brazil or the Volga river in Europe, the system has been converted into a cascade of reservoirs with very little of the original free flowing channel left. Fish populations in the new reservoirs are very different from those in the original river. The dominant elements are often drawn from formerly insignificant species whilst former dominants regress or disappear. In particular there is the emergence of a strong pelagic community in reservoirs, which is usually very much reduced in rivers. In some rivers the elements needed to successfully colonise lacustrine environments are frequently absent (Fernando and Holcik 1982) and exotic species, such as the demersal tilapias and pelagic forms such as *Limnothrissa*, are introduced to fill the otherwise vacant niches.

Secondly, by barring the river they create an insurmountable obstacle to the passage on migratory species. These then can not reach their spawning grounds and may become locally extinct. Certainly diadromous fishes seem to be the most vulnerable of all groups of fishes. Damming and flow modification, together in some cases with excessive fishing, have decimated migrating shad, salmon and sturgeon populations around the world. Attempts have been made to limit the impact of dams on migrating fish through the construction of fish passes. Fish ladders may be successful for some energetic migrants such as the salmon but other types of structure need to be developed for other species.

Thirdly, dams and their operation for power generation and irrigation change discharge patterns in rivers.

Levee Construction

Levees may be regarded as linear dams whose function is to keep water off of the floodplain. They may be extended to enclose complete areas of wetland as polders for the same purpose. In so doing they also prevent fish from migrating laterally to the richest breeding, feeding and nursery sites in the system. Great reductions in overall productivity and the local disappearance of species from black fish guilds usually follow levee construction. The enclosure of the channel, which is a natural extension of the channelization process, also alters the discharge pattern in the river.

Wetland Area and Quality

River training works such as those described above rob the system of wetlands through the prevention of seasonal flooding and the interruption of connectivity between the floodplain system and the river. While temperate rivers in Europe, Asia, North America and Oceania have largely lost their floodplains, many tropical rivers have retained extensive wetlands. Even here far reaching changes are underway in many parts of the world through the conversion of the wetland from its wild, forested state to some form of agriculture. In Southeast Asian rivers such as the Mekong forested wetlands are being changed into rice paddies at an alarming rate (see Figure 3). In the Amazon basin riparian forests are being lost to small scale agriculture and large scale cattle ranching.

Conversion of floodplains in this way impacts on the fish fauna in a number of ways. Forested wetland fish faunas have elements specialised in feeding on fruit and seeds whose life cycle is intimately linked with the survival and dispersion of the tree species. Changes from a forested to a more open savannah landscape will inevitably reduce the abundance of such species creating changes in the relative composition of the fish assemblages. The change from natural nutrient cycling in forested wetlands to human uses, where nutrients are added to the system as fertilizers and domestic wastes, also changes the type of fish community that can survive. Further intensification through use of pesticides and double cropping of rice can further stress the fish communities. The more uniform environment also further selects for certain black fish species which are also resistant to the increased vulnerability to the intensive fishing that is usual in such systems.

Management of river biodiversity

Conservation of biological diversity is now the obligation of all nations ratifying the Convention on Biological Diversity (UNEP 1994). The mode in which the provisions of the Convention can be applied to fisheries is set out in the FAO Code of Conduct for Responsible Fisheries (FAO 1995) and in the guidelines to the Code for Inland Fisheries (FAO 1997). Whilst the Convention aims at striking a balance between conservation and use its general tenor tends to be conservationist, whereas the Code of Conduct is aimed more at containing fisheries within sustainable limits. It is unrealistic to demand that valuable sources of food and recreation such as are found in rivers throughout the world remain unexploited solely to protect their biodiversity. Unfortunately the process of fishing together with management practices for the improvement of the yield or recreational value of chosen elements of fish assemblages do erode a biodiversity that is also under threat from pollution and general environmental deterioration. Because of this freshwater fishes are the most threatened group of animals utilised by humans (Bruton 1995) with 20% either extinct, threatened or vulnerable (Moyle and Leidy 1992). Management of inland waters now must consist in managing the diversity of the fish populations of all types of water as well as the original task of managing the yield. The management function also is no longer only the domain of those responsible for the fishery but also concerns all those other users who can impact the water and the living organisms inhabiting it. River management has now become a national (and international in the case of transnational river basins) enterprise in which all interests should negotiate to maintain the quantity and quality of water in the rivers, the connectivity and diversity of fluvial habitats and the sustainability of the fish communities.

Indicators of change

Management of biodiversity depends on an adequate evaluation of its status. In rivers with few species it is relatively easy to identify one that is endangered and to make appropriate arrangements for its protection. However, in rivers with large numbers of species it is almost impossible to keep track of any but the few very large species that are normally the first targeted by the fisheries. In such cases the general health of the biodiversity has to be measured using indicators of trends within the population (Table 4)

Table 4. Indicators of change occurring in fish populations in response to fishing and environmental stress.

Indicator	Trend
Level of catch	• Falling levels of total catch levels in single species fisheries, however catch levels can be maintained over a wide range of effort and can only be interpreted relative to the catch composition
Mean length	• Disappearance of larger fish and falling mean size within species • Disappearance of larger species and falling mean size of catch as a whole
Number of species	• Initially rise in number of species in catch from a few large ones to many small ones. • Later falling numbers until the fishery is confined to few very small species
Type of species	• Decline and disappearance of anadromous and long distance riverine migrants • Decline and disappearance of native species in favour of exotics where introductions have occurred • Decline and disappearance of higher trophic levels (predators) and their replacement by lower food chain species • Decline and disappearance of species with high oxygen requirements and their replacement by species tolerant of low oxygen [eutrophication]
Response time	• In rivers and river-driven lakes and reservoirs shortened time between flood events and response by population
Other indicators:	• P/B ratios rise • Mortality rates(z and f) increase • Higher incidence of diseased and deformed individuals [extreme eutrophication and pollution]

Management of the Fishery

One of the major causes of deterioration in the diversity of river fish is the fishery. In most of the tropical world rivers are fished at extremely high level and probably produce about 3 million tons of protein rich food per year. This heavy fishing pressure has degraded stocks of many species to a point where they are heavily compromised. The main policy for fishery managers must be to reduce access to the overburdened fisheries and thus to allow them to recover. Such a relief of pressure on the wild stocks will inevitably be accompanied by a parallel intensification through aquaculture under controlled conditions. In temperate areas fishing pressure is mainly exerted through recreational fisheries, which, because of the demand for specific species, can also deform populations through management to favour the preferred target. In such cases education can produce shifts in perception on the part of the fishing community. In both cases, current thinking is that success in managing wild fish stocks can only be achieved by fully involving the fishing communities through co-management systems. In its turn co-management involves a transfer of ownership to the people that actually fish the resources. It would be simplistic to view this type of approach in isolation, as it must be accompanied by incentives for the fishing communities and supported through education, research and other infrastructure.

Rehabilitation of the Environment

As we have seen fishing is not alone in its capacity to damage biodiversity. In most areas of the world by far the greatest harm has been done by non-fishery activities. Clearly the economic power of activities such as power generation, navigation, agriculture and industry is very difficult to counter balance. In such cases the fish community has to make the best of a bad job. Such measures as are possible should be taken to mitigate effects such as the installation of fish passes at dams and weirs, or the creation of artificial gravel substrates where these are eroded. When pressure on the natural resource is released through better conduct of industry and agriculture, steps should be taken to rehabilitate aquatic environments. This should firstly involve removing pollution as no matter what other changes are made fish will not survive long in contaminated water. Secondly diversity should be recreated in the main channel with a reestablishment of sinuosity, meander bends and pool-riffle structure. Connectivity should be restored to the system both longitudinally with the installation of better passage for migrating fish and laterally with the reconnection of the floodplain.

Rehabilitation usually carries a price in that it is more land-hungry then the channelized river. This means that to work decisions have to be taken at national level for buy-back or set-aside schemes which enable flooding to be restored and the rivers to meander more or less freely over a large area. Fortunately, the dynamics of floodplain productivity are such that even small areas of plain can produce fish for a much wider area of river. Restoration areas then are seen as resembling a string of beads along the river channel. The disposition of such areas must however, create conditions favourable to the fish and their design has to be such that current is not excessive.

Parks And Reserves

One mechanism to conserve fish in-situ is to establish parks or reserves. This method is particularly valuable for grey and black fishes and river residents as the park can encompass all necessary habitats within one area. However, with white fishes and long distance anadromes parks will only succeed if there are reserved areas at both ends of the fish's range of movement and if the pathway between them remains unobstructed. This implies that for reserves to be truly successful, a unified approach has to be taken to their siting as well as to the conservation of favourable conditions in the watershed as a whole. The principle of establishing aquatic reserves for fish has recently been reinforced by RAMSAR's decision that the conservation of fish species alone is sufficient to justify the setting up of a RAMSAR site.

Conclusion

The fish biodiversity of rivers and their associated wetlands is under severe threat at the present moment making them among the most endangered ecosystems on the planet. Riverine wetlands are under attack from excessive and badly managed fisheries, from environmental degradation and from alternative demands for water. As a result many species are threatened with local extinction and other may disappear entirely. To reverse this situation will require a major effort. Firstly, fisheries will have to be better managed for sustainability. Secondly pressure from other sectors of the economy that use water will have to ease, and thirdly damaged ecosystems will have to be restored. All this requires a concerted effort at national level consistent with the undertakings to the Convention on Biodiversity.

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