The guild approach to categorizing estuarine fish assemblages: a global review

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Abstract

Many studies have recently described and interpreted the community structure and function of fishes inhabiting estuaries and other transitional waters in terms of categories or guilds. The latter describe the main features of the fishes' biology and the way in which they use an estuary. However, the approach has been developed by different workers in different geographical areas and with differing emphasis such that there is now a need to review the guilds proposed and used worldwide. The previous wide use of the guild approach has involved increasing overlap and/or confusion between different studies, which therefore increases the need for standardization while at the same time providing the opportunity to reconsider the types and their use worldwide. Against a conceptual model of the importance of the main features of fish use in estuaries and other transitional waters, this review further develops the guild approach to community classification of fish communities inhabiting those areas. The approach increases the understanding of the use of estuaries by fishes, their interactions and connectivity with adjacent areas (the open sea, coastal zone and freshwater catchments) and the estuarine resources required by fishes. This paper gives a global perspective on this categorization by presenting new or refined definitions for the categories, lists the synonyms from the literature and illustrates the concepts using examples from geographical areas covering north and central America, north and southern Europe, central and southern Africa, Australia and the Indo-Pacific.

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Introduction

The description and classification of biological communities usually uses one or more of three sets of attributes: first, and most commonly, are taxonomic-based entities, as summarized by traditional species/site/abundance matrices; secondly, on the size and biomass spectra of the individuals present and thirdly, on the functional attributes of the recorded organisms (Nagelkerken and van der Velde 2004; Akin *et al.* 2005). When used in combination, these attributes give a large amount of information about the structure and functioning of communities. While it is valuable to compare communities within small geographical areas based on taxonomic identities, it is less valuable for comparing communities across biogeographic regions, and hence for determining common features of community functioning within- and between-habitats and ecosystems.

The fish communities inhabiting estuaries have been studied worldwide and there have been several attempts to indicate the common features of those communities (Yáñez-Arancibia *et al.* 1980, 1988; Whitfield 1990, 2005; Blaber 1991, 2000; Potter and Hyndes 1999; Elliott and Hemingway 2002). In addition to supporting their own resident fish community, estuaries are nursery grounds, migration routes and refuge areas for a variety of fish species (Whitfield 1990, 1998; Blaber 1997; Potter and Hyndes 1999; McLusky and Elliott 2004). Given the increasing wealth of data, it is now possible to start determining similarities and differences between biogeographical areas and thus to examine the features of estuarine fish community structure on a global basis (Potter and Hyndes 1999; Whitfield 1999).

This type of information on estuarine fish community structure and functioning is important for an understanding of the biological features of estuaries, but it is becoming increasingly important to classify and categorize those estuarine faunae as an aid to the understanding and management of the effects of human activities in estuaries (Whitfield and Elliott 2002; McLusky and Elliott 2004). For example, the Water Framework Directive presently being implemented in Europe (Apitz *et al.* 2006; Breine *et al.* 2007; Coates *et al.* 2007), the National Land and Water Resources Audit in Australia (Heap *et al.* 2001), the Clean Water Act in the US (United States Environmental Protection Agency 2002) and the 1998 Water Act in South Africa (Adams *et al.*

2002) all rely on an ability to detect a change in estuarine faunae from a defined reference condition. Furthermore, the responses to natural and anthropogenic stressors need to be identified (Greenwood *et al.* 2006). Within each of these initiatives, biologists have been given the task of defining which attributes are used in assessing that degree of change. Hence, there is an increasing demand to devise classification schemes which indicate the structure and functioning of biological communities, to determine their departure from reference conditions and to implement management plans to ensure maintenance and recovery of communities affected by human activities (Whitfield and Elliott 2002; McLusky and Elliott 2004).

Many studies have dealt with the taxonomic entities within estuaries, i.e. the species composition of fish communities and their seasonal and spatial variation (Nordlie 1979, 2003; Yáñez-Arancibia *et al.* 1980, 1988; Marshall and Elliott 1996, 1998; Potter *et al.* 1997; Blaber 2000; Albaret *et al.* 2004; Ecoutin *et al.* 2005). More recently, studies have concentrated on a functional analysis of community structure in which the species present are assigned to groupings or guilds, each of which denotes certain attributes. Root (1967) defined a guild as a group of species that exploit the same class of environmental resources in a similar way. Albaret (1999) used bio-ecological categories, essentially guilds, to define and compare the fundamental estuarine fish community. Hence, guilds have been used to provide information on functioning, hierarchical structure and connectivity and to simplify complex ecosystems (Elliott and Dewailly 1995; Albaret 1999; Garrison and Link 2000; Lobry *et al.* 2003; Franco *et al.* 2006). Several authors (Claridge *et al.* 1986; Potter and Hyndes 1999; Thiel *et al.* 2003) have used the term life cycle categories to describe natural groupings of species based primarily on reproductive strategies and the different habitats occupied at different stages of their life cycle. Bond *et al.* (1999), Nagelkerken and van der Velde (2004) and Akin *et al.* (2005) have applied similar groupings to the quantitative functional analysis of marine habitats, whereas Maes *et al.* (2004) incorporated the guilds in a statistical and modelling analysis of estuarine fish community structure. These approaches bear some similarity to that undertaken for freshwater fish assemblages by Welcomme *et al.* (2006), which also indicate the connectivity with estuarine fish faunae. The latter authors present their guilds for freshwater fishes

and use a salinity-based classification for freshwater-dominated estuarine systems.

The concept of guilds was first developed for fishes inhabiting estuaries in the early classical works by McHugh (1967), Perkins (1974), Wallace and van der Elst (1975) and Haedrich (1983), which separated the components of the estuarine nekton into ecological groupings. The concept was also used by de Sylva (1975), who defined groupings of estuarine fishes based on their feeding preferences and food web structure. This type of analysis was then extended to include descriptions of the migration, feeding, reproduction and habitat preferences of species (Potter *et al.* 1990; Elliott and Dewailly 1995; Potter and Hyndes 1999). Consequently, the approach to classifying fish into guilds/categories in terms of the way they use estuaries has now been attempted worldwide for many individual biogeographic areas and types of estuaries and using a variety of terms. The approach adopted by the present authors and associates over the last 25 years for this type of classification of species in European, American, Australian and African estuaries has essentially been the same or a development of that of Cronin and Mansueti (1971), the latter undertaking being one of the first attempts to categorize estuary-associated fishes according to the characteristics of their life cycle.

This paper presents a classification scheme that is a logical extension of previous conceptual models and which focuses especially on a revision and standardization of previous categorizations. As such, this review is necessary in drawing out those cases where the classification of a particular guild has to be adapted to meet differences between the ichthyofaunae in very different regions (e.g. temperate vs. tropical) or where new information necessitates a revision of previous categories (e.g. where certain estuarine gobies have been discovered to have marine larval phases). The present treatment therefore fully acknowledges the systematic development of estuary-associated fish guild terminology and thus proposes a revision around the foundations that have already been laid. Our approach is aimed at incorporating recent research on the life cycles of fishes in estuaries, thus increasing our understanding of estuarine functioning and informing management strategies for these valuable ecosystems.

The present authors have collectively been involved in many studies of fishes in estuaries in different geographical areas, and take the view that the guild approach presents an opportunity to compare and contrast estuarine and other transitional habitats worldwide. In this way, an understanding of the features of estuarine fish communities central to the functioning of estuaries can be determined. Despite this, several variations of estuarine fish guilds have been given by the present and other authors, and hence there is a need to consider the nature of the categories, their synonyms and areas of confusion, and thus rectify any discrepancies. The present paper therefore aims to bring together the views of the authors to propose a set of guilds which may be used worldwide in estuarine areas. The use of similar terms, but with different definitions, is not conducive to attempting to understand the structure and functioning of estuarine fish communities on a worldwide basis and hence there is a need for an agreed set of terms. It is emphasized that while this is the collective opinion of the present authors, the guild definitions indicated here are the result of extensive discussions with estuarine fish biologists worldwide whose help and advice is gratefully acknowledged.

Within the present context, it is acknowledged that there is not a single and suitable definition which covers all types of estuaries worldwide (for further discussion see Day 1980; Elliott and McLusky 2002; Ray 2005; McLusky and Elliott 2004, 2007). Ray (2005) discusses the value of estuaries without defining them, other than to say that they are transitional systems, although he did illustrate the different types of estuaries. Hence, the present authors take the pragmatic view that a water body is an estuary when experts regard it as such, and thus it is an accepted geographical, hydrodynamic and biological term. Within Europe, under the implementation of the Water Framework Directive, the term 'transitional water bodies' is now being used to include the various types of estuaries (open and closed, positive and negative), deltas, rias, fjords, fjards, and coastal and brackish lagoons. Hence, for the present discussion, it is necessary and useful to take a pragmatic approach and accept the term transitional waters for all intermediate habitats under the influence of both freshwater and marine systems. The discussion here relates to those transitional waters worldwide that are usually located within the coastal zone but note that transitional waters also apply to the estuarine plume which may extend a considerable distance away from the coast (Ketchum 1983). At the other end of the continuum, we take the view that

estuaries and transitional waters also include fresh-water tidal areas, i.e. those places where although there is no saline influence and the tidal water movement occurs through hydrostatic changes further down the estuary (McLusky and Elliott 2007). Such tidal freshwater areas are likely to be either at or upstream of turbidity maximum areas and also upstream of the freshwater–seawater interface, both areas of high importance in habitat use by fishes in estuaries.

While there are many options for functional guilds, such as one for habitat preference and another relating to position inhabited within the water column (Elliott and Dewailly 1995), the present paper proposes and concentrates on three groups of functional guilds, viz. the Estuarine Use Functional Group (EUFG) which defines the overall ecological use of an estuary by a given species (Table 1); the Feeding Mode Functional Group (FMFG) which defines the primary method of feeding used by a given species (Table 2) and the Reproductive Mode Functional Group which indicates how and, in some cases, where an estuarine species reproduces (Table 3). Within each of these major categories, subcategories have been defined and, where possible, examples are given which illustrate the use of that mode by fishes in cool temperate, warm temperate, subtropical and tropical estuarine areas. In this way, the approach is used to show the similarities worldwide in estuarine fish faunal community structure despite the different taxa encountered. As an aid to the future numerical analysis of the groups, and in line with previous uses of this approach, each subcategory has been assigned an identifier code (given in Tables 1–3). Furthermore, the tables giving the definitions of the guilds proposed here also include synonyms used in the literature by ourselves and other authors.

In previous uses of the guild approach, species were assigned within a local or regional geographical context (Wallace and van der Elst 1975; Potter and Hyndes 1999; Albaret *et al.* 2004). However, recent research indicates that certain fish species may have different life history styles in different biogeographic regions, e.g. the cosmopolitan flat-head mullet (*Mugil cephalus*, Mugilidae) may be catadromous in one region, an estuarine migrant in another and marine in a third. Despite this anomaly, there is a need to unify the terms for use across geographical boundaries. A preliminary attempt at such a global classification was undertaken by

Whitfield (1999) but was limited to an EUFG categorization.

It is emphasized that, where possible, a detailed knowledge of the biology of a species is required and used to place it within a guild. However, where there is no published knowledge it is necessary to use best-judgement or unpublished data on a species' biology, to place a species in a guild. As indicated in the appended reference list, the present authors and their collaborators have a background knowledge of the biology of many fish species within their areas. Under the present development of these categories, it has not been considered necessary to include a catch-all category (i.e. for species which cannot be assigned) although the future use of such an approach may require this in cases where the biology and habits of a species are unknown, as is likely to be the case for rare species.

Estuarine Use Functional Group

Estuaries have well-defined roles as nursery and feeding areas, areas of refuge and migration routes, and these fundamental properties of estuaries have been shown worldwide, e.g. for North America by Haedrich (1983), Nordlie (1979, 2003) and Able (2005); the tropical Indo-Pacific by Blaber (2000); European areas by Elliott and Hemingway (2002); tropical Africa by Albaret (1999) and Albaret *et al.* (2004); temperate and subtropical Australia by Potter and Hyndes (1999), and subtropical and temperate southern Africa by Whitfield (1999). The seasonal and spatial occurrence of species and their biological attributes are well-known (Claridge *et al.* 1985, 1986) such that species can be assigned to guilds, which denote the primary estuarine use made by different species (Table 1, Fig. 1). These terms have been widely used (see Whitfield 1999 for a preliminary review) but have been revised here to allow for more recent information and account for the subtle differences worldwide. The revisions indicate the short- and long-term migration patterns, the physiological adaptations required to occupy estuarine areas and the multifaceted use made of these areas by estuary-associated fish species.

The selected categories cover all of the dominant groups of fishes found in estuaries, as well as describing the links between the estuary and areas downstream (along the coast and in the open sea) and upstream (into freshwaters) of the estuarine environment. Potter *et al.* (2001) indicated the

Table 1 Estuarine Use Functional Group.

Term	Definition	Synonyms	Examples	
			Cool/warm temperate	Subtropical/tropical
Marine stragglers (MS)	Species that spawn at sea and typically enter estuaries only in low numbers and occur most frequently in the lower reaches where salinities are approximately 35 PSU. These species are often stenohaline and associated with coastal marine waters	Marine adventitious, marine visitors, marine transients, marine occasional species	Western school sillago (*Sillago bassensis*, Sillaginidae), Blue runner (*Caranx crysos*, Carangidae), Whiting (*Merlangius merlangus*, Gadidae), Striped seabream (*Lithognathus mormyrus*, Sparidae), Zebra seabream (*Diplodus cervinus*, Sparidae)	Spanish mackerel (*Scomberomorus maculatus*, Scombridae), Bengal sergeant (*Abudefduf bengalensis*, Pomacentridae), Colorado snapper (*Lutjanus colorado*, Lutjanidae), Concertina fish (*Drepane longimanus*, Drepanidae), Atlantic tripletail (*Lobotes surinamensis*, Lobotidae)
Marine migrants (MM)	Species that spawn at sea and often enter estuaries in large numbers and particularly as juveniles. Some of these species are highly euryhaline and move throughout the full length of the estuary. This category can be subdivided into: 1. Marine estuarine-opportunist (MMO): marine species that regularly enter estuaries in substantial numbers, particularly as juveniles, but use, to varying degrees, nearshore marine waters as an alternative habitat 2. Marine estuarine dependent (MMD): marine species that require sheltered estuarine habitats as juveniles but live along coasts where there are no such habitats and these species are thus dependent on the habitats of that type that are present in estuaries)	Marine estuarine-opportunists, marine estuarine dependents, marine seasonal, marine juveniles, marine immigrants, estuarine species of marine origin, marine estuarine species, marine species accessory in estuaries	Atlantic herring (*Clupea harengus*, Clupeidae), European seabass (*Dicentrarchus labrax*, Moronidae), Atlantic menhaden (*Brevoortia tyrannus*, Clupeidae), Thinlip mullet (*Liza ramada*, Mugilidae), Cape stumpnose (*Rhabdosargus holubi*, Sparidae), Spotted sillago (*Sillaginodes punctatus*, Sillaginidae), Weeping toado (*Torquigener pleurogramma*, Tetraodontidae), Yellow-eye mullet (*Aldrichetta fosteri*, Mugilidae), Bluefish (*Pomatomus saltatrix*, Pomatomidae), Leerfish (*Lichia amia*, Carangidae)	Mangrove red snapper (*Lutjanus argentimaculatus*, Lutjanidae), Tenpounder (*Elops machnata*, Elopidae), Giant trevally (*Caranx ignobilis*, Carangidae), Japanese meagre (*Argyrosomus japonicus*, Sciaenidae), Milkfish (*Chanos chanos*, Chanidae), Largescale mullet (*Liza macrolepis*, Mugilidae), Smallspotted grunter (*Pomadasys commersonnii*, Haemulidae), Goldlined seabream (*Rhabdosargus sarba*, Sparidae), Longarm mullet (*Valamugil cunnesius*, Mugilidae), Jenny mojarra (*Eucinostomus gula*, Gerreidae)

Table 1 Continued.

			Examples	
Term	Definition	Synonyms	Cool/warm temperate	Subtropical/tropical
Estuarine species (ES)	This category can be subdivided into: 1. Estuarine residents (ER): estuarine species capable of completing their entire life cycle within the estuarine environment. 2. Estuarine migrants (EM): Estuarine species that have larval stages of their life cycle completed outside the estuary or are also represented by discrete marine or freshwater populations	Estuarine, estuarine residents, estuarine migrants, strictly estuarine species	Common goby (*Pomatoschistus microps*, Gobiidae), Atlantic silverside (*Menidia menidia*, Atherinopsidae), Gilchrist's round herring (*Gilchristella aestuaria*, Clupeidae), Black bream (*Acanthopagrus butcheri*, Sparidae), Wallace's hardyhead (*Leptatherina wallacei*, Atherinidae), Swan River goby (*Pseudogobius olorum*, Gobiidae), Estuarine pipefish (*Syngnathus watermeyeri*, Syngnathidae)	Commerson's glassy (*Ambassis ambassis*, Ambassidae), Cooman's grenadier anchovy (*Coilia coomansi*, Engraulidae), Celebes goby (*Glossogobius celebius*, Gobiidae), River goby (*Glossogobius callidus*, Gobiidae), Indo-Pacific tropical sandgoby (*Favonigobius reichei*, Gobiidae), Dusky sleeper (*Eleotris fusca*, Eleotridae)
Anadromous (AN)	Species that undergo their greatest growth at sea and which, prior to the attainment of maturity, migrate into rivers where spawning subsequently occurs		Chinook salmon (*Oncorhynchus tshawytscha*, Salmonidae), Pouched lamprey (*Geotria australis*, Petromyzontidae), Allis shad (*Alosa alosa*, Clupeidae)	Hilsa shad (*Tenualosa ilisha*, Clupeidae), Chacunda gizzard shad (*Anodontostoma chacunda*, Clupeidae)
Semi-anadromous (SA)	Species whose spawning run from the sea extends only as far as the upper estuary rather than going into freshwater		Western Australian gizzard shad (*Nematalosa vlaminghi*, Clupeidae)	Toli shad (*Tenualosa toli*, Clupeidae)
Catadromous (CA)	Species that spend all of their trophic life in freshwater and which subsequently migrate out to sea to spawn		European eel (*Anguilla anguilla*, Anguillidae), American eel (*Anguilla rostrata*, Anguillidae)	African longfin eel (*Anguilla mossambica*, Anguillidae), Indian short-finned eel (*Anguilla bicolor pacifica*, Anguillidae) Barramundi (*Lates calcarifer*, Latidae)
Semi-catadromous (SC)	Species whose spawning run extends only to estuarine areas rather than the marine environment			
Amphidromous (AM)	Species which migrate between the sea and freshwater and in which the migration in neither direction is related to reproduction		Bay anchovy (*Anchoa mitchilli*, Engraulidae)	Fat sleeper (*Dormitator maculatus*, Eleotridae), Blacktip sardinella (*Sardinella melanura*, Clupeidae)

Table 1 Continued.

Term	Definition	Synonyms	Examples	
			Cool/warm temperate	Subtropical/tropical
Freshwater migrants (FM)	Freshwater species found regularly and in moderate numbers in estuaries and whose distribution can extend beyond the oligohaline sections of these systems	Freshwater species, freshwater immigrants, estuarine species of freshwater origin, freshwater species with estuarine affinities	Three-spined Stickleback (*Gasterosteus aculeatus*, Gasterosteidae), American gizzard shad (*Dorosoma cepedianum*, Clupeidae)	Mozambique tilapia (*Oreochromis mossambicus*, Cichlidae), Neotropical silverside (*Atherinella chagresi*, Atherinopsidae)
Freshwater stragglers (FS)	Freshwater species found in low numbers in estuaries and whose distribution is usually limited to the low salinity, upper reaches of estuaries	Freshwater species, freshwater species occasional in estuaries	Least killifish (*Heterandria formosa*, Poeciliidae), Northern pike (*Esox lucius*, Esocidae)	North African catfish (*Clarias gariepinus*, Clariidae), Redbreast tilapia (*Tilapia rendalli*, Cichlidae)

quantitative links between marine and estuarine areas and the importance of connectivity. Since connectivity has been the subject of recent articles by Able (2005) and Ray (2005), it is not discussed in further detail here. As expected, much of the estuarine fish community originates from marine areas and the guild approach reflects this. This approach has previously taken several different forms, for example, the bio-ecological categories defined by Albaret (1999) for tropical African estuaries and lagoons distributed according to two gradients based on the group of strictly estuarine species. These gradients, of species of marine affinity and species of freshwater affinity, indicate the sources of the species inhabiting the estuary and thus indicate the influence of natural and anthropogenic influences external to the estuary, e.g. damming of freshwaters affecting those estuarine species with freshwater affinity (Chícharo and Chícharo 2006).

Some marine and freshwater species have a well-defined and regular use of estuaries, whether for seasonal migrations, nursery or feeding migrations, reproductive migrations through the estuary or the use of the estuary as a refuge. However, other marine and freshwater species occur 'occasionally' (Albaret 1999) or 'adventitiously' (Elliott and Hemingway 2002), terms previously used to denote an almost accidental or at best an unexplained and infrequent use of estuaries. The term 'stragglers' has been used for fish in both Northern and Southern Hemisphere estuaries (Claridge *et al.* 1986; Potter *et al.* 1990) and is preferred here to denote a low-level and almost accidental introduction by species from either coastal or freshwater areas and for species that are often predominantly stenohaline or freshwater in their tolerances. Hence, these guild categories frequently relate to salinity tolerances of the species, thus reflecting the physiologically stressful nature of transitional waters. The majority of stragglers are thus restricted to the ends of the salinity continuum (seawater or freshwater) and generally occupy an estuary for only very short periods of time and in limited areas (Fig. 1a,b). In contrast, those fish taxa with euryoecious tolerances (i.e. wide tolerances to several environmental variables), especially euryhaline characteristics, are best adapted to an estuarine existence. Both estuarine resident and marine migrant species are euryoecious and have the ability to tolerate the spatially and temporally widely varying conditions found within estuaries. This feature was shown by

Table 2 Feeding Mode Functional Group (FMFG).

Category	Definition	Examples	
		Cool/warm temperate	Subtropical/tropical
Zooplanktivore (ZP)	Feeding predominantly on zooplankton (e.g. hydroids, planktonic crustaceans, fish eggs/larvae)	European sprat (*Sprattus sprattus*, Clupeidae), Australian anchovy (*Engraulis australis*, Engraulidae), Gilchrist's round herring (*Gilchristella aestuaria*, Clupeidae)	Toli shad (*Tenualosa toli*, Clupeidae), Orangemouth glassnose (*Thryssa vitrirostris*, Engraulidae), Kelee shad (*Hilsa kelee*, Clupeidae)
Detritivore (DV)	Feeding predominantly on detritus and/or microphytobenthos	White mullet (*Mugil curema*, Mugilidae), South African mullet (*Liza richardsonii*, Mugilidae)	Flathead mullet (*Mugil cephalus*, Mugilidae), Mozambique tilapia (*Oreochromis mossambicus*, Cichlidae)
Herbivore (HV): herbivore-phytoplankton (HV-P), herbivore- macroalgae/macrophytes (HV-M)	Grazing predominantly on living macroalgal and macrophyte material or phytoplankton	Southern sea garfish (*Hyporhamphus melanochir*, Hemiramphidae)	Redbreast tilapia (*Tilapia rendalli*, Cichlidae)
Omnivore (OV)	Feeding predominantly on filamentous algae, macrophytes, periphyton, epifauna and infauna	White seabream (*Diplodus sargus*, Sparidae), Cape stumpnose (*Rhabdosargus holubi*, Sparidae), Cape halfbeak (*Hyporhamphus capensis*, Hemiramphidae)	Milkfish (*Chanos chanos*, Chanidae), Northern snubnose garfish (*Arrhamphus sclerolepis*, Hemiramphidae), Vermiculated spinefoot (*Siganus vermiculatus*, Siganidae)
Piscivore (PV)	Feeding predominantly on finfish but may include large nektonic invertebrates	Japanese meagre (*Argyrosomus japonicus*, Sciaenidae), Leerfish (*Lichia amia*, Carangidae), Bluefish (*Pomatomus saltatrix*, Pomatomidae)	Pickhandle barracuda (*Sphyraena jello*, Sphyraenidae), Bigeye trevally (*Caranx sexfasciatus*, Carangidae), Talang queenfish (*Scomberoides commersoniannus*, Scombridae)
Zoobenthivore (ZB): zoobenthivore- hyperbenthos (ZB-H), zoobenthivore-epifauna (ZB-E), zoobenthivore-infauna (ZB-I)	Feeding predominantly on invertebrates associated with the substratum, including animals that live just above the sediment (hyperbenthos), on the sediment (epifauna) or in the sediment (infauna)	European plaice (*Platichthys flesus*, Pleuronectidae), Cobbler (*Cnidoglanis macrocephalus*, Plotosidae), Spotted sillago (*Sillaginodes punctata*, Sillaginidae), Atlantic cod (*Gadus morhua*, Gadidae), Yank flathead (*Platycephalus speculator*, Platycephalidae)	Surf bream (*Acanthopagrus australis*, Sparidae), Smallspotted grunter (*Pomadasys commersonnii*, Haemulidae), Javelin grunter (*Pomadasys kaakan*, Haemulidae), Red Drum (*Sciaenops ocellatus*, Sciaenidae), Bay anchovy (*Anchoa mitchilli*, Engraulidae)
Miscellaneous/opportunist (OP)	Feeding on such a diverse range of food that it cannot be readily assigned to one of the above specialized FMFG	Flounder (*Platichthys flesus*, Pleuronectidae), Southern black bream (*Acanthopagrus butcheri*, Sparidae), Yellowtail trumpeter (*Amniataba caudavittata*, Terapontidae)	Sheepshead minnow (*Cyprinodon variegatus*, Cyprinodontidae), Silver croaker (*Bairdiella chrysoura*, Sciaenidae), Jarbua terapon (*Terapon jarbua*, Terapontidae)

Table 3 Reproductive Mode Functional Group.

Term	Subterm	Definition	Examples	
			Cool/warm temperate	Subtropical/tropical
Viviparous (V)		Species in which the female produces live progeny	Viviparous blenny (*Zoarces viviparus*, Zoarcidae), Super klipfish (*Clinus superciliosus*, Clinidae)	Mosquitofish (*Gambusia affinis*, Poeciliidae), Bull shark (*Carcharhinus leucas*, Carcharhinidae)
Ovoviviparous (W)		Species producing an egg case in which the young develop	Piked dogfish (*Squalus acanthias*, Squalidae)	Common eagle ray (*Myliobatus Aquila*, Myliobatidae)
Oviparous (O)		Producing eggs that are liberated into the surrounding waters. The species in this group can be subdivided into the following five categories		
	Op	Species producing pelagic eggs	Flounder (*Platichthys flesus*, Pleuronectidae), White mullet (*Mugil curema*, Mugilidae), Bluefish (*Pomatomus saltatrix*, Pomatomidae)	Flathead mullet (*Mugil cephalus*, Mugilidae), Hilsa shad (*Tenualosa ilisha*, Clupeidae), Goldlined seabream (*Rhabdosargus sarba*, Sparidae)
	Ob	Species that produce eggs which settle on the substratum	European smelt (*Osmerus eperlanus*, Osmeridae), American shad (*Alosa sapidissima*, Clupeidae)	Australian river gizzard shad (*Nematalosa erebi*, Clupeidae), Tropical silverside (*Atherinomorus duodecimalis*, Atherinidae)
	Ov	Species that produce adhesive eggs that become attached to substrata and/or vegetation	Striped seasnail (*Liparis liparis*, Liparidae), Inland silverside (*Menidia beryllina*, Atherinopsidae), Knysna sandgoby (*Psammogobius knysnaensis*, Gobiidae)	Burrowing goby (*Croilia mossambica*, Gobiidae), Cape silverside (*Atherina breviceps*, Atherinidae), Topsmelt silverside (*Atherinops affinis*, Atherinopsidae)
	Og	Species in which one or the other parent guards their eggs externally, e.g. in a nest	Common goby (*Pomatoschistus microps*, Gobiidae), Three-spined Stickleback (*Gasterosteus aculeatus*, Gasterosteidae)	Mozambique tilapia (*Oreochromis mossambicus*, Cichlidae), Barred mudskipper (*Periophthalmus argentilineatus*, Gobiidae)
	Os	Species that shed their eggs and then protect them for a period in a part of their body, e.g. brood pouch or mouth, where they develop into a post-larva or juvenile and then released into the surrounding waters	Nilsson's pipefish (*Syngnathus rostellatus*, Syngnathidae), Hardhead sea catfish (*Ariopsis felis*, Ariidae), White baggar (*Galeichthys feliceps*, Ariidae)	Belly pipefish (*Hippichthys heptagonus*, Syngnathidae), Bellybarred pipefish (*Hippichthys spicifer*, Syngnathidae), Blue-spotted pipefish (*Hippichthys cynospilos*, Syngnathidae)
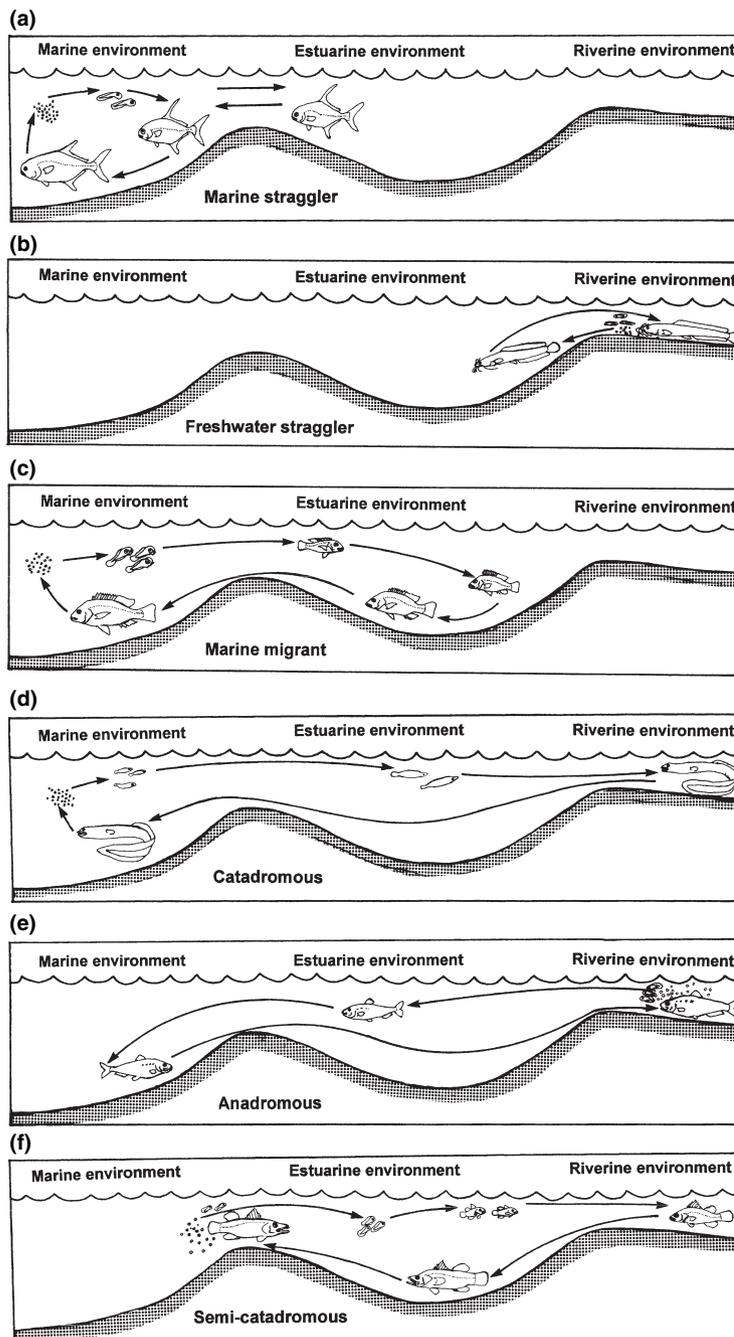
Figure 1 Life cycle categories of estuarine fishes: (a) marine straggler; (b) freshwater straggler; (c) marine migrant; (d) catadromous; (e) anadromous; (f) semi-catadromous; (g) semi-anadromous; (h) amphidromous; (i) freshwater migrant; (j) estuarine resident; (k) estuarine migrant.

the multivariate analysis of salinity tolerances amongst estuarine fishes carried out by Bulger *et al.* (1993), where estuarine salinity regions were defined according to their biological characteristics. In that analysis, many estuarine species were shown to have a wide salinity tolerance such that salinity regions in estuaries were overlapping in distribution.

In the present synthesis, the convention has been adopted whereby the first part of the guild title denotes the original source of the species. For example, a marine migrant originates in the fully saline area, whereas a freshwater straggler has come into the estuary from upstream. The term marine migrant is used in preference to marine immigrant as the latter is taken to imply a permanent residency
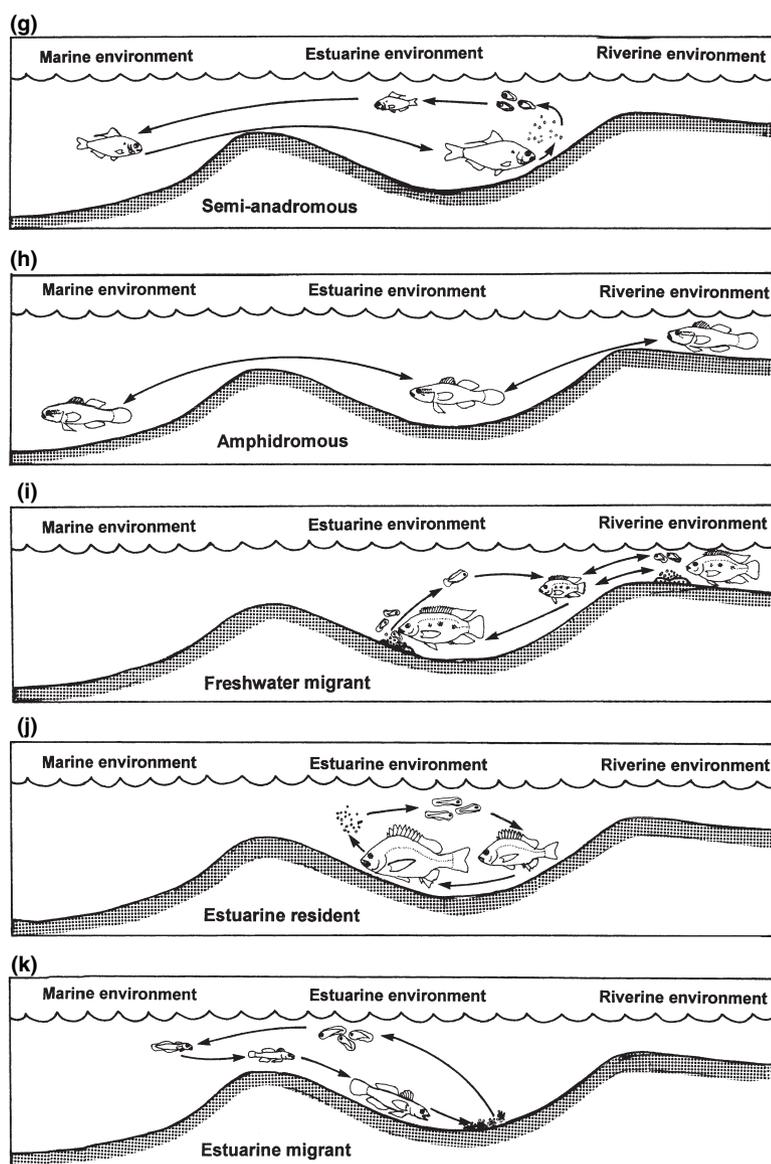
Figure 1 (*Continued*).

after migration, whereas migrant is used here to imply a temporary residence and thus a return to the original habitat at some future stage. The term migrant could refer to a few or many individuals, depending on the distribution of each species and the locality of a particular estuary in a biogeographical region. Therefore, it is as important to consider the use of estuaries by both the occasional occurrence of a few individuals of a species and the large abundance of a regularly occurring species.

Although most marine migrants use estuaries opportunistically, there are some marine species that are dependent on estuaries during their juvenile stages and are therefore not using estuaries opportunistically. Ray (2005) emphasizes the need to determine which fishes 'must' use estuaries (i.e. obligative dependents), and which therefore will be at risk if estuarine habitats are lost, from those which 'may' use estuaries (i.e. facultative dependents). Hence, here the term marine migrant is separated into marine estuarine-opportunists and marine estuarine dependents (Table 1, Fig. 1c). Marine estuarine-opportunists are able to use alternative marine nursery areas, whereas marine estuarine dependents do not have suitable nursery habitats nearby. For example, the 0+ juveniles of *M. cephalus* in Western Australia are almost exclusively found in estuaries in south-western Australia,

where there are numerous rivers (Lenanton and Potter 1987). However, similar-sized juvenile *M. cephalus* are also abundant in nearshore waters of regions further north where there are no estuaries. Hence, this species does not have to rely on estuaries as a nursery area but uses them opportunistically when they are present. Similarly, juvenile European plaice (*Pleuronectes platessa*, Pleuronectidae) in the North Sea use estuaries opportunistically as nursery grounds but also use other suitable shallow, sandbank habitats (Elliott and Hemingway 2002). In contrast, the 0+ juveniles of the Cape stumpnose (*Rhabdosargus holubi*, Sparidae) are abundant in South African estuaries but seldom recorded in marine waters (Wallace *et al.* 1984). The terms opportunist and dependent therefore illustrate fundamental differences in the importance of estuaries to particular species (Blaber *et al.* 1989).

Estuaries have a highly important role as migration routes for diadromous species (Elliott and Hemingway 2002; Able 2005). The term diadromy is taken here, and by others such as McDowall (1988), not to imply a tolerance to stable, variable or low salinities, but rather an ability of a fish to change its physiology while moving between water bodies of different and stable salinities. Hence, the classical diadromous species such as eels moving from freshwater to seawater to breed (catadromy) and salmonids and lampreys moving in the opposite direction (anadromy) undergo a major physiological adjustment to tolerate the new salinities. Diadromy has been used to imply transfer from seawater to freshwater or vice versa and so the established diadromous terms anadromy and catadromy have been retained here for species which, for reproduction, undertake migrations between freshwaters and the sea (Fig. 1d,e). However, it has been necessary to adopt the terms semi-anadromous and semi-catadromous for those few species whose landward or seaward migrations for spawning, respectively, stops within the estuary or other transitional water body (Fig. 1f,g). This concept is further complicated by the fact that estuaries can include tidal freshwater areas (McLusky and Elliott 2004) such that a migration by species into these areas rather than into the river upstream of these areas should be regarded as catadromy and anadromy *sensu strictu*.

In addition to anadromy and catadromy, the term amphidromy is also used (McDowall 1988, 1992; Keith 2003) which may be subject to confusion. Myers (1949) defines an amphidromous strategy as

'Diadromous fishes whose migration from fresh water to the sea, or vice versa, is not for the purpose of breeding but occurs regularly at some other definite stage of the life cycle' (Fig. 1h). In estuaries studied by the authors there are fishes that live in rivers and estuaries but whose eggs, larvae and post-larvae may be swept out to sea on the ebb-tide. This could be regarded as amphidromy (*sensu strictu* McDowall 1988), but we believe the term should be reserved for those species where there is movement between freshwater and the sea that is not related to breeding migrations (see McDowall 1997, 2004, 2007 for further information on amphidromy).

There are several species of fishes that reproduce in estuaries but whose larvae and post-larvae may be found in nearshore marine waters, apparently feeding and developing there, before returning to estuarine systems where they develop into adults. Examples of this phenomenon have been noted along the Gulf of Mexico and the Caribbean coast of Central America, where aggregations entering estuaries include not only post-larval fishes, but also several types of invertebrates, especially larval and post-larval crustaceans (Pattillo *et al.* 1997). Such aggregations have been referred to as 'tismiche'. Examples of post-larval fishes that have been identified from the aggregations at Tortuguero, Costa Rica, have included the fat sleeper (*Dormitator maculatus*, Eleotridae) and the sand fish (*Awaous tajasica*, Gobiidae) (Gilbert and Kelso 1971; Nordlie 1981; Winemiller and Ponwith 1998). These species are considered to be amphidromous. Similarly, Keith (2003) extensively discusses the amphidromous gobiid fishes of Indo-Pacific and Caribbean areas. After being spawned in freshwaters, the embryos drift seaward for a planktonic phase before returning to freshwaters for growth and reproduction, e.g. the genera *Lentipes*, *Sicyopterus* and *Stenogobius* in the Indo-Pacific and *Sicydium* and *Awaous* in the Caribbean.

Similar return migrations have been observed in South African systems where estuarine spawning gobies possess eggs that hatch on the high tide and are carried out to sea on the ebb-tide (Whitfield 1989). At the post-larval stage these fishes then return to the estuarine environment to complete their life cycle, e.g. prison goby (*Caffrogobius gilchristi*, Gobiidae). Such species have been termed estuarine migrants by Whitfield (1999). The lack of the larvae of certain estuary-associated gobies, e.g. Knysna sandgoby (*Psammogobius knysnaensis*,

Gobiidae), from mainly closed systems in South Africa may indicate that the marine larval phase is obligatory for these species (Whitfield 1999).

The primary use of estuaries as feeding, refugia and seasonal-migration areas has previously led to a separation of marine species which migrate into estuaries on a seasonal basis from those that migrate as juveniles (McHugh 1967; Elliott *et al.* 1990). However, as the larval and 0+ juvenile migrations of many marine species into estuaries also tend to be seasonal, it is not satisfactory to make this distinction, hence the term marine migrants are suggested here (Fig. 1c). Similarly, the combination of all freshwater species into a single group (McHugh 1967) has been rejected to separate those freshwater species which often migrate into estuaries (freshwater migrants) from those freshwater species which accidentally occur in these systems, possibly as the result of large freshwater flows or river flooding (freshwater straggler) (Fig. 1i). In all geographic areas there are freshwater species which are found in estuaries either in small or larger numbers (Miller 1966) but the inclusion of any species in the estuarine fauna relies on its degree of association with and penetration into the estuary. Hence, a freshwater straggler is therefore analogous to a marine straggler (MS) but these enter the estuary from opposite ends. It is important to note that not all freshwater fishes extend only into the low salinity upper reaches; some species, e.g. Mozambique tilapia (*Oreochromis mossambicus*, Cichlidae), can tolerate high salinities and be found in the upper, middle and lower reaches of estuaries when conditions are suitable (Whitfield and Blaber 1979).

Those species capable of spending all of their lives within estuaries have been termed estuarine residents (Fig. 1j) and there appear to be differences between regions. For example, in southern Africa there are relatively few estuarine resident species conducting their entire life cycle within an estuary, although such species, e.g. Gilchrist's round herring (*Gilchristella aestuaria*, Clupeidae) may be locally abundant (Whitfield 1998). In some transitional waters such as the West African coastal lagoon systems, some estuarine residents such as the blackchin tilapia (*Sarotherodon melanotheron*, Cichlidae) form the basis for intensive and important fisheries. In contrast to areas having relatively few truly and fully estuarine resident species, in south-western Australian estuaries there are several species which are found only in estuaries or are represented by discrete estuarine populations, i.e. true estuarine residents (Potter and Hyndes 1999). Furthermore, none of these has a marine larval phase. Indeed, certain gobiids and atherinids are predominantly found in the upper reaches of these Australian estuaries throughout their entire life cycle (Prince *et al.* 1982; Gill and Potter 1993). In the United Kingdom, only two of the 73 species recorded amongst nearly 18 500 fish in the Severn Estuary were estuarine, and their contribution to that total number of individuals was only 0.7% (Potter *et al.* 1997). The probability is that egg and larval retention in the macrotidal Severn is less conducive to maintaining an estuarine life cycle than in the microtidal estuaries of south-western Australia. Unfortunately, this explanation does not appear to be the only reason for regional differences in resident estuarine fish species diversity since southern African estuaries are also microtidal and have relatively few exclusively estuarine taxa.

As an example of the subtleties of defining an estuarine resident, Cape silverside (*Atherina breviceps*, Atherinidae) and the clupeid *Gilchristella aestuaria* are abundant in most South African estuaries, spawn in these systems, and their larvae, juveniles and adults do not require any other environment to complete their life cycle (Ratte 1989). *Gilchristella* is an estuarine resident because it is not found in the sea at any stage of its life cycle (unless temporarily flushed into the sea following river flood events) and is regarded as a permanent resident of estuaries in the region (Talbot 1982). In contrast, the larvae, juveniles and adults of *A. breviceps* are also abundant in the sea (Whitfield 1998) and there is strong exchange of genetic material between the marine and estuarine populations of this species (Norton 2005). Hence, *A. breviceps* is regarded as an estuarine migrant even though this species can also complete its entire life cycle within estuaries. Many estuarine residents have a marine dispersal phase, often larval, but this dispersal can also be during the juvenile or adult life stages. In the tropics this dispersal often takes place in the wet season when coastal salinities are lower (Albaret *et al.* 2004). Hence, it is possible to use the term estuarine migrants for those estuarine species with an apparent strategy for using the adjoining marine (or freshwater) areas at some stage of their life cycle (Fig. 1k). However, in this it is necessary to separate species accidentally washed out of the estuary from those which have a well-defined

strategy for moving out. Similarly, it is of value to separate the facultative use of estuaries, possibly with an element of opportunistic behaviour, from obligate estuarine residents.

Some species classically regarded as estuarine residents have a restricted seaward migration only for spawning. For example, the flounder (*Platichthys flesus*, Pleuronectidae) spends most of its life within estuaries and then spawns in the coastal zone before the larvae use selective tidal stream transport (STST) to migrate into the estuary (Elliott and Hemingway 2002). Flounder are an abundant fish component within the Bristol Channel, a marine embayment outside the Severn Estuary, as well as in the Severn Estuary. There is thus a strong case to categorize this species as a marine estuarine-opportunist in the Severn Estuary. However, some authors (McDowall 1988) include *P. flesus* and other pleuronectiids in the catadromous category, despite the fact that there is no obligate freshwater phase in their life cycles. It is also debatable whether *P. flesus* is semi-catadromous because it does not occupy rivers as a first choice habitat at any stage in its life cycle, although it is sometimes found in these areas (unpublished observations). If the coastal spawning migration is ignored then *P. flesus* can also be regarded as an estuarine migrant, i.e. spends most of its life in an estuary but migrates between the estuarine and marine environments at certain stages of its life cycle.

In future analyses of estuarine functioning it is suggested that all of the groups described above, and in Table 1 and Fig. 1a–k, should be used in conjunction with the feeding and reproduction guilds below, given that each description only indicates a part of the species' biology.

Feeding Mode Functional Group

The overall aim of the approach described here is to help understand, explain and eventually use in a management context, the functioning of estuarine areas and especially the use of estuarine areas which may be perturbed by human activities. Hence, it is particularly important to determine the food webs, predator–prey relationships and carrying capacity of estuaries and the effects on these as a result of anthropogenic, hydromorphological and chemical modifications, through an understanding of trophic relationships within these systems. This requires an understanding of the feeding mode of fish species when they are within

the estuary, irrespective of their mode of feeding while in any adjacent habitat. For example, Hostens and Mees (1999) analysed feeding guilds in an estuarine environment and found a dependence on the hyperbenthos (the mobile forms on or above the estuary substratum) by fishes that may take other prey when outside the estuary. Therefore, in the approach used here the FMFG relates to a species while in the estuary, but it is acknowledged that, given the often opportunistic nature of feeding by fishes, some taxa will be difficult to assign to a particular group. If it is not possible to assign a species because of such a wide set of feeding preferences, that species should be regarded as miscellaneous/opportunistic and hence the inclusion of this category in Table 2.

Essentially the FMFG classification is a trophic guild system designed to allow the aggregation of fish species that utilize similar food resources. The classification draws upon other fish feeding guilds such as that developed by Elliott and Dewailly (1995) for European fishes as well a standardized table of fish food items provided in FishBase (Froese and Pauly 2006). Over 800 references were used to develop the food items table in FishBase and to accommodate the range of information found in the literature. Food items were classified into three hierarchical levels, from six very broad food groups at the highest level to 55 food (taxonomic) groups at the lowest level. The broad food categories provided in FishBase included detritus, plants, zooplankton, zoobenthos, nekton and others (Froese and Pauly 2006). The Feeding Functional Groups (FMFG) proposed here identifies seven broad categories: detritivore, herbivore, omnivore, zooplanktivore, zoobenthivore, piscivore and miscellaneous/opportunist (Table 2).

The detritivore category includes those species that feed on decaying organic (plant or animal) matter together with the associated bacteria and fungi. Most detritivores, however, also consume benthic microalgae (microphytobenthos; Whitfield and Blaber 1978a) and it is often unclear whether the detritus/benthic floc or microphytobenthos is the targeted food source. Mugilids, for example, feed on organic matter and diatoms off the substratum and have a muscular gizzard-like stomach designed for grinding (using ingested sediment) this algal and detrital material. Similarly, the term illiophagous (sediment-feeding, *sensu* Bowen 1979) can be used as an indication that fish are taking the sediment together with its detritus, microphytobenthos and

benthophagous (BP). Zoobenthos includes animals that live in the sediment (infauna), on the sediment (epifauna) or immediately above the sediment (hyperbenthos) and the term BP can also include flora associated with the benthos. In recent decades hyperbenthophagous (HP) fish species have been identified since their method of feeding is centred on the hyperbenthos, i.e. those mobile organisms living just above the substratum. Thus, while the guild HP feeders could be regarded as a subgroup of the BP feeders, their prey sources will require different methods of feeding and so have been kept separate. In general, many benthic/demersal species feed on fauna that are associated with the sediment. Since much of the zoobenthos (especially the epifauna) is sometimes in, sometimes on and sometimes above the sediment (e.g. many amphipods) according to time of day, tidal regime, current flow rates, etc., it is often difficult in practice to separate these two compartments. Furthermore, for most fish species, their very detailed feeding behaviour is unknown.

While it is difficult to separate the zoobenthic components, this FMFG classification has provided three subdivisions: zoobenthivore-hyperbenthos, zoobenthivore-epifauna and zoobenthivore-infauna. These subdivisions were created such that they may be accommodated should new information on fish diets become available. For example, in recent decades, HP fish species have been identified since their diet and method of feeding is centred on those mobile organisms living just above the estuary bottom. In addition, certain fish species have developed specialized feeding mechanisms which enable them to exploit infauna. For example, spotted grunter (Pomadasys commersonnii, Haemulidae) and white steenbras (Lithognathus lithognathus, Sparidae) both have protusible mouthparts and employ a gill chamber pump action to extract mud prawns (Upogebia) from their burrows (Whitfield 1998). Some fishes also deliberately target certain infaunal prey; members of the Gerreidae in southern Africa (Cyrus and Blaber 1982) and common sole (Solea solea, Soleidae) in the Humber estuary, UK (Marshall 1995), for example, feed by cropping bivalve siphons.

The piscivore category includes carnivorous species that feed mainly on other fishes. Although estuaries provide shelter from major fish predators, several estuary-associated fishes are piscivorous. Examples include members of the Carangidae, Elopidae, Gadidae, Pomatomidae and Sciaenidae

(Table 2). While piscivores feed primarily on fishes, they will also consume other prey items. In South African estuaries, for example, swimming prawns (Peneaidae) can form a substantial component of the diet of both A. japonicus and E. machnata at certain times (Whitfield and Blaber 1978b). In addition to finfish, FishBase also includes cephalopods (squid and cuttlefish) within the nekton food category (Froese and Pauly 2006). FishBase also contains a category 'others' which includes food items such as reptiles, birds and mammals that are typically consumed by apex predators such as sharks. Apex fish predators are generally absent from estuaries although the bull shark (Carcharhinus leucas, Carcharhinidae) is reported to enter large estuarine bays, lakes and rivers. In South Africa, however, the individuals that enter estuaries are usually juveniles whose diet is mainly composed of fishes (Whitfield 1998).

Those species that fit into the other categories should be fairly consistent in their prey/food choice in a range of estuaries. Given the nature of feeding by many estuarine species, however, there is a need for an opportunist category which should be separated from the omnivore category to be used for those species that are actually omnivorous and not necessarily opportunists. An opportunist species is likely to feed on very different prey/food in different estuaries depending on food availability, whereas omnivores will probably have dietary mix of plant and animal material in different areas. Examples of estuarine omnivores include Diplodus capensis from southern Africa (Coetzee 1986; Whitfield 1988) and Acanthopagrus butcheri in south-western Australian estuaries (Sarre et al. 2000). Both species ingest a wide spectrum of plant and animal food items, especially aquatic macrophytes, filamentous algae and the associated epifauna and periphyton. Although these species are opportunistic in that the proportions of major dietary categories consumed varies greatly amongst estuaries, this opportunism should not influence the primary FMFG categorization which is driven at a higher level of resolution.

The term opportunistic has been used here to indicate both the feeding behaviour and food preferences, rather than food preferences alone. It is increasingly observed that many estuarine fishes take almost any suitably sized prey that they encounter and thus should be regarded as opportunists. Thus, while the EUFG reflects the migratory behaviour and physiological tolerances of fishes, the

FMFG reflects the feeding behaviour and their body structure as an adaptation to feeding on particular prey, i.e. their ecotrophomorphology or ecomorphology (Wootton 1990). For example, streamlined clupeids inhabiting the upper water column and feeding on zooplankton have a very different ecomorphology when compared with demersal gadoids preying on hyperbenthic crustaceans (Costa and Elliott 1991).

The South African species *R. holubi* is an omnivore and will always select both plants and animals in its diet where both food sources are available (Blaber 1974). Where aquatic macrophytes are unavailable it will actively search for alternative plant material in its diet, e.g. feeding on filamentous algae growing on the stems of *Phragmites* reeds in the Mhlanga Estuary (Whitfield 1980). In the Swartvlei system, *R. holubi* previously fed consistently on both *Potamogeton* and associated epifauna but when the macrophytes disappeared it consumed the filamentous algal mats that replaced the *Potamogeton* and the epifauna associated with the sediments. When the algal mats also disappeared, the species was obviously restricted to a carnivorous diet (epifauna associated with the sediments) and the body condition, as reflected in the length/weight relationship, declined (Whitfield 1984). Thus, juvenile *R. holubi* may survive on a carnivorous diet but they require an omnivorous diet to thrive and they deliberately (not opportunistically) select both plant and animal material when available.

The FMFG classification presented here provides a method of grouping fishes according to common broad food categories. However, it is increasingly observed that many estuarine-associated fishes are opportunistic in that they switch their diet beyond their 'normal' spectrum, as and when opportunities arise, or have no food preference whatsoever and take any prey that they encounter. The European flounder, *Platichthys flesus*, for example, may take infaunal benthos, epifaunal shrimps or zooplankton, depending on availability (Costa and Elliott 1991; Marshall 1995). Such opportunistic feeding behaviour sometimes makes it difficult to assign a species to a particular feeding category. While most estuarine-associated fishes are somewhat opportunistic, it is suggested that a FMFG classification should be based on a species normal or preferred diet. A miscellaneous/opportunistic category has been created, however, to accommodate situations where a species cannot be placed in one of the more conventional FMFG categories. This miscellaneous/opportunistic category should not be confused with the omnivore category, which includes those species with a regular, varied diet of both plant and animal material.

Most estuary-associated fish species also show ontogenetic shifts in diet. During their larval stages most fishes are planktivorous but switch to juvenile diets at lengths that vary according to the taxa (Whitfield 1985). Some species such as *M. cephalus* retain the same feeding mode through the juvenile and/or adult life stages. The types of food consumed by certain other species, however, change markedly with growth. For example, the Atlantic cod (*Gadus morhua*, Gadidae) appears to be a planktonic feeder as a larva, BP as a 0+ juvenile, then take hyperbenthic crustaceans such as mysids and pericarid shrimp before becoming a piscivore when mature (Costa and Elliott 1991). Thus, this group of species will move from one feeding category to another during their life. Where possible, ontogenetic changes in diet should be accounted for through allocating various size classes to the appropriate FMFG category. In practice, however, this may be difficult and an alternative may be to allocate a FMFG category to a particular species based on the diet of the predominant size classes or life cycle stage (e.g. mostly juveniles) present within an estuary.

Furthermore, some species ingest different species during the day and night and this may result in a temporal change in the FMFG. It should also be recognized that many species are opportunistic feeders in that, at any one time, they will target organisms that are abundant and constitute an appropriate food source. These FMFG shifts and combinations can be denoted by using the codes for two or more FMFG subgroups which reflect diel and opportunistic shifts in diet.

While it is recognized that estuaries play an important role in the life cycle of a number of fish species, many species that are reported in estuaries are marine vagrants and are not dependent on these environments. Furthermore, many diadromous species such as certain salmonids do not feed while passing through the estuary, especially the mature individuals on their final spawning migrations (Froese and Pauly 2006). It is recommended that a feeding guild analysis should be restricted to the dominant EUFG occupying a particular system, i.e. those fish species foraging mainly within the estuary. For example, marine stragglers, catadromous

even smaller macrofauna and meiofauna. In view of this, and to prevent the creation of a large number of terms, the detritivore category has been extended from previous analyses (Elliott and Dewailly 1995; Potter and Hyndes 1999) to include those fish also consuming microphytobenthos, detritus and sediment.

The category herbivore includes fishes that consume plant material (see below) and although few, if any, estuarine-associated fish are reported to consume only phytoplankton, the subcategory herbivore–phytoplankton is included to accommodate phytoplanktivorous fishes should new information on fish diets become available. Hajisamae *et al.* (2003), for example, reported that phytoplankton dominated the diet of the Chacunda gizzard shad (*Anodontostoma chacunda*, Clupeidae) in the Johor Strait estuarine system in Singapore, south-east Asia. FishBase also includes phytoplankton as a subcategory of the plants food item (Froese and Pauly 2006), for example, in the diet of *Brevoortia* (Friedland *et al.* 2005). Hence, in the present assessment, the subcategory herbivore–macroalgae/macrophytes is also included to accommodate those fishes that have a mainly herbivorous diet comprising large plants.

In the estuaries studied by the authors, there appear to be very few examples of exclusive herbivory, possibly because of the fact that fish lack a cellulase with which to digest the cell walls of plants (Kapoor *et al.* 1975). However, sparids, for example, have been shown to possess both the amylase required for digesting carbohydrates in plant material (see Fernandez *et al.* 2001) and the ability to incorporate plant carbon in their tissues (see Havelange *et al.* 1997). Hence, the designation of the herbivorous FMFG may be difficult, especially as most herbivorous fishes in estuaries also consume animal material, often small invertebrates associated with macrophytic plants and filamentous algae. In some cases, there may be a temporal separation of food, e.g. the Cape halfbeak (*Hyporhamphus capensis*, Hemiramphidae) consumes mainly zooplankton in late winter and macrophytic plants in late summer (Coetzee 1981). In addition, there is the need for an energetic assessment of this type of feeding in that, although a large amount of plant material is ingested by these species, the relatively small amount of animal material may be more important because of the higher food value and assimilation rate. While there may not be many true herbivores in estuaries there are some, such as

certain Hemiramphidae, Sparidae, Siganidae and Kyphosidae, which have a diet dominated by plant material (Nordlie and Kelso 1975). It is therefore proposed that the herbivore category be retained for further testing, especially as a means of comparing systems.

The designation of herbivorous species can be compounded by the fact that many fishes that feed on macrophytes and/or filamentous algae are actually targeting the periphyton and epifauna associated with the plants. Examples include the Cape white seabream (*Diplodus capensis*, Sparidae) from southern Africa (Coetzee 1986; Whitfield 1988) and Southern black bream (*Acanthopagrus butcheri*, Sparidae) in south-western Australian estuaries (Sarre *et al.* 2000). Both species ingest a wide spectrum of plant and animal food items, especially aquatic macrophytes, filamentous algae and the associated epifauna and periphyton. Although FishBase contains a subcategory 'other plants', which includes food items such as benthic algae/weeds, terrestrial plants and periphyton within the plant food categories (Froese and Pauly 2006), it is felt that the term omnivore better describes the feeding guild of this group of fishes.

The category zooplanktivore includes fishes that typically feed on small crustaceans in the water column; for example, the Bay anchovy (*Anchoa mitchilli*, Engraulidae) diet comprises mainly zooplankton but may also include fish eggs and larvae (Froese and Pauly 2006). Typical zooplanktivores found in estuaries include members of the Clupeidae and the Engraulidae (Table 2). Zooplankton is also a major component of the diet of larval fishes and most, if not all estuary-associated fish species, are planktivorous during their larval stages but change to juvenile/adult diets with growth (Whitfield 1985). The larvae of many anadromous, semi-anadromous and estuarine-spawning fishes also prey predominantly on zooplankton. Many fishes that utilize estuaries, however, enter these systems as juveniles and are therefore already at a stage where they have or are about to switch to their juvenile/adult diet. In addition, there are examples of pelagic fish taxa such as *Alosa* and *Brevoortia* which consume zooplankton during both the larval and juvenile stages and so this may be an important component in some areas and for some species (Friedland *et al.* 2005).

Many bottom-dwelling fishes feed on organisms associated with the substratum (zoobenthos) and hence the terms zoobenthivore (ZB) and

and anadromous groups should not be included in an FMFG analysis.

Another consideration is the fact that the diet of some species during the estuarine phase of their life cycle differs from that in the marine environment. For example, *R. holubi* in South African estuaries feed mainly on filamentous algae, aquatic macrophytes and epibenthic invertebrates (Whitfield 1998). The tricuspid incisors of juvenile *R. holubi* are specifically adapted for cutting vegetation and the loss of these and replacement with molariform teeth to crush bivalves as adults coincides with their migration from estuaries to the marine environment (Blaber 1974). The classification and analysis of estuarine fish feeding guilds should therefore be confined to the estuarine phase of a particular species life cycle, i.e. food consumed while in an estuary.

Reproductive Mode Functional Group

The use of reproductive guilds for fishes in general was first proposed by the seminal work of Balon (1975) although the present assessment has attempted an independent use of the approach as it relates to estuarine fishes. In particular, the definition of a species' mode of reproduction as a guild is related to a fundamental understanding of the functioning of estuaries. In the case of estuarine spawners, it is aimed at determining first, the importance of the estuary as a breeding area and, secondly, the strategies employed by these species in response to environmental conditions, especially the hydrodynamic regime of the transitional waters (Potter *et al.* 1993). In particular, the strategies employed by estuarine spawners to retain their young within an estuary are especially important. Where the flushing rate through an estuary is too high, and thus the hydrographic residence or retention time too short, the successful development of pelagic eggs or larvae may be compromised (Elliott and Dewailly 1995; Nordlie 2000; Strydom *et al.* 2002; McLusky and Elliott 2004).

Functional reproductive guilds allow a comparison of the estuarine resident species, most of which are hypothesized to require egg and larval retention strategies within estuaries, with marine migrant species which appear to have a greater reliance on egg and larval development occurring within the marine environment (Whitfield 1980). In an analysis of reproductive guilds, it is especially important to consider mechanisms for successful reproduction in an estuary and strategies for facilitating the maintenance of the young stages within the estuary and thus preventing their being flushed out to sea (Melville-Smith *et al.* 1981). However, if it was advantageous for some estuarine residents to become widely dispersed, this would be facilitated by the release of pelagic eggs or larvae on the spring high tide (Whitfield 1989). Similarly, the apparent necessity for most marine migrant species to spawn at sea rather than in estuaries is an area of research that has not been properly explored.

The fishes found in estuaries can be allocated to one of three functional reproductive groups: viviparous, ovoviviparous and oviparous, although it is valuable to subdivide the latter into variations based on the reproductive strategy of the species (Table 3). Analysis of these guilds should be restricted to the dominant estuarine resident and migrant taxa or those which spawn in the estuary, such as the semi-diadromous species. Most estuary-associated fish species are sea-borne spawners and posses strategies which ensure estuarine recruitment on both a spatial and temporal basis. A few southern African marine migrant species, e.g. the picnic seabream *Acanthopagrus berda*, have been recorded spawning in the mouth region of marine-dominated systems (Garratt 1993), but generally the marine taxa have extended spawning periods in this part of the world and release their eggs relatively close to the coast/ estuaries (Wallace 1975).

The classical strategy of retaining brood in a location with the highest level of protection is reflected by viviparous species. Examples of this strategy in estuaries range from small species such as the viviparous blenny (*Zoarces viviparous*, Zoarcidae) in temperate waters to the bull shark *Carcharhinus leucas* in tropical and subtropical areas (Table 3). In the previous use of this guild, brooding species, such as the syngnathids (pipefishes and seahorses) in which the male has a ventral brood chamber, were also grouped with viviparous or ovoviviparous (Elliott and Dewailly 1995). However, for consistency, and given that this reproductive mode represents a similar strategy to other brooders, such as mouth-brooding cichlids and ariids, then the brooders of fertilized eggs and young have been grouped under the guild Os (Table 3).

In many estuaries the dominant group of spawners are oviparous marine migrants which breed at sea, followed by an onshore migration of post-flexion larvae and early juveniles (Boehlert and

Mundy 1988). Most of this groups are serial spawners that release large numbers of pelagic eggs which are fertilized within the water column during mass spawning aggregations (Wallace 1975). The immigration of larvae and post-larvae into large, well-flushed estuaries of the Northern Hemisphere mainly takes place using passive and/or selective tidal stream transport (STST) for entry to and retention within these systems (Weinstein *et al.* 1980; Fortier and Leggett 1982). For example, the pelagic spawner *Platichthys flesus* has coastal spawning followed by STST which enables a larval and post-larval migration into the nursery area. Even in the microtidal estuaries of South Africa, Australia and New Zealand, where for much of the year the two-layered circulation pattern is less pronounced or absent, the larvae and juveniles of some marine species enter these systems on the flood tide and are retained by rapidly settling along the banks or on the bottom where water movements are reduced (Beckley 1985; Roper 1986; Neira and Potter 1994).

In most large estuaries worldwide there are oviparous, ovoviparous and viviparous breeders, although it is important to determine which reproductive strategies are particularly suited to the specific hydrographic conditions encountered within these systems. As indicated in Table 3, there are several reproductive strategies to ensure that eggs and young are retained within an estuary. For example, egg and brood protection by mouth, pouches or nest building, or by fixing eggs to the substratum or weed, prevents washout and loss of these vulnerable life stages into the marine environment. Similarly, the production of large, demersal and neutrally buoyant eggs such as by the European smelt (*Osmerus eperlanus*, Osmeridae) also leads to a greater retention within transitional waters. By attaching eggs to some element of the substratum, such as debris, rock, sand, shell or vegetation, washout is prevented but this does mean that these fertilized eggs are exposed to the highly variable conditions within the estuary. However, while egg and larval retention strategies may be employed by some species, others such as certain blennies and gobies may release larvae into the water column at peak high tide so that they are flushed by the ebb-tide out to sea (Whitfield 1989). A different strategy is adopted by those marine migrants that use estuaries as juvenile nursery areas, with their eggs often being released in coastal waters, or in the vicinity of estuary mouths, so that the distance

between the larval and juvenile habitats is reduced to a minimum (Wallace 1975).

Discussion

This review has reinforced the point made in many papers regarding the value and utility of the guild approach in helping to describe and explain community structure. However, the approach further developed here shows that despite the estuarine continuum (i.e. the gradual change in environmental variables such as salinity, temperature, depth, turbidity, dissolved oxygen and substratum type), it is still possible to group species into categories, each with similar life history characteristics, modes of reproduction or trophic demands on the available resources. In all estuary-associated fish taxa there are ontogenetic shifts and species therefore can change guilds during their lifespan, especially with respect to feeding.

It is emphasized here that the value of standardization of terms makes it much easier to compare systems in a range of areas with completely different species, thus showing the utility of this approach on a global scale and across estuaries on different continents. While comparisons in terms of taxonomy give important information, this is regarded as less important for an understanding of the functioning of estuaries, especially where different biogeographic regions are being studied. As an example, hyperbenthic feeders appear to be more prevalent in northern temperate estuaries, especially in the upper regions of these systems where these fishes are consuming mysids and shrimps (Mees and Jones 1997). Similarly, research in the Scheldt Estuary shows the dominance of shrimp, mysid and swimming prawn prey in the diet of several predatory fish species. In contrast, there seems to be no bottom-dwelling fish species in southern African estuaries that are exclusively hyperbenthophagic feeders. There are many species that feed on both benthic and hyperbenthic invertebrates (Blaber 1984; Marais 1984; Whitfield 1988), but none that fit neatly into the latter category only. Using the FMFG classification outlined in this review, species that utilize similar food resources will be aggregated, and thus provide a greater understanding of estuarine trophic functioning in different estuaries.

A primary aim of this synthesis has been to lay the foundations for examining the similarities and differences between estuaries in different

geographical areas and especially to understand strategies employed by fishes in estuaries. Such an analysis could benefit from that carried out by Bulger *et al.* (1993) in which multivariate ordination analyses were used to locate the salinity tolerances of estuarine fishes within one geographical region. Despite this, in attempting to understand and interpret the use of estuaries by fishes, we are reluctant to over-emphasize the adoption of strategies by fishes but the value of the guild approach relies on the ability to separate such strategies from an accidental behaviour. Some fish species appear to have certain strategies and may even have specialized mouthparts or dentition to deal with particular foods, while others merely take whatever they encounter as long as they can manipulate and consume the prey. For example, some fishes target certain prey, e.g. cropping of bivalve siphons by *S. solea* in the Humber (Marshall 1995) when compared to flatfish incidentally taking prey such as polychaetes during benthic foraging.

However, two of the functional group types have included the term opportunistic as a strategy for taking advantage of resources such as space, food and other environmental conditions found in estuaries. As is shown throughout this review, semantics cannot be ignored, so the use of the term opportunistic has to be used with caution. From an estuarine management perspective, the case for estuarine conservation is considerably weakened if all marine fish utilising estuaries as nursery areas are 'opportunists', as such a pejorative use of the word could imply that the loss of estuarine habitats can be easily compensated for by the fish moving to non-estuarine areas or feeding on other types of prey if the preferred prey have been removed or destroyed.

The initial discussion here has indicated differences between biogeographic areas that are worthy of further study. For example, in southern African estuaries there seem to be only a few fish species that are true estuarine residents (Whitfield 1998), in contrast to estuaries in Western Australia where a much higher proportion of the fish community are found only in estuaries or are represented by genetically distinct populations that complete their entire life cycles within these systems (Potter and Hyndes 1999). In terms of number of individuals, these two groups of species collectively make a large contribution to the ichthyofaunae of many estuaries in Western Australia (Potter and Hyndes 1999) and, in southern Africa, *Gilchristella aestuaria*, an

estuarine resident, is probably the most abundant fish species despite the much more diverse marine migrant group within these systems (Harrison 2003).

This review has also indicated the links between estuaries and adjacent marine and freshwater habitats, and the creation of the estuarine fish community originating from those adjacent areas (Albaret 1999). The repercussions of these links and origins for speciation within estuaries has been little studied. Although our estuaries in their current form are of recent origin, there are clear genetic differences between the marine and estuarine populations of species, such as the plotosid *Cnidoglanis macrocephalus* (Watts and Johnson 2004). This also raises the question of the extent to which the speciation of fish can occur in estuarine environments (Whitfield 1994).

It is hoped that the present assessment will enable a quantitative global assessment of the contribution by different guilds, especially estuarine residents and marine migrants, and further determine the species associated with estuaries and thus the importance of these transitional environments. It is suggested that such an agreed definition of guilds provides an important addition to the catalogue FishBase and in turn will allow further refining of the terms used. For example, it is expected that the estuarine resident guild is likely to be a 'graded' grouping from true estuarine residents (spending 100% of their time in estuaries) to estuarine migrants with varying percentages of time spent in estuaries. More research on a global basis may show that many species previously thought to be restricted to estuaries (especially within the family Gobiidae) have obligate marine larval stages while yet others will be found to undertake migrations between estuaries and the sea and/or between estuaries along various coasts. It is emphasized that molecular, genetic and behavioural approaches will be required to provide insights into the latter aspects, for example, the tagging of individuals to determine their salinity preferences and migration routes and the use of otolith elemental tracers to determine their life history. Similarly, there is a need to know the differences in environmental tolerances (e.g. with respect to salinity for migratory species) and the way in which this determines the estuarine strategies adopted by the different taxa.

In most of the areas studied by the present authors and others, the species categorized as marine migrants are overwhelmingly dominant in

terms of biomass and typically also numerically, e.g. the large influx of gadoids or clupeids into north-west European estuaries (Claridge *et al.* 1985, 1986; Elliott *et al.* 1990). This emphasizes the importance of estuaries as feeding and refuge areas for marine fishes, often as juveniles but also as adults. The generally small estuarine species form a less dominant group in terms of biomass but are often numerically very abundant (Harrison and Whitfield 1995; Harrison 2003) and while some of these may be termed as estuarine migrants, in that they have larval stages which move from the estuary to adjacent marine areas, it is difficult to know whether this is a recognized strategy or is merely an accidental occurrence whereby the larvae get washed out of estuaries under high flows or ebb-tide conditions.

The present review has indicated uncertainty in the ecology of many estuarine species and confusion in the terms used to categorize them. For example, it indicates the need to reconsider or revise certain diadromous terms such as marine amphidromy which has been taken to be refer to reproduction occurring in estuaries rather than fresh water (McDowall 1988). If the directed movements of the estuarine migrants are related to spawning strategies of those species, these taxa do not fall into McDowall's amphidromous grouping of species that undergo migrations 'not for reproduction'. It would appear that the original definition of amphidromy (McDowall 1987), which refers only to fishes that migrate between fresh water and the sea, is more appropriate. All of this indicates that the term amphidromy for estuarine spawners is inappropriate. Here, we regard amphidromous species as those that move between freshwater and marine environments in a manner not related to reproduction.

Although certain freshwater spawning tropical gobies and eleotrids that have larvae occurring in the marine environment are the prime examples of amphidromy, there does appear to be a case for other species to be also placed in this category. For example, *M. cephalus*, which has sometimes been referred to as catadromous because of its tendency to enter freshwater areas (Riede 2004), should perhaps also be considered amphidromous. This is because *M. cephalus* occurs in freshwater, estuarine and marine environments as both juveniles and adults (Bok 1979), and its occurrence in rivers and estuaries is not linked to reproduction. Similarly, the Indo-Pacific tarpon (*Megalops cyprinoides*, Megalopi-dae) is found in freshwater, estuaries and the sea

(Whitfield 1998), with movements between these environments not being directly related to breeding activities. Although the Bonga shad (*Ethmalosa fimbriata*, Clupeidae) breeds in rivers, estuaries and the sea, and is regarded by Riede (2004) as catadromous, this species is actually amphidromous because the movements between the various areas are not dictated by spawning activities. A recent definition of amphidromy by McDowall (2007) limits its use to those species breeding in freshwater, which is contrary to the above interpretation of amphidromy that includes marine, estuarine and freshwater spawning species moving between rivers and the sea in a manner not linked to breeding activities. All of this shows the confusion relating to the term amphidromy and, because of this, we are not confident that the term will continue to be useful.

In presenting this classification of guilds pertaining to the different species, the present review has encountered limitations in our knowledge of fish life cycles, especially the changes in preferences occurring during a life cycle and between populations. For example, while the European eel (*Anguilla anguilla*, Anguillidae) has always been regarded as a classical catadromous species, requiring freshwater passage to complete its life cycle, there is now increasing evidence that it often omits the freshwater phase and can live as an adult in brackish and even coastal areas (Professor Leif Pihl, University of Gothenburg, Sweden, pers. comm.; Tsukamoto *et al.* 2002). Similarly, the southern barramundi shows a diversity and variability in the extent to which individuals within populations use marine and estuarine environments. Further examples such as this will require a re-analysis of the terms catadromy and estuarine residence (Tsukamoto *et al.* 2002).

Similarly, the initial set of examples given here suggests that some guilds are present in only some geographical regions and in some estuaries within an area and not others. In reinforcing our thesis that the guilds reflect a fundamental character of estuaries, it is of note that at present very few of the boxes in the tables are empty. Further analysis is required to determine whether this is a real feature. For example, there appears to be a lack of anadromous species from South African estuaries and it has been suggested that this may be linked to the ephemeral nature of freshwater flow in many of the region's rivers (Bruton *et al.* 1987). However, Australia, which is also an arid country, appears

to have anadromous taxa, again indicating the need for further investigation of the development of estuarine fish community structure.

The proposed guilds reinforce the role of estuaries as migration routes, feeding and refuge areas, and further highlight the importance of this understanding in contributing to fish ecology and estuarine management (Botton *et al.* 2005). While it is likely that estuarine managers will continue to require indices of estuarine health based on the species present, it is emphasized here that the guild approach has a more direct link with estuarine ecological functioning. In particular, the hydromorphological and pollution-related changes in estuaries (e.g. abstraction, industrial discharges, barriers to migration, etc.) will be reflected in changes to the availability of resources and thus the presence of guilds using those resources. Furthermore, the assessment of guilds is required to determine the resilience of estuaries and their response to anthropogenic stressors. Hence, the morphological, behavioural and physiological variability within- and between-taxa, which will allow individuals to tolerate changing environmental conditions (Ray 2005), will contribute to an estuarine system's

resilience to anthropogenic change. The increased tolerance of estuarine fishes to natural stressors has therefore created a characteristic estuarine fish community which may have the same features as anthropogenically stressed areas, a feature termed the 'estuarine quality paradox' which has to be taken into account when using biological information in estuarine management (Elliott and Quintino 2007).

The current understanding of the central role of fishes and their links between the various factors in relation to the management of estuaries is summarized in the conceptual model in Fig. 2. This follows Deegan *et al.* (1997) and Whitfield and Elliott (2002) who emphasized the need for 'functional' fish information in management initiatives and its relationship to indicators of estuarine health and change, including the type of information presented here. The guilds advocated here are embedded within the boxes 'dominant uses' in Fig. 2, thus illustrating the need for an understanding of the fundamental nature of estuarine fish assemblages and the use of that information. Because of this, there is an increasing need and tendency to represent such features quantitatively and numerically;
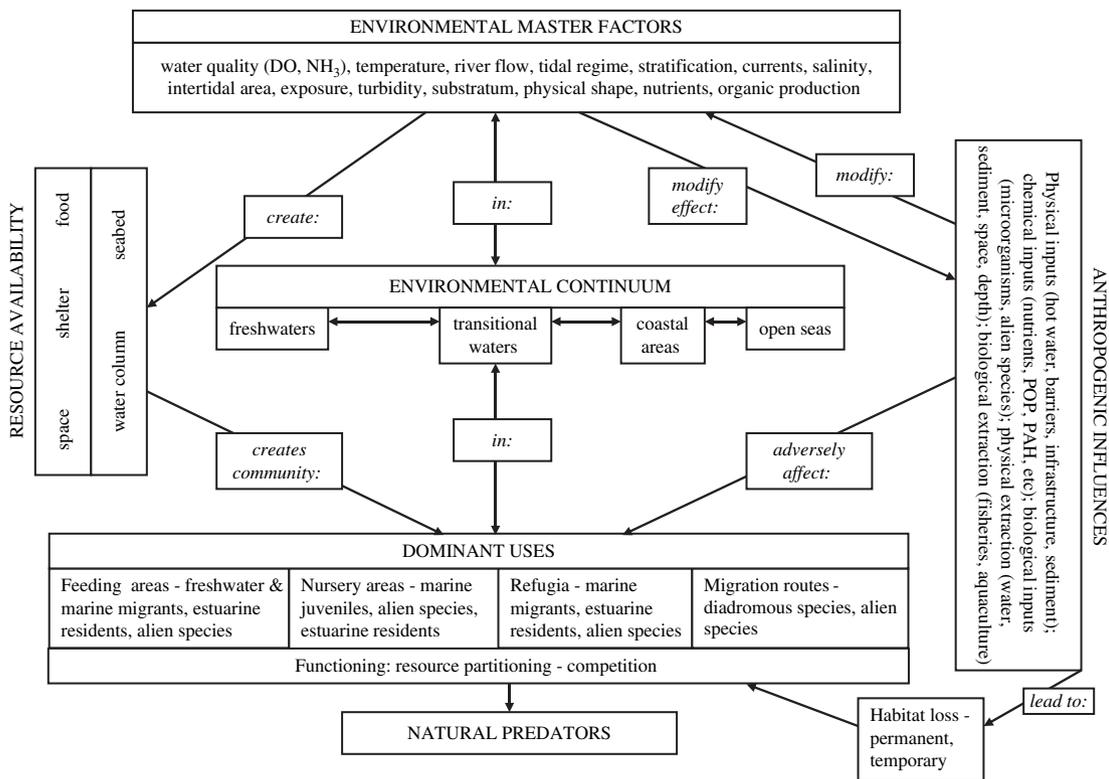

Figure 2 Conceptual model of the anthropogenic, environmental and biological influences on fishes in estuaries.

for example, Harrison and Whitfield (2004), Coates *et al.* (2007) and Breine *et al.* (2007) included fish guild information within a multimetric approach aimed at assessing change in estuaries in different biogeographic areas and Bulger *et al.* (1993) used a multivariate analysis of the salinity tolerances of estuarine fishes. In addition, Maes *et al.* (2004) indicated that guild information was a valuable approach to numerical regression modelling of estuarine fish species in relation to environmental variables. Similarly, Pombo *et al.* (2002) indicated changes in species identities but similarities in guilds over a long period tended to emphasize the stability of community structure according to functional guilds. Finally, given the importance of assessments of habitat loss and habitat gain in estuaries, and management initiatives to decrease that loss and increase the gain (Elliott and Cutts 2004; Botton *et al.* 2005), there is an increasing importance of guild studies to assess differences and changes in habitats (Franco *et al.* 2006). We emphasize that the greatest use of guilds is related to their contribution in searching for differences in biogeographical areas and at the same time similarities in estuarine fish assemblage structure irrespective of that global position.

The influence of natural and anthropogenic stressors on the structure of estuarine fish communities, as characterized by guilds, has yet to be fully quantified. In particular, there is a need to assess to what degree a reduction in guilds can occur under such stressors and whether such an analysis will indicate the resilience of estuarine systems to change and even any redundancy within estuaries. Ray (2005) suggests that an estuarine-dependent set of species, which may have opportunistic life histories, may inherently include redundancy which confers greater resilience to the estuarine community. However, it is also suggested that a euryoecious tolerance, characteristic of estuarine species, also confers both resistance to anthropogenic stressors and resilience (Elliott and Quintino 2007).

In using the fish guild approach, as with similar assessments in other areas, there are problems of interpretation and data availability. The concepts described here have been derived using extensive spatial and temporal data series for many well-studied estuaries worldwide but there is still the need for good and comprehensive biological information for each species, including data on spatial and temporal patterns. The use of the guild approach relies on a detailed understanding of

ichthyofaunae and in those areas of the world where we have this for the life cycles of estuary-associated fishes we can probably divide them into appropriate groups. Elliott and Dewailly (1995) and Whitfield (2005) show how a broad categorization of guilds similar to that described here can be very effectively used with simple presence/absence data to demonstrate similarities and differences between estuaries in different regions and their functioning. It is concluded that the categorization outlined in this review should be sufficiently broad to be globally applicable now and then refined at a future date when we know more about the biology and ecology of most species. As indicated here, there is the need for further work on the variability in life history styles of some marine migrant species in different areas, i.e. a species may be a marine estuarine-opportunist in area A but a marine estuarine-dependent species in area B. A broad categorization that encapsulates the continuum aspect with regard to estuary associations is valuable and will facilitate immediate analyses and comparisons between estuary-associated species around the world. It will also be of considerable value for further study and hypothesis generation to determine what determines whether a marine estuarine-opportunist becomes a marine estuarine-dependent species. Similarly, a rigorous treatment of these new guilds will determine any redundancy or a need for additional categories in the classification.

It is relevant, from an evolutionary perspective, to emphasize the value of obtaining sound quantitative data on the contribution by different fish to the functioning of estuaries. Variations in these contributions can then be used to hypothesize as to how differences in selective pressures in different types of estuary (e.g. macrotidal vs. microtidal and permanently open vs. intermittently open) have led to differences in the characteristics of ichthyofaunae in those estuaries. Such quantitative data have proved invaluable for facilitating comparisons between the ichthyofaunae of macrotidal European and microtidal south-western Australian estuaries and of those within a range of estuarine types in temperate Western Australia and South Africa (Potter *et al.* 1990; Potter and Hyndes 1999; Sarre and Potter 1999). The current assessment has created guilds and hopefully simplified and advanced our understanding of guild terminology for fishes in estuaries. It is our aim to encourage fish biologists from different regions to quantify the contributions made by both the number of species and number of

individuals of different guilds to the fish assemblages in the estuaries of their region. Although it is not the aim of this paper to provide such quantitative data, a rigorous 'classification' scheme as proposed here will make it more feasible to produce data that will facilitate reliable quantitative comparisons between the characteristics of estuarine ichthyofaunae in different regions. We hope that the use of our guilds in a quantitative way (numbers and/or biomass) could be a primary goal of estuarine ichthyologists worldwide. However, in the absence of comparable quantifiable data, qualitative data can also provide useful insights into both evolutionary and current estuarine fish assemblages on both a local and global scale.

Acknowledgements

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