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FISH ENVIRONMENTAL GUILDS AS A TOOL FOR ASSESSMENT OF ECOLOGICAL CONDITION OF RIVERS

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ABSTRACT

The form, hydrology and functioning of rivers worldwide have been increasingly modified by a range of human activities. The impacts of these changes on the fish faunas of rivers need to be assessed for biodiversity conservation and fisheries management. Reliable and cost effective indicators of fish assemblage responses to hydrological, morphological and functional changes in a river are required. Given the large number of fish species present in many rivers, reliance on a single indicator species is problematic. The present paper proposes the use of environmental guilds for this purpose. Building on prior studies, we propose a series of environmental guilds based on common patterns of response by fish species to changes in river flow and geomorphology. A general framework consisting of two upland stream guilds, three lowland lentic guilds, four lowland lotic guilds, two generalist guilds and five estuarine guilds is proposed. Considering the large numbers of species present in many river and estuarine systems and the flexibility of their behaviour, many species will be difficult to classify. Further development of the proposed guild classification at the level of individual basins is anticipated, particularly in river systems with highly variable hydrology and many opportunistic species. Nevertheless, this general scheme would be easily and rapidly applied to a wide variety of local circumstance, as well as to the description of the general trends in fish population and assemblage structure occurring during river development. Copyright © 2005 John Wiley & Sons, Ltd.

KEY WORDS: guilds; environmental flows; rehabilitation; biodiversity conservation; environmental assessment; hydrological alteration; floodplain fisheries

INTRODUCTION

Human activities have modified rivers worldwide (see Cowx, 2002). Over 70% of all temperate rivers are heavily regulated (Dynesius and Nilsson, 1994), and similar trends are occurring in tropical, sub-tropical and arid-zone systems (Arthington and Pusey, 2003; Revenga and Kura, 2003). Changes to the morphology, hydrology and functioning of river ecosystems may be produced directly by engineering of the river channels by river straightening, channel deepening and isolation of the floodplain by poldering (creation of dyked plots within which there is full control of the hydrology usually for agriculture) and levee construction. Hydrology and geomorphology may also be influenced directly and indirectly by changes to flow regimes induced by dams and water extraction abstractions that interfere with natural dynamic equilibrium between the generation of new channel and floodplain features and their disappearance through deposition and vegetation growth. Geomorphic and hydrologic changes influence the structure and dynamics of biological communities living in the river (Petts, 1996; Cowx and Welcomme, 1998; Bunn and Arthington, 2002).The impacts of proposed public works projects influencing river form and function must be assessed prior to the granting of a licence to abstract or divert water or construct flow modifying structures. Assessments of environmental flows also support the growing trend to mitigate for activities that alter hydrological regimes by regulated releases from dams for ecosystem maintenance, and to guide efforts to rehabilitate damaged rivers, especially in temperate regions. These needs are becoming increasingly important because there are

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growing pressures on countries to improve the ecological status of rivers and lakes to meet their obligations under international conventions such as the European Union Water Framework Directive 2000/60/EC, as well as the impetus to contribute towards protection of biodiversity under the Habitats Directive 92/43/EEC, Agenda 21 of the Rio Convention and the Convention of Biological Diversity.

Concern about the amount of water required for the maintenance of fish and fisheries in rivers (environmental flows) is reflected in the extensive, and growing, literature devoted to environmental flow assessment that has been reviewed by Parsons *et al.* (2002), Tharme (2003) and Dyson *et al.* (2003). Major developments to date have been in the United States, Northern Europe and Australia, which have all been affected for many years by dams, river control works and water abstractions (e.g. Arthington and Pusey, 2003; King *et al.*, 2003). However, there is increasing concern about the state of tropical rivers, where large quantities of water are being withdrawn for irrigated agriculture and there is a growing programme of large dam construction. This is leading countries such as South Africa to develop assessment methodologies adapted to the needs of such regions. Many of the methods developed to date are for organisms other than fish, and most fish-oriented methodologies have been usually been applied in relatively small upland rivers and headwater streams with few species. Currently there is a lack of methodologies capable of dealing with the greater ecological diversity of species of larger rivers, especially lowland floodplain rivers.

Welcomme and Halls (2001, 2005) and Bunn and Arthington (2002) emphasized the significance of changes in the timing, duration, amplitude and other characteristics of flood regimes on various fish species. There is also a vast literature on the responses of some fish species to changes in the morphology of rivers, the availability of habitats and the connectivity between them. Nevertheless, because of the greater numbers of species in many large rivers around the world, especially in tropical regions, it is impossible to assess the impacts of changes in hydrology or morphology on most species (see Welcomme, 1979; Hugueny, 1989; Oberdorff *et al.*, 1995). Even in temperate zones, where there are relatively fewer species, there has been a search for 'indicator' species that summarize impacts on characteristic groupings. This has proved equally difficult because of the wide range of habitat types occupied by many species (Grandmott[Q1], 1983). Nonetheless, it has long been recognized that groups of species behave in a sufficiently similar manner as to be classed into a common group. The classification of Mekong river species by the local fisher folk into 'black' and 'white' fish groupings is an example of such a classification (Chevey and Le Poulain[Q2], 1940).

In view of the present and future challenges for the sustainability of river ecosystems and their fish faunas, there is a need for cheap, rapid appraisal methods to assess impacts on fluvial ecosystems, particularly in regions of the world where biodiversity is high and knowledge of the biota is poor. This paper examines the possibility of expanding functional-group classifications into a more generalized tool that can assist in predicting responses of river fish biota to changes in flow and geomorphology resulting from dams and water diversion/extraction.

HISTORY AND DEFINITIONS

The ecological guild concept identifies subsets within species assemblages having high potential for competition (Simberloff and Dayan[Q3], 1991), and also may provide a means to identify species with similar responses to environmental variation (Leonard and Orth, 1988; Austen *et al.*, 1992[Q4]). Kryzhanovsky (1948) appears to have been the first person to group fish species according to preferred habitat requirements at various stages of their life cycles. Balon (1975, 1990) grouped fishes into 'reproductive guilds' according to their breeding behaviour, and Bain *et al.* (1988) and Leonard and Orth (1988) grouped North American stream fishes into habitat guilds based on responses to stream flow conditions. Regier *et al.* (1989) generalized the blackfish–whitefish separations of the Mekong River to other systems using the term 'ecological assemblages' mainly to guide river restoration and fisheries management. Aarts *et al.* (2004) used the term 'ecological guilds' to explain the failure of certain behavioural groups of fish to return to European large rivers, despite improvements in water quality.

In a review of the application of the guild concept in fisheries management, Austen *et al.* (1994) distinguished between structural guilds (groups of species that use similar resources) versus guilds that function as a 'super species' (groups of fishes that collectively respond to environmental variation in a more or less consistent manner). Although consistent with the classical definition of the ecological guild, structural guilds may have inconsistent or limited application for ecological assessment, because the resource or characteristic used to define the guild may be largely unresponsive to major sources of environmental impact. For example, species within guilds based on dietary similarity or ecomorphology would likely respond differently to key abiotic impacts such as flow alteration.

Karr *et al.* (1986) used trophic and other groupings of fish as indicators of the ecological state of a river or stream reach though the index of biological integrity (IBI), and Schmutz *et al.* (see www.FAM.boku.ac.uk) used 'functional groupings' or 'ecological guilds' to define fish community typologies for assessment of ecosystem health of European rivers for compliance with the Water Framework Directive. Developing further the concept proposed by Regier *et al.* (1989), the term 'environmental guild' is proposed here for identifying fish species that respond in a similar manner to changing hydrology and geomorphology of river ecosystems.

CRITERIA

The following criteria are used to describe fish environmental guilds.

Location in river system

This criterion considers the location of various life stages of a species in the fluvial ecosystem. Welcomme (1979) listed a wide range of habitats that occur in lowland rivers, and Amoros *et al.* (1982) described functional units of European river–floodplain systems. In addition, Rosgen (1994) and Schmutz *et al.* (2000) proposed river zones based on flow characteristics and morphology associated with topography, geology and longitudinal position in the watershed. Although these are not universally applicable, they do provide a general nomenclature that can be used to describe the various components of river systems. The following categories from the scheme of Amoros *et al.* (Figure 1) provide a foundation for identification of fish environmental guilds.

Main channel (eupotamon). The main channel consists of the central course of the river (main stem and tributaries) with two lateral zones: (i) the centre of the channel and (ii) the riparian zone. The channel can be further broken down longitudinally into upper (rhithron) and middle and lower (potamon) sectors, each of which can be further broken down into upper (epi-), middle (meta-) and lower (hypo-) reaches (Illies and Botosaneanu, 1963) (in European rivers, for example, the epi- and metarhithral zones represent upper and lower trout zones and the hyporhithral zone is equivalent to the grayling zone; Huet, 1949). The epi- and metapotamal zones represent the 'barbel' and 'bream' zones, respectively, and the hypopotamon is equivalent to the brackish-water estuarine or coastal–deltaic region.

Seasonal flowing anabranches and backwaters of the main channel (parapotamon). These are backwaters and slack shallows that are the remains of old anabranches. These areas tend to be silted and separated from the eupotamon during low-flow periods, at least at their upstream end. Consequently, these habitats are lentic during periods of isolation. Parapotamon evolve into plesiopotamon when the separation process is complete.

Floodplain pools seasonally connected to the main river (plesiopotamon). In the stabilized rivers of Europe, floodplain lakes are usually the remains of oxbow lakes. In the tropics, a range of scroll and scour lakes are also regularly flooded by the main channel. Floodplain lakes may be permanent or temporary, but even permanent lakes decrease substantially in area by the end of prolonged dry periods. Several recent studies have shown that the nature of fish populations in floodplain lakes depends strongly on the distance from the main channel and the frequency of connection (Winemiller *et al.*, 2000; Pouilly and Rodriguez[Q5], 2005; Arthington *et al.*, 2005). Q5

Floodplain pools disconnected from the main river (paleopotamon). In Europe the floodplain features furthest separated from the main river are fed mainly by ground water and have clear water. Spring-fed and groundwater-fed lakes also occur at the margins of the floodplain, but these usually are connected to the main channel only during high floods. In the tropics, seasonal floodplain pools provide important nursery habitats for many fish species, and local assemblages are influenced by local environmental factors and fish movement (Winemiller and Jepsen, 1998; Okada *et al.*, 2003; Arthington *et al.*, 2005).

The floodplain. This is a surface that is inundated seasonally according to the hydrological cycle. In their pristine condition, floodplains of many of the world's rivers were forested. Although some forested floodplains remain, more

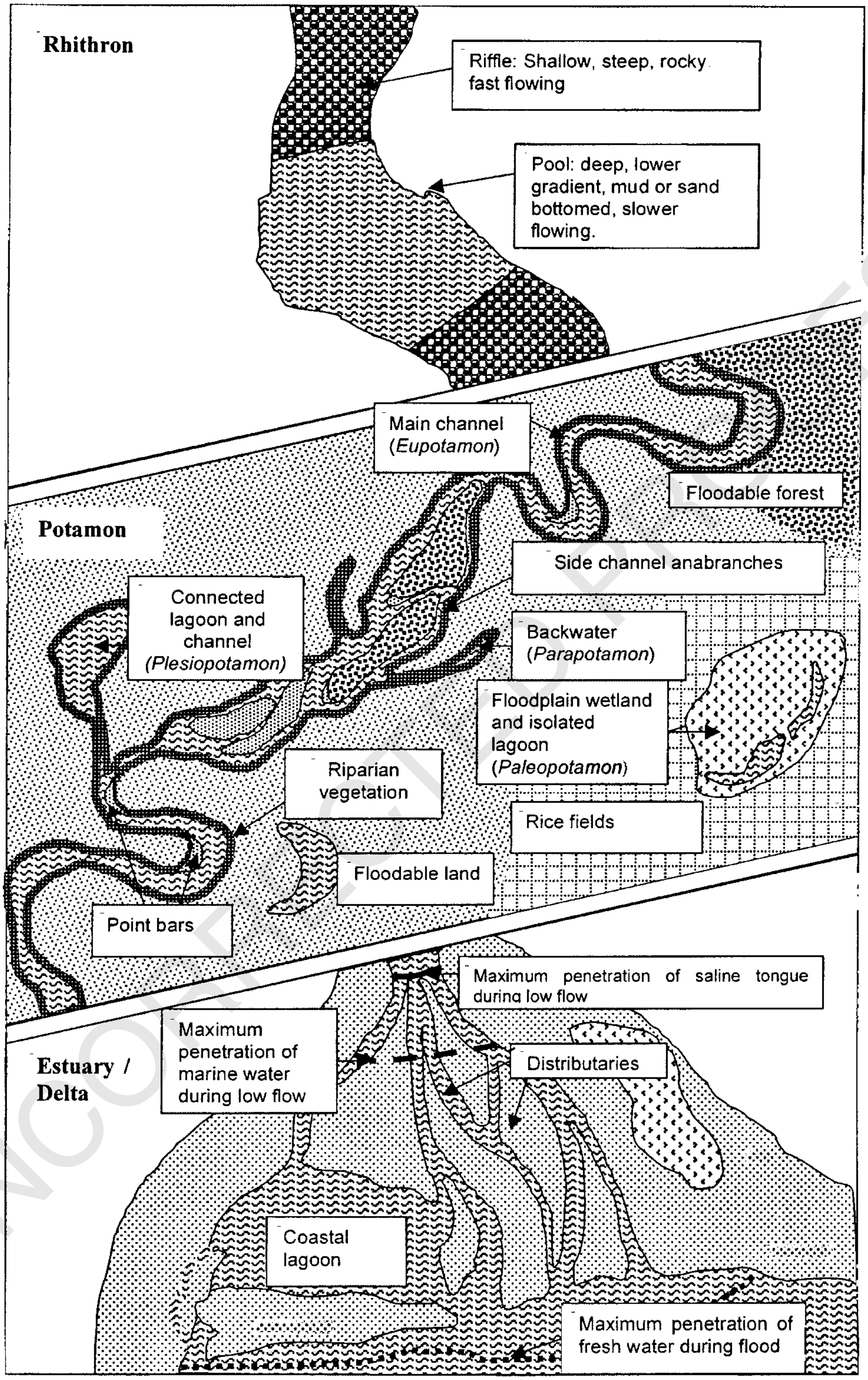

Figure 1. Q13

Q13

commonly these have been cleared for agriculture or cattle grazing. Floodplain pools are embedded in landscapes that are highly heterogeneous with respect to topography and vegetation, often transected by networks of drainage channels that connect the floodplain pools to the river channel. Large areas of permanent, semi-permanent or seasonal wetlands are found in floodplains of lowland rivers with unperturbed hydrology. There are great differences in the area flooded from year to year, and this greatly influences the population dynamics of many fish species (Welcomme, 1979; Gomes and Agostinho, 1997; Arthington *et al.*, 2005; Agostinho *et al.*, in press[Q6]). Q6

Migration and movement

The following patterns of migration, following the nomenclature of Daget (1960), are recognized.

Longitudinal migrations are those taking place up and down the main river channel, usually between breeding, feeding and refuge locations. Such migrations can be extremely long (see Lucas and Baras, 2001, for a review). Longitudinal migrations can take place entirely within the river channel, from large lakes up rivers (potamodromous) or from the sea to rivers (diadromous). Diadromous migrations can either be anadromous or catadromous (Gross *et al.*, 1988). Poddubnyi (1979) also recognized a category of semi-anadromous or semi-migratory species that undertake much shorter migrations of tens of kilometres, usually for breeding purposes. A further category that needs consideration is amphidromy (running between rivers and the ocean), which refers to fishes that spend appreciable parts of their life in both fresh and sea waters, feeding and growing in both, and whose migrations seem to have no direct relationship to reproduction (McDowall, 1988). Despite this categorization, care must be taken because some species, e.g. *Salmo trutta* L., exhibit a range of migratory traits including iteroparous and semelparous life histories.

Lateral migrations are those taking place from the main river channel to and from the floodplain and its waterbodies, usually between breeding, feeding and refuge locations (Winemiller and Jepsen, 1998).

Movements. Many species do not undergo structured migration but move onto and off floodplains in response to the seasonal expansion and contraction in flooded area. Some species, such as *Colossoma macropomum* (Cuvier) (Araujo-Lima[Q7] and Goulding, 1998) and *Semaprochilodus spp*. (Goulding, 1980), show complex migration patterns between the main channel, tributaries and flooded areas. Q7

Drift. Downstream drift of eggs and larvae is an important component of the life cycles of many species. Drifting eggs and larvae of riverine migrant, anadromous and amphidromous species have been described from rivers from all continents (see Lucas and Baras, 2001, for a review).

Reproductive strategy

Balon's (1975, 1990) system of reproductive guilds is used here. Many of Balon's guilds are found in rivers, but the most important are various substrate spawners (lithopophils, psammophils and phytophils), open-water spawners (pelagophils) and species showing varying degrees of parental care from nest building to viviparity (Table I).

Resistance to anoxia

Some river fish species are well adapted for survival under conditions of low dissolved oxygen. Adaptations may be physiological, morphological and/or behavioural, including lungs (lungfishes) and ancillary-breathing tissues derived from gills, gut lining, swim bladders or the skin.

Criteria not included

Feeding. The concept of IBIs (Karr *et al.*, 1986) is largely orientated around feeding guilds, and Aarts *et al.* (2004) included feeding in their behavioural guilds. Due to observed flexibility in diets of many river fish species, feeding guilds are not considered a major correlate of the environmental guilds proposed here. Dietary flexibility may be related to fish size, season and location within the system or most likely a combination of all three (Pusey *et al.*, 1995). Despite the specific exclusion of feeding ecology here as major determinant in guild composition, it should be noted that trophic ecology often is affected by human impacts to fluvial ecosystems. For example, a fish population may be restricted to channel habitats, yet still dependent on inputs (transport) of food resources from upstream or floodplain habitats, perhaps even on a seasonal basis. Furthermore, human perturbations often affect

Table I. Classification of main reproductive strategies of river fish based on spawning habits (after Balon, 1975, 1990)

I. Non-guarders	*II. Guarders*	*III. Bearers*
A. Open substrate spawners	A. Substratum choosers‘A. External bearers	
1. Pelagic spawners	1. Rock tenders (*lithophils*)	1. Transfer brooders
i. Pelagic eggs and larvae (*pelagophils*)	2. Plant tenders (*phytophils*)	2. Auxillary brooders
ii. Rock and gravel spawners with pelagic larvae (*lithopelagophils*)	3. Terrestial tenders (*aerophils*)	3. Mouth brooders
	4. Pelagic tenders (*pelagophils*)	4. Gill-chamber brooders
2. Benthic spawners	B. Nest spawners	5. Pouch brooders
i. Spawners on coarse bottoms with benthic larvae (*lithophils*)	1. Rock and gravel nesters (*lithophils*)	B. Internal bearers
	2. Sand nesters (*psammophils*)	1. Facultative internal bearers
ii. spawners on sand bottoms (*psammophils*)	3. Plant material nesters (*phytophils*)	2. Obligate internal bearers
	a. Gluemakers (*ariadnophils*)	3. Live bearers
iii. Spawners on plants	4. Froth nesters (*aphrophils*)	
A Obligate spawners on plants (*phytophils*)	5. Hole nesters (*speleophils*)	
B Non-obligatory spawners on plants (*phytolithophils*)	6. Miscellaneous-materials nesters (*polyphils*)	
3. Terrestial spawners (*aerophils*)		
B. Brood hiders		
1. Spawners on invertebrates (*ostracophils*)		
2. Annual fishes (*xerophils*)		

overall system productivity. Thus, all habitat and breeding requirements could be provided for a population, yet its numbers may still decline if critical food resources are eliminated by human alterations to the system.

Taxonomic relationships. Multiple taxonomic groups are clearly represented in each of the environmental guilds, therefore taxonomic affiliations are not considered in derivation of the framework.

PROPOSED ENVIRONMENTAL GUILDS

The previous attempts to identify guild structures are either based on single attributes (e.g. reproductive guilds) or on characteristics that tend to be plastic (e.g. trophic guilds). Consequently, a more integrated strategy is required. Given that river geomorphology, hydrology and the quality and quantity of aquatic habitats are critical elements influencing fish populations and community structure, the guild structure summarized in Table II is proposed.

Guilds in rhithronic communities

The rhithron has the predominant form of a succession of pools and riffles that give a longitudinal alternation of habitat types. This region of the river is relatively fast flowing and turbulent, with calmer stretches and occasional slack waters in the pools. Rhithronic reaches are visited by migratory potamonic and anadromous species that use the gravel riffles for breeding and the pools as nurseries. Resident species are usually small and migrate little outside of the rhithronic zone. Differences between the guilds lie in their location in the system.

Riffle guild. Species in this guild are rheophilic, main channel residents that inhabit rapids and riffle areas. They are generally sedentary, of small size and are equipped with suckers or spines to enable them to grip rocks and other submersed objects. They may also have elongated or laterally flattened forms that allow them to live in the interstitial spaces of the rock and cobble substrate. Riffle species are generally non-guarding and guarding lithophils with extended breeding seasons depositing their eggs among the rocky riffles where they live. They are generally insectivorous or specialists such as algal scrapers or filter feeders. Species inhabiting riffles usually require very well oxygenated water.

Table II. Response of the main ecological guilds to changes in flow regimes

Ecological guild	Typical behaviour	Reaction to changes in hydrograph	Typical species
Rhithronic guilds • Rheophilic, main channel residents • Inhabit torrent and rapids areas			
Riffle guild	• Inhabit rapids and rocky areas	• Sensitive to catastrophic and habitat flows (see Welcomme and Halls, 2005)	*Chiloglanis*, *Garra*, *Phractura* (Africa), *Botia* and balitorinids (Asia); loaches and sculpins (Europe); *Percina*, *Etheostoma* (N. America); *Characidium*, *Parodon*, and *Trichomycterus* (S. America)
	• Generally small size and equipped with suckers or spines, may also have elongated or flattened forms	• Damaged by disturbances to pool-riffle structure, such as seasonal desiccation or increases in sediment load that choke the interstitial spaces	
	• Generally lithophilic with extended breeding seasons depositing their eggs among gravel and rocks	• Damaged by wash-out or submergence of gravel reaches	
	• Generally insectivorous or specialists such as algal scrapers or filter feeders	• Species can be restored by rehabilitation of rapids and the pool-riffle structure • Species have fairly well defined flow requirements	
Pool guild	• Inhabit pools, often very micro-habitat specific	• Disturbed by changes to the flow regime that desiccate the pools or leave them for long periods without flow	Many small cyprinids, characins, salmonids, *Schizothorax* (Asia), catfishes and loaches
	• More limnophilic in habit	• Changes in water level can disturb habitat structure	
	• Some species inhabit slack regions of back eddies where there is emergent and floating vegetation	• Generally rely on delicate balance of pool-riffle structure of the rhithron and respond negatively to any influence that changes this balance	
	• Other species inhabit the deeper waters • Tend to feeding on the drift dislodged from the riffles or on insects falling into the river • Either lithophilic, breeding in the riffles, or phytophilic, attaching their eggs to vegetation		

Continues

Table 2. Continued

Ecological guild	Typical behaviour	Reaction to changes in hydrograph	Typical species
Lowland river (potamonic) guilds *Lentic guilds* • Floodplain residents move little between floodplain pools, swamps and inundated floodplain • Repeat breeders with specialized reproductive behaviour • Predominantly polyphils, nest builders, parental carers or live bearers • Generally resistant to low dissolved oxygen			
Plesiopotamonic guild	• Tolerant of low dissolved oxygen tensions only	• Sensitive to the drawdown phase of the hydrological cycle. Sensitive also to the amplitude of flooding that regulates connectivity to the river and extent of inundated floodplain	*Polypterus*, *Oreochromis mossambicus* (Africa); many small characins, cyprinids, catfishes and cichlids (Asia); *Tinca tinca* L. (Europe); *Astyanax*, *Markiana* and other characids, *Astronotus ocellatus* (Agaasiz) and other cichlids, *Rhamdia* and other pimelodids (S. America); *Gambusia affinis* Baird and Girard), *Lepomis humilis* Girard), *Ameiurus melas* (Raffinesque) (N. America)
	• May be lateral migrants moving from river margins, de-oxygenated backwaters and floodplain water-bodies onto floodplain	• Tend to disappear when floodplain disconnected and desiccated through poldering and levee construction • May increase in number in shallow, isolated wetlands, rice-fields and drainage ditches	
Paleopotamonic guild	• Tolerant of complete anoxia	• Sensitive to the drawdown phase of the hydrological cycle and to risks of desiccation	*Trichogaster*, *Ophicephalus* (Asia); *Protopterus*, *Heterobranchus*, *Parophicephalus* (Africa); *Clarias*, *Ctenopoma* (Africa and Asia); *Misgurnus fossilis* (L.) (Europe); *Hoplerythrinus*, *Brachyhypopomus*, *Corydoras*, *Hoplosternum*, *Brachyhypopomus*, *Hypostomus* and other loricariids (Latin America); *Umbra*, *Lepisosteus* (N. America)

	• Usually non-migratory	• Persist in residual floodplain water bodies • Principal component of rice field and ditch faunas	
Annual guild	• Inhabit seasonal, isolated, water bodies	• Sensitive to land reclamation schemes that permanently suppress seasonal water bodies	*Rachovia* and other annual killifishes
	• Have aestivating eggs with diapause • Complete life cycle in one rainy season		
Lotic guilds • Migratory fishes, moving often over long distances with sometimes complex migration patterns • One breeding season a year • Intolerant of low oxygen			
Eupotamonic pelagophilic guild	• Main channel residents not entering floodplain	• Tend to disappear when river dammed to prevent migration	Lates calcarifer (Bloch) (barramundi) (Australia); *Salminus maxillosus* (Valenciennes), *Brachyplatystoma* and other pimelodid catfishes (Latin America); Asian major barbs, *Hilsa*, some pangasiid catfishes (South and Southeast Asia); *Alosa* (Northern Hemisphere); *Polyodon* (North America)
	• Longitudinal migrants between a usually downstream feeding site and an upstream breeding one	• Sensitive to the timing and velocity of flow when these are inappropriate to breeding seasonality	
	• Predominantly pelagophils	• Recruitment success lessened if flow excessive or too slow for the needs of drifting larvae	
	• Often have drifting eggs and larvae	• Sensitive to low temperature discharges from dams	
	• May use backwaters or slacks downstream of point bars as nurseries	• May respond positively to fish passes	
Eupotamonic lithophilic guild	• Longitudinal migrants, often anadromous between a usually downstream feeding site and an upstream breeding one	• Tend to disappear when river dammed to prevent migration or when timing of flood inappropriate to their breeding seasonality	*Salmo salar* L., anadromous sturgeons (Acipenseridae) (Europe and N. America); *Onchorhynchus* spp. (Northwestern N. America); *Tor tor* (Hamilton) (India)
	• Lithophils and psammophils	• Sensitive to habitat flows if upstream breeding substrates destroyed or degraded	

Continues

Table 2. Continued

Ecological guild	Typical behaviour	Reaction to changes in hydrograph	Typical species
	• Fry may be resident at upstream site for a certain period and may occupy upstream floodplain	• Sensitive to structure of upstream habitats particularly presence of absence of woody debris • May respond positively to fish passes	
Eupotamonic phytophilic guild	• Use floodplain for breeding, nursery grounds and feeding of juvenile and adult fish	• Tend to disappear when river dammed to prevent migration	*Alestes*, *Hydrocynus*, *Citharinus* (Africa); percichthyids (Australia); many large cyprinids throughout the Paleotropics including *Barbus*, *Labeo*, *Catla*; *Leporinus*, *Colossoma*, *Piaractus*, *Prochilodus*, *Semaprochilodus*, *Pseudoplatystoma* (S. America); some species of suckers (Catastomidae) and large western minnows (Cyprinidae) (N. America)
	• Longitudinal/lateral migrants between floodplain spawning and feeding areas and main channel refugia	• Damaged when access to floodplain denied to developing fry and juveniles	
	• Predominantly phytophils	• Influenced by amplitude and duration of flooding	
	• Usually spawn at floodplain margin or on floodplain; sometimes have semi-pelagic drifting eggs and larvae		
Parapotamonic (semi-lotic) guild	• Intermediate between rheophilic and limnophilic habit	• Sensitive to river straightening and bank revetments	Many small cyprinids and characins; *Cyprinus carpio* (wild form), *Rutilus rutilus*, *Abramis brama* (L.) (Europe); *Esox lucius* (L.) (Northern Hemisphere)
	• Short distance, but often non-obligate migrants • Predominantly lithophils, psamophils, phytophils • Prefer anabranches and backwaters with low or seasonal flows • Use backwaters or slacks downstream of point bars as breeding grounds and nurseries	• Sensitive to stress flows and habitat flows needed for flushing the system	
Eurytopic guilds • Generalist species with very flexible behaviour			

• Tolerant of low dissolved oxygen • Repeat breeders • Predominantly phytophils, lithophils, psammophils, but some nesters or parental carers • Short distance migrants (semi-migratory) often with local populations			
Eupotamonic benthic guild	• Occupy main channel generally benthic sites	• Able to adapt behaviourally to altered hydrograph	Some *mormyrids*, some *Synodontis* (Africa): *Ancistrus*, *Chaetostoma*, *Pekoltia*, *Apteronotus*, *Sternarchorhynchus*, *Rhabdolichops* (S. America); *Dorossoma*, *Ictiobus*, *Ictalurus* (N. America)
	• May be tolerant of low dissolved oxygen but not necessarily so	• Generally increase in number as other species decline • Impacted negatively to flows that change depositional siltation processes and alter the nature of the bottom	
Eupotamonic riparian guild	• Occupy main channel riparian vegetation	• Able to adapt behaviourally to altered hydrograph	*Heterotis niloticus* (Cuvier) and many *Tilapia* and *Oreochromis* species (Africa); *Cyprinus carpio*, *Scardinius erythrophthalmus* (L.) (Europe); *Apistogramma*, *Crenicichla*, *Hemigrammus*, *Nannostomus*, *Microglanis*, various small doradid and loricariid catfishes (S. America); *Fundulus*, some *Lepomis* spp. (N. America)
	• Usually tolerant of low dissolved oxygen • May be lateral migrants or semi-migratory but often flexible with resident elements	• Generally increase in number as other species decline • Impacted negatively by flows and management that changes riparian structure	
Estuarine and coastal lagoon guilds			
Freshwater estuarine guild	• Stenohaline species that inhabit the freshwater component of the estuarine system	• Sensitive to changes in flow that affect fresh–salt water balance in the estuarine system	*Chrysichthys aureus* (Pfaff) (Africa); some ariid catfishes (Australia and West Africa); *Herichthys maculicauda* (Regan), (Central America),

Continues

Table 2. Continued

Ecological guild	Typical behaviour	Reaction to changes in hydrograph	Typical species
			Brachyplatystoma vaillanti (Valenciennes) (S. America), *Rutilus rutilus*, *Abramis brama*, *Esox lucius* (Baltic and Black Seas)
	• Semi-migratory species that move according to salinity and flood strength • Usually breed and feed in freshwater component of system	• Affected negatively by lowered flows permit greater penetration of saline water • Excessive flows may carry adults and fry into excessively saline environments • Influenced positively by river mouth dams that impound freshwater in the estuary	
Brackish water estuarine guild	• Permanent residents of estuary and lagoon system	• Influenced negatively by river mouth dams that impound freshwater in the estuary and remove the brackish component	Milkfish *Chanos chanos* (Forsskal) (Asia); *Ethmalosa fimbriata* (Bowditch), *Sarotherodon melanotheron* (Ruppel), *Chrysichthys nigrodigitatus* (Lacepede) (West Africa); *Anableps anableps* (L.) (Central America); *Jenynsia multidentata* (Jenyns) (S. America); Eleotridae and Mugilidae (global)
	• Euryhaline, able to tolerate both fresh and marine water phases • Usually confined to brackish part of the system		
Semi-anadromous estuarine guild	• Stenohaline and euryhaline species	• Stenohaline species may be adversely affected by increased river flows that convert the system to freshwater	*Hilsa*, Reeves shad many Eleotridae and Gobiidae (global); *Dormitator lebretonis* (Steindachner) (West Africa); this guild also includes many crustaceans of economic importance
	• Enter fresh/brackish water system to breed	• Excessive flows may carry adults and fry into excessively saline environments	
	• Enter freshwaters as larvae/juveniles to use the area as a nursery—either obligate or opportunistic	• Influenced negatively by river mouth dams that impound freshwater in the estuary and stop migration into the river	
Amphidromous guild	• Species that enter fresh or brackish waters to feed either as adults or as fry and juveniles	• Euryhaline species	*Dicentrachus*, *Polynemus*, *Monodactylus* (Asia); this guild also includes many crustaceans of economic importance

		• Excessive flows may eject adults and fry from the freshwater system	
Catadromous guild	• Feed in the freshwater environment, often penetrating far into freshwaters	• Affected by much the same conditions as affect the eupotamonic guilds and are threatened by interruptions to longitudinal connectivity and by changes to the hydrograph at times critical to migration. They are equally affected by adverse changes to the marine ecosystems	Anguilid eels (Africa); *Anguilla anguilla*. L. (Europe and N. America) and flounder (*Platichthys flesus* L.)
Marine guilds *Opportunistic marine fishes*	• Breed in the marine environment • Enter estuaries opportunistically		Bullsharks (*Carcharinus leucas*), sawfish (*Pristis pectinatus*), many skates and rays, as well as diverse bony fishes

Any activities that disturb the pool-riffle structure, such as seasonal desiccation of riffles, increases in sediment load that choke the interstitial spaces, erosion of gravel or complete submergence of the riffle will affect this group. Populations can be recovered by mitigative rehabilitation of rapids and the pool-riffle structures of the main channel, and/or sediment removal. This guild can also be affected by loss in longitudinal connectivity preventing anadromous species reaching these upstream spawning and nursery habitats. This loss can take the form of low flows (natural or artificial) restricting the ability of fish to negotiate obstructions (natural or artificial).

The larval and young forms of some migratory species (eupotamonic lithophilic guild) also inhabit riffle areas. Variations in this guild may occur resulting from the velocity and turbulence of the water, with larger species and individuals occurring where the river gradient lessens and the channel widens (see for example the structure of Schmutz *et al.*, 2000).

Pool guild. Species in this guild are slightly more limnophilic in habit and generally seek to inhabit the slack regions of back eddies where emergent and floating vegetation may occur. Other species inhabit the deeper waters. They tend to be insectivorous, feeding on the drift dislodged from the riffles or on insects falling into the river from riparian vegetation. They may be either limnophilic, breeding in the riffles, or phytophilic, attaching their eggs to vegetation. The various species inhabiting rhithronic pools usually have well defined home ranges, and appear to have defined habitats delimited by depth, current strength and the distribution of vegetation. As with the riffle guild, variations may occur resulting from the lessening gradient and widening of the channel.

These species are also disturbed by changes to the flow regime that desiccate the pools or leave them for long periods without flow so they become anoxic. They also generally rely on the delicate balance between pool and riffle of the rhithron and respond negatively to any influence that changes this balance. Again this guild can be affected by loss of longitudinal connectivity.

Guilds in potamonic communities

Lentic guilds. Lentic species are mainly floodplain residents that do not migrate but may move between floodplain pools, swamps dead arm backwaters and the inundated floodplain. They frequently are tolerant to low dissolved oxygen concentrations or even to complete anoxia. As such they may tolerate reduced water quality and even extreme eutrophication. They are generally repeat breeders that may breed at both high and low water phases of the hydrograph. They have specialized reproductive behaviour and have highly diverse reproductive strategies, including fish that are unselective about their spawning substrate (phytolithophils), nest builders, brood guarders or livebearers. In the Mekong these species are usually termed 'black fish' because of the dark colour of the various species in the guild (e.g., *Mastacembelus*, *Ophicephalus* and *Osphronemus spp.*). Such species are sometimes armoured, have prominent scutes or spines, or may be naked skinned. Many interspecific behavioural differences within the guild are associated with alternative strategies of response to lowered dissolved oxygen levels and the degree of isolation from the main channel.

Plesiopotamonic guild. This guild consists of species that are tolerant to reduced dissolved oxygen concentrations but cannot resist complete anoxia. They usually inhabit relatively well oxygenated water bodies that are regularly connected to the main river by flooding, where they may be found in open waters as well as in the riparian vegetation. Some species may also occupy riparian vegetation of still-water channels and canals. They are often sedentary but may show a limited amount of lateral migration that permits them to escape the worst of deoxygenated conditions. They include guarding and non-guarding phytophilic and nest building as well as the one ostracophilic species (*Rhodeus sericeus* (Pallas)).

Species in this guild tend to disappear when the floodplain is disconnected from the main channel and desiccated through poldering and levee construction. Limited populations may continue in riparian vegetation in the main channel or in backwaters whose upper end is silted. They may also increase in number in shallow, isolated wetlands, rice-fields and drainage ditches. The species may be recovered by reconnection of floodplain water bodies to the main channel or establishment of flow regimes that allow for seasonal filling of the floodplain lakes.

Paleopotamonic guild. This guild consists of species tolerant of complete anoxia that are found in isolated floodplain pools and wetlands. They are usually sedentary and sometimes show extremes of parental care with nest building and viviparity. In slightly modified systems they persist in residual floodplain water bodies isolated from the main river and may resist complete desiccation (xerophils). They may also survive in low numbers in deoxygenated backwaters and in marginal and floating vegetation, and form important components in rice field and ditch faunas. Some of these species have been used for intensive aquaculture because of the readiness with which they adapt to pond conditions and to extremely dense populations. The guild is impacted negatively by floodplain reclamation schemes that drain or fill the marginal waterbodies and wetlands in which component species live.

Annual guild. Species in this guild are found in seasonal water bodies that are completely dry during part of the year and are usually found at the outermost limits of the floodplain. The species are characterized by a dormant phase, usually with diapausing eggs that are able to survive prolonged drought. At the onset of flooding, or seasonal rains, the eggs hatch to produce fish that mature and lay eggs during the following wet phase, thus completing the life cycle within the year.

Lotic guilds. These are generally longitudinal migrants that move within the main river channel or up and down tributaries. They require relatively high dissolved oxygen levels and as such they are sensitive to reductions in water quality and many species have locally disappeared under eutrophic conditions. Most lotic guild species have one breeding season a year that is closely linked to peak flows and rely of increased flow as cues for migration and maturation. Species in this guild are usually termed white fish in Southeast Asia because of their light colour and reflective scales (e.g. *Cirrhinus* and other cyprinids). Different groups within the guild may be defined on the basis of reproductive behaviour and the degree of floodplain dependence.

Eupotamonic pelagophilic guild. This guild is composed of main channel residents that do not enter the floodplain. They are long distance, longitudinal migrants that breed in a single event annually and are predominantly lithopelagophils and some pelagophils. They have drifting eggs and larvae that may use backwaters or slacks downstream of point bars as nurseries. Some of the species in this guild are piscivorous, having complex migratory behaviour associated with movement patterns of their principal prey (see, e.g., Fuentes, 1998).

Species in this guild frequently are vulnerable to overexploitation and other human disturbances, and many have become locally extinct. They tend to disappear when their river is dammed and prevents migration, although they may respond favourably to fish passage facilities. They are also vulnerable to changes in the timing of high flow events that are inappropriate to their breeding seasonality. They may be affected if flow rates are excessive or too slow for the needs of drifting larvae. The species may be recovered by ensuring longitudinal connectivity by fish passage facilities or removal of cross channel dams, or by ensuring the timing and quantity of flows are adequate to promote breeding and ensure the arrival of fry at the adult habitats.

Eupotamonic lithophilic guild. Species in this guild are often longitudinal migrants, including many anadromous species. They differ from the eupotamonic pelagophilic species in that they are predominantly lithophils and psammophils with a single breeding season. They may be semelparous, having one breeding season only. Fry may be resident at upstream sites for a certain period and may occupy upstream floodplains (West Coast N. American salmonids).

These species are also vulnerable to damming and to lowered water quality that prevents migration, although they may respond favourably to appropriately designed fish passes. They are also adversely affected by changes in the timing of high flow events that are inappropriate to their breeding seasonality, as well as to changes in the quality of upstream breeding habitats, which may become choked with silt or have insufficient flow to aerate the developing eggs. The species may be recovered by ensuring longitudinal connectivity by fish passage facilities or removal of cross channel dams, or by ensuring the timing and quantity of flows are adequate to promote migration and ensure the development of eggs and larvae by providing aerating flows in the spawning gravels.

Eupotamonic phytophilic guild. Species in this guild are long distance or short distance longitudinal migrants that also undertake lateral migrations onto and off the floodplain, which they use for breeding, nursery grounds and feeding by juvenile and adult fish. Adult and juvenile populations may be found in floodplain lagoons as dry season residents. They are predominantly phytophils or phytolithophils, spawning at floodplain margins, in inflowing channels or on the floodplain itself. Eggs and larvae of some species are semi-pelagic and are carried onto the floodplain by passive drift with the rising flood.

Species in this guild tend to disappear or become greatly diminished in abundance when the river is dammed and prevents migration, or when access to the floodplain is denied to developing fry and juveniles because flow levels are inadequate to flood riparian lands or these are cut off by levees. The species may be recovered by ensuring longitudinal and lateral connectivity by fish passes, removal of cross channel dams or removal of lateral levees or by ensuring the timing and quantity of flows are adequate to ensure access to the floodplain.

Parapotamonic guild. Species in this guild may be termed semi-lotic in that their behaviour is intermediate between the long distance migrants of the other three lotic guilds and the lentic groupings. They are sometimes sedentary but also show semi-migratory behaviour. They include lithophils, phytophils, phytolithophils and psammophils. They prefer slow flowing anabranches of the main river or backwaters with low or seasonal flows. They can also use tributary creeks, blind backwaters or slacks downstream of point bars as breeding grounds and nurseries. The parapotamon is also used as a refuge for many rheophilic species during times of excessive main channel flow.

Species in this guild are usually fairly resistant to change and as such could be considered eurytopic (generalist). However, they are sensitive to river straightening and bank revetments that suppress main channel diversity and bank structure. Species can be recovered by rehabilitating main channel diversity, particularly by reconnection of abandoned side arms and active backwaters.

Eurytopic guilds. These are generalized and extremely adaptable species that are often tolerant of low dissolved oxygen concentrations. They are generally repeat breeders or may breed during both high and low flow phases of the hydrograph, as such breeding may be independent of flow clues. They may have either rheophilic or limnophilic characteristics. They are predominantly phytophils, phytolithophils, lithophils, or psammophils, but some species are nesters or parental carers. They may be short distance migrants (semi-migratory) often with sedentary, local populations. There is evidence (Bouvet *et al.*, 1985; Linfield, 1985), however, that some species at least have both mobile and static elements in their genome and are thus able to adapt to drastic changes in flow type. Differences in the guild lie in their location within the system.

Eupotamonic benthic guild. Many species in this guild are benthic and occupy the centre of the main channel. They are generally intolerant of lowered dissolved oxygen concentrations, although they may have to resist periodic lowering of oxygen tensions during the hot, dry season. They are able to adapt behaviourally to altered hydrographs, existing in a quasi-lacustrine condition and generally increase in number as other species decline. They are impacted negatively by modifications that change deposition–siltation processes and alter the nature of the substratum, and may also be sensitive to deoxygenated conditions in the deeper, refuge areas of the channel during the dry season. They are predominantly psammophils and lithophils.

Eupotamonic riparian guild. This guild occupies the riparian zone and particularly the vegetation of the main channel and floodplain waterbodies; and may move onto the floodplain to occupy similar habitats during flooding. Populations may have lateral migratory or semi-migratory components, with resident elements that become dominant in controlled conditions. These species usually tolerate low dissolved oxygen. They show a wide range of breeding behaviour but are predominantly phytophils although they also include species showing various degrees of nest building and parental care. They are able to adapt behaviourally to altered hydrographs, are extremely flexible and may adopt other habitats as river conditions change and generally increase in number as other species decline. This guild is especially well represented in most rivers. For example, in the Cinaruco River, Venezuela, almost half the 280 species can be found in shallow water littoral/shoreline habitats (Arrington and Winemiller, 2003).

Species in this guild are colonizers of regulated systems and often increase to pest levels following control of flooding and stabilization of river hydrographs, or declines in water quality through eutrophication.

The habits of this guild make them suitable for rearing in ponds and they have been widely distributed for aquaculture (Welcomme, 1988). Some species in this group, such as *Plagioscion squamossissimus* (Haekel) and *Cichla ocellaris* (Bloch & Schneider) (South America); small pelagic clupeids and cyprinids, *Cyprinus carpio* L. (domesticated form), *Oreochromis niloticus* L. and *Clarias gariepinus* (Burchell) (Africa); and certain *Lepomis* spp. (North America), form the basic colonizers when rivers are impounded and converted to reservoirs and dams.

Species in this guild may be affected negatively by changes in riparian structure that suppress vegetation.

Guilds in estuarine and coastal lagoon communities

Five main guilds dominate the estuarine portion of rivers (Quinn *et al.*, 1999). The lower reaches of many fluvial systems form coastal lagoons or brackish lagoon systems associated with marine deltas. The five guilds are distinguished by their responses to salinity. The species comprising the various guilds move with daily and seasonal changes in salinity and are sensitive to interventions, such as river mouth barrages or changes in the connectivity of lagoon systems with the sea and flow changes.

Freshwater estuarine guild. These are basically stenohaline, freshwater species that inhabit the lower reaches of rivers, although the guild may include some species that are able to breed in fresh and brackish waters. They generally breed and feed in fresh water but move up and down the estuarine system depending on flow and their tolerance to salinity. At times of high flow the species expand their range to occupy the estuary and coastal lagoon systems. In some areas, such as the Amazon, the freshwater plume allows freshwater species to penetrate far into the marine system. In freshwater seas, such as the Baltic and Black Seas, freshwater species are able to maintain extensive populations.

Species in this guild are affected negatively by reductions in flow that allow saline waters to penetrate upstream or to permanently occupy the lower estuary and lagoon systems.

Brackish water estuarine guild. A group of euryhaline species permanently inhabits the estuary and coastal lagoon system. These species breed and feed in the brackish water systems and are able to support a considerable range of salinities. They may, however, be displaced if the waterbody is converted to a permanent marine or freshwater environment by changes in flow or connectivity to the marine system.

Marine estuarine guilds. These guilds consist of marine species that may penetrate far into fresh waters. They may be stenohaline or euryhaline and differences between the guilds are based on the relative use they make of the marine and freshwater habitats.

Semi-anadromous estuarine guild. This group of species enters fresh or brackish water to breed or to use the lower reaches of the river as a nursery.

Amphidromous estuarine guild. This group of species enters the freshwater phase of the system to feed, often opportunistically.

Catadromous species. These species require a lower salinity residence phase in their development, or species that use estuaries as transit routes between the marine and freshwater environments, They are distinguished from semi-anadromous species by the greater dependence on the freshwater phase of their life cycle and by the greater distance they penetrate into freshwaters. These species are affected by much the same conditions as affect the eupotamonic guilds and are threatened by interruptions to longitudinal connectivity, although they may respond favourably to fish passes, and by changes to the hydrograph at times critical to migration. They are equally affected by adverse changes to the marine ecosystems.

Opportunistic marine guild. These are marine species that occur opportunistically in estuaries in small numbers, but are not dependent on these systems. This guild is largely unaffected by changes to the river.

CONCLUSIONS

The use of guilds to group fish species with similar patterns of habitat use is intended to provide indicators and predictors of response to changes in river hydrographs and to modification of geomorphology, habitat structure and ecological functions of river ecosystems. As such it conforms to the suggestion by Austen *et al.* (1994) that guilds function as 'super-species' in as far as their responses to flow and morphological changes are concerned. Although the scheme is not tested statistically here, some of the references we cite do, such as Aarts *et al.* (2004) and descriptions of species assemblage changes due to flow variations in poldered areas on the Bangladesh floodplain (Halls, 1998), changes in dominance of floodplain and river spawning guilds during the Sahelian drought (Dansoko *et al.*, 1976), and the failure of various anadromous and potamodrous migratory guilds in response to damming in many areas of the world. Furthermore the scheme may be applied retroactively to historical changes in river systems following changes in flow regime, such as the restoration of many eupotamonic lithophils and pelagophils in the Mun River, Thailand, after the gates of the Pak Mun dam were opened to allow flows during the breeding season of the fish (Jutagate *et al.*, 2005). The scheme is also well adapted to holistic environmental flow assessment framework methodologies such a DRIFT (Arthington *et al.*, 2003; King *et al.*, 2003) that rely on limited knowledge and expert opinion rather than detailed local study. Assessment may lead to positive outcomes where understanding of fish guild responses can guide river rehabilitation and restoration projects as well as releases of water for environmental maintenance. Negative impacts of the effects of river modification activities, such as dam building, river training and flow regulation, on the various guilds can also be assessed. Other changes may be less accessible to the application of guild classifications. For example the transition from forested to Savannah River conditions is accompanied by an increase in insolation that increases the productivity of the system. This may involve guild independent changes in populations in that many of the smaller, obligate species inhabiting floodplains, pools and small streams in forested rivers may be lost, such as *Pantodon* buccholzii (Peters)i, nandidae and cichlids (Africa); *Hephysobrycon* and many other small, ornament characins and cichlids (Latin America), barbs and loaches (African and South East Asia) and cyprinodonts (tropical). Similarly, the possibility of competition and predation within guilds remarked on by Simberloff and Davan (1991) and Austen *et al.* (1994) is evidenced by examples such as the interactions between *Salminus* and *Prochilodus* larvae in the drift for the channel pelagophilic guild in the Uruguay river (Fuentes, 1998) or the devastating impact of a few *Hoplias* on the other fish of isolated Orinoco lagoons.

With the large numbers of species that are present in many systems and the flexibility of intra-specific behaviour, it is sometimes difficult to assign species among guilds. In some instances, the same species could be considered a member of more than one guild. This is especially likely with eurytopic (grey) fishes, and the opportunistic species that inhabit floodplain rivers in arid and semi-arid regions of Australia (Arthington *et al.*, 2005). For example, the Prussian carp, *Carassius carrasius* L., may exist as two forms—long or deep bodied—each of which behaves in a different manner (Balon, 2004). It is this difference of behaviour that confers the flexibility that characterizes some of these species in the eurytopic group. In these circumstances, local knowledge of the life history traits may prove useful for allocation of a species to a guild and for identification of the environmental guilds of species about which little is known. Some river habitats are important for more than one guild. The floodplain is of significance for many lotic, lentic and eurytopic groupings and in some arid-zone rivers all species may use the main channel, backwaters, anabranches and the inundated floodplain at various stages of the hydrograph and life cycle (Arthington *et al.*, 2005). Similarly, habitat diversity is important in the main channel, as species in several guilds use backwaters and blind arms either as primary habitat or to compensate for losses of their preferred floodplain habitats

Such flexibility of behaviour is necessary in fishes that occupy systems that have high inter-annual variability in environmental characteristics such as rivers of arid and semi-arid regions (Puckridge *et al.*, 2000; Arthington *et al.*, 2005. In some cases this flexibility emerges at the species level. For example, in the Niger River several genera have main channel and floodplain forms whose relative dominance varies according the flood regime in any particular year (Dansoko *et al.*, 1976; Lae, 1992). In other fish faunas, this flexibility is apparently expressed within a single species at genetic level where both migratory and static components exist in the population, e.g. *Salmo trutta*. This explains the behaviour of fish such as roach, *Rutilus Rutilus* L., that were classified as semi-migrants in pristine Ponto-Caspian rivers, but which have adapted readily to life in static water canals and regulated rivers. Such changes may correspond to genetic shifts experienced by domesticated species, reared in aquaculture facilities and used to stock rivers and lakes described by Utter (2001, 2002). It is perhaps significant that such species show evidence of re-establishing migratory populations when the occasion arises, and this confers with the recent isolation of genes that control migration in salmonids (Utter, 2001, 2002).

Despite the flexibility of behaviour exhibited by some species, a general classification of fish response to changing hydrology and river form is possible and advantageous for the assessment of the impacts of projects that influence these factors. The classification system offered here is based on a preliminary synthesis of knowledge of fish behaviour in tropical and temperate rivers, with comment on fishes from semi-arid and arid zone rivers. It is hierarchical in the sense that the more generalized lentic, lotic and eurytopic guilds can be subdivided into subordinate groupings and these, in turn, may be further sub-divided. Based on detailed patterns of habitat use, species may be assigned to habitat guilds at finer scales of spatial resolution (see, e.g., Orth and Leonard, 1988[Q8]). The species cited here are intended as simple examples, and many fish faunas could be classified into guilds in this manner based on currently available information. The trade-off is that more-detailed guild classifications require a much greater amount of time and effort to derive predictions useful for assessment of instream flow requirements. Q8

A general scheme, such as the one proposed, could be more easily and rapidly applied to a wide variety of local circumstance, as well as to the description of the general trends in fish population and assemblage structure expected to occur during river development and flow regulation. It can also be used to illustrate to policy makers the consequences on biodiversity of decisions they make on the allocation of water and the modification of fluvial ecosystems.

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