SESSION 3 REVIEW

RIVER FISHERIES: ECOLOGICAL BASIS FOR MANAGEMENT AND CONSERVATION

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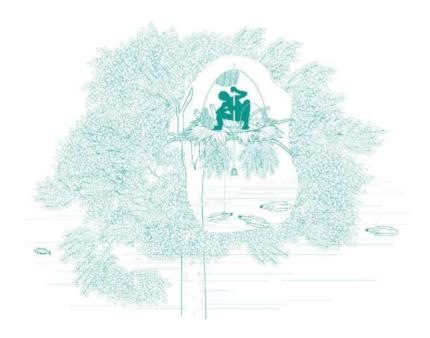
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ABSTRACT

Large rivers and their floodplains support a significant proportion of the world's biodiversity and provide important goods and ecological services to society, including fisheries. Riverine ecosystems and fisheries are subject to intense pressure from a wide range of anthropogenic disturbances, the main ones being impacts from altered land use, modifications to river flow regimes, riparian and physical habitat loss, water pollution, exotic species invasions and intensive exploitation of fish stocks. As a consequence, a far greater proportion of freshwater species are threat-

ened or endangered than terrestrial or marine species in the same taxonomic groups. In this paper we review ecological processes sustaining river and floodplain biodiversity and productivity. We also outline the status of knowledge of fundamental issues in fish ecology, including fish habitat requirements, trophic ecology, life history strategies, migration, the population biology of riverine fish and modelling of fish populations and assemblages. We evaluate threats to the productivity and diversity of large river systems, as well as conservation and rehabilitation measures and discuss ecological approaches and tools for management decision support. The final summary highlights knowledge gaps and research priorities and new research frontiers that demand more attention in river ecosystem studies, conservation efforts and fisheries management.

INTRODUCTION

Large rivers and floodplain ecosystems support a significant proportion of the world's aquatic biodiversity. Species richness within some tropical systems surpasses that of marine ecosystems, including coral reefs. The Mekong River, for example, contains 500 known fish species, with several hundred more species lacking formal definition (Dudgeon 2000). The floodplains of large rivers are also amongst the most productive landscapes on earth (Bayley 1988a; Welcomme 2001). Fisheries in large rivers and their associated wetlands and floodplains provide a major source of food, employment and/or income that is crucial to sustaining the livelihoods of multitudes of people, particularly the rural poor in large areas of the world. For example, fisheries are the single most important source of income for floodplain dwellers in the Amazon (Almeida, Lorenzen and McGrath 2002) and match income from rice farming in rural households in Cambodia and Laos (Lorenzen *et al.* 2000). H o w e v e r , due to their diffuse and inconspicuous nature, inland fisheries are often grossly underreported and undervalued.

Freshwater species are, on average worldwide, more imperilled than their terrestrial and marine coun-

terparts (McAllister, Hamilton and Harvey 1997; Stein, Kutner and Adams 2000). Of those species considered in the 2000 IUCN (The World Conservation Union) Red List, approximately 30 percent of fishes (mostly freshwater) are threatened (IUCN Species Survival Commission 2000). At a regional scale, the projected mean future extinction rate for North American freshwater fauna is about five times greater than that for terrestrial fauna and three times that for coastal marine mammals. This rate is comparable to the range of estimates predicted for tropical rainforest communities (Ricciardi and Rasmussen 1999). Such inventories can account only for described forms and even within well-known groups such as fish, species could be going extinct before they can be classified (McAllister, Parker and McKee 1985).

Rarely is a given species imperilled as a result of a single threat and it is often impossible to tease out the intertwined effects of the many disturbances occurring within a given watershed (Malmqvist and Rundle 2002). Only seven of forty recent extinctions of North American fishes were judged to have a single cause (Miller, Williams and Williams 1989). In a more recent global analysis of fishes, Harrison and Stiassny (1999) estimated that 71 percent of extinctions were related to habitat alteration, 54 percent to exotic species, 26 percent to pollution and the rest to hybridization, parasites and diseases, or intentional eradication. On the Iberian Peninsula, habitat alteration and water pollution were identified as the most important causes of degradation of native fish communities (Aparicio, Vargas, Olmo and de Sostoa 2000), a pattern that may be typical of developed countries. Exploitation, however, may be more important as a threat to freshwater fish diversity in some developing countries (Welcomme 1979; 1985). In analyses of threats, the categories themselves often overlap, signalling the difficulty of isolating proximate causes. As any conservation planner knows, mitigating threats to freshwater biodiversity requires understanding of a complex set of biophysical interactions operating over a range of spatial and temporal scales.

Fisheries production and ecosystem conservation interests are often, but not necessarily, identical. Certainly, intensive exploitation can be detrimental to ecological integrity. A somewhat more insidious conflict arises when habitat modifications or species introductions impair ecological integrity but result in increased fisheries production. For example, reservoirs in the Sri Lanka dry zone retain significant amounts of water in the upper basin for much longer than would naturally be the case and support productive fisheries based largely on introduced tilapias. Overall, this type of modification of habitats and biota in small river basins is likely to increase basin-wide fish production (Lévêque1995; Lorenzen, Smith, Nguyen Khoa *et al.* 2002). However, impacts on native biodiversity and ecological integrity, although rarely quantified, are likely to be negative (World Commission on Dams 2000; Bunn and Arthington 2002; Naiman, Bunn, Nilsson *et al.* 2002). As a result, conflicts may arise between fisheries production and related livelihood issues *versus* the maintenance or restoration of habitats and river flow patterns that are critically important from a conservation perspective.

Similar examples of divergence between fisheries and biodiversity conservation interests have been reported from North American and European rivers (Walters 1997; Arlinghaus, Mehner and Cowx 2002), in particular where modified systems favour certain species of particular fisheries or conservation interest. Hence it is important to distinguish clearly between fisheries production and conservation aspects of rivers where the former are important, particularly in a developing country context.

To provide effective support for management, river fisheries ecologists must analyse and predict processes and impacts at the level of species, assemblages and ecosystem processes, in systems of high spatial and temporal heterogeneity. This paper reviews aspects of fish biology and ecology of importance to biodiversity conservation and sustainable fisheries and provides a perspective on the role of ecological knowl-

edge in river and fisheries management. We identify key areas where ecological information is demanded by managers and/or where scientists believe it should be taken into account. The global water crisis and the threat to riverine biota increase the necessity to deliver models that serve science, management and policy. We review the need to understand and predict river fish population and assemblage dynamics, particularly in relation to forecasting and mitigating the impacts of human activities (such as flow regulation) and sustaining fishery yields. Theoretical concepts describing river ecosystems and ecological processes sustaining biodiversity and productivity in large rivers must also progress if we are to protect and restore damaged ecosystems and sustain their fisheries production.

After reviewing recent developments, we discuss ecological approaches and tools for management decision support, methods for integrating information and novel approaches to resolving uncertainty. We conclude with a summary of major points arising from this review and the discussions held during LARS 2, beginning with general statements to emphasize the importance of rivers and fisheries and ending with a perspective on conspicuous gaps in the science discussed at LARS. Throughout this summary we highlight research priorities and new research frontiers that demand more attention in river ecosystem studies, conservation efforts and fisheries management.

THE ECOLOGICAL BASIS OF RIVER FISHERIES AND BIODIVERSITY

River hydrology and geomorphology

A fluvial hydrosystem comprises the whole river corridor - the river channel, riparian zone, floodplain and alluvial aquifer. This hydrosystem can be considered as four-dimensional, being influenced not only by longitudinal processes, but also by lateral and vertical fluxes and by strong temporal changes (Ward 1989; Arthington and Welcomme 1995). Rivers and their floodplains are disturbance-dominated ecosystems characterised by a high level of habitat heterogeneity and spatial-temporal fluxes of materials,

energy and organisms are driven largely by fluvial dynamics (Tockner and Standford 2002). Fluvial hydrosystems provide corridors through the landscape (Gregory, Swanson, McKee and Cummins 1991) and the marginal zones (ecotones) provide buffers between the watercourse and the variety of land uses within the catchment (Cowx and Welcomme 1998).

A river basin can be characterised in a variety of ways (Frissell, Liss, Warren and Hurley 1986). A useful broad categorisation breaks the basin into three longitudinal sections (upper/headwater, middle and lower) and two lateral sections (upland and flood-plain). Floodwaters and their silt load are dispersed laterally within the middle and lower catchment, extending over the floodplain and carrying with them nutrients, organic matter and organisms. The annual (or more erratic) cycles of flooding and flow pulses ensure the connectivity of river channels and their floodplains and the silt, nutrients and organic load carried in the floodwaters form and maintain the floodplain ecosystems (Ward and Stanford 1995; Tockner and Stanford 2002).

The habitat components of the fluvial hydrosystem include the main channel with its different habitats: backwaters, side arms; floodplain lakes and wetlands; estuaries and intermittent coastal lagoons, man-made reservoirs and canals land subject to seasonal flooding and non-floodable land that nonetheless influences the quantity and quality of r u n o f f received (Cowx and Welcomme 1998). Temporal variation in discharge and habitat heterogeneity are closely linked and such linkages span a wide range of time frames, from that of daily changes associated with short-term floods or spates, to seasonal and decadal changes (e.g. creation of oxbows and wetlands).

Hydrological variations associated with longer time frames are also important. For example, drought associated with El Nino events has been reported to greatly influence riverine and estuarine fishes in Suriname (Mol, Resida, Ramlal and Becker 2000). Processes occurring over historical time spans may continue to influence contemporary riverine ecology. The Mary River of southeastern Queensland, Australia, has cut down over 70 m into its bed in response to sea level lowering during the Pleistocene. Subsequent aggradation in the middle reaches has raised the bed by 40 m but the river remains deeply incised into the landscape (Bridges, Ross and Thompson 1990). Such conformation has consequences for the dissipation of flows during floods and may influence in-stream production by limiting light penetration. Long-term changes in discharge, channel morphology and habitat and their interrelationship, need to be carefully considered in light of projected changes in global climate.

River ecosystems and processes sustaining biodiversity and productivity

River ecologists have investigated various functional linkages among riparian, floodplain and river ecosystem components since the earliest studies on large European rivers, but it is only relatively recently that integrative frameworks have been proposed for lotic ecosystems. The initial conceptual frameworks were linear, particularly the River Continuum Concept (Vannote *et al.* 1980), modified for large rivers by Sedell, Ritchie and Swanson (1989), the idea of nutrient "spiralling" (Elwood, Newbold, O'Neill and van Winkle 1983) and the Serial Discontinuity Concept (Ward and Stanford 1983).

Junk, Bayley and Sparks (1989) formalised the "flood pulse concept" (FPC) at the first LARS meeting, distinguishing lateral processes from concepts of ecological continua along the length of rivers. According to this model, flood conditions should be associated with greater nutrient availability, aquatic primary production (dominated by macrophytes), allochthonous inputs and secondary production (espe-

cially among juvenile fishes) in floodplain habitats. The degree to which flooding occurs in phase with warm temperatures and enhanced system productivity influences selection for alternative life history strategies of fish and other biota (Winemiller 2003). In strongly seasonal floodplain systems, reproductive cycles and associated migrations of fish have evolved to exploit relatively predictable habitats and resources on the floodplain (Welcomme 1985; Lowe-McConnell 1987; Junk *et al.* 1989; Winemiller and Rose 1992). Physiological adaptation is also possible in response to seasonal fluctuations in habitat condition and patterns of distribution may be influenced by tolerance to naturally fluctuating water quality (Hickley and Bailey 1987). In aseasonal flood-pulse regimes, fish are "more challenged to respond appropriately to relatively unpredictable patterns of resource variation" (Winemiller 2003). One strategy shared by many species in highly variable systems is to spawn and recruit in main channels and backwaters under relatively low flow conditions (Humphries, King and Koehn 1999).

While the FPC has undoubtedly provided an integrating paradigm for highly diverse and complex ecological processes in river-floodplain-systems, new perspectives have emerged from studies on floodplain processes in different latitudes and continents (Junk and Wantzen 2003). Walker, Sheldon and Puckridge (1995); Dettmers, Wahl, Soluk and Gutreuter (2001) and Ward, Tockner, Uehlinger and Malard (2001) suggest that energy flow in large river systems might best be viewed as an interaction of three concepts, the RCC (downstream transport), the FPC (lateral transport to and from floodplains) and the "riverine productivity model" of Thorpe and Delong (1994), which describes the role of autochthonous production. Some of the major new developments in floodplain theory and management include the importance of hydrological connectivity (Ward, Tockner and Schiemer 1999; Robinson, Tockner and Ward 2002; Winemiller 2003); alternatives to the "highway analogy" with respect to

the ecological functions of the main river channel (Galat and Zweimuller 2001); the ecological consequences of erratic flow pulses (Puckridge, Sheldon, Walker and Boulton 1998; Walker *et al.* 1995); and the Multiple Use Concept developed for the central Amazon River floodplain (Junk and Wantzen 2003).

A pervasive theme in river ecology and management is the importance of hydrological variability, perceived by Walker *et al.* (1995) to operate at three temporal scales: the flood pulse (days to weeks), flow history (weeks to years) and the long-term statistical pattern of flows, or flow regime (decades or longer). Many ecologists perceive that the ecological integrity and long-term evolutionary potential of rivers and their floodplains depends upon the spatial and temporal variability of the natural flow regime (e.g. Arthington *et al.* 1992; Sparks 1992; Poff *et al.* 1997; Richter, Baumgartner, Wigington and Braun 1997; Ward *et al.* 2001; Olden and Poff 2003). Poff *et al.* (1997) proposed the "natural flows paradigm" as a blueprint for management of river flows and river corridor restoration and several methods for determining flow regimes intended to protect or restore river ecosystems (i.e. by providing environmental flows) are founded upon it (Arthington and Pusey 2003; Arthington *et al.* 2003; Brizga *et al.* 2002; Arthington and Pusey 2003; King, Brown and Sabet 2003). Likewise, the UNESCO conceptual tool "ecohydrology" (Zalewski 2003) suggests that the sustainable development of water resources is dependent on our ability to maintain established evolutionary processes of water and nutrient circulation and energy flow at the basin scale.

The ecological roles of littoral and riparian ecotones have received much attention in the recent literature on river-floodplain studies (Naiman and Decamps 1997; Naiman *et al.* 2002). Riparian zone processes influence river fish communities by way of effects on individual fitness and species diversity, mediated by changes in light and shade, water quality, habitat quality and heterogeneity and trophic dynamics

(Pusey and Arthington 2003). Sustaining the processes linking riparian and river systems is crucial to the management, rehabilitation and conservation of river landscapes (Cummins 1992; Bunn, Pusey and Price 1993; Wissmar and Beschta 1998; Naiman, Bilb and Bisson 2000).

Riverine fish assemblages: diversity, habitats and trophic ecology

Biodiversity

Species richness in relation to area of habitat is extremely high in many freshwater groups with an estimated 10 000 fish, 5 000 amphibians and 6 000 mollusc species dependant on freshwater habitats which account for only 0.01 percent of the earth's total aquatic habitat. Other major groups dependent upon freshwaters include bacteria, fungi, plants, additional invertebrate taxa, reptiles, birds and mammals. River conservation and management activities in most countries suffer from an inadequate knowledge of the constituent biota, especially in large, poorly investigated tropical river systems (e.g. the Amazon, Saint-Paul 2003), many Asian and southern African rivers (e.g. Dudgeon 2000; Shrestha 2003) and tropical Australian rivers (Pusey 1998).

Rivers are islands of freshwater aquatic habitat isolated from one another by terrestrial and marine ecosystems. Studies of geographic variation in riverine fish diversity have established significant relationships between species richness and catchment area or discharge (Welcomme 1985; Hugueny 1989; Oberdorff, Guegan and Hugueny 1995; Oberdorff, Huegeny and Guegan 1997; Guegan, Lek and Oberdorff 1998; Pusey and Kennard 1996). In lowland rivers of the southern llanos of Venezuela, interactions among seasonal hydrology, variability in habitat structural complexity and landscape heterogeneity appear to maintain high aquatic species richness (Arrington and Winemiller 2003). Likewise, multivariate models of fish assemblage structure in Australian rivers demonstrate the importance of catchment and local scale

habitat structure and hydrological variability (Pusey, Arthington and Read 1995; Pusey, Arthington and Read 1998; Pusey, Kennard and Arthington 2000). Diversity of hydrological pattern appears to be central to the maintenance of habitat heterogeneity and species diversity (Ward *et al.* 2001; Tockner and Stanford 2002).

Alteration of water quantity, seasonal flows and patterns of flow variability (e.g. by damming and abstraction, or inter-basin transfers - IBTs) have substantial and negative consequences for the maintenance of biodiversity in many rivers (Arrington and Winemiller 2003; Pusey *et al.* 2000; Bunn and Arthington 2002). The disconnection of river channels from their floodplains also affects biodiversity (Halls, Hoggarth and Debnath 1998; Toth, Melvin, Arrington and Chaimberlain 1998; Galat and Zweimuller 2001; Robinson *et al.* 2002), with the magnitude of effect likely to be greater in tropical and temperate seasonal rivers than for temperate aseasonal rivers (Winemiller 2003). The further development of macro-ecological models predicting regional variation in freshwater fish diversity remains a task of major importance, given that conservation plans to protect species from current and impending threats (such as water use and global environmental change) often seek to identify areas of highest biological importance (Oberdorff *et al.* 1995).

Genetic analysis of the major populations of fish species can reveal the geographic location, extent and connectivity of genetically distinct stocks (Hogan 2003; So and Volckaert 2003) and thus inform fisheries management and environmental impact assessments. For example, dams and barriers to fish migration (Das 2003) may disconnect populations that now intermingle and breed freely thus leading to depression of genetic diversity (Jager, Chandler, Lepla and van Winkle 2001; Matsubara, Sakai and Iwata 2001). IBTs may connect distinct stocks with a long history of separation, undermining their genetic integrity and long-term evolutionary potential (Davies, Thoms and

Meador 1992; Bunn and Hughes 1997). Dams often reduce the extent of downstream flooding and thereby reduce the extent of connectivity between adjacent river systems, with consequences for the genetic structure of regional fish populations.

Genetic studies can assist in the identification of unique assemblages of species and genetic strains and in the management of rare, endangered, "flagship" or indicator species. Genetic analysis may also aid the identification of processes threatening the genetic integrity of metapopulations (e.g. unidirectional gene flow) and mechanisms to minimise such impacts (Jager *et al.* 2001; Matsubara *et al.* 2001). Resolution of the systematics of many groups of fishes is needed also to identify evolutionary significant units (ESUs) and to identify at what scale conservation and fisheries management strategies should be aimed (i.e. ESUs, species or species complexes) (Mayden and Wood 1995). Neglect of such fundamental investigations will inevitably result in management strategies lacking an adequate biological foundation, with loss of biodiversity and ecosystem services in the long term.

Distribution and habitat requirements

River networks have provided many opportunities for allopatric speciation of aquatic taxa and also serve as reservoirs that accumulate species over evolutionary time (Winemiller 2003). To assess the habitats, populations and communities being managed and opportunities for biodiversity conservation (Abell 2002), detailed surveys of the fish faunal composition of individual river basins are needed, including major tributary systems as well as main channels (Shrestha 2003). Ideally, such surveys should be undertaken within a rigorous quantitative framework, in order to provide meaningful and useful information on as many aspects of organism biology as possible (density, micro and macrohabitat use, population size structure) in addition to distribution at the macrohabitat scale. This type of information is proving immensely useful in

devising strategies to mitigate the impacts of flow regime change in regulated rivers. Pusey (1998) and Arthington, Rall, Kennard and Pusey (2003a) have recommended fish data sets considered essential for the determination of the flow requirements of river fishes.

Specific habitat requirements of aquatic organisms may be characterized by many factors, including water depth, flow velocity, temperature and substrate. Habitat preferences of different life stages of many temperate fish species have been established and expressed in the form of preference curves. Data on habitat preferences are the crux of the earliest and most widely applied methods to predict the ecological consequences of flow regulation and water abstraction, most notably the Instream Flow Incremental Methodology (IFIM) and its physical habitat component, PHABSIM (Bovee 1982; Stalnaker, Lamb, Henriksen *et al.* 1994). As well as physical attributes, water quality factors, in-stream and bank cover (Crook and Robertson 1999; Pusey 1998; Pusey *et al.* 2000) and biotic features/processes merit more investigation to ensure suitable conditions of space, shelter and food supplies for each life history stage (Power 1992; King 2002). For example, the distribution of some species may be better predicted from knowledge of the factors that determine the distribution of food items than it is by habitat preferences defined by depth, flow and substrate composition (Petty and Grossman 1996). Habitat-centred methods for the assessment of minimal and optimal stream flow requirements are discussed in more detail below.

Trophic ecology and food web structure

Sustaining river ecosystems and productive fisheries depends upon understanding the energetic basis of their productivity, linked to the trophic ecology of fish and to food web structure. In many habitats, algae seem to provide the most important source of primary production entering the grazer web (Lewis *et al.* 2001; Winemiller 2003), even in the highly turbid

rivers of Australia's arid-zone (Bunn, Davies and Winning 2003). In contrast, fine suspended organic matter apparently fuels the food web of the constricted-channel region of the Ohio River (Thorp, Delong, Greenwood and Casper 1998). Even in species-rich tropical rivers, most material transfer in food webs involves relatively few species and short food chains (3-4 levels, 2-3 links), i.e. remarkable "trophic compression" (Lewis *et al.* 2001). Although longer food chains that involve small or rare species are common and increase ecological complexity, they probably have minor effects on total primary and secondary production (Winemiller 2003).

Seasonal rivers in nutrient-rich landscapes can sustain greater harvest than aseasonal rivers or seasonal rivers in nutrient-poor landscapes (e.g. Carvalho de Lima and Araujo-Lima 2003). However, the productivity of oligotrophic ecosystems can be enhanced by "spatial food web subsidies" (Polis Anderson and Holt 1997; Winemiller 2003). For example, fishes that migrate out of tributaries draining the floodplain during the falling water period subsidize the food web of the flowing channel by providing an abundant food source for resident piscivores (Winemiller and Jepsen 2002). Food web subsidies can have major effects on food web dynamics, even inducing trophic cascades (Polis *et al.* 1997; Winemiller and Jepsen 1998; 2002) and stabilising complex systems (Huxel and McCann 1998; Jefferies 2000).

The food web paradigm provides an approach that allows us to model complex communities and ecosystems with the ultimate aim of understanding relationships and predicting dynamics (Woodward and Hildrew 2002). To inform management, multispecies fisheries in large rivers require a food web perspective because stock dynamics are influenced by both bottom-up factors related to ecosystem productivity and by top-down factors influenced by relative densities of predator and prey populations (Winemiller 2003). Water resource infrastructure can modify aquatic food

webs by regulating downstream transport of organic carbon, modifying water transparency and changing the extent of movement of fishes throughout the riverine landscape (Jordan and Arrington 2001), such changes impacting river fisheries (Barbarino Duque, Taphorn and Winemiller 1998). Empirical models relating fish diversity to discharge (e.g. Guegan *et al.* 1998) suggest that reductions in discharge will necessarily result in reductions in diversity and this effect is, at least in part, likely to be due to changes in food web complexity (Livingston 1997).

POPULATION BIOLOGY OF RIVERINE FISH

Life histories

Most fish (and other exploited aquatic organisms such as crustaceans and molluscs) have complex life cycles involving several morphologically distinct, free-living stages such as eggs, larvae, juveniles and adults. In the course of their lives, many organisms will grow by several orders of magnitude in mass and their resource and other ecological requirements may change drastically. As a consequence, many aquatic organisms undergo ontogenetic shifts in habitat requirements. Even so, habitat requirements and even life cycles are not necessarily set in stone. Some species, such as tilapias (Arthington and Bluhdorn 1994; Lorenzen 2000), display considerable plasticity in their life histories and can cope well (or even benefit from) changes in habitat availability. Others show very little plasticity and may become locally extinct as a result of even small environmental changes. For example, the introduction of novel predators caused the local extinction of the Lake Eacham rainbowfish, *Melanotaenia eachamensis*, in Australia (Barlow, Hogan and Rogers 1987).

Life history characteristics of fish, including maximum size, growth rate, size at maturity, fecundity and migratory behaviour, have important implications for populations as well as their risk of extinction (Winemiller and Rose 1992; Parent and Schriml 1995; Denney, Jennings and Reynolds 2002). While life his-

tory theory has been increasingly used to assess exploitation threats to marine fish stocks arising from fishing pressure, there has been far less work on freshwater populations that face a far wider set of threats.

In the following sections we review key aspects of fish life histories and population ecology.

Habitat use and migrations

To meet the different requirements of different life history stages, most aquatic organisms require access to a variety of habitats in the course of their life cycle. This requirement has two implications: (1) a variety of habitats must exist and (2) organisms must be able to migrate between them (actively or passively). Migration requires some degree of connectivity between aquatic habitats, which can be highly fragmented and separated spatially.

Migration has evolved as an adaptive response to natural environmental variation on a daily, seasonal and multi-annual basis, with biomes and habitats visited during the life cycle and distance travelled being essential characteristics of fish migration. Migrants must respond to the right cues, travel at the right pace and arrive at their destination within a certain time interval. Embryos, larvae and juveniles must find appropriate shelter and feeding grounds in order to reach the size threshold at which they maximize their survivorship. Migration also acts as a mechanism of e n e r gy transfer ("subsidy") between biomes and ecosystems (Winemiller 2003) as discussed above. Gross, Coleman and McDowall (1988) suggest that various forms of diadromy (i.e. catadromy, anadromy) have evolved in response to differences in marine and freshwater productivity and it seems likely that the evolution of potamodromy may also reflect spatial differences in aquatic production within river networks.

Many fisheries in large rivers are based mainly on migratory species. For example, medium to large-sized characiforms with wide distribution on the flood-plains of the Amazon/Solimões and other rivers migrate by descending the nutrient-poor, clear and black-water rivers to spawn in the nutrient-rich, white-water rivers that originate in the Andean ridge. The high abundance attained by these species may be a consequence of their tactic of migrating towards nutrient-rich habitats to spawn and using floodplain habitats as nursery grounds (Carvalho de Lima and Araujo-Lima 2003). The study of fish migrations has emerged as a key area of fisheries research in the Mekong River Basin (Warren, Chapman and Singhanouvong 1998; Baird, Flaherty and Phylavanh 2000). Preliminary evidence suggests that changes in fishing activities in Cambodia may have resulted in changes in fish catches in southern Laos (Baird and Flaherty 2003), highlighting the need for fish management strategies that transcend national jurisdictions.

Similarly, in rivers where diadromous fishes are an important component of the overall riverine fishery, management strategies (and river fisheries valuation studies) need to transcend the distinction between freshwater, estuarine and marine habitats and to more properly consider critical chains of habitats. Over-exploitation of piscivorous migratory species in marine or estuarine systems may potentially affect far-removed populations of fishes in freshwaters by altering top-down processes of regulation (Winemiller and Jepsen 2002). Fully integrated (freshwater/estuary /coastal) biological monitoring programs would address these dependencies but appear to be lacking in most large river systems, even though the close relationship between discharge and coastal fish production has been documented in both temperate and tropical rivers (e.g. Loneragan and Bunn 1999 and references therein).

Determination and regulation of abundance

Management for both exploitative and conservation purposes requires an understanding of the dynamics of populations as a whole. Losses, through emigration and death and gains, through immigration

and birth, are integral to an understanding of population dynamics and have received much attention in the ecological literature (Humphries *et al.* 1999).

The abundance of fish populations is determined by a combination of density-dependent and density-independent factors. Compensatory density dependence regulates the abundance of populations and its magnitude has important implications for the population dynamics of exploitation and disturbances (Rose *et al.* 2001). The sustainable exploitation of populations is possible only because populations compensate for the removal of animals by density-dependent improvements in natural mortality, growth and reproductive rates. Likewise, populations can compensate for the loss of individuals as a result of pollution and other environmental catastrophes. Density-dependence has been detected in mortality, growth and reproductive traits of fish populations (Bayley 1988b; Rose *et al.* 2001). While traditional age-structured models of fish population dynamics assume that regulation occurs predominantly through density-dependent mortality at the juvenile stage, recent studies have pointed to the importance of density-dependent growth and reproductive parameters in the recruited population (Post, Parkinson and Johnston 1999; Lorenzen and Enberg 2002). Regulation in the late juvenile and adult population implies a greater potential to compensation for increased mortality rates in juveniles (e.g. as a result of juvenile habitat loss, or losses due to entrainment), but also lower potential benefits of increasing juvenile survival or abundance (e.g. by stocking of hatchery fish) as compared to populations regulated only at the juvenile stage. A good quantitative understanding of regulatory mechanisms is therefore important to management and conservation decisions, but our knowledge base in this respect remains relatively poor.

The relative importance of density-dependent and density-independent processes in determining population abundance is difficult to assess and model.

This is particularly so in river systems characterized by extreme environmental variability, where disturbance can be a major factor (Reeves *et al.* 1995). Recovery from disturbance is typically rapid in temperate fish populations, although rates of recovery vary according to the types of disturbance (i.e. pulse or press) (Detenbeck, DeVore, Niemi and Lima 1992; Winemiller 1989b; 1996; Winemiller and Rose 1992).

Population processes

Reproduction and recruitment

Various recruitment models or hypotheses have been put forward, attempting to explain how fish in early life history stages encounter sufficient quantities of food of the right size, while avoiding predation. One of the pre-eminent hypotheses is the "match/mismatch" hypothesis of Cushing (1990), which recognizes that fish spawn at approximately the same time each year, but that prey abundance is less predictable and more responsive to the vagaries of oceanic conditions. Thus, in years when larvae and prey coincide or 'match', there will be strong recruitment, whereas in years when larvae and prey do not coincide ('mismatch'), there will be poor recruitment. Under experimental conditions in dry season waterbodies in Bangladesh, Halls *et al.* (2000) found the recruitment of a typical floodplain fish to be strongly dependent upon both spawning stock biomass (egg density) and biolimiting nutrient concentrations. These responses were believed to reflect cannibalism by adult fish on larvae and juveniles, competition for shelter from predators and the abundance of food organisms for developing larvae.

Harris and Gehrke (1994) proposed a 'flood recruitment model' similar to the flood pulse concept (Junk *et al.* 1989), to explain how some species of fish in the Murray-Darling Basin, Australia, respond to rises in flow and flooding. Humphries *et al.* (1999) questioned the generality of this model, based mainly on the fact that flooding in large areas of the Murray-Darling Basin does not coincide with peak spawning

times for many species and there are no published accounts of larvae being found on the floodplain. Whilst not dismissing the potential importance of the floodplain, Humphries *et al.* (1999) proposed the 'low flow recruitment hypothesis', which describes how some fish species spawn in the main channel and backwaters during periods of low flow and rising water temperatures. Ironically, only the introduced carp (*Cyprinus carpio*) seemed to respond to flood events in the Murray-Darling system with a renewed bout of spawning. More recently, King (2002) proposed five reproductive strategies among fishes of Australian floodplain rivers (generalists, flood opportunists, low flow specialists, main channel specialists and floodplain specialists).

Establishment and defence of territories, feeding, cues for reproduction and rearing of young are all critical for the production of the next generation. Yet our ignorance of these processes and how they are affected by environmental disturbances caused by the actions of humans is profound.

Mortality

Numerous and often interacting factors affect natural mortality rates in fish (including predation, disease, starvation, abiotic factors, spawning stress and senescence), yet our understanding of the importance of different sources of mortality remains poor, particularly for riverine fish. Mortality is strongly dependent on body size in fish (Lorenzen 1996). It is greatest in early life history stages, where variation in mortality rates plays a major role in determining the strength of cohorts. Whereas predation and starvation are assumed to be the primary reasons for high mortality, information on the links between these processes and alteration to the natural environment is virtually non-existent. Overall mortality rates decline as juveniles grow, but mortality at the juvenile stage is generally believed to be most strongly density-dependent. Moreover, juveniles may also disperse considerable distances and thus are vulnerable to artificial barriers and other anthropogenic as well as natural threats (Gallagher 1999).

The juvenile stage in fishes is often the most difficult to study and hence knowledge of this stage (including mortality rates and the factors influencing them) remain particularly poor. In seasonal river-floodplain systems, extremely high density-dependent and density-independent mortality rates may be associated with the period of receding water levels, when fish may become stranded and densities in remnant water bodies can increase by several orders of magnitude relative to flood conditions (Welcomme 1985; Halls 1998). This seasonal mortality pattern has major fisheries management implications. Intensive harvesting during receding floods may replace rather than add to the high natural mortality at this stage and consequently, floodplain fisheries may be able to sustain very high levels of exploitation during the recession phase. Conversely, however, these fisheries may be very vulnerable to exploitation of the remnant dry season stocks that form the basis for future recruitment.

Growth

Body growth is an important population process in fish, because it has a major impact on population biomass development as well as reproduction. Growth in river and floodplain fish is strongly influenced by environmental conditions, including hydrology (Bayley 1988a and b; De Graf *et al.* 2001), food resources and population density (Halls 1998; Jenkins *et al.* 1999). In at least one highly channelized river (Kissimmee River, Florida, USA), the restoration of a more natural hydrologic regime has resulted in increased growth rate and maximum size of a target game fish, *Micropterus salmoides* (Arrington and Jepsen 2001).

Population dynamics

There are two aspects that set the dynamics of river-floodplain fish populations apart from those of fish populations in other habitats: the strong influence of hydrological variation and the dendritic structure of riverine metapopulations (Dunham and Rieman 1999).

The influence of hydrology on population dynamics is most striking in seasonal floodplain systems where aquatic habitat may expand and contract by over three orders of magnitude and populations may respond with extreme cycles of production and mortality (Welcomme and Hagborg 1977; Halls, Kirkwood and Payne 2001; Halls and Welcomme 2003). As a direct consequence of this response, floodplain fish stocks can withstand very high levels of harvesting during the period of receding waters. Indeed, simulation studies described by Welcomme and Hagborg (1977) and Halls *et al.* (2001) both indicate that yields from floodplain fisheries can be maximized by removing a significant proportion (up to 85 percent) of the population just prior to the draw-down period. Perhaps not surprisingly, this corresponds to the period of maximum fishing activity in most floodplain fisheries (de Graaf *et al.* 2001).

Overall, quantitative modelling of population dynamics in relation to habitat factors, such as hydrological variables and land use change, is a relatively recent development (Welcomme and Hagborg 1977; Peterson and Kwak 1989; van Winkle *et al.* 1998; Jager, van Winkle, Holcomb 1999; Gouraud *et al.* 2001; Halls *et al.* 2001; Lorenzen, de Graf and Halls 2003a; Halls and Welcomme 2003; Minte-Vera 2003). Whilst validation of the models is required, good fits have been achieved using long time-series data sets from Bangladesh. Individual-based simulation models provide a powerful means of exploring any effects of different hydrological conditions on the dynamics and production of riverine fish, providing valuable insights to improve water use management at local and basin-wide scales. More work is required, in particular with respect to systems where large-scale hydrological modifications are likely in the future and/or restoration of natural hydrological regimes is but a distant possibility (i.e. in many areas of the developing world). However, even in pristine or restored river systems, climate change is likely to lead to significant hydrological change within the next few decades and under-

standing population responses to such changes will become increasingly central to fisheries management and conservation.

Most river fish populations have a metapopulation structure, i.e. they are comprised of local-scale sub-populations that are subject to relatively frequent extinction and re-colonization (Schmutz and Jungwirth 1999; Matsubara, Sakai and Iwata 2001). Gotelli and Taylor (1999) show that conventional metapopulation models that do not account for gradients may poorly describe the behaviour of riverine metapopulations. Connectivity patterns in river systems differ from those found in terrestrial habitats. The dendritic structure of the river habitat implies that fragmentation of rivers results in smaller and more variable fragment sizes than in two-dimensional landscapes and a possible mismatch on the geometries of dispersal and disturbance (Fagan 2002). As a result, fragmentation of riverine habitats can have more severe consequences for population persistence than would be predicted from models for two-dimensional landscapes.

ANTHROPOGENIC IMPACTS ON RIVER ECOLOGY AND FISHERIES

Many types of river ecosystem have been lost and populations of many riverine species have become highly fragmented due to human intervention (Dynesius and Nilsson 1994; Bunn and Arthington 2002). Over three quarters of the 139 major river systems in North America, Mexico, Europe and Republics of the former Soviet Union are affected by dams, reservoir operation for different purposes, interbasin diversions and irrigation (Dynesius and Nilsson 1994). The range of human activities known to damage and degrade river systems includes: (1) supra-catchment effects such as inter-basin transfers of water, acid deposition, climate change, (2) catchment land-use change, (3) river corridor 'engineering' and (4) instream impacts (Boon, Calow and Petts 1992; Arthington and Welcomme 1995; Junk 2002). Increasingly, aquatic ecosystems are being impacted

by recreation and tourism (Mosisch and Arthington 1998). The following sections briefly review anthropogenic impacts on river ecosystems and fisheries and measures for the mitigation of impacts.

Supra-catchment effects

Supra-catchment effects such as acid deposition, inter-basin transfers and climate change increasingly affect river ecosystems and fisheries in multiple catchments and bioregions simultaneously. Acidification of surface waters has caused a suite of new pollution problems in industrialized areas, with massive impacts on aquatic habitats and fisheries (Brocksen and Wisniewski 1988). The general effects of toxic pollution and acidification are first, the elimination of the most sensitive aquatic species and, as the loading increases, the production of large tracts of river that do not support fish. Climate change affects temperature, but most importantly the spatial and temporal distribution of rainfall and consequently river hydrology and ultimately geomorphology, habitat and biotic processes. Climatic or man-made changes to the environment may compromise finely adapted fish reproductive and migratory strategies, to an extent largely depending on the intensity and recurrence of the perturbation and on the adaptability of the species.

Catchment land-use and river corridor engineering

Changes in catchment land-use affecting rivers include afforestation and deforestation, urbanisation, agricultural development, land drainage and flood protection. Corridor engineering includes flow and flood transformation by dams, weirs and levees, channelization and dredging, water abstraction and the removal or deterioration of riparian vegetation.

In many river systems land use change and corridor engineering are the most important factors affecting fish ecology and fisheries. These impacts arise primarily from changes in habitat availability (both quantity and quality) and habitat connectivity (Trexler 1995; Toth *et al.* 1995; Toth, *et al.*1998; Bunn and

Arthington 2002; FAO 2000). Loss of habitat connectivity has resulted in the local extinction of many migratory species including shads, salmonids and sturgeons (Boisneau and Mennesson-Boisneau 2003; Faisal 2003; Fashchevsky 2003; Gopal 2003) and the diminished abundance of floodplain migrant species (Halls *et al.* 1998). Many rivers still face the threat of loss of connectivity and its ecological consequences. For example, the largest dam in the world, the Three Gorges Dam in the Yangtze River basin of China, will create a reservoir 600 km in length, reaching from Sangliping to Chongqing. Closure of this dam will cause blockage of fish migrations, extensive loss of riverine habitat and profound ecological changes that will threaten fish biodiversity in the river (Fu Cuizhang *et al.* 2003).

The impacts of hydrological change (e.g. by damming of rivers) may affect individual fish in any history stage, biotic assemblage structure and ecosystem processes. These impacts have been observed at multiple spatial and temporal scales (World Commission on Dams 2000; Bunn and Arthington 2002). Only a brief review of key issues can be provided here. Pulsed reservoir discharges associated with on-demand hydroelectric power generation limit the quality and quantity of habitat available (Valentin *et al.* 1994), causing fish to become stranded on gravel bars or trapped in off-channel habitats during rapid decreases in flow. The timing of rising flows serves as a cue to the spawning of certain fish species and loss of these cues may inhibit reproduction (King, Cambray and Dean Impson 1998), whereas cold-water releases from dams have been found to delay spawning by up to 30 days in some fish species (Zhong and Power 1996) or even inhibit spawning entirely. Larval development can be inhibited by cold-water releases. Furthermore, anoxic waters are often released from reservoirs in which the vegetation has not been removed prior to filling (e.g. Petit Saut Dam, Sinnamary River, French Guyana), causing mortality in many river species. Changes in river hydrology that are not in natural har-

mony with seasonal cycles of temperature and day-length may influence many critical life history events and have negative impacts on fish and other biota (Bunn and Arthington 2002). Natural flood regimes (and other aspects of the natural flow regime) are critical for maintaining biodiversity and fisheries, especially in strongly seasonal systems (Welcomme 1985; Junk *et al.* 1989; Agostinho and Gomes 2003; Winemiller 2003), but also in rivers with less predictable flooding regimes (Puckridge *et al.* 1998; Pusey *et al.* 2000). Ecological restoration of hydrologically degraded river floodplain systems should pay careful attention to restoration of the historical hydrologic regime including natural periods of low and high flow and periodic extreme flood and drought events (Toth *et al.* 1997).

In-stream impacts

Exploitation

Many fisheries, particularly in the tropics, exploit a wide range of species. In such multi-species fisheries, the relationship between total effort and long-term total yield (obtained from a range of different species) tends to be asymptotic, i.e. yield increases initially with effort but approaches a constant maximum over a wide range of higher effort levels (Welcomme 1985, 1999; Lae 1997). This is because, as exploitation increases, large and slow-growing species are depleted and replaced by smaller, fast-growing species that can produce high yields even at very high levels of exploitation. Even though multi-species yields can be maintained at very high levels of fishing effort, it is neither economically nor ecologically desirable to operate at very high effort. Economically, the returns to individual fishers tend to diminish with increasing effort (albeit not linearly) and at the level of the overall fishery, unnecessarily high levels of resources are expended to achieve the same fish catch that would be achieved at much lower effort levels. However, where access is open and opportunity costs are low, fisheries tend to be over-exploited in this way. The small fast-growing species that dominate catches

at high effort levels are usually less valuable in monetary terms than the large species they have replaced, but the nutritional value of small fish eaten whole is extremely high (Larsen *et al. 2000;* Roos *et al.* 2002). Ecologically the overexploitation of larger species - "fishing down" the food web (Pauly *et al.* 1998) is obviously undesirable because it may threaten the very existence of some of these species. Of course, even multi-species yield must decline at very high levels of fishing effort (when even the most productive species are overexploited), but whether this point has been reached in many fisheries is questionable.

Recreational fisheries tend to have less drastic impacts than food fisheries in that the target species are generally limited and when these species are over-exploited there are rarely shifts to smaller elements of the community. It is also likely that loss of much genetic variability occurs before a species is eliminated from the fishery or the community. Total disappearance of species through this process is comparatively rare, although in some cases such as the Oueme River in Benin, Africa, species (e.g. Nile perch, *Lates niloticus*) have become commercially and ecologically extinct at the local scale (Welcomme 1999). Where biological extinctions follow, this is usually the result of combined environmental and fishing pressures.

Introduced species

With progressive deterioration of native fish stocks as a result of over-exploitation and other environmental impacts, many countries have turned to exotic species as substitutes, rather than addressing the underlying causes of fisheries degradation (Welcomme 1988). In many instances fish have been introduced to satisfy local anglers with strong preferences for exotic angling species of international repute (e.g. salmonids and bass). Fish have also been introduced deliberately for pest and disease control (especially the mosquito fishes), as ornamental species for aquariums, parks and botanic gardens (Lobon-Cervia, Elvira and Rincon 1989; Arthington 1991) and as a source of protein for

human populations (e.g. tilapias, carps). Fish intro-duced for fish-farming have also escaped and colonised local waterbodies and even most of some large drainage basins (e.g. carp in the Murray-Darling Basin, Australia).

The major modes of impact associated with introduced fishes (both exotic and translocated) are genetic effects via hybridisation, alterations of habitat and water quality, consequences to native populations of competition for space and food and from predation and impaired health from imported parasites and dis-eases (Moyle and Light 1986; Arthington 1991; Pusey *et al.* 2003). Environmental impacts due to introduced fishes frequently exacerbate the effects of over-fishing, river regulation, habitat destruction and water pollu-tion and these disturbances themselves often provide ideal conditions for introduced species (Arthington, Hamlet and Bluhdorn 1990; Bunn and Arthington 2002). However, despite decades of empirical studies and some experimental work, our capacity to predict the species most likely to become established, spread and impact of introduced species is still very limited (Moyle and Light 1996; Williamson and Fitter 1996). Many countries have used risk assessments to identify potentially invasive species (see Arthington *et al.* 1999; Leung *et al.* 2002) and then placed restrictions on the range of species imported from other continents. The translocation of native fish species that are not endemic to particular basins should also be restricted (Pusey *et al.* 2003).

Fisheries enhancement and supplementation

Aquaculture-based fisheries enhancement and supplementation programs are frequently used in river and floodplain systems. Such programmes may serve a variety of purposes, from supplementation of indige-nous populations for conservation to culture-based fisheries of exotic species exclusively for fisheries pro-duction (Cowx 1994; Welcomme and Bartley 1998). Particularly common are programmes to maintain pop-ulations of large migratory species threatened by loss of habitat connectivity (e.g. salmonids, sturgeons, major carps) and/or to enhance fisheries production in storage reservoirs and floodplain habitats. There are good examples where the stocking of hatchery fish has contributed to the conservation or restoration of popu-lations (Philippart 1995), or led to substantial increas-es in fisheries production with little environmental cost (Lorenzen *et al.* 1998). However, many aquaculture-based enhancements have proved ineffective and/or ecologically and genetically problematic (Meffe 1992; Lorenzen in press). Compensatory density-dependent mechanisms imply that stocking into naturally repro-ducing populations tends to reduce vital rates (growth, survival, reproduction) of wild fish unless their densi-ty is far below the environmental carrying capacity. Stocking of hatchery fish may also increase the trans-mission of infectious diseases or introduce new dis-eases into wild stocks. Genetic risks to natural popula-tions arise from low effective population size of hatch-ery-reared fish (leading to inbreeding depression) and from loss of local genetic distinctiveness and adapta-tion if hatchery fish are not derived from local popula-tions (leading to outbreeding depression). Where exot-ic species are used for enhancement, this may give rise to strong and sometimes unexpected ecological inter-actions with native species, as well as to hybridization between the exotic and related native species (Arthington and Bluhdorn 1996). However, there is lit-tle evidence for the common assumption that ecologi-cal and genetic risks of stocking native species are nec-essarily lower than those of stocking exotics (see also Pusey *et al.* 2003). Potential and actual benefits and risks of any stocking programme should be assessed carefully and there are now several frameworks to assist in this task (Cowx 1994; Lorenzen and Garaway 1988).

Aquaculture

Aquaculture is the farming of aquatic organ-isms, usually confined in facilities such as ponds or cages. Where cultured organisms escape into natural systems in significant numbers, this may raise ecolog-

ical and genetic concerns similar to those encountered in fisheries enhancement and supplementation (Arthington and Bluhdorn 1996). Most aquaculture systems rely on external inputs of feeds and/or fertilizers and large-scale aquaculture can be a significant source of nutrient pollution (Baird *et al.* 1996).

CONSERVATION, MITIGATION AND REHABILITATION PRIORITIES

The global assessments of the World Resources Institute (Revenga *et al.* 2000), the IUCN (Darwall and Vié 2003) and others (Miller *et al.* 1989) all indicate the serious vulnerability and degradation of inland water habitats world-wide. To address these issues, three levels of intervention - preservation/protection, mitigation and rehabilitation/restoration - are appropriate for the protection of lotic systems, depending upon the degree and type of modification and the level of investment society chooses to make. Here we review methods, opportunities and progress with river conservation, mitigation and rehabilitation.

Identifying conservation areas

There is widespread agreement that it is far cheaper for society to prevent degradation of rivers and their floodplains in the first place than it is to restore degraded aquatic ecosystems. The first challenge for managers and policy makers is therefore to review the legislative and institutional background to biodiversity conservation and river protection and then to identify and protect relatively undisturbed large rivers and river basins that are representative of the world's lotic biodiversity (Arthington *et al.* 2003a). Apart from their heritage values, conserved rivers and wetlands will serve in the future as the major sources of propagules and colonists for degraded rivers and wetlands that have already lost much of their biological diversity (Frissell 1997; Arthington and Pusey 2003). Clearly a method is needed for prioritising inland water sites for conservation at both local and regional scales.

Several major conservation organisations, including WWF and The Nature Conservancy, identify priority areas and strategies through ecoregion planning (Groves *et al.* 2002; Abell *et al.* 2002). Conservation strategies formulated at the ecoregional scale have the potential to address the fundamental goals of biodiversity conservation: (1) representation of all distinct natural communities within conservation landscapes and protected-area networks; (2) maintenance of ecological and evolutionary processes that create and sustain biodiversity; (3) maintenance of viable populations of species; and (4) conservation of blocks of natural habitat that are large enough to be resilient to large-scale stochastic and deterministic disturbances as well as to long-term changes. Freshwater ecoregions have been delineated largely on the basis of fish distributions and planning approaches incorporating the broader dynamics of freshwater systems are evolving (Abell *et al.* 2003). Areas of future work include, but are not limited to, designing strategies to address threats posed by supra-catchment stresses and by catchment land uses. While supra-catchment impacts cannot be mitigated through the designation of traditional protected areas, there is largely untapped potential to develop protected areas to address terrestrial impacts.

Based on a review of existing site prioritisation schemes such as the ecoregion approach, as well as on consultations with experts, the IUCN Species Programme has developed an integrative method for terrestrial, marine and freshwater ecosystems (Darwall and Vié 2003). Similar approaches are being instituted in Australia (Dunn 2003), the UK (Boon 2000) and elsewhere.

Focal species protection

Species-focused conservation measures are particularly important where threatened species cannot be conserved through protected areas. This is the case for many of the large migratory species spending much of their life cycle outside protected areas and those that may also be heavily exploited. Species-focused strategies will typically involve multiple measures such as

protection of key habitats and provision of passage facilities (Galat and Zweimuller 2001), as well as restrictions on fisheries exploitation. Chang *et al.* (2003) used an adaptive learning algorithm, the self-organizing map (SOM) to pattern the distribution of endemic fish species found in the Upper Yangtze and to identify alternative reserve areas for their conservation.

Mitigation

Attempts to mitigate, rather than remove, existing threats are probably the most common approach to conservation of river resources. Most mitigation measures aim to retain something of the original diversity of the ecosystem.

Only very limited mitigation or compensation for supra-catchment effects can be carried out at the level of aquatic ecosystems, such as liming of water bodies affected by acid deposition, or management of regulated rivers to compensate for hydrological effects of climate change.

A range of mitigation measures is available for effects of catchment land use and river corridor engineering. These include buffer strips to protect rivers from direct agricultural runoff, agricultural land and waste management to minimize erosion and pollution (Large and Petts 1996). A wide range of habitat protection and creation techniques have been described (Cowx and Welcomme 1998), although their effectiveness in achieving biological conservation objectives requires further investigation. Details in the design and operation of dams, weirs and flood control embankments can make a great deal of difference to the integrity of riverine ecosystems Larinier, Trevade and Porcher 2002; de Graaf 2002). Much experience is available now in the design of fishways (Larinier *et al.* 2002, FAO/DVWK 2002), although this is focused on temperate climates and the common designs may not be appropriate for tropical systems. Other measures include creation of spawning substrate for focal fish

species (e.g. salmonids), instituting fish stocking programs, providing simulated flood discharges and flushing flows for particular ecological and water quality objectives (Reiser, Ramey and Lambert 1989) and implementing more comprehensive flow prescriptions to protect river ecosystems (for method see Arthington *et al.* 2003a and b; King *et al.* 2003). Maintenance or restoration of key hydrological patterns is crucial to conservation and methods for assessing such patterns are discussed in section 5. Large rivers can be protected from further deterioration by limiting development on the floodplains, prohibiting mainstream dams and limiting activities designed to constrain the main channel, such as dredging, straightening and hardening of banks.

Exploitation impacts are addressed by regulating fishing activities through restrictions on total effort, gear types and seasonal or spatial closures. In multi-species fisheries, determining appropriate exploitation levels is difficult even in principle because vulnerability to fishing differs greatly between species that may be harvested fairly indiscriminately by fishing gear. Even moderate levels of overall effort may be too high for the most vulnerable (usually long-lived) species, while aggregated yields may be maximized at much higher effort levels. The inherent problem of deciding what level of exploitation is sustainable or desirable (Rochet and Trenkel 2003) is further confounded by the practical difficulties of assessing exploitation status and options in often data-poor inland fisheries. Methods for assessing exploitation are reviewed in section 5, while the human aspects of managing fisheries are dealt with in other chapters of this volume.

Worldwide, fish introductions and translocations are strongly restricted by national and international laws and codes of conduct. Where such measures are considered, a risk assessment should be conducted following established frameworks such as those reviewed by Coates (1998).

Rehabilitation and restoration

Rehabilitation and restoration are assuming a high profile in many countries as an extension of soil conservation programs and initiatives to improve water quality. Interventions focused on the morphology of river systems are also increasing (Brookes 1992; Clifford 2001), for instance by restoring portions of the floodplains by local piercing of dykes, setting back levees from the main channel and removing revetments and wing dykes from river banks. Many of these strategies are based on the recognition of the importance of connected side-arm channels and their role in sustaining the fish biodiversity of large rivers (Humphries *et al.* 1999; Brosse *et al.* 2003). Adequate protection and management of riparian zones, based on sound ecological principles, is another effective strategy for addressing many existing problems of river ecosystem degradation (Bunn *et al.* 1993; Kauffman, Beschta, Otting and Lytjen 1997) and is essential to the maintenance and management of freshwater fishes (Pusey and Arthington 2003). However, various studies have produced conflicting results regarding the relative impacts to aquatic ecological integrity of land uses in the riparian zone versus activities in the wider catchment (Hughes and Hunsaker 2002).

Numerous examples of how these and other restorative measures have been implemented exist, principally from developed countries. Among the most famous is the ongoing restoration of the channelled Kissimmee River in Florida, which involves integration of hydrological, hydraulic and water quality principles with concepts of ecological integrity (Koebel, Harris and Arrington 1998). The primary goal of the project is to re-establish the river's historical flow characteristics and its connectivity to the floodplain (Toth *et al.* 1993). A method for rehabilitating smaller rivers has been articulated in the stepwise ("Building Block") approach (Petersen *et al.* 1992) and there is a growing literature on principles and guidelines for river corridor restoration (e.g. Ward *et al.* 2001).

ECOLOGICAL APPROACHES AND TOOLS FOR
MANAGEMENT DECISION SUPPORT

Clearly, the conservation of river ecosystems and the sustainable exploitation of their fisheries require integrating ecological knowledge into river and fisheries management. In this section we review approaches and tools for making such ecological knowledge available to management and decision processes.

The challenge of providing ecological decision support

There are four important requirements for effective decision-support tools: (1) tools must be relevant, i.e. they must address the specific issues encountered by decision makers; (2) tools must be scientifically and ecologically sound, i.e. they must reflect current knowledge including uncertainties/ ignorance; (3) tools must be practical, i.e. they must be easily parameterised and understood; and (4) tools must be appropriate in the context of the decision-making process, i.e. they must be usable by some of the stakeholders involved and should be transparent to most. Failure of any management approach or tool to satisfy these criteria will render it ineffective. This implies that factors such as the degree of stakeholder participation in management and the extent of local ecological knowledge are just as important to consider in the design of decision-support tools as the underlying ecology.

Habitat-centered assessment

Many approaches for assessing ecological impacts of corridor engineering and other disturbances focus on habitat availability and suitability rather than aquatic population abundance or assemblage structure as such (e.g. Clifford 2001). This reflects the reasonable (but not always accurate) assumption that populations are likely to persist as long as habitats are maintained. Predicting population or assemblage dynamics is a complex task and will introduce additional uncer-

tainty, without necessarily producing additional insight into the problem at hand. However, it is unlikely that any single assessment of habitat will encompass the myriad different ways or scales at which habitat is perceived or used by aquatic organisms. There is always the potential for a habitat-based approach to define a reach as suitable for one taxon but completely unsuitable or less suitable for another and in the case where the former taxon is critically dependent on the latter, it is unlikely that a good conservation outcome will be achieved. The maintenance of a desired proportion of "optimum habitat" at a series of river reaches may result in the situation where it is impossible to simultaneously accommodate each reach because of spatial variation in the overarching factor determining habitat suitability (i.e. discharge). Habitat-centred assessments may not be sufficiently holistic in outlook to advise managers strategically.

Nonetheless, habitat approaches have value in identifying critical elements for individual species. For example, discharge-based modelling of habitat structure may be used to identify the magnitude of critical flow events necessary to allow the passage of migratory species. In addition, time series of habitat suitability based on the flow duration curve may be useful (Tharme 1996) in assessing the importance (defined by the frequency of occurrence) of particular conditions or the desirability of maintaining such conditions. In her discussion of physical habitat/discharge modelling, Tharme (1996) recommended that a wide array of trophic levels be included so as to improve the generality of habitat-based assessments.

Some larger-scale habitats, such as floodplains, are accepted as being important to a wide range of riverine biota. In this case, assessments of habitat a v a i l a b i l i t y , for example through combinations of hydrologic and terrain topographic modelling, may present a useful approach.

Modeling fish populations and assemblages

Empirical models

Empirical models are statistical representations of variables or relationships of interest, without reference to underlying processes. Average fisheries yield per area estimates (e.g. from different habitat types) may be regarded as the simplest of empirical models, but can be extremely useful in decision-making about habitat protection or creation (Jackson and Marmulla 2001; Lorenzen *et al.* 2003b).

Most empirical models are regression models that relate parameters such as yield, abundance, or diversity to one or more factors of interest, usually exploitation intensity (effort) and/or environmental characteristics. Regression models are appropriate for comparative studies involving independent observations, while time-series models are appropriate where data are auto-correlated (i.e. time series of observations from a single system). Fishing intensity tends to be the single most important factor determining yields in comparative studies of floodplain rivers (Bayley 1989) and lagoons (Joyeux and Ward 1998). However, hydrological factors may be dominant in system-specific models, particularly where fishing effort is either stable or itself related to hydrology (as in the floodplains of Banglasdesh). Empirical models relating river or estuarine fisheries yields to hydrological variables such as discharge have been derived for many systems (e.g. Welcomme 1985; Loneragan and Bunn 1999; de Graaf *et al.* 2001).

Rule-based and Bayesian network models

Rule-based and Bayesian network models are logical representations of the relationships between cause and effect variables, hence they occupy an intermediate position between purely empirical models and mechanistic (e.g. population dynamics) models. In the case of Bayesian networks, probability distributions are attached to all variables and the distributions of response variables are modified by applying Bayes

theorem (Jensen 1996). Bayesian network models for predicting (co)-management performance are described by Halls *et al.* (2001b). These models use multidisciplinary explanatory variables to predict a range of performance measures or outcomes, including sustainability, equity and compliance and are designed to support adaptive management approaches. Baran, Makin and Baird (2003) present a Bayesian network model to assess impacts of environmental factors, migration patterns and land use options on fisheries production in the Mekong River. The natural production levels that can be expected for each fish group (black fishes, white fishes and opportunists and three geographic sectors (Upper Mekong, Tonle Sap system and the Mekong Delta), are qualitatively expressed by a percentage between "bad" and "good". Such a result can be converted into tons of fish when statistical time series are available.

Bayesian network models are increasingly being incorporated into decision support systems for the determination of river flow regimes that will sustain river ecosystems and their fish populations (Arthington *et al.* 2003a and b).

Population dynamics models

Population dynamics models have been central to decision analysis in marine fisheries management for a long time, but they have not been widely used in rivers. This is likely to reflect differences in management requirements (annual setting of exploitation targets in marine fisheries versus more focus on environmental factors and a longer term perspective in freshwater systems) and the fact that models developed for marine fisheries are largely unsuitable for addressing the river fisheries issues.

The development of models addressing the linkages between fish populations and abiotic processes central to the management of rivers for fisheries began with Welcomme and Hagborg's (1977) model. Over the past few years, there has been an upsurge of interest in population models for river and floodplain fish stocks. Halls *et al.* (2001a) and Halls and Welcomme (2003) present an age-structured model incorporating sub-models describing density-dependent growth, mortality and recruitment to explore how various hydrographical parameters affect the dynamics of a common floodplain river fishes. The results of the simulations offer insights into hydrological criteria for the maintenance of floodplain-river fish faunas and can be used to design appropriate flooding regimes that maximise benefits from the water available. Minte-Vera (2003) developed a lagged recruitment, survival and growth model (LRSG - Hilborn and Mangel 1997) for the migratory curimba *P r ochilodus lineatus* (Valenciennes 1847) in the high Paraná River Basin (Brazil), with recruitment as a function of flood and stock size. Distributions obtained were used to evaluate the risk to the population from various fisheries and dam-operation management decisions. Lorenzen *et al.* (2003a) developed a biomass dynamics model for fisheries and hydrological management of floodplain lakes and reservoirs. The model accounts explicitly for production and catchability effects of water area fluctuations. Models of population dynamics in relation to flow in non-floodplain rivers have been developed by van Winkle *et al.* (1998); Jager *et al.* (1999); Peterson and Kwak (1989) and Gouraud *et al.* (2001).

Model development and testing are still at a relatively early stage; more validation is required and the relative importance of compensatory processes remains largely uncertain. However, initial results appear promising, particularly with respect to biomass dynamics and dynamic pool models. Certainly, density-independent effects on fish populations require further investigation, particularly the effect of different flooding patterns on primary and secondary production per unit area or volume flooded. Other factors such as the influence of hydrology on processes such as spawning success need further evaluation and consideration in models of this type.

Many tropical river-floodplain fisheries are inherently multi-species and multi-gear fisheries. In such systems it is difficult to manage species in isolation, due to technical and biological interactions. Technical interactions arise because a range of species are harvested by the same fishing gear and it is not therefore possible to optimize exploitation for individual species independently. Biological interactions arise from predation and competition. The assessment of multi-species fisheries remains a major challenge, but several tools are now available to aid their analysis. Technical interactions can be analyzed using BEAM4 (Sparre and Willmann 1991) for river fisheries applications see Hoggarth and Kirkwood (1995). The ECO-PATH family of models has emerged as widely used too for assessing biological interactions. Often, however, data available for river fisheries will be too limited to allow even simple applications of such models. Simple and robust indicators for assessing such fisheries based on aggregated catch/effort and possibly size structure or species composition data should receive more attention. All of the models discussed above focus on the dynamics of populations at relatively high abundance, where populations are subject to compensatory density dependence and demographic stochasticity can be ignored. Such models are important to decision-making in fisheries management contexts, but the dynamics of populations at risk of extinction are not captured well. Methods of population viability analysis have been used to prioritize salmon stocks for conservation (Allendorf *et al.* 1997), but further development of these approaches for freshwater fish populations is highly desirable.

Integrating information

The integration of biological and environmental data in models (conceptual, rule-based, statistical, predictive) is increasingly being used to underpin audits of aquatic ecosystem health (Bunn, Davies and Mosisch 1999), in environmental impact assessments and in river restoration activities (e.g. the restoration of important characteristics of river flow regimes; Toth,

Arrington, Brady and Muszick 1995; Toth *et al.* 1997). The quantification of modified flow regimes that will maintain or restore biodiversity and key ecological functions in river systems is increasingly concerned with the integration of information on river hydrology, geomorphology, sediment dynamics and ecology, all linked to the social consequences of changing river flows (Arthington *et al.* 2003a and b; King *et al.* 2003). The so-called holistic environmental flow methods that make use of many types of information, including local ecological knowledge, models and professional judgement, are the most suitable for large river systems. Examples include the environmental flow methodology DRIFT (Downstream Response to Imposed Flow Transformations) originating in South Africa (King *et al.* 2003) and similar A u s t r a l i a n approaches (Cottingham, Thoms and Quinn 2002; Arthington and Pusey 2003). For reviews of such methods and recent innovations see Arthington *et al.* (2003a and b) and Tharme (1996, 2003).

Resolving uncertainty

Major theoretical advances have been made in understanding how large rivers and their fisheries function, yet the science underlying river and fisheries management is still beset by fundamental problems of uncertain knowledge and limited predictive capability (Poff *et al.* 2003). Uncertainly arises both from irreducible ecosystem complexity and from uncertain transferability of general ecological understanding to specific situations. Uncertainty is such a pervasive factor in ecological management that it must be dealt with explicitly and constructively by, we suggest, process research and tools such as adaptive management, strategic assessment and meta-analysis.

Process research

More research on many of the key ecological processes discussed above is clearly warranted (see priorities discussed below), but this will take time and may not reduce uncertainty enough to allow reliable predictions at the scale required for management decision-making.

Adaptive management

In the long term we may reduce uncertainty and increase the effectiveness of management measures, if their consequences are monitored and management measures adapted accordingly. Adaptive management is a process of systematic "learning by doing" (Walters 1997). It involves three main aspects: (1) uncertainty is made explicit, (2) management measures are considered as experiments, designed to yield information as well as material benefits and (3) management measures and procedures are modified in light of results from management experiments. Adaptive management may be implemented within just a single site, but it is often advantageous to work across a number of similar sites in order to increase replication and, possibly, test a range of management options in parallel, thus achieving results more quickly than through sequential experimentation. The costs of adequate monitoring can be considerable and therefore experimental management should be considered only where the costs of the intervention or the anticipated benefits warrant this expenditure.

Strategic assessment and meta-analysis

Strategic assessments of impacts or mitigation measures synthesize results from individual projects as well as wider relevant knowledge. Strategic assessments carried out on a national or regional basis are likely to improve the effectiveness of future assessments and management interventions substantially. Meta-analysis is an approach increasingly used to synthesize and integrate ecological research conducted in separate experiments and holds great promise for identifying key factors affecting river ecosystems and effective conservation measures (Arnqvist and Wooster 1995; Halls *et al.* 2001b). Fuzzy Cognitive Mapping (Hobbs *et al.* 2002) is a promising new technique for integrating disconnected case studies to guide ecosystem management. Bayesian networks, which express complex system behaviour probabilistically, can facilitate predictive modelling based on knowledge and judgement, thereby enhancing basic understanding without the requirement of excessive detail (e.g. Reckhow 1999).

SUMMARY AND RECOMMENDATIONS

Although major advances have been achieved across the broad field of river ecology and fisheries, substantial information gaps characterize every fundamental aspect of fish biology and the ecological processes sustaining fisheries in large river systems. Here we summarize the major points and conclusions arising from our review and the discussions held during LARS 2, beginning with general statements intended to emphasize the importance of healthy rivers and their fisheries. The main research priorities identified in this review are given emphasis (see also Dugan *et al.* 2002).

Large rivers and their floodplains provide a wide range of ecosystem goods and services to society. Many of these services, fisheries production in particular, depend upon the biodiversity and ecological integrity of aquatic ecosystems. The harnessing, development and management of rivers and their natural resources have contributed to economic development for some segments of society, but usually such development is accompanied by severe degradation of ecological integrity. There is evidence that the true value of fisheries has often been underestimated compared to the value of river development.

Biodiversity of large rivers are threatened by climate change, deforestation, agricultural and urban land use, pollution, channel modifications, inter-basin transfers of water and modified flow regimes, loss of habitat and habitat connectivity, introduced species and fishing pressure. These impacts are of particular concern in tropical floodplain rivers, which are home to over 50 percent of the world's freshwater fish species. There is a critical need to define the factors and processes that maintain biodiversity and ecosystem services at river basin and regional scales.

Tropical floodplain rivers present a rare opportunity to conserve important areas of biological diversity and aquatic resources before they deteriorate under pressure from development. The conservation of important genetic stocks, species and species complexes is a priority. Methods are evolving to define conservation and restoration priorities in large rivers but theoretical and methodological considerations merit more attention (Abell 2002). Major data gaps for species distributions prevent identification of hotspots for richness, endemism and other conservation targets, hindering effective conservation planning. Further, planners are challenged to design strategies that will maintain the often large-scale abiotic and biotic processes that shape habitats and support the persistence of biodiversity.

In many cases, the maintenance of healthy river ecosystems and all components of biodiversity (species, genetic stocks, ecological and evolutionary processes) are synonymous with maintaining healthy productive fisheries and sustaining livelihoods. Occasionally, however, modified systems can provide high levels of fishery production (e.g. via stock enhancement programs in modified habitats, particularly water storage reservoirs) even though their biodiversity is compromised. Hence, it is important to distinguish clearly between fisheries production and conservation aspects of rivers where the former are important, particularly in a developing country context.

Natural flow regimes and hydrological variability (quantity, timing and duration of flows and floods and periods of low flows) are considered essential for maintaining biodiversity and fisheries, especially in strongly seasonal river systems (Poff *et al.* 1997). The Flood Pulse Concept (Junk *et al.* 1989) remains a robust and widely applicable paradigm in tropical floodplain rivers with predictable annual flood pulses, governing maintenance of biodiversity, energy flow and fisheries productivity. Maintaining the annual flood pulse in tropical floodplain rivers and the vari-

able patterns of flows and floods in rivers with more erratic flow regimes should be the first priority in water management.

Research on flow-ecological relationships in large rivers and further development of conceptual, empirical and dynamic ecological models, are urgent research priorities (Arthington and Pusey 2003). Interim environmental flow prescriptions should be set now, in major rivers of conservation concern and those sustaining fisheries and livelihoods. Holistic ecosystem environmental flow methods such as DRIFT (King *et al.* 2003) and its fish component (Arthington *et al.* 2003a), using all information, including local ecological knowledge, models and professional judgement, are the most suitable methods for defining flow regimes in large river systems.

Sustaining river ecosystems and productive fisheries depends in part upon understanding the energetic basis of their productivity, linked to the trophic ecology of fish and food web structure. Food webs in large rivers are complex and influenced by many abiotic and biotic factors. Nevertheless, to inform management, we need a food web perspective on multispecies fisheries in large rivers, because stock dynamics are influenced by both bottom-up factors related to ecosystem productivity and by top-down factors influenced by relative densities of predator and prey populations. Research into the productive basis of fish populations and fisheries in different habitats is a priority (Winemiller 2003).

There is evidence of ecosystem overfishing in many tropical rivers and large long-lived species are endangered as a result. The implications of "fishing down the food web" (Pauly *et al.* 1998) and species loss for the sustainability, variability and management of fisheries, as well as for biodiversity protection, need to be explored further.

More research is required to understand basin-wide threat mechanisms, interactions and scales of response. Mitigation measures include the restoration of hydrological and sediment dynamics, riparian vegetation, river habitat diversity and floodplain connectivity (Tockner and Stanford 2002). More investment in monitoring and evaluation is required to determine the success of such efforts.

For most large river systems, essential information is lacking on biodiversity (of all aquatic biota), species distributions and habitat requirements of fishes, migration and spawning cues, all aspects of migration patterns, reproductive biology and population dynamics. Habitat (in its very broadest sense) may be used in assessments of ecological integrity, in quantifying environmental flows and in planning conservation strategies, as a surrogate for biotic requirements where data on the latter are limited. If habitat-based assessments must be used, a wide array of trophic levels should be included to improve the generality of habitat-based assessments (Tharme 1996).

Quantitative measures at the population level (yield, abundance, extinction risk) are important for decision-making on many issues, including trade-offs between water resources development and fisheries. Despite some fundamental gaps in ecological knowledge (e.g. the basis of floodplain production), fisheries models accounting for hydrological variability and exploitation impacts on large populations are becoming available and will allow a more detailed analysis of water management-fisheries interactions (Halls and Welcomme 2003). Further elucidating density-dependent and density-independent mechanisms that regulate and determine fish abundance is a key challenge. Understanding of proximate mechanisms underlying life history plasticity (including migration cues) requires further research.

A significant gap is the lack of data, theory and models for small and endangered populations where demographic stochasticity, depensation and metapopulation structure are significant factors in dynamics. This area should be addressed as a matter of priority, given the imperilled status of a significant proportion of riverine biota.

Major theoretical advances have been made in understanding how large rivers and their fisheries function. Further development of ecological theory for river biota and fisheries will provide a better basis for management and conservation in the longer term. This will require integration of field data collection, management experiments (i.e. "learning by doing" Walters 1997) and modelling.

Routine fisheries data collection should be focused more strongly on providing information relevant to key issues in river management. This will require a closer link between research, management and administration. Modelling should play a key role in synthesising information, formulating and testing hypotheses and improving data collection, experimental design and management actions.

Despite recent advances, the science underlying river and fisheries management is still beset by fundamental problems of uncertain knowledge and limited predictive capability (Bunn and Arthington 2002). Uncertainty arises both from irreducible ecosystem complexity and from uncertain transferability of general ecological understanding to specific situations (Poff *et al.* 2003). Uncertainty is such a pervasive factor in ecological management that it must be dealt with explicitly and constructively.

Adaptive management will often be the most effective way of resolving uncertainties, improving management and generating key ecological knowledge. Well-planned management experiments should be carried out and comprehensively documented far more widely than hitherto (Poff *et al.* 2003).

Meta-analysis also holds great potential to answer key ecological questions from the combined analysis of studies on individual sites and river basins. Studies in individual systems should report averages as well as variability, minimum and maximum values, to be amenable for inclusion in such quantitative syntheses. A paucity of comparative analyses was a conspicuous gap in papers submitted to LARS 2.

Already a range of modelling tools is available to support decision-making in river basin and fisheries management. Risk assessment can provide a framework for decision-making by explicitly including uncertainties, data and previous knowledge in quantitative frameworks. Modelling approaches can facilitate communication between stakeholders.

Beyond general principles at the conceptual level and volumes of international recommendations, there is a dearth of practical guidelines for managers to apply at the operational level. There are also few tools to help stakeholders assess various management options and trade-offs. A compendium of decision tools for river ecological and fisheries management should be compiled and maintained, to provide managers, stakeholders and decision makers with an up-to-date guide to available resources.

Conspicuous gaps at LARS 2 concern the ecological linkages between uplands, rivers, lowland floodplains, estuaries and coastal systems, even though recent research has highlighted the importance of flow-related and land-based processes affecting estuarine ecosystems and their fish stocks. The ecological roles of groundwater and surface-groundwater processes and the consequences of climate change for aquatic ecosystems and fisheries, also received very little attention in submitted papers. The design of fishery management practices, environmental flows, restoration strategies and conservation reserves to cope with potential impacts of climate change is a largely unexplored research frontier.

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