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The ways in which fish use estuaries: a refinement and
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27 **Abstract**

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

40

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

42 **Introduction**

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

51 Several workers have progressively built on the pioneering proposal of Cronin and Manuseti
52 (1971) for characterising the ways in which fish employ estuaries (*e.g.* Haedrich, 1983, Potter *et al.*,
53 1990, Elliott and Dewailly, 1995, Potter and Hyndes, 1999, Whitfield, 1999). The gradual refinement
54 eventually led to the review of Elliott *et al.* (2007), which integrated and harmonised the various
55 terminologies for describing these ways into a scheme that would be applicable to estuarine
56 ichthyofaunas worldwide and which has subsequently been widely cited and used (Scopus, 2013).
57 This paper brought together the different life cycle categories of fishes found in these systems under
58 the umbrella of an Estuarine Usage Functional Group (EUFG), with a similar approach being adopted
59 for functional groups related to feeding and reproduction.

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

68 has also been placed on building on the views of Able (2005) and Ray (2005) as to what constitutes
69 estuarine dependence by determining which fish guilds strictly represent such dependence.

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

75

76 **Marine category**

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

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

103 Marine stragglers and marine estuarine-opportunists are invariably represented in estuaries
104 throughout the world (Potter *et al.*, 1990, Franco *et al.*, 2008, Blaber and Blaber, 1980, Nordlie,
105 2003), whereas true estuarine dependence by marine species is a far more restricted phenomenon. One
106 such example is provided by some marine species along the southern African coast, where the highly
107 exposed waters are considered not conducive to successful habitation by its young juveniles, which
108 thus rely on the protected waters of estuaries for providing a suitable nursery habitat (Blaber, 1981).
109 They are therefore designated as belonging to the *marine estuarine-dependent* guild. Blaber (2007)
110 has also proposed that, as certain marine species in the tropics are found almost exclusively at some
111 stage of their life cycle in mangrove habitats, which tend to dominate the estuarine environment in
112 those waters, these species may also be estuarine-dependent. He recognises, however, that the
113 evidence for this view is, at present, circumstantial.

114

115 **Estuarine category**

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

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

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

150 The *estuarine migrant* guild comprises species such as the prison goby (*Caffrogobius*
151 *gilchristi*, Gobiidae) whose larvae are flushed out to sea and substantial numbers of which survive and

152 return to the estuary as relatively small juveniles (Whitfield, 1989; Fig.1f). This migratory pattern
153 corresponds to that of the amphidromous guild, whose characteristics are described below, except that
154 spawning and the main part of the life cycle takes place in the estuary rather than the river. It is thus
155 relevant that *C. gilchristi* belongs to the Gobiidae, whose species make such a large contribution to
156 the amphidromous guild (McDowall, 2004) and that *C. gilchristi* also occurs in certain islands of the
157 Indo-Pacific, where many species are amphidromous (Ryan, 1991, Thuesen *et al.*, 2011, Keith, 2003,
158 Tweedley *et al.*, 2013).

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

167

168 **Diadromous category**

169 In his classic book on diadromy in fishes, McDowall (1988) essentially reiterated Myers
170 (1949) in defining diadromy as “*truly migratory species which migrate between the sea and*
171 *freshwater*” and in regarding it as containing three types, *i.e.* anadromy, catadromy and amphidromy
172 (Table 1). **Anadromous** species were thus described as those “*diadromous fishes which spend most of*
173 *their lives at sea and which migrate to fresh water to breed*” (Fig. 1g) and which are represented, for
174 example, by several species of lampreys and salmonids (Banks, 1969, Hardisty and Potter, 1971,
175 Thorstad *et al.*, 2010,). In contrast, **catadromous** species, such as anguillid eels (Tsukamoto *et al.*,
176 2002, Ginneken and Maes, 2005), were those “*diadromous fishes which spend most of their lives in*
177 *fresh water and which migrate to the sea to breed*” (Fig. 1i). The upstream migration from the sea of
178 a small number of anadromous species does not extend, however, beyond the upper reaches of the
179 estuary and such species are thus termed **semi-anadromous** (Table 1; Fig.1h). Likewise, those few

180 catadromous species whose downstream migration to the sea does not extend beyond the lower
181 estuary are designated **semi-catadromous** (Table 1; Fig.1j).

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

199 McDowall (1988), again following Myers (1949), defines **amphidromous** species as those
200 “*diadromous fishes whose migration from fresh water to the sea, or vice versa, is not for the purpose*
201 *of breeding, but occurs regularly at some other definite stage of the life cycle*”. There is consequently
202 a bi-directional movement, involving a migration both from one biome to another, in which breeding
203 does not occur, and then back to the original biome (Fig. 1k), which thus contrasts with the migrations
204 involved in anadromy (Fig. 1g) and catadromy (Fig. 1i) that are for the purpose of spawning. Myers
205 (1949), Gross (1987) and McDowall (1988) recognised two types of amphidromy, *i.e.* freshwater and
206 marine. Freshwater amphidromy involves the migration of the recently-hatched larvae of species from
207 riverine environments to the sea, where they typically grow and feed for a short period (weeks to

208 months), before returning to rivers, where most of the growth occurs and they subsequently reach
209 maturity and spawn (Keith, 2003, McDowall, 2007; Fig. 2). In contrast, marine amphidromy was
210 considered to represent the reverse migration, with spawning taking place in marine waters and the
211 larvae/juveniles then living temporarily in fresh water before returning to the sea to grow to maturity.
212 McDowall (1997) later concluded that there were no definitive examples of marine amphidromy and
213 thus considered freshwater amphidromy the only form of amphidromy and consequently no longer
214 required the prefix freshwater (McDowall, 2010, McDowall, 2009, McDowall, 2007).

215 Comprehensive details of the life cycles of several species with characteristics that fall under
216 the umbrella of amphidromy and are represented in a number of families, including the Galaxiidae,
217 Gobiidae and Eleotridae, demonstrated that these species all possess similar and distinctive life cycle
218 traits (McDowall, 1988, Maeda and Tachihara, 2005, Keith, 2003, Bell, 2009). Indeed, McDowall
219 (2010) was able to compile a list of eight essential features of amphidromy, including those listed in
220 the previous paragraph, which distinguished this type of diadromy from anadromy and catadromy.
221 While the adults of amphidromous species, which are often iteroparous, may migrate downstream to
222 the lower rivers to spawn, this never leads to a reinvasion of the sea. As amphidromy is found mainly
223 among species in young or volcanic islands, in which the streams have ephemeral flows, it represents
224 an adaptation that enables such species to avoid problems posed by perturbations in these dynamic
225 fluvial environments and provides the potential for dispersal and colonisation of new habitats
226 (Ryan, 1991, Thuesen *et al.*, 2011, Keith, 2003, McDowall, 2010, Tweedley *et al.*, 2013). While Bell
227 (2009) considered amphidromy to be a form of anadromy, McDowall (2007) had earlier pointed out
228 that “the return to freshwater of small juveniles of amphidromous species is functionally and
229 strategically different from the return of large mature adults, as happens in anadromy”, a view with
230 which we entirely concur. McDowall (2007, 2010) also found no evidence to support the view of
231 Gross (1987) that amphidromy represented a stepping stone to anadromy. Indeed, he suggested that,
232 because the majority of the growth phase of amphidromous species was spent in freshwater,
233 amphidromy was more akin to catadromy.

234

235 **Freshwater category**

236 This category comprises two guilds (Table 1). The freshwater species that are typically found
237 only in low numbers in estuaries represent the *freshwater straggler* guild (Fig. 11), while the
238 freshwater species found regularly in estuaries, but generally in moderate numbers, are assigned to the
239 *freshwater estuarine-opportunist* guild (Fig.1m). This latter guild, previously referred to as
240 freshwater migrant (Elliott *et al.*, 2007), is therefore analogous to the marine estuarine-opportunist
241 guild.

242

243 **Which guilds are strictly estuarine dependent**

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

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

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

266

267 **References**

268 Able, K.W. (2005) A re-examination of fish estuarine dependence: evidence for connectivity between
269 estuarine and ocean habitats. *Estuarine, Coastal and Shelf Science* **64**, 5-17.

270 Able, K.W., Fahay, M.P. (2010) *Ecology of estuarine fishes: temperate waters of the western north*
271 *Atlantic*, Johns Hopkins University Press, Baltimore, USA.

272 Araujo, F.G., Bailey, R.G., Williams, W.P. (1998) Seasonal and between-year variations of fish
273 populations in the middle Thames estuary: 1980-1989. *Fisheries Management and Ecology* **5**,
274 1-21.

275 Ayvazian, S.G., Johnson, M.S., McGlashan, D.J. (1994) High levels of genetic subdivision of marine
276 and estuarine populations of the estuarine catfish *Cnidoglanis macrocephalus* (Plotosidae) in
277 southwestern Australia. *Marine Biology* **118**, 25-31.

278 Banks, J.W. (1969) A review of the literature on the upstream migration of adult salmonids. *Journal*
279 *of Fish Biology* **1**, 85-136.

280 Bell, K.N.I. (2009) What comes down must go up: the migration cycle of juvenile-return anadromous
281 taxa. *American Fisheries Society Symposium* **69**, 321-341.

282 Blaber, S.J.M. (1981) The zoogeographical affinities of estuarine fishes in south east Africa. *South*
283 *African Journal of Science* **77**, 305-307.

284 Blaber, S.J.M. (2007) Mangroves and fishes: issues of diversity, dependence, and dogma. *Bulletin of*
285 *Marine Science* **80**, 457-472.

286 Blaber, S.J.M., Blaber, T.G. (1980) Factors affecting the distribution of juvenile estuarine and inshore
287 fish. *Journal of Fish Biology* **17**, 143-162.

- 288 Boileau, M.G. (1985) The expansion of white perch, *Morone americana*, in the lower Great Lakes.
289 *Fisheries* **10**, 6-10.
- 290 Claridge, P.N., Potter, I.C., Hardisty, M.W. (1986) Seasonal changes in movements, abundance, size
291 composition and diversity of the fish fauna of the Severn Estuary. *Journal of the Marine*
292 *Biological Association of the United Kingdom* **66**, 229-258.
- 293 Cronin, L.E., Mansueti, A.J. (1971) The biology of the estuary. In: *A symposium on the biological*
294 *significance of estuaries*. (Eds. P.A. Douglas, R.H. Stroud), Sport Fishing Institute,
295 Washington DC, pp. 14-39.
- 296 Elliott, M., Dewailly, F. (1995) Structure and components of European estuarine fish assemblages.
297 *Netherlands Journal of Aquatic Ecology* **29**, 397-417.
- 298 Elliott, M., Whitfield, A.K., Potter, I.C., Blaber, S.J.M., Cyrus, D.P., Nordlie, F.G., Harrison, T.D.
299 (2007) The guild approach to categorizing estuarine fish assemblages: A global review. *Fish*
300 *and Fisheries* **8**, 241-268.
- 301 Franco, A., Elliott, M., Franzoi, P., Torricelli, P. (2008) Life strategies of fishes in European estuaries:
302 the functional guild approach. *Marine Ecology Progress Series* **354**, 219-228.
- 303 Gillanders, B.M. (2002) Connectivity between juvenile and adult fish populations: do adults remain
304 near their recruitment estuaries? *Marine Ecology Progress Series* **240**, 215–223.
- 305 Gillanders, B.M., Able, K.W., Brown, J.A., Eggleston, D.B., Sheridan, P.F. (2003) Evidence for
306 connectivity between juvenile & adult habitats for mobile marine fauna: an important
307 component of nurseries. *Marine Ecology Progress Series* **247**, 281-295.
- 308 Ginneken, V.J.T., Maes, G.E. (2005) The European eel (*Anguilla anguilla*, Linnaeus), its lifecycle,
309 evolution and reproduction: a literature review. *Reviews in Fish Biology and Fisheries* **15**,
310 367-398.

311 Gross, M.R. Evolution of diadromy in fishes. (Proceedings of the Common strategies of anadromous
312 and catadromous fishes, Bethesda, Maryland., 1987). (Eds. M.J. Dadswell, C.R.J. Klauda, M.
313 Moffitt, R.L. Saunders), American Fisheries Society, Maryland, pp. 14-24.

314 Haedrich, R.L. (1983) Estuarine fishes. In: *Estuaries and enclosed seas*. (Ed. B. Ketchum), Elsevier,
315 Amsterdam, pp. 183-207.

316 Hagan, S.M., Able, K.W. (2003) Seasonal changes of the pelagic fish assemblage in a temperate
317 estuary. *Estuarine, Coastal and Shelf Science* **56**, 15-29.

318 Hardisty, M.W., Potter, I.C. (1971) The general biology of adult lampreys. In: *The biology of*
319 *lampreys*. Vol. 1. (Eds. M.W. Hardisty, I.C. Potter), Academic Press, London, pp. 127-206.

320 Keith, P. (2003) Biology and ecology of amphidromous Gobiidae of the Indo-Pacific and the
321 Caribbean regions. *Journal of Fish Biology* **63**, 831-847.

322 Lellis-Dibble, K.A., McGlynn, K.E., Bigford, T.E. (2008) Estuarine fish and shellfish species in U.S.
323 commercial and recreational fisheries: economic value as an incentive to protect and restore
324 estuarine habitat. pp. 94. Available from <http://spo.nmfs.noaa.gov/tm/TM90.pdf> [last accessed
325 July 2013].

326 Lenanton, R., Potter, I. (1987) Contribution of estuaries to commercial fisheries in temperate Western
327 Australia and the concept of estuarine dependence. *Estuaries and Coasts* **10**, 28-35.

328 Maeda, K., Tachihara, K. (2005) Recruitment of amphidromous sleepers *Eleotris acanthopoma*,
329 *Eleotris melanosoma*, and *Eleotris fusca* into the Teima River, Okinawa Island.
330 *Ichthyological Research* **52**, 325-335.

331 Maes, J., Stevens, M., Ollevier, F. (2005) The composition and community structure of the
332 ichthyofauna of the upper Scheldt Estuary: synthesis of a 10-year data collection (1991-2001).
333 *Journal of Applied Ichthyology* **21**, 86-93.

- 334 McDowall, R.M. (1988) *Diadromy in fishes: migration between freshwater and marine environments*.
335 Croom Helm, London.
- 336 McDowall, R.M. (1997) The evolution of diadromy in fishes (revisited) and its place in phylogenetic
337 analysis. *Reviews in Fish Biology and Fisheries* **7**, 443-462.
- 338 McDowall, R.M. (2004) Ancestry and amphidromy in island freshwater fish faunas. *Fish and*
339 *Fisheries* **5**, 75-85.
- 340 McDowall, R.M. (2007) On amphidromy, a distinct form of diadromy in aquatic organisms. *Fish and*
341 *Fisheries* **8**, 1-13.
- 342 McDowall, R.M. (2009) Early hatch: a strategy for safe downstream larval transport in amphidromous
343 gobies. *Reviews in Fish Biology and Fisheries* **19**, 1-8.
- 344 McDowall, R.M. (2010) Why be amphidromous: expatrial dispersal and the place of source and sink
345 population dynamics? *Reviews in Fish Biology and Fisheries* **20**, 87-100.
- 346 McHugh, J.L. (1976) Estuarine fisheries: are they doomed? In: *Estuarine processes*. (Ed. M. Wiley),
347 Academic Press, New York, pp. 15-27.
- 348 Myers, G.S. (1949) Usage of anadromous, catadromous and allied terms for migratory fishes. *Copeia*
349 **1949**, 89-97.
- 350 Neira, F.J., Potter, I.C. (1992) Movement of larval fishes through the entrance channel of a seasonally
351 open estuary in Western Australia. *Estuarine, Coastal and Shelf Science* **35**, 213-224.
- 352 Neira, P., Beckley, L.E., Whitfield, A.K. (1988) Larval development of the Cape silverside *Atherina*
353 *breviceps* Cuv. & Val. 1875 (Teleostei, Atherinidae) from southern Africa. *South African*
354 *Journal of Zoology* **23**, 176-183.
- 355 Nordlie, F.G. (2003) Fish communities of estuarine salt marshes of eastern North America, and
356 comparisons with temperate estuaries of other continents. *Reviews in Fish Biology and*
357 *Fisheries* **13**, 281-325.

358 Pearsall, J., Trumble, B. (2002) *Oxford English reference dictionary*. Oxford University Press,
359 Oxford.

360 Potter, I.C., Claridge, P.N., Warwick, R.M. (1986) Consistency of seasonal changes in an estuarine
361 fish assemblage. *Marine Ecology Progress Series* **32**, 217-228.

362 Potter, I.C., Beckley, L.E., Whitfield, A.K., Lenanton, R.C. (1990) Comparisons between the roles
363 played by estuaries in the life cycles of fishes in temperate Western Australia and Southern
364 Africa. *Environmental Biology of Fishes* **28**, 143-178.

365 Potter, I.C., Chuwen, B.M., Hoeksema, S.D., Elliott, M. (2010) The concept of an estuary: a definition
366 that incorporates systems which can become closed to the ocean and hypersaline. *Estuarine,
367 Coastal and Shelf Science* **87**, 497-500.

368 Potter, I.C., Hyndes, G.A. (1999) Characteristics of the ichthyofaunas of southwestern Australian
369 estuaries, including comparisons with holarctic estuaries and estuaries elsewhere in temperate
370 Australia: a review. *Austral Ecology* **24**, 395-421.

371 Ray, G.C. (2005) Connectivities of estuarine fishes to the coastal realm. *Estuarine, Coastal and Shelf
372 Science* **64**, 18-32.

373 Ryan, P.A. (1991) The success of the Gobiidae in tropical Pacific insular streams. *New Zealand
374 Journal of Zoology* **18**, 25-30.

375 Scopus (2013) Available from <http://www.scopus.com> [last accessed July 2013].

376 Secor, D. H., Piccoli, P. M. (1996) Age- and sex-dependent migrations of the Hudson River striped
377 bass population determined from otolith microanalysis. *Estuaries* **19**, 778-793.

378 Secor, D. H., Rooker, J. R., Zlokovitz, E., Zdanovwcz, V. S. (2001) Identification of riverine,
379 estuarine and coastal contingents of Hudson River striped bass based on elemental
380 fingerprints. *Marine Ecology Progress Series* **211**, 245-253.

- 381 Secor, D.H., Kerr, L.A. (2009) A lexicon of life cycle diversity in diadromous and other fishes. In
382 *Challenges for diadromous fishes in a dynamic global environment* (Eds. Haro, A.J., Smith,
383 K. L., Rulifson, R. A., Moffitt, C. M., Klauda, R. J., Dadswell, M. J., Cunjak, R. A., Cooper,
384 J. E., Beal, K. L., Avery, T. S.), American Fisheries Society, Symposium 69, Bethesda,
385 Maryland, pp. 537-556.
- 386 Thiel, R., Potter, I.C. (2001) The ichthyofaunal composition of the Elbe Estuary: an analysis in space
387 and time. *Marine Biology* **138**, 603-616.
- 388 Thorstad, E.B., Whoriskey, F., Rikardsen, A.H., Aarestrup, K. (2010) Aquatic nomads: the life and
389 migrations of the Atlantic Salmon. In: *Atlantic salmon ecology*. (Eds. Ø. Aas, S. Einum, A.
390 Klemetsen, J. Skurdal), Wiley-Blackwell, Oxford, pp. 1-32.
- 391 Thuesen, P.A., Ebner, B.C., Larson, H., Keith, P., Silcock, R.M., Prince, J., Russell, D.J. (2011)
392 Amphidromy links a newly documented fish community of continental Australian streams, to
393 oceanic islands of the west Pacific. *PLoS ONE* **6**, e26685.
- 394 Tsukamoto, K., Aoyama, J., Miller, M.J. (2002) Migration, speciation, and the evolution of diadromy
395 in anguillid eels. *Canadian Journal of Fisheries and Aquatic Sciences* **59**, 1989-1998.
- 396 Tweedley, J.R., Bird, D.J., Potter, I.C., Gill, H.S., Miller, P.J., O'Donovan, G., Tjakrawidjaja, A.H.
397 (2013) Species compositions and ecology of the riverine ichthyofaunas on two Sulawesian
398 islands in the biodiversity hotspot of Wallacea. *Journal of Fish Biology* **82**, 1916-1950.
- 399 Whitfield, A.K. (1989) Ichthyoplankton interchange in the mouth region of a southern African
400 estuary. *Marine Ecology Progress Series* **54**, 25-33.
- 401 Whitfield, A.K. (1999) Ichthyofaunal assemblages in estuaries: a South African case study. *Reviews*
402 *in Fish Biology and Fisheries* **9**, 151-186.

403 **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
 404 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
 405 ‘accidentally’ stray into estuaries.

406

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 (<i>Scomberomorus maculatus</i> , Scombridae), Sand steenbras (<i>Lithognathus mormyrus</i> , Sparidae), Colorado snapper (<i>Lutjanus colorado</i> , 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 (<i>Pomatomus saltatrix</i> , Pomatomidae), Flathead mullet (<i>Mugil cephalus</i> , Mugilidae), European seabass (<i>Dicentrarchus labrax</i> , 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 (<i>Rhabdosargus holubi</i> , Sparidae), Oval moony (<i>Monodactylus falciformis</i> , 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 (<i>Atherinosoma elongate</i> , Atherinidae), Common goby (<i>Pomatoschistus microps</i> , Gobiidae), Estuarine round herring (<i>Gilchristella aestuaria</i> , Clupeidae).
Estuarine & marine	O*	Also represented by marine populations	Estuary Cobbler (<i>Cnidoglanis macrocephalus</i> , Plotosidae), Super klipfish (<i>Clinus superciliosus</i> , Clinidae), Longsnout pipefish (<i>Syngnathus temmincki</i> , Syngnathidae).
Estuarine & freshwater	O*	Also represented by freshwater populations	White perch (<i>Morone americana</i> , Moronidae), Western hardyhead (<i>Leptatherina wallacei</i> , Atherinidae), River goby (<i>Glossogobius callidus</i> , 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 (<i>Caffrogobius gilchristi</i> , Gobiidae), Knysna sandgoby (<i>Psammogobius knysnaensis</i> , 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 (<i>Oncorhynchus tshawytscha</i> , Salmonidae), Sea lamprey (<i>Petromyzon marinus</i> , Petromyzontidae), Chacunda gizzard shad (<i>Anodontostoma chacunda</i> 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 (<i>Nematalosa vlaminghi</i> , Clupeidae), Threadfin shad (<i>Dorosoma petenense</i> , Clupeidae), Toli shad (<i>Tenuالosa toli</i> , Clupeidae).
Catadromous	O	Spend their trophic life in fresh water and subsequently migrate out to sea to spawn	American eel (<i>Anguilla rostrata</i> , Anguillidae), European eel (<i>Anguilla anguilla</i> , Anguillidae), Indian short-finned eel (<i>Anguilla bicolor pacifica</i> , Anguillidae).
Semi-catadromous	O	Spawning run extends only as far as downstream estuarine areas rather than into the marine environment	Barramundi (<i>Lates calcarifer</i> , 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, (<i>Sicyopterus stimpsoni</i> , Gobiidae), Banded kokopu (<i>Galaxias fasciatus</i> , Galaxiidae), Ayu (<i>Plecoglossus altivelis</i> , 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 (<i>Carassius auratus</i> , Cyprinidae), Northern pike (<i>Esox lucius</i> , Esocidae), Redbreast tilapia (<i>Tilapia rendalli</i> , 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 (<i>Oreochromis mossambicus</i> , Cichlidae), Three-spined Stickleback (<i>Gasterosteus aculeatus</i> , Gasterosteidae), Checked goby (<i>Redigobius dewaali</i> , 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).

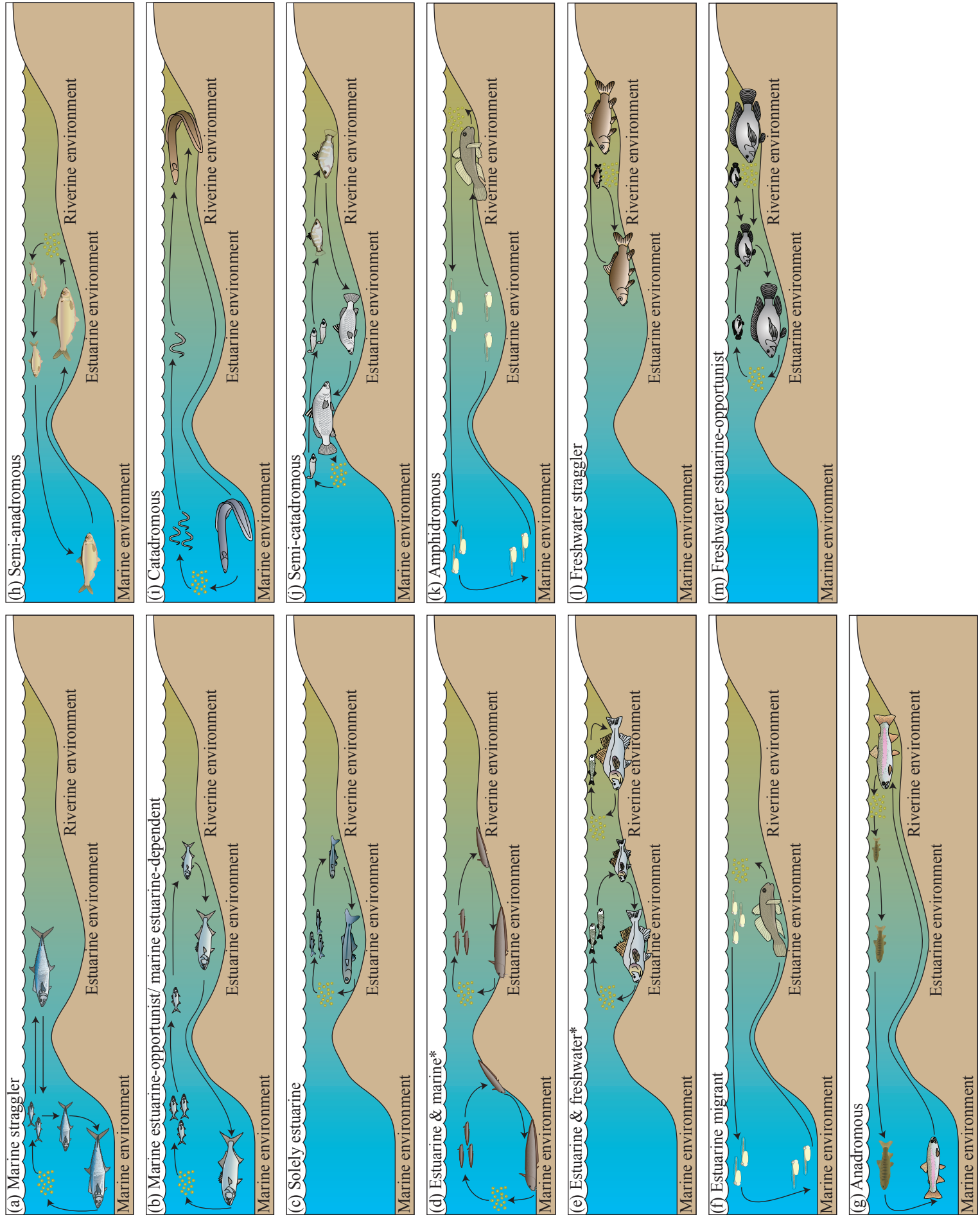


Figure 1

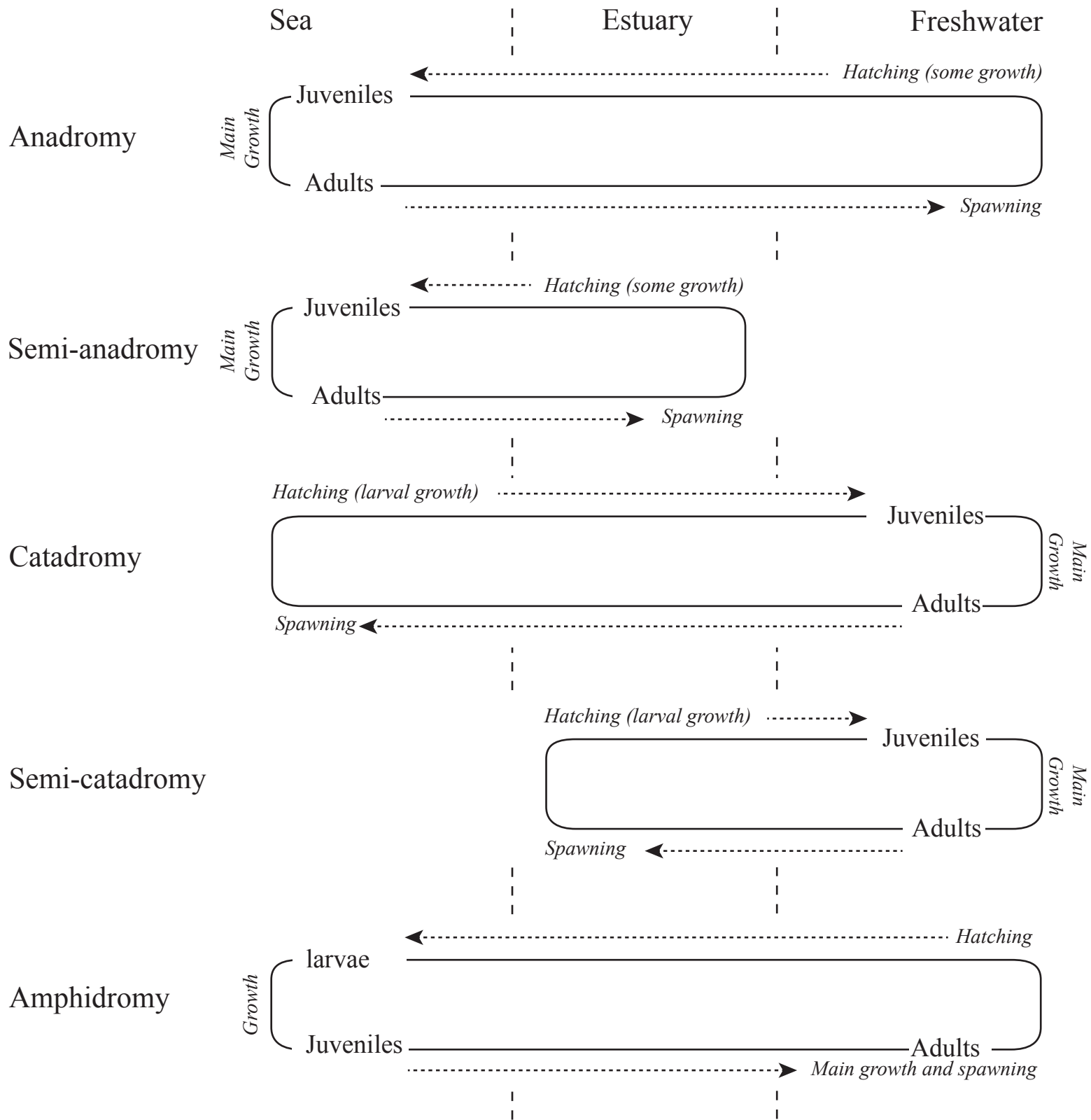


Figure 2