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The ways in which fish use estuaries: a refinement and expansion of the guild approach

Alternative Title 1: *Guilds representing the different ways fish use estuaries: a refinement and expansion*

Alternative title 2: *The* u*se of estuaries by fish: a refinement and expansion of the guild approach*

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Abstract

This paper refines, clarifies and, where necessary, expands details of the guild approach developed by Elliott *et al*. (2007) for the ways in which fish use estuaries. The estuarine usage functional group is now considered to comprise four categories, *i.e.* marine, estuarine, diadromous and freshwater, with each containing multiple guilds. Emphasis has been placed on ensuring that the terminology and definitions of the guilds follow a consistent pattern, on highlighting the characteristics that identify the different guilds belonging to the estuarine category and in clarifying issues related to amphidromy. As the widely-employed term 'estuarine dependent' has frequently been imprecisely used, the proposal that the species found in estuaries can be regarded as either obligate or facultative users of these systems is supported and considered in the guild context. Thus, for example, species in the five guilds comprising the diadromous category and those in the guilds containing species or populations confined to estuaries are obligate users, whereas those in the marine and freshwater estuarine-opportunistic guilds are facultative users.

Keywords: Estuaries, estuarine dependence, estuarine usage, fishes, guilds

Introduction

The numerous fish species found in estuaries *sensu* Potter *et al.* (2010) use these systems in a variety of ways (Elliott *et al.*, 2007). For example, many are spawned in marine waters and enter estuaries for variable periods, while others complete their life cycle within the estuary and yet others employ the estuary as a migratory route from their spawning areas in the sea to their main feeding areas in freshwater or *vice versa*. An understanding of the structure and function of estuaries and an ability to manage these ecosystems and their faunas thus requires, in the case of fishes, a sound grasp of the stages in their life cycles at which the different species use estuaries and whether that usage changes at different stages and throughout the year and, if so, in what manner.

Several workers have progressively built on the pioneering proposal of Cronin and Manuseti (1971) for characterising the ways in which fish employ estuaries (*e.g.* Haedrich, 1983, Potter *et al*., 1990, Elliott and Dewailly, 1995, Potter and Hyndes, 1999, Whitfield, 1999). The gradual refinement eventually led to the review of Elliott *et al.* (2007), which integrated and harmonised the various terminologies for describing these ways into a scheme that would be applicable to estuarine ichthyofaunas worldwide and which has subsequently been widely cited and used (Scopus, 2013). This paper brought together the different life cycle categories of fishes found in these systems under the umbrella of an Estuarine Usage Functional Group (EUFG), with a similar approach being adopted for functional groups related to feeding and reproduction.

Discussions at the Estuarine and Coastal Sciences Association conference in Grahamstown, South Africa, in 2010 led to the conclusion that the terminology and definitions of some of the guilds under the EUFG required refinement, clarification and/or extension to facilitate a more rigorous understanding of estuarine structure and function and to place managers in a better position to develop more effective measures for conserving these ecosystems and their fish faunas. In this update, particular emphasis has thus been placed on refining terminology, defining the guilds that represent the species which spawn in estuaries and discussing the amphidromous guild, whose origin and relationships are still disputed (Keith, 2003, McDowall, 2007, Gross, 1987, McDowall, 2010). Focus has also been placed on building on the views of Able (2005) and Ray (2005) as to what constitutes estuarine dependence by determining which fish guilds strictly represent such dependence.

We now feel that it is valuable to recognise that the fishes that use estuaries, constituting the EUFG, can each be allocated to one of four broad categories, *i.e.* marine, estuarine, diadromous and freshwater (Table 1). Each of these categories is considered to contain two or more guilds that represent characteristics associated with the locations of spawning, feeding and/or refuge and, which, in some cases, involve migratory movements between estuaries and other ecosystems.

Marine category

In our original scheme, we considered the marine species found in estuaries to comprise either stragglers or migrants and subdivided the latter guild into marine estuarine-opportunist and marine estuarine-dependent species (Elliott *et al.*, 2007). It is now considered prudent to eliminate the term migrant and elevate the marine estuarine-opportunist and marine estuarine-dependent species to guild status (Table 1). The three guilds in the marine category thus then form a sequence, ranging from species that occur 'accidentally' in estuaries (***marine straggler***) to those that tend to enter estuaries in large numbers at some stage in their life cycle and typically during juvenile life (***marine estuarine-opportunist***) and, in turn, to those that depend on these systems for survival at a critical stage in their life cycle (***marine estuarine-dependent***) (Fig.1a, b). In the case of marine estuarine-opportunists, the migration into and emigration from estuaries by each of the species belonging to this guild is often seasonal, with the phasing varying among those species (Claridge *et al.*, 1986, Araujo *et al.,* 1998; Maes *et al.*, 2005, Hagan and Able, 2003) and thus making a major contribution to the pronounced annual cyclical changes that typically occur in the compositions of the fish faunas of estuaries each year (Potter *et al.*, 1986; Thiel and Potter, 2001; Maes *et al.*, 2005). The importance of increasing our understanding of the relationship between the habitats occupied by marine estuarine-opportunist species in estuaries and ocean environments has been emphasised by Gillanders (2002), Gillanders *et al.* (2003) and Able (2005). In the case of the snapper (*Pagrus auratus*, Sparidae), Gillanders (2002) provided strong circumstantial evidence that the adults found on reefs in eastern Australia were derived from nearby estuaries and had thus not travelled far from their nursery habitats.

It should be recognised that marine estuarine-opportunist species also frequently use coastal marine waters as an alternative nursery habitat and the relative extents to which these waters and those of estuaries are employed for this purpose vary among species (Lenanton and Potter, 1987). Moreover, even in the case of teleosts such as the flathead mullet (*Mugil cephalus,* Mugilidae), which exhibits a very marked tendency to enter estuaries, the waters along the coast can provide the sole nursery habitat in areas where there are no estuaries and still help support substantial populations of that species (Lenanton and Potter, 1987).

Marine stragglers and marine estuarine-opportunists are invariably represented in estuaries throughout the world (Potter *et al*., 1990, Franco *et al*., 2008, Blaber and Blaber, 1980, Nordlie, 2003), whereas true estuarine dependence by marine species is a far more restricted phenomenon. One such example is provided by some marine species along the southern African coast, where the highly exposed waters are considered not conducive to successful habitation by its young juveniles, which thus rely on the protected waters of estuaries for providing a suitable nursery habitat (Blaber, 1981). They are therefore designated as belonging to the ***marine estuarine-dependent*** guild. Blaber (2007) has also proposed that, as certain marine species in the tropics are found almost exclusively at some stage of their life cycle in mangrove habitats, which tend to dominate the estuarine environment in those waters, these species may also be estuarine-dependent. He recognises, however, that the evidence for this view is, at present, circumstantial.

Estuarine category

In our previous scheme, we identified two guilds, *i.e.* estuarine residents and estuarine migrants (Elliott *et al.*, 2007). While it is true that the species which always complete their entire life cycle within the estuarine environment are appropriately termed estuarine residents, this term likewise applies to the populations of some other species, that are also represented by populations which are confined either to marine or freshwater environments. It was thus inappropriate for these latter important species to have been included in the estuarine migrant guild, which also otherwise correctly contained species that spawned within the estuary but whose larval life was completed in marine waters outside the estuary.

For the above reasons, the estuarine category is now considered to comprise four guilds (Table 1). The ***solely estuarine*** guild represents those species that are confined to estuaries, *i.e.* complete their entire life cycle within the estuarine environment (Fig. 1c). The species that contain populations in which the individuals likewise complete their life cycles within the estuary, but which are also represented by populations in either marine or freshwater environments, constitute the ***estuarine & marine*** guild (Fig. 1d) and the ***estuarine & freshwater*** guild, respectively (Fig.1e). Species representing the estuarine & marine guild are far more prevalent than the estuarine & freshwater guild and, in some regions, can be very abundant (Potter and Hyndes, 1999). As such species are also represented in the marine environment and may even have been derived from individuals in populations in that environment, caution should be exercised in referring to such taxa as estuarine species. The view that these species may have had a marine origin is consistent with that fact that, in those microtidal estuaries where there are very distinct morphological differences between their regions and thus also in their environmental characteristics, such species are typically found in the lower region where salinities are elevated and often equivalent to full strength seawater (Potter and Hyndes, 1999). In contrast, species belonging to the solely estuarine guild tend to live predominantly in the middle or even upper regions, where salinities decline markedly in winter. While the estuarine populations of species such as the estuary cobbler (*Cnidoglanis macrocephalus*, Plotsidae) have been shown to be genetically distinct from those in nearshore, coastal waters (Ayvazian *et al.*, 1994), there is clearly a need to explore the extent to which such a distinction applies to a range of species and different types of estuary.

Among the few species capable of completing their life cycle in fresh water as well as estuaries is the white perch (*Morone americana*, Moronidae), which is represented in freshwater by landlocked populations in lakes (Boileau, 1985). Furthermore, biological data for the Cape silverside (*Atherina breviceps*, Atherinidae) strongly indicate that this atherinid is highly atypical in that it is capable of breeding not only in estuaries but also in marine and freshwater (coastal lake) environments (Neira *et al.*, 1988).

The ***estuarine migrant*** guild comprises species such as the prison goby (*Caffrogobius gilchristi,* Gobiidae) whose larvae are flushed out to sea and substantial numbers of which survive and return to the estuary as relatively small juveniles (Whitfield, 1989; Fig.1f). This migratory pattern corresponds to that of the amphidromous guild, whose characteristics are described below, except that spawning and the main part of the life cycle takes place in the estuary rather than the river. It is thus relevant that *C. gilchristi* belongs to the Gobiidae, whose species make such a large contribution to the amphidromous guild (McDowall, 2004) and that *C. gilchristi* also occurs in certain islands of the Indo-Pacific, where many species are amphidromous (Ryan, 1991, Thuesen *et al*., 2011, Keith, 2003, Tweedley *et al*., 2013).

In the microtidal estuaries of south-western Australia, substantial numbers of another goby, *Favonigobius lateralis*, are swept out of the estuary on the ebb tide as pre-flexion larvae and return later as post-flexion larvae on a flood tide (Neira and Potter, 1992). Such movements by *F. lateralis* and *C. gilchristi* contrast with those of other species that spawn in Southern Hemisphere estuaries, such as *Pesudogobius olorum* (Gobbidae), *Engraulis australis* (Engraulidae), *Urocampus carinirostris* (Syngnathinae) and *Gilchristella aestuaria* (Clupeidae), which, while similarly flushed out on ebb tides, rarely return on flood tides and are thus not regarded as representatives of the estuarine migrant guild.

Diadromous category

In his classic book on diadromy in fishes, McDowall (1988) essentially reiterated Myers (1949) in defining diadromy as "*truly migratory species which migrate between the sea and freshwater*" and in regarding it as containing three types, *i.e.* anadromy, catadromy and amphidromy (Table 1). **Anadromous** species were thus described as those "*diadromous fishes which spend most of their lives at sea and which migrate to fresh water to breed"* (Fig. 1g) and which are represented, for example, by several species of lampreys and salmonids (Banks, 1969, Hardisty and Potter, 1971, Thorstad *et al*., 2010,). In contrast, **catadromous** species, such as anguillid eels (Tsukamoto *et al*., 2002, Ginneken and Maes, 2005), were those "*diadromous fishes which spend most of their lives in fresh water and which migrate to the sea to breed"* (Fig. 1i). The upstream migration from the sea of a small number of anadromous species does not extend, however, beyond the upper reaches of the estuary and such species are thus termed **semi-anadromous** (Table 1; Fig.1h). Likewise, those few catadromous species whose downstream migration to the sea does not extend beyond the lower estuary are designated **semi-catadromous** (Table 1; Fig.1j).

In a recent review, Secor and Kerr (2009) drew attention to the fact that some diadromous species, in particular, exhibit life cycle diversity, *i.e.* all individuals within the populations of such species do not conform to a single life cycle pattern. The results of extensive studies on the striped bass (*Morone saxatilis,* Moronidae) on the eastern seaboard of North America provide a good example of this phenomenon. These studies, which employed elemental fingerprints in otoliths, demonstrated that the population of this species in the Hudson River comprised different contingents, with some individuals, for example, typically remaining in fresh waters and estuarine waters, rather than migrating into coastal waters as with other individuals, and that this population could thus be regarded as facultatively anadromous (Secor and Piccoli, 1996; Secor *et al.*, 2001). Furthermore, the extent to which migrating individuals move towards coastal habitats increases with age and can vary among years in response to inter-annual differences in environmental conditions. Secor *et al*. (2001) hypothesised that the maintenance of divergent life cycle pathways by anadromous species such as *M. saxatilis* confers to its populations a resilience to exploitation and environmental change. From the above, it follows that the possibility that the populations of a given diadromous species may exhibit sex, age and annual variations in migratory movements needs to be born in mind when assigning a species to a guild within the EUFG, with the qualifying term facultative for the population(s) of certain anadromous and catadromous species likely to become more prevalent.

McDowall (1988), again following Myers (1949), defines **amphidromous** species as those "*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"*. There is consequently a bi-directional movement, involving a migration both from one biome to another, in which breeding does not occur, and then back to the original biome (Fig. 1k), which thus contrasts with the migrations involved in anadromy (Fig. 1g) and catadromy (Fig. 1i) that are for the purpose of spawning. Myers (1949), Gross (1987) and McDowall (1988) recognised two types of amphidromy, *i.e.* freshwater and marine. Freshwater amphidromy involves the migration of the recently-hatched larvae of species from riverine environments to the sea, where they typically grow and feed for a short period (weeks to months), before returning to rivers, where most of the growth occurs and they subsequently reach maturity and spawn (Keith, 2003, McDowall, 2007; Fig. 2). In contrast, marine amphidromy was considered to represent the reverse migration, with spawning taking place in marine waters and the larvae/juveniles then living temporarily in fresh water before returning to the sea to grow to maturity. McDowall (1997) later concluded that there were no definitive examples of marine amphidromy and thus considered freshwater amphidromy the only form of amphidromy and consequently no longer required the prefix freshwater (McDowall, 2010, McDowall, 2009, McDowall, 2007).

Comprehensive details of the life cycles of several species with characteristics that fall under the umbrella of amphidromy and are represented in a number of families, including the Galaxiidae, Gobiidae and Eleotridae, demonstrated that these species all possess similar and distinctive life cycle traits (McDowall, 1988, Maeda and Tachihara, 2005, Keith, 2003, Bell, 2009). Indeed, McDowall (2010) was able to compile a list of eight essential features of amphidromy, including those listed in the previous paragraph, which distinguished this type of diadromy from anadromy and catadromy. While the adults of amphidromous species, which are often iteroparous, may migrate downstream to the lower rivers to spawn, this never leads to a reinvasion of the sea. As amphidromy is found mainly among species in young or volcanic islands, in which the streams have ephemeral flows, it represents an adaptation that enables such species to avoid problems posed by perturbations in these dynamic fluviatile environments and provides the potential for dispersal and colonisation of new habitats (Ryan, 1991, Thuesen *et al*., 2011, Keith, 2003, McDowall, 2010, Tweedley *et al*., 2013). While Bell (2009) considered amphidromy to be a form of anadromy, McDowall (2007) had earlier pointed out that "the return to freshwater of small juveniles of amphidromous species is functionally and strategically different from the return of large mature adults, as happens in anadromy", a view with which we entirely concur. McDowall (2007, 2010) also found no evidence to support the view of Gross (1987) that amphidromy represented a stepping stone to anadromy. Indeed, he suggested that, because the majority of the growth phase of amphidromous species was spent in freshwater, amphidromy was more akin to catadromy.

Freshwater category

This category comprises two guilds (Table 1). The freshwater species that are typically found only in low numbers in estuaries represent the ***freshwater straggler*** guild (Fig. 1l), while the freshwater species found regularly in estuaries, but generally in moderate numbers, are assigned to the ***freshwater estuarine-opportunist*** guild (Fig.1m). This latter guild, previously referred to as freshwater migrant (Elliott *et al.*, 2007), is therefore analogous to the marine estuarine-opportunist guild.

Which guilds are strictly estuarine dependent

Recognition that many commercial fish species are found in estuaries at some stage of their life cycle has led numerous authors to categorise them as 'estuarine dependent' or 'estuarine species' when discussing and quantifying the importance of this ecosystem to such species. Thus, for example, McHugh (1976) and Lellis-Dibble *et al.* (2008) calculated that these species contributed 69 and 46% to the weight of the total commercial fishery catch in the United States in 1970 and 2000-2004, respectively, and that, in the latter period, they contributed 68% to its value. The latter authors also estimated that ~80% by weight of the total recreational catch were represented by such species, but with the percentage varying markedly between regions.

It must be emphasised that the groupings used for the above corresponding 'estuarine dependent' species and 'estuarine species' are very broad and comprise marine species, estuarine residents and diadromous species. The marine category thus includes some species that are not strictly dependent on estuaries in the formal sense of the word (Pearsall and Trumble, 2002), *i.e.* estuaries are essential for the survival of the species. Indeed, we reiterate the conclusion of Able & Fahay (2010) that "estuarine dependent has become a part of resource managers' lexicons, despite a lack of critical testing or exacting definition". We also support the view of Able (2005) and Ray (2005) that the species that use estuaries extensively are best regarded as either obligate or facultative users. Thus, species belonging to the marine estuarine-dependent guild, the solely estuarine guild and the estuarine migrant guild, and all five guilds within the diadromous species category, are obligate users of estuaries. This also applies, however, to those populations of species in the estuarine & marine and estuarine & freshwater guilds in which the individuals complete their life cycles in estuaries (Table 1).

In contrast, the species in the marine estuarine-opportunist and freshwater estuarine-opportunist guilds constitute facultative users of estuaries.

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Table 1. Definitions of the different categories and guilds of the Estuarine Usage Functional Group. O and F refer to obligate and facultative users of estuaries, respectively. * refers only to the estuarine populations of the guild. NB: The absence of a designation of O and F for a guild implies that the species ‘accidentally’ stray into estuaries.

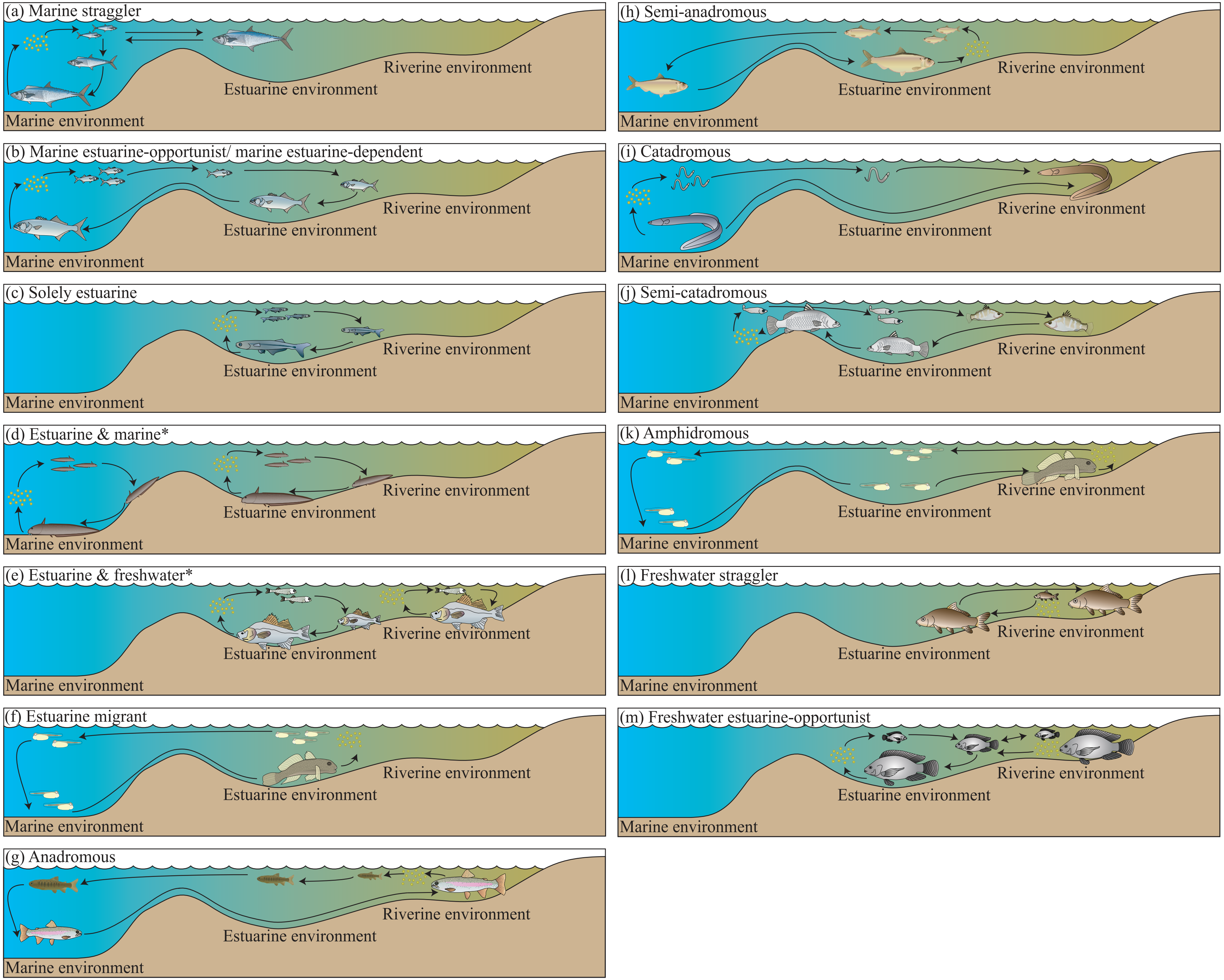
Category and guild		**Definition**	**Examples**
Marine category		Species that spawn at sea	
Marine straggler		Typically enter estuaries sporadically and in low numbers and are most common in the lower reaches where salinities typically do not decline far below ~ 35. Often stenohaline	Spanish mackerel (*Scomberomorus maculatus*, Scombridae), Sand steenbras (*Lithognathus mormyrus*, Sparidae), Colorado snapper (*Lutjanus colorado*, Lutjanidae).
Marine estuarine-opportunist	F	Regularly enter estuaries in substantial numbers, particularly as juveniles, but use, to varying degrees, coastal marine waters as alternative nursery areas	Bluefish (*Pomatomus saltatrix*, Pomatomidae), Flathead mullet (*Mugil cephalus,* Mugilidae), European seabass (*Dicentrarchus labrax*, Moronidae).
Marine estuarine-dependent	O	Juveniles require sheltered estuarine habitats and are thus not present along exposed coasts where they spend the rest of their life	Cape stumpnose (*Rhabdosargus holubi*, Sparidae), Oval moony (*Monodactylus falciformis*, Monodactylidae).
Estuarine category		Species with populations in which the individuals complete their life cycles within the estuary	
Solely estuarine	O	Found only in estuaries	Elongate hardyhead (*Atherinosoma elongate*, Atherinidae), Common goby (*Pomatoschistus microps*, Gobiidae) Estuarine round herring (*Gilchristella aestuaria*, Clupeidae).
Estuarine & marine	O*	Also represented by marine populations	Estuary Cobbler (*Cnidoglanis macroceplalus*, Plotosidae). Super klipfish (*Clinus supercilious*, Clinidae), Longsnout pipefish (*Syngnathus temmincki*, Syngnathidae).
Estuarine & freshwater	O*	Also represented by freshwater populations	White perch (*Morone americana*, Moronidae), Western hardyhead (*Leptatherina wallacei* Atherinidae), River goby (*Glossogobius callidus*, Gobiidae).

Estuarine migrant	O	Spawn in estuaries but may be flushed out to sea as larvae and later return at some stage to the estuary	Prison goby (*Caffrogobius gilchristi*, Gobiidae), Knysna sandgoby (*Psammogobius knysnaensis,* Gobiidae).
Diadromous category		Species that migrate between the sea and fresh water	
Anadromous	O	Most of their growth at sea and migrate into rivers to spawn	Chinook salmon (*Oncorhynchus tshawytscha*, Salmonidae), Sea lamprey (*Petromyzon marinus*, Petromyzontidae), Chacunda gizzard shad (*Anodontostoma chacunda* Clupeidae).
Semi-anadromous	O	Spawning run from the sea extends only as far as the upper estuary rather than into fresh water	Western Australian gizzard shad (*Nematalosa vlaminghi*, Clupeidae), Threadfin shad (*Dorosoma petenense*, Clupeidae), Toli shad (*Tenualosa toli*, Clupeidae).
Catadromous	O	Spend their trophic life in fresh water and subsequently migrate out to sea to spawn	American eel (*Anguilla rostrata*, Anguillidae), European eel (*Anguilla anguilla*, Anguillidae), Indian short-finned eel (*Anguilla bicolor pacifica*, Anguillidae).
Semi-catadromous	O	Spawning run extends only as far as downstream estuarine areas rather than into the marine environment	Barramundi (*Lates calcarifer*, Latidae).
Amphidromous	O	Spawn in fresh water, with the larvae flushed out to sea, where feeding occurs, followed by a migration back into fresh water, where most somatic growth and spawning occurs	Stimpson's goby, (*Sicyopterus stimpsoni*, Gobiidae), Banded kokopu (*Galaxias fasciatus*, Galaxiidae), Ayu (*Plecoglossus altivelis*, Plecoglossidae).
Freshwater category		Species that spawn in freshwater	
Freshwater straggler		Found in low numbers in estuaries and whose distribution is usually limited to the low salinity, upper reaches of estuaries	Goldfish (*Carassius auratus*, Cyprinidae), Northern pike (*Esox lucius*, Esocidae), Redbreast tilapia (*Tilapia rendalli*, Cichlidae).
Freshwater estuarine-opportunist	F	Found regularly and in moderate numbers in estuaries and whose distribution can extend well beyond the oligohaline sections of these systems	Mozambique tilapia (*Oreochromis mossambicus*, Cichlidae), Three-spined Stickleback (*Gasterosteus aculeatus*, Gasterosteidae), Checked goby (*Redigobius dewaali*, Gobiidae).

Figure legends

Figure 1. Guilds of fishes found in estuaries using the Estuarine Usage Functional Group approach. * refers only to the estuarine populations of the guild.

Figure 2. Migratory movements that characterise the main diadromous guilds of the Estuarine Usage Functional Group, emphasising the locations where growth mainly occurs and spawning takes place. Developed, in part, from McDowall (1988).



(a) Marine straggler
(b) Marine estuarine-opportunist/ marine estuarine-dependent
(c) Solely estuarine
(d) Estuarine & marine*
(e) Estuarine & freshwater*
(f) Estuarine migrant
(g) Anadromous
(h) Semi-anadromous
(i) Catadromous
(j) Semi-catadromous
(k) Amphidromous
(l) Freshwater straggler
(m) Freshwater estuarine-opportunist
Marine environment
Estuarine environment
Riverine environment

Figure 1

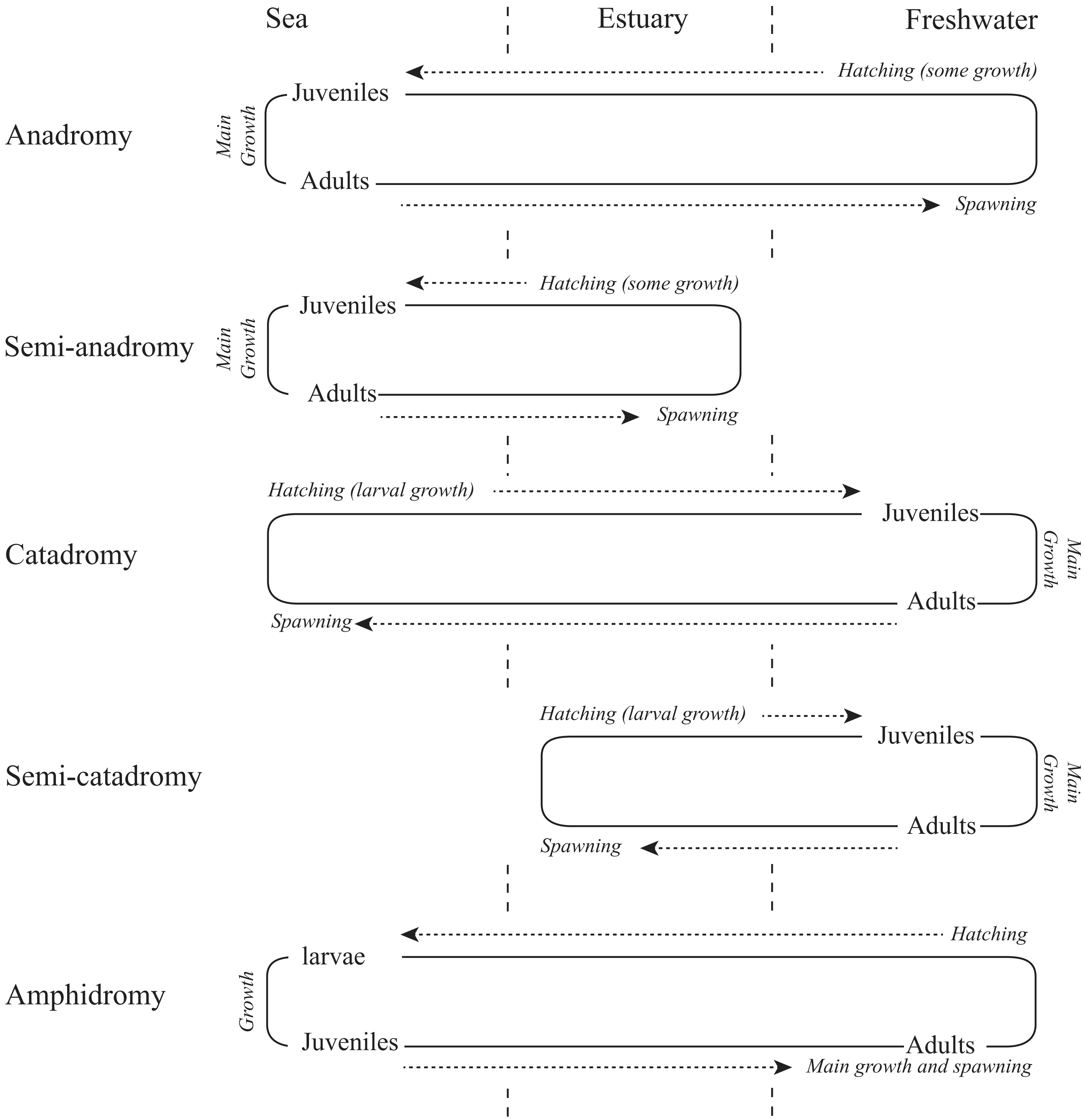

Sea
Estuary
Freshwater
Anadromy
Hatching (some growth)
Juveniles
Main Growth
Adults
Spawning
Semi-anadromy
Hatching (some growth)
Juveniles
Main Growth
Adults
Spawning
Catadromy
Hatching (larval growth)
Juveniles
Main Growth
Adults
Spawning
Semi-catadromy
Hatching (larval growth)
Juveniles
Main Growth
Adults
Spawning
Amphidromy
Hatching
larvae
Growth
Juveniles
Adults
Main growth and spawning

Figure 2