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2.4. The physico-chemical characteristics, biota and fisheries of estuaries

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Abstract

The characteristics of the biota and fisheries of estuaries are considered in the context of a contemporary definition that recognizes the physico-chemical features of the different estuary types found worldwide, *i.e.* macrotidal *v.* microtidal and permanently-open *v.* seasonally-open *v.* normally-closed. The ways in which fishes use estuaries, feed and reproduce are categorized and exemplified by fishery-important species from their constituent guilds. Marine species, and particularly their juveniles, dominate the fish faunas of permanently-open estuaries. The prevalence and abundance of species either confined to estuaries or represented by estuarine populations that are discrete from their marine counterparts are far greater in systems that are periodically closed to the sea by sand bars at their mouths. Anthropogenic activities are continuing to have marked effects on estuarine environments and, in extreme circumstances, have had highly deleterious impacts on the fish faunas and fisheries of these systems.

Keywords macro- and meso-tidal estuaries; fishes; invertebrates; reproduction; life cycle categories and guilds; fisheries; case histories; estuarine dependence; connectivity; anthropogenic effects and threats

INTRODUCTION

Estuaries are among the most productive of all aquatic ecosystems (Schelske & Odum, 1961; Whittaker & Likens, 1975; Whitfield & Elliott, 2011) and yet represent the most degraded of all marine ecosystems (Jackson *et al.*, 2001a). They constitute, in particular, an important nursery area for many marine species of fishes, several of which are of commercial and recreational importance (Haedrich, 1983; Potter *et al.*, 1990; Elliott & Hemingway, 2002; Able & Fahay, 2010), as well as providing an essential route for diadromous species to migrate between their spawning and main feeding areas (McDowall, 1988). The high productivity of estuaries enables the juveniles of marine species to grow rapidly and thereby become less susceptible to predation (Sogard, 1992; Potter *et al.*, 2011), while the high turbidity in those estuaries with a strong tidal influence reduces the visibility of fishes to visual avian and fish piscivores (Blaber & Blaber, 1980; Robertson & Blaber, 1992; Elliott *et al.*, 2002). Macrophytes, such as seagrass and mangroves, also provide cover as well as a habitat for the prey of juvenile fishes in certain estuaries (Odum & Heald, 1972; Boesch & Turner, 1984; Humphries *et al.*, 1992; Humphries & Potter, 1993; Nagelkerken *et al.*, 2000; Jackson *et al.*, 2001b). In addition to their crucial nursery function for certain fish species, estuaries also house commercial and recreational fisheries for a number of species and are becoming increasingly important in facilitating the aquaculture of valuable finfish, crustacean and mollusc species (Wilson, 2002). From a fisheries perspective, it has been estimated that, in the U.S.A., the combined biomass of the wild species that are found in estuaries at some stage of their life cycles made a very substantial contribution to the commercial fishery in that country in 1970 (McHugh, 1976) and continues to do so (Lellis-Dibble *et al.*, 2008).

Salinity undergoes pronounced changes during each tidal cycle in those estuaries with a strong tidal regime, and also throughout the year in most estuaries as freshwater discharge either increases or decreases substantially, as often occurs on a seasonal basis. The estuaries with a strong tidal flow are also highly turbulent and turbid. While the estuarine environment thus poses considerable physiological and physical challenges to its fauna, it does provide an excellent environment for rapid growth by those species that possess the osmoregulatory, physical and behavioural characteristics required to cope effectively with those stresses and the ability to exploit

effectively the high productivity of these water bodies (Elliott & Quintino, 2007). As a consequence, estuaries are typically characterized by a greater density but lower diversity of organisms than the local marine environment into which they discharge (Snelgrove, 2001; Josefson & Hansen, 2004; McLusky & Elliott, 2004; Hourston *et al.*, 2011).

As this chapter on fishes and fisheries deals specifically with estuaries, which represent the interface between rivers and the sea, and the other chapters in this book focus on freshwater fishes and fisheries, emphasis is first placed on outlining the range of physico-chemical characteristics that distinguish this complex type of system. The resultant definition is crucial for developing effective and appropriate management plans for estuaries and their fisheries (Elliott & McLusky, 2002), noting that management strategies for the fisheries may vary among the estuaries in a given region and among jurisdictions. This definition, and the subsequent sections that deal with the fauna, emphasizes the characteristics of the very different types of estuary found throughout the world. It thus includes, in particular, details of the permanently-open, seasonally-open and normally-closed estuaries often found along the same coasts in microtidal regions and for which we have extensive first-hand experience, rather than concentrating predominantly on the permanently-open and often macrotidal systems in temperate regions of the northern hemisphere, which have been the focus of many studies and reviews (Cronin & Mansueti, 1971; Haedrich, 1983; Elliott & Hemingway, 2002; Able & Fahay, 2010).

In this review, we follow Elliott *et al.* (2007) who considered the biology of the fish species found in estuaries in the context of the following three functional groups. (1) estuarine use, *i.e.* how and at what life cycle stages the estuary is used, (2) feeding mode and (3) reproductive mode, each of which is then separated into a number of guilds. Attention is drawn to examples of the constituent species of each life cycle guild *sensu* Potter *et al.*, (2013) and particularly those of commercial and recreational value. The biota of estuaries, which comprise the main food types of fishes, *e.g.* detritus, microphytobenthos, invertebrate meio- and macrofaunas and other fishes, and also their characteristics and origins are then highlighted.

The development of methods for catching fishes in estuaries and the fishery for diadromous species in marine, estuarine and riverine environments is next described. This is followed by an

account of the decline and subsequent restoration of the environment and fisheries in the Thames Estuary and its tributary rivers, which provides a classical example of the impacts of extreme anthropogenic influences and the resultant success of massive efforts to restore a system that had undergone huge perturbations. The broad life cycle characteristics of a few exploited species that use estuaries and represent selected life cycle guilds of the estuarine use functional group are discussed, together with very broad outlines of certain relevant features of their fisheries. Finally, the major threats to estuarine environments and their faunas and the challenges that managers thus face are summarized.

DEFINITION OF AN ESTUARY

In Europe, the term transitional waters is becoming increasingly used to describe all water bodies between fresh water and the marine environment and thus include not only estuaries, but rias, fjords, lagoons and intermittently closed and open lakes and lagoons (ICOLLs) (McLusky & Elliott, 2007). There has long been a recognition, however, that it is crucial for both scientists and environmental and fisheries managers to have a reliable definition of estuaries (Elliott & McLusky, 2002; Potter *et al.*, 2010). The wide variation in the physico-chemical characteristics of estuarine ecosystems has meant that this was not an easy task.

The need to have a reliable definition of an estuary led, in 1964, to the convening of a special committee of the American Association for the Advancement of Science to address this issue (Lauff, 1967) and this produced the following definition: ‘An estuary is a semi-enclosed coastal body of water which has a free connection with the open sea and within which sea water is measurably diluted with fresh water derived from land drainage’ (Pritchard, 1967). This definition was largely based, however, on experience with permanently-open and predominantly macrotidal estuaries in temperate regions of the Northern Hemisphere and did not take into account the very different characteristics of estuaries along, for example, the temperate southern coasts of Australia and Africa. Some of the latter estuaries become closed from the ocean through the formation of sand bars at their mouths, either seasonally or intermittently, and, in some cases, now even remain normally closed. Consequently, Day (1980, 1981) proposed that the above definition should be modified to the following: ‘An estuary

is a partially enclosed coastal body of water which is either permanently or periodically open to the sea and within which there is a measurable variation of salinity due to the mixture of sea water with fresh water derived from land drainage’.

It should also be recognized that the waters of some estuaries in southern Australia and Africa can become markedly hypersaline as a result of high rates of evaporation during the warmer and drier months of the year (Day, 1980; Cooper, 2001; Young & Potter, 2002). Furthermore, the definitions of Pritchard (1967) and Day (1980, 1981) do not specifically state that freshwater input should be derived directly from a riverine source. For these reasons, the definition of the estuary provided by those workers was further modified to the following: ‘An estuary is a partially enclosed coastal body of water that is either permanently or periodically open to the sea and which receives at least periodic discharge from a river(s), and thus, while its salinity is typically less than that of natural sea water and varies temporally and along its length, it can become hypersaline in regions when evaporative water loss is high and freshwater and tidal inputs are negligible’ (Potter *et al.*, 2010). Recently, Elliott & Whitfield (2011), have generated eight paradigms that summarize the main characteristics of the structure, functioning and management of estuaries.

The question of what constitutes the precise boundaries of the estuary with the river and the sea has still to be fully resolved (Wolanski, 2007). For example, in the case of its seawards boundary, some workers prefer to use morphological or geomorphological criteria while others prefer those based on salinity regimes (Whitfield & Elliott, 2011).

COMPARISONS OF THE CHARACTERISTICS OF MACROTIDAL AND MICROTIDAL ESTUARIES

Estuaries can be broadly separated into macrotidal and microtidal systems. For convenience, macrotidal estuaries are considered to be those having a tidal range > 2 m, and thus include the mesotidal (2-4 m) and hypertidal estuaries (>6 m) of McLusky & Elliott (2004), while microtidal estuaries are those with a tidal range < 2 m. The complex pattern of distribution of these different types of estuaries worldwide is shown in Whitfield & Elliott (2011), which was derived from Perillo *et al.* (1999).

As the most common type of macrotidal estuary throughout temperate regions of the world is the positive estuary, *i.e.* where freshwater input is greater than evaporation (McLusky & Elliott, 2004), it is used as the exemplar for the comparisons between the main characteristics of macrotidal and microtidal systems shown in Table 2.4.1. While the microtidal estuaries employed for these comparisons are those that are permanently-open to the sea, attention is drawn, when relevant, to the particular characteristics of intermittently, seasonally and normally-closed estuaries. Some important implications of the differences between macro- and microtidal estuaries are as follows.

The upstream movement of salt water during each flood tide, in those macrotidal estuaries in which tidal currents are particularly strong, provides a mechanism by which the larvae of certain marine fish species can be transported rapidly through the estuary using passive and active tidal transport (Weinstein *et al.*, 1980; Norcross & Shaw, 1984; Aprahamian & Barr, 1985; Jager, 1999). Thus, for example, in temperate microtidal estuaries of the northern hemisphere, the smallest larvae of the herring *Clupea herengus* remain in the deeper waters, where there is a net upstream flow, but, when larger, migrate across the pycnocline into the upper part of the water body during the strong flood tide and are thus transported upstream at a faster overall rate (Fortier & Leggett, 1982). The absence of such pronounced tidal action in microtidal estuaries means that, to penetrate their upper reaches, the larvae and juveniles of marine species must swim through the main body of these systems (Neira & Potter, 1992a; Neira *et al.*, 1992). The larvae and juveniles of some of these species are carried, however, into the mouths of microtidal estuaries on the flood tide and then settle along the banks or on the bottom where water movements are reduced (Beckley, 1985; Whitfield, 1989; Neira & Potter, 1992b; Neira & Potter, 1994).

The large tidal range in macrotidal estuaries results in the formation of wide intertidal areas at low tide. The very extensive production of microphytobenthos in these areas (Warwick *et al.*, 1979) facilitates the development of large colonies of polychaetes, *e.g.* species of *Nereis*, *Nephtys* and *Arenicola*, amphipods *e.g.* *Corophium* spp. and bivalve molluscs *e.g.* species of *Cerastoderma* and *Macoma* (Elliott *et al.*, 2002). The densities of these benthic macroinvertebrates are greater than in the intertidal than subtidal areas and these species provide particularly important sources of prey for many of the fish species found in estuaries (Elliott *et al.*, 2002). Although the intertidal area is at best

limited in microtidal estuaries, microphytobenthos is relatively abundant in the shallow, subtidal and less turbulent waters of microtidal estuaries (Masini & McComb, 2001) and this acts a source of food for benthic macroinvertebrates (Fauchald & Jumars, 1979; Jensen, 1987).

The high turbidity that characterizes most macrotidal estuaries reduces the visibility of the juveniles of the many fish species that use estuaries as nursery areas to potential avian and piscivorous predators, and thus presumably makes them less susceptible to predation (Blaber & Blaber, 1980; Robertson & Blaber, 1992; Elliott *et al.*, 2002). This is particularly important on the wide unvegetated open mudflats of these systems when they are covered at high tide. While microtidal estuaries are less turbid, they often contain areas of seagrass which offer refuge to juvenile fishes.

The compositions of the fish faunas of macrotidal estuaries undergo similar pronounced cyclical changes each year, due to a sequential immigration and emigration of diadromous and marine species, the latter being dominated by the 0+ year age class (Fig. 2.4.1; van den Broek, 1979; Potter *et al.*, 1997; Araújo *et al.*, 1998; Thiel & Potter, 2001; Maes *et al.*, 2005). While these changes are not strongly correlated with variations in either water temperature or salinity, their pattern can be modified by extreme environmental conditions, *e.g.* very dry winters and thus higher salinities than normal at that time. Cyclical seasonal changes in ichthyofaunal composition are far less pronounced in microtidal estuaries, with the composition throughout the estuary being related more to region, but with the compositions within the main regions varying between systems (Fig. 2.4.2) (Potter & Hyndes, 1999). The deep and wide artificial entrance channel, which was constructed in the large Peel-Harvey Estuary on the lower-west coast of Australia in order to increase markedly the tidal exchange with the ocean and thus flush nutrients out of that estuary resulted, however, in the composition of the ichthyofauna in that estuary then undergoing the same type of pronounced cyclical changes each year as those exhibited by the ichthyofaunas of macrotidal estuaries (Claridge *et al.*, 1986; Young & Potter, 2003).

In macrotidal estuaries, the composition of the fish fauna changes in a progressive manner from the mouth to the apex of these systems, reflecting, for example in the Elbe Estuary, a sequential decline in the number and abundance of marine species and an increase in the contributions of both anadromous and freshwater species (Thiel & Potter, 2001). The composition of the fauna in

195 microtidal estuaries, such as those on the lower-west coast of Australia and south coast of South
196 Africa, where the narrow and shallow entrance channel leads to a very pronounced attenuation of the
197 tidal effect (Hodgkin & Hesp, 1998), reflect to a large degree the marked differences in the physico-
198 chemical characteristics of the different regions of these estuaries, which comprise the entrance
199 channel (lower estuary), expansive basins (middle estuary) and the lower saline reaches of rivers
200 (upper estuary) (Fig. 2.4.2). These regional differences are attributable to certain species being largely
201 distributed in a particular region or regions of the estuary. Thus, for example, in the Swan-Canning
202 Estuary, atherinids, such as *Atherinomorus vaigiensis*, *Leptatherina presbyteroides* and the goby
203 *Favonigobius lateralis*, which are each represented by marine as well as estuarine populations, are
204 most abundant in the lower estuary and rarely found in the upper estuary, whereas the reverse is true
205 for species such as the atherinid *Leptatherina wallacei* and the gobies *Afurcagobius suppositus* and
206 *Arenigobius bifrenatus*, which are entirely restricted to estuaries (Prince *et al.*, 1982; Gill & Potter,
207 1993; Potter & Hyndes, 1999).

208 Irrespective of whether the estuary is located in a macro- or micro-tidal region, it contains a
209 complex range of inter-connected habitats defined by a myriad of environmental characteristics such
210 as substratum type, submerged vegetation type and water physico-chemistry (Pihl *et al.*, 2002;
211 Cicchetti & Greening, 2011; Fulford *et al.*, 2011). Various studies have demonstrated that the
212 compositions of the fish faunas varies among these habitats throughout the world (Humphries *et al.*,
213 1992; Marshall & Elliott, 1998; Mattila *et al.*, 1999; França *et al.*, 2009). On the basis of a series of
214 environmental characteristics and the associated fish fauna at a large number of sites throughout
215 various estuaries in south-western Australia, Valesini *et al.* (2010) developed a scheme whereby it
216 was possible to identify statistically the different habitats present in those systems and to predict the
217 fish species likely to occur at any unsampled site on the basis of its habitat characteristics.

218 The strong tidal action in macrotidal estuaries, and the resultant net upstream flow of sea
219 water at the bottom of the water column, facilitates the transport of detritus and sediment from the sea
220 into and through these estuaries. As the tidal influence is small and largely restricted to the lower
221 reaches of microtidal estuaries, this cannot be the case in these systems. Thus, in these estuaries, the
222 detritus is derived mainly from the other sources that also supply that component to macrotidal

estuaries, *i.e.* the catchments *via* rivers and erosion and *in situ* degradation of biota, sewage and various industrial wastes.

Although the salinity during each tidal cycle varies markedly at any one point along a macrotidal estuary, it declines progressively overall from the mouth of the system to its junction with the river (Uncles, 1984; Damme *et al.*, 2005). This is by no means, however, always the case in estuaries in microtidal regions, such as those located along the south coast of Western Australia (Chuwen *et al.*, 2009a). Furthermore, salinity can vary markedly among those latter estuaries. Thus, during the periods they were sampled, the maximum of the mean seasonal salinities ranged from *c.* 27 in the seasonally-open Wilson Inlet, to *c.* 36 in the permanently-open Oyster Harbour to *c.* 40 in the seasonally-open Broke & Irwin inlets, to *c.* 45 in the normally-closed Wellstead Estuary, and to *c.* 64 in the normally-closed Stokes Inlet and, following a protracted period of closure and low rainfall and thus freshwater discharge, to as high as *c.* 145 in Hamersley Inlet and nearly 300 in Culham Inlet (Chuwen *et al.*, 2009a). These differences are related to variations in a combination of the amount of local rainfall, the size of the catchment, the extent of land clearing and the amount of intrusion by sea water, the last of which is related to the size and duration of the mouth opening.

Increases in the salinity in the last three of the above estuaries have a very pronounced effect on their fish faunas. For example, on the basis of the relationship between the mortalities of the black bream *Acanthopagrus butcheri* and increasing salinities in the main tributary of Culham Inlet in the austral summer and autumn of 2001, this sparid becomes stressed at salinities of *c.* 60 and dies by *c.* 83-85 (Hoeksema *et al.*, 2006). It is estimated that *c.* 1.3 million *A. butcheri* were killed in that upper estuarine region of Culham Inlet during those early months in 2001 (Fig. 2.4.3; Hoeksema *et al.*, 2006).

Because of their relatively poor flushing by tidal action, microtidal estuaries are particularly prone to becoming highly eutrophic when surrounded by agricultural land and urban development from which large amounts of nutrients pass into these systems. A particularly striking example is provided by the Peel-Harvey Estuary on the lower-west coast of Australia, in which large volumes of phosphorous and nitrogen entered the two large basins of this system from surrounding agricultural land during the 1960s to 1980s (McComb & Lukatelich, 1995). This led to the production of massive

growths of macroalgae, principally of *Chaetomorpha* and *Cladophora* species, and to the development of prolific seasonal blooms of the cyanobacterium *Nodularia spumigena* in one of the basins. Catch per unit effort data strongly indicate that increasing eutrophication, which had presumably increased the amount of food and protection for fishes, was accompanied by an increase in the abundance of commercial fish species (Steckis *et al.*, 1995). In addition to the overpowering stench produced by *N. spumigena*, the onset of the blooms led to mortalities among the less mobile bottom-living fishes and also crabs and to the movement of more active species into other parts of the system (Potter *et al.*, 1983a; Steckis *et al.*, 1995). Fishers also moved their fishing activities to the other basin where water clarity was not impeded by the dense blooms.

The effects of eutrophication in the Peel-Harvey Estuary became so severe that it was decided to construct, at great cost, a large artificial entrance channel in order to increase tidal exchange markedly, and thus the amount of nutrients flushed out of the estuary, and to elevate the salinity, in the basin where *N. spumigena* blooms, to levels that are far less conducive to the growth of this cyanobacterium. This channel, which was opened in 1994, has ameliorated the extent of eutrophication and eliminated pronounced blooms of *N. spumigena*.

THE DIFFERENT WAYS IN WHICH FISHES USE ESTUARIES

The estuarine use functional group of Elliott *et al.* (2007) integrated and developed the schemes produced by several workers in different parts of the world and in different types of system (Cronin & Mansueti, 1971; Haedrich, 1983; Potter *et al.*, 1990; Elliott & Dewailly, 1995; Potter & Hyndes, 1999; Whitfield, 1999) to accommodate the different ways in which fish species use estuaries. This approach has been refined and developed in Potter *et al.* (2013).

MARINE SPECIES AND THE QUESTION OF THEIR ESTUARINE DEPENDENCE

The fish faunas of estuaries are typically dominated by marine species, both in terms of abundance and number of species. Such species have now been separated by Potter *et al.* (2013) into three guilds, *i.e.* marine straggler, marine estuarine-opportunist and marine estuarine-dependent [Fig. 2.4.4(a), (b)].

Marine stragglers are those species that spawn at sea and typically enter estuaries only in low numbers and are most frequently found in their lower reaches, where salinities are similar to those in the marine environment, *i.e.* *c.* 35 [Fig. 2.4.4(a)]. In estuaries in temperate regions of the northern hemisphere, these species include teleosts, such as the Atlantic mackerel *Scomber scombrus*, the European conger *Conger conger* and the red mullet *Mullus surmuletus*, and elasmobranchs such as the smooth hound *Mustelus mustelus* and the little skate *Leucoraja erinacea* (Potter *et al.*, 1986; Elliott & Dewailly, 1995; Thiel & Potter, 2001; Nordlie, 2003). Their counterparts in temperate regions of the southern hemisphere include the southern eagle ray *Myliobatis australis*, the western school whiting *Sillago bassensis* and the sand steenbras *Lithognathus mormyrus* (Whitfield, 2005; Chuwen *et al.*, 2009b). Within the tropics, the Spanish mackerel *Scomberomorus maculatus*, the Bengal sergeant *Abudefduf bengalensis* and the Colorado snapper *Lutjanus colorado* are occasionally found in low numbers in estuaries (Whitfield, 1999; Elliott *et al.*, 2007). Because the species within this life cycle guild are, by definition, rarely abundant in estuaries, they do not make a significant contribution to estuarine fisheries (McLusky & Elliott, 2004).

The marine estuarine-opportunist guild, which is by far the most abundant of the marine category guilds, are defined as those species that spawn at sea and often enter estuaries in large numbers and particularly during early life [Fig. 2.4.4(b)]. These species are typically euryhaline and thus able to become distributed throughout much of the estuary. While such species do not typically contribute in a major way directly to estuarine fisheries, the juveniles of some larger species, *e.g.* the Atlantic herring *Clupea harengus* and the Atlantic menhaden *Brevoortia tyrannus*, are fished commercially and some do remain in estuaries for a sufficient time to attain sizes that enable them also to contribute to estuarine fisheries. Two of the latter such species, *i.e.* the sea mullet *Mugil cephalus* and the bluefish *Pomatomus saltatrix*, are abundant in temperate estuaries throughout the world and contribute to fisheries within these systems (Nordlie, 2003; Gillson *et al.*, 2009; Robillard *et al.*, 2009). Such species may leave just prior to reaching maturity and not return, *e.g.* the King George whiting *Sillaginodes punctatus* (Potter *et al.*, 2011), while others, *e.g.* *M. cephalus*, can re-enter an estuary after spawning in the marine environment and thus when also of fishable size (Thomson, 1955).

The term estuarine-opportunist recognizes the fact that some individuals of such marine species never enter estuaries and often utilize, for example, protected coastal waters or embayments as alternative nursery habitats. Indeed, while the juveniles of some species typically use estuaries in regions where these systems are prevalent, they are still abundant in other areas where estuaries are not present. Such an example is provided in Western Australia by the juveniles of *M. cephalus*, which exhibit a very strong tendency to enter estuaries on the lower west coast and yet are still numerous in the protected waters of embayments further north, where there are no rivers (Lenanton & Potter, 1987).

The fact that, in most parts of the world, the juveniles of marine estuarine-opportunistic species, which make such an important contribution to the faunas of estuaries (Blaber & Blaber, 1980, Potter *et al.*, 1990; Nordlie, 2003; Franco *et al.*, 2008), can also use marine coastal waters as a nursery area implies that such species are not strictly estuarine dependent (Potter *et al.*, 2013). Indeed, Hedgpeth (1982) has proposed that, from a geological point of view, estuaries are of such recent origin that it would be unlikely that any marine species is strictly estuarine dependent, *i.e.* requires the presence of an estuary for the completion of its life cycle. Ray (2005), however, has noted that, although estuaries have changed in their characteristics over time, they are very old features in one form or another, pre-dating the Holocene and have therefore allowed ample time for the evolution of estuarine dependence. In the case of southern Africa, it has been argued that, because its coastline lacks sheltered shores and is exposed to turbulent wave action, certain marine species in that region are dependent on the more protected waters of estuaries for the survival of their juveniles (Blaber, 1981; Wallace *et al.*, 1984; Bennett *et al.*, 1985; Whitfield, 1999). Furthermore, because a number of fish species are found almost exclusively at some stage of their life cycle in mangrove habitats, which dominate the estuarine environment in tropical waters, Blaber (2007) proposed that such species may also be estuarine dependent, but recognizes that the evidence for this view is, at present, circumstantial. The above South African and tropical examples would thus belong to the category defined as marine estuarine-dependent [Fig. 2.4.4(b)]. As pointed out by Able (2005), however, the term estuarine dependent has been used in ways other than implying a total dependency on estuaries. For example, estuarine-dependent fish species have been defined by Whitfield & Cowley (2010) as

those species whose populations would be adversely affected by the loss of estuarine habitats (Ray, 2005).

Irrespective of whether a species is regarded as an estuarine-opportunist or estuarine-dependent, estuaries clearly provide important habitats for numerous commercial and recreational species and frequently during their early life. They thus play a crucial role in maintaining the stocks of such species in the marine environment (Haedrich, 1983; Wilson, 2002). It is not clear, however, to what extent the removal, in a region, of estuarine habitats and thus important fish nursery areas would have on the biomass and other stock characteristics of commercial fish species which enter estuaries in large numbers.

ESTUARINE, DIADROMOUS AND FRESHWATER CATEGORIES

The estuarine category comprises those species with populations in which the individuals complete their life cycles in estuaries. It contains species that are essentially confined to estuaries, *i.e.* solely estuarine species [Fig. 2.4.4(c)], and those that are represented by discrete populations in both estuaries and marine waters, *i.e.* estuarine & marine [Fig. 2.4.4(d)]. In the case of the estuarine & marine species, the marine populations probably represent the ancestral condition. The former guild is represented by relatively few species in the macrotidal estuaries of temperate regions of the northern hemisphere, which could reflect the recent origin of these systems in their form today and thus only a short period of time for facilitating the evolution of any type of estuarine dependence (Hedgpeth, 1982). Indeed, detailed biological studies of the fish species in the Severn Estuary in the U. K. indicated that the common goby *Pomatoschistus microps* and the black goby *Gobius niger* were the only fish species among the 97 caught in that system that could be definitively regarded as strictly estuarine (Claridge *et al.*, 1986).

Microtidal regions, such as south-western Australia, do entertain, however, several species which are either entirely confined to estuaries or are represented in estuaries by populations in which the individuals complete their life cycles in these systems and some of which are very abundant (Potter & Hyndes, 1999; Hoeksema *et al.*, 2009). This feature could be related to the fact that, as these estuaries frequently become closed to the ocean, either intermittently, seasonally or for longer periods,

there would have been strong selection for those individuals to be able to adapt by breeding within the estuary and this would have been particularly the case with short-lived species (Potter & Hyndes, 1999; Hoeksema *et al.*, 2009). One small and strictly estuarine species, the estuarine round herring *Gilchristella aestuaria*, is one of the most abundant fish species in the microtidal estuaries of southern Africa (Whitfield, 1998). Another strictly estuarine species, *A. butcheri*, which has a far greater longevity, *i.e.* 20-30 years (Morrison *et al.*, 1998; Potter *et al.*, 2008), is one of the most important recreational and commercial fish species in the microtidal estuaries of southern Australia (Kailola *et al.*, 1993; Gixti *et al.*, 2007; Gixti *et al.*, 2010).

A collation of data on the contribution of the various life cycle guilds to the suite of estuaries in a range of different estuary types on the south-western Australian coast demonstrated that as many as 19 and 17 of the species found in the shallows of the large and permanently-open Peel-Harvey and Swan-Canning Estuaries, respectively, were represented by populations whose individuals were confined to the estuaries and that about half of those species were also not represented in the marine environment (Potter & Hyndes, 1999). These species contributed about one third of the individuals to the seine catches obtained from the shallows of those two estuaries. While the numbers of species was less in the shallows of the intermittently-open Moore River estuary (nine) and the seasonally-open Wilson Inlet (11), the contributions of species with populations confined to estuaries to the total catches was far greater, *i.e.* 95 and 98.5%, respectively (Potter & Hyndes, 1999). These very high percentage contributions reflected, in particular, the presence of large numbers of several species of atherinid and goby. The gillnet catches from deeper waters, which included considerable numbers of several larger and often marine species, contained fewer species that were confined to estuaries. The five such species found in Wilson Inlet did contribute, however, over 60 and 40% of the catch from that seasonally-open system in 1987-89 and 2006 - 2007, respectively (Potter *et al.*, 1993; Chuwen *et al.*, 2009b), and these included *Cnidogobius macrocephalus*, *Platycephalus speculator* and *A. butcheri* which are of fishery importance. The above comparisons clearly demonstrate that the composition of the ichthyofauna is influenced by estuary type, *i.e.* the extent to which it is open to the sea.

Studies encompassing nearly 200 estuaries across three zoogeographical regions in South Africa also emphasised the importance of estuary type, *e.g.* permanently-open *v.* normally-closed, in

defining the characteristics of the ichthyofaunas in those systems (Harrison & Whitfield, 2006, 2008). Thus, species richness was greatest in estuaries that are permanently-open to the sea, reflecting the fact that this enables marine species more readily to enter the estuary than is the case with those in which a sand bar at the estuary mouth blocks such movements for substantial periods. Species which can complete their life cycle in estuaries are more important, however, than marine species in seasonally-open or normally-closed estuaries than in permanently-open systems.

The estuary cobbler *C. macrocephalus*, which is the greatest contributor to the overall value of the commercial estuarine gillnet fishery on the south coast of Western Australia (Chuwen *et al.*, 2011), was shown by the genetic studies of Ayvazian *et al.* (1994) to comprise discrete estuarine and marine populations [Fig. 2.4.4(d)]. The question of the connectivity of the estuarine and marine assemblages of other species, whose life cycle can be completed in both types of environment, clearly requires further investigation.

In addition to the solely estuarine and estuarine & marine guilds, the estuarine category also includes the estuarine & freshwater and estuarine migrant guilds. The estuarine & freshwater guild contains those species that are represented by species that can complete their life cycles in freshwater as well as estuaries, *e.g.* the western hardyhead *Leptatherina wallacei* [Fig. 2.4.4(e)]. The estuarine migrant guild comprises species that spawn in estuaries but may be flushed out to sea as larvae but later return at some stage to the estuary, *e.g.* the prison goby *Caffrogobius gilchristi* and the Knysna sandgoby *Psammogobius knysnaensis* [Fig. 2.4.4(f)].

The two main categories of diadromous species are the anadromous and catadromous species. The anadromous category comprises species that undergo all or most of their growth at sea and, prior to attaining maturity, migrate through estuaries and into fresh water where they subsequently spawn [Fig. 2.4.5(a)]. It includes several species of salmonid, lamprey and clupeid, many of which are commercially and recreationally important (Wilson, 2002). Species such as the sockeye salmon *Oncorhynchus nerka*, the pink salmon *Oncorhynchus gorbuscha* and the Chinook salmon *Oncorhynchus tshawytscha* are fished in the marine environment and after entering fresh water, and also sometimes in estuaries (Miller, 2000; Chinook Technical Committee, 2003; Eggers *et al.*, 2005). Lampreys such as the sea lamprey *Petromyzon marinus*, the river lamprey *Lampetra fluviatilis* and the

Caspian lamprey *Caspiomyzon wagneri* used to be caught in substantial numbers during their upstream spawning migration in various European countries and, in some areas, are still regarded as a great delicacy (Hardisty, 2006). Such species have declined markedly in numbers as a result of damming and other anthropogenic effects, which have reduced their ability to reach their typical spawning grounds. Several of the clupeid species that comprise the anadromous category and are fished in estuaries belong to the genus *Alosa* and include the allis shad *Alosa alosa* and the twaite shad *Alosa fallax* in Europe, the blueback herring *Alosa aestivalis* and the American shad *Alosa sapidissima* in North America. While another shad, the chacunda gizzard shad *Anodontostoma chacunda*, contributes to estuarine fisheries in the tropics and the hilsa shad *Tenualosa ilisha* constitutes the largest estuarine fishery in Bangladesh (Facey & Avyle, 1986; Blaber *et al.*, 1989; Groot, 1990; Klauda *et al.*, 1991; Blaber, 2011). An example of a decline in the estuarine fishery for an anadromous species is provided by *A. alosa* in France, a decline considered to be due to a combination of habitat modification and overfishing (Blaber, 2011).

A few species have a similar life cycle to those above, but differ in that their upstream migration does not extend into rivers and spawning consequently occurs in the upper reaches of estuaries [Fig. 2.4.5(b)]. These species, which have thus been termed semi-anadromous, include clupeids such as the Perth herring *Nematalosa vlaminghi* (Chubb & Potter, 1984).

The most notable component of the catadromous category, which comprises species that spend all of their trophic life in fresh water and subsequently migrate out to sea to spawn [Fig. 2.4.5(c)], are various species of eel belonging to the family Anguillidae. Such species, which are widely fished throughout the world, include the European eel *Anguilla anguilla*, the American eel *Anguilla rostrata*, the Japanese eel *Anguilla japonica* and the New Zealand longfin eel *Anguilla dieffenbachii*, the last being of particular significance to the Māori population. While these species are caught mainly as juveniles and immature adults, the glass eel stage of *A. anguilla* is occasionally taken in very large numbers such that it constituted 14% of the French catch of this species (Costa *et al.*, 2002); they are sometimes also taken as elvers soon after their entry into fresh water (Tzeng, 2004; Aprahamian & Walker, 2008).

The semi-catadromous category, which comprises species whose downstream spawning run extends only as far as the lowest part of the estuary, rather than into marine waters [Fig. 2.4.5(d)], contains the barramundi *Lates calcarifer* (Elliott *et al.*, 2007).

The last of the diadromous categories, *i.e.* amphidromous, constitutes those species that migrate between the sea and fresh water and in which the migration in neither direction is related to reproduction. Amphidromy refers to those species that spawn in fresh water, after which the resultant larvae and juveniles migrate temporarily into marine waters before returning to fresh water to grow to maturity [Fig. 2.4.5(e)]. A particularly good example is provided by the banded kokopu *Galaxias fasciatus*, whose life cycle is illustrated by McDowall (1988).

The vast majority of freshwater species do not possess the mechanisms required for osmoregulating in the saline conditions found in estuaries. Some species, termed freshwater stragglers, are typically found in low numbers in estuaries and are usually restricted to their low salinity upper reaches [Fig. 2.5.5(f)]. The few species that are found regularly in estuaries and whose distributions can extend past the oligohaline sections of these systems are termed freshwater estuarine-opportunists [Fig. 2.4.5(g)]. They include species such as the three-spined stickleback *Gasterosteus aculeatus* and the American gizzard shad *Dorosoma cepedianum* in temperate waters and the Mozambique tilapia *Oreochromis mossambicus* and the neotropical silverside *Atherinella chagresi* in subtropical and tropical waters (Elliott *et al.*, 2007).

THE DIFFERENT WAYS IN WHICH BENTHIC MACROINVERTEBRATES USE ESTUARIES

The ways in which invertebrates use estuaries can each be assigned to one of the same estuarine use guilds as those described above for fishes. Thus, crabs such as *Callinectes sapidus* and *Portunus armatus* (formerly *Portunus pelagicus*; Lai *et al.*, 2010) and prawns such as *Melicertus plebejus*, *Melicertus latisulcatus* and *Penaeus monodon* can all be considered marine estuarine-opportunists. While the above crabs mate in the estuary and release their fertilized eggs in the marine environment [Fig. 2.5.6(a); Darnell, 1959; Potter *et al.*, 1983b], the above prawns use the estuary exclusively as a nursery area [Fig. 2.5.6(b); Dall *et al.*, 1990; Potter *et al.*, 1991). In contrast, bivalve

molluscs, such as the oyster *Crassostera virginica* and the mussel *Mytilus edulis* are represented by populations in which their individuals complete their life cycles in either the marine or estuarine environment [Fig 2.4.6(c)]. The western school prawn *Metapenaeus dalli* provides an example of an invertebrate species that is confined to estuaries in the southern part of its range [Fig. 2.5.6(d); Potter *et al.*, 1989].

FISHERY CATCHES AND THE CONCEPT OF ESTUARINE DEPENDENCE

The contribution of fishes that use estuaries at some stage in their life cycle to the total commercial catches in an area varies among regions. Thus, for example, between the 1980s and early 1990s, such fishes, which were termed estuarine dependent, contributed between 15 and 90% to the total catch in various regions throughout Europe (Costa *et al.*, 2002). McHugh (1976) calculated that, in 1970, 69% by mass of the catches taken by the commercial fishery in the U. S., comprising fishes and shellfish, was based on what he termed estuarine dependent species. More recently, Lellis-Dibble *et al.* (2008) estimated that 'estuarine species' contributed *c.* 46% by mass and 68% to the fishery in the same country between 2000 and 2004. McHugh (1976) defined estuarine dependent species as those 'that spend at least a part of their lives within land-bound estuaries', which corresponds to the above category of Costa *et al.* (2002) and the same as the estuarine species of Lellis-Dibble *et al.* (2008). Such a group is therefore very broad, comprising marine species which use estuaries, as well as estuarine species *sensu stricto*, *i.e.* those in which all of their individuals complete their life cycle in estuaries, and also diadromous species. Indeed, as pointed out by Able & Fahay (2010), the term estuarine dependent has become an uncritical and loosely defined component of resource managers' lexicons.

Since estuaries are the only environment in which certain fish species complete their life cycle and provide the sole route for the migration of diadromous species from their main feeding areas in rivers to their spawning areas in the sea or *vice versa*, such species can be regarded as truly estuarine dependent. These species, and the few marine species that are apparently estuarine dependent, can be considered obligate users of the estuary, whereas the marine estuarine-opportunists are facultative users of the estuary and others are simply strays that occasionally find their way into

the estuary from either the sea or the rivers (Able, 2005). In the case of marine estuarine-opportunists, a lack of comparative data on the habitats they use in estuarine and marine environments at different stages in their life cycle means that it is difficult to determine the relative importance of these two environments to the overall abundance and recruitment success of such species (Beck *et al.*, 2001; Able, 2005; Ray, 2005). Furthermore, assessments of the role of estuaries in the life cycles of fish species have sometimes been confounded by a lack of a clear understanding of what constitutes the seaward limits of the estuary (Able, 2005) and consequently fishes that were considered to have been caught in the lower reaches of the estuary were in fact taken in waters, which for most of the time, corresponded to full strength sea water and thus belong to the marine environment. In the case of non-diadromous species, a thorough understanding of the location of their spawning areas is also required before assigning such species with certainty to either the marine, estuarine or freshwater categories.

For the above reasons, our preference is to use the term dependent in its formal sense and thus to restrict the term estuarine dependent to the obligate users of the estuary as identified by Able (2005). At the same time, it is recognized that one of the most important issues facing ecologists and managers of estuarine environments is establishing the extent of connectivity between the assemblages of species in estuarine and marine waters (Ray, 2005).

THE BIOTA AND FOOD SOURCES OF FISHES IN ESTUARIES

The need to adopt an ecosystems-based approach to fisheries management (EBFM) led a committee convened by the U. S. Congress to recommend a series of actions that would provide data for facilitating the sustainability of aquatic ecosystems and thus of their fishery resources (U.S. Commission on Ocean Policy, 2004; Sanchirico *et al.*, 2008; Essington & Punt, 2011). These actions included the acquisition of data on the predators and prey of the main commercial fish species and the construction of a food web showing the interactions between those predators and their prey. The overall trends exhibited by such data for various estuaries have been condensed to produce a simplified flow diagram representing the biota that constitute the broad dietary groups, providing the main energy sources for fishes in estuarine ecosystems. This figure has not been extended to produce a traditional food web as these often constitute complex spider-web patterns, representing the myriad

of interactions between ecosystem components (Elliott *et al.*, 2002) and thereby obscure the main trends (Raffaelli, 2000). Attention is drawn in the text, however, to the origin of the food source of fishes, *e.g.* detritus, and to the interactions between the dietary components, *e.g.* meiofauna and macrofauna. While birds play a particularly important role in estuaries and contribute greatly to predation of the fish and invertebrates in those water bodies and may even have led to overfishing in certain of these systems (Vetemaa *et al.*, 2010).

The main food sources in estuaries are diverse (Fig. 2.4.7). This diversity is reflected in the feeding modes of fishes represented by the following specific guilds, *i.e.* zooplanktivore, detritivore, herbivore, omnivore, piscivore and zoobenthivore, of which several examples are given in Elliott *et al.* (2007). A number of species are highly adaptable in their feeding behaviour, however, and thus the suites of biota they ingest can vary markedly among estuaries, depending on what food source is most available and particularly prevalent in estuaries (Sarre *et al.*, 2000; Elliott *et al.*, 2002; Chuwen *et al.*, 2007). This particular group is assigned to the miscellaneous and opportunist guild (Elliott *et al.*, 2007). An account of the various food sources for fishes in estuaries, together with a few selected examples of the species, representing the different dietary guilds are given below.

DETRITUS

Detritus, whose importance in estuaries has been emphasized by numerous authors (Wolanski, 2007), has been defined as all types of biogenic material that are in various stages of microbial decomposition (McLusky & Elliott, 2004). It is derived from the breakdown of a wide range of plant material, *i.e.* microphytobenthos, macrophytes, macroalgae and phytoplankton, and animal material, *i.e.* meiofauna, macrofauna, fishes and other vertebrates, together with faeces and heterotrophic bacteria. During recent times, the detrital pool has frequently been enhanced by products derived from anthropogenic activities, *e.g.* domestic, agricultural and industrial sewage and paper pulp mills. Detrital material enters the estuary both as tidal inputs from the sea and *via* the catchments, *i.e.* rivers and surrounding land, as well as being generated *in situ*. When considering the role of detritus in food webs, it is important to recognize that a substantial proportion of this particulate organic matter is refractile rather than labile and thus not readily available to consumers

(Warwick *et al.*, 1979; McLusky & Elliott, 2004). Although detritus is used directly as a food source by only a few fish species, such as *M. cephalus* (Odum, 1968; Eggold & Motta, 1992), it does play this role for deposit feeding benthic meiofauna, *e.g.* nematodes and harpacticoid copepods (Jensen, 1987) and macrofauna, *e.g.* polychaete worms (Fauchald & Jumars, 1979), which constitute such an important food source for numerous fish species in estuaries (Gee, 1989; Baldoa & Drake, 2002; Nemerson & Able, 2004). Furthermore, as microphytobenthos is ingested with detritus, it would also contribute to the diets of detritivorous fishes and invertebrates (Fauchald & Jumars, 1979; Whitfield, 1998; Lin *et al.*, 2007).

MICROPHYTOBENTHOS

The very high levels of primary production by the abundant micophytobenthic flora on the extensive intertidal areas of the sediments in macrotidal estuaries and in the relatively clear shallow waters of microtidal estuaries (Table 2.4.I; Warwick *et al.*, 1979; Masini & McComb, 2001) provide an abundant food source for the benthic macroinvertebrates in those systems (Warwick *et al.*, 1979) and even for some fish species directly (Krumme *et al.*, 2008). In macrotidal estuaries, production takes place during low tide when the sediment is exposed and in daylight when photosynthesis can occur, and is negligible when the sediment is flooded (Warwick *et al.*, 1979). The annual production of microphytobenthos may far exceed that of primary production from any other source. On an estuarine mudflat in south-western England, for example, the annual production by microphytobenthos was 143 g carbon.m⁻².year⁻¹ compared with 2.8 g carbon.m⁻².year⁻¹ by heterotrophic bacteria in the sediment and 11 g carbon.m⁻².year⁻¹ by detritus. Some of the various benthic meiofaunal species feed selectively on different components of the benthic microflora, resulting in resource partitioning that facilitates the maintenance of the high diversity of this crucial group in estuarine food webs. Surface deposit-feeding macrofauna, *e.g.* the bivalve mollusc *Scrobilularia plana*, may siphon off the surface film of sediment which is rich in microphytobenthos (Hughes, 1969), while subsurface deposit-feeders, *e.g.* the polychaetes *Capitella capitata* and *Arenicola marina*, ingest sediment from which they extract nutrients (Fauchald & Jumars, 1979).

MACROPHYTES AND MACROALGAE

Although salt marshes in temperate latitudes and mangroves in the tropics are found at the highest extent of the tides, the principal flowering plants in the main bodies of estuaries are seagrasses, which include species of *Thalassia*, *Posidonia* and *Cymodocea* in tropical waters and of *Zostera*, *Ruppia* and *Potamogeton* in temperate areas (Green & Short, 2003). Seagrasses can be highly productive, with an annual yield typically twice that of their maximum biomass, but this energy source may be obtained by animals mainly through the detritus route rather than by direct grazing (McLusky & Elliott, 2004). The shallow, quiet sublittoral waters of microtidal estuaries are far more conducive for seagrass growth, however, than macrotidal estuaries in which there is high tidal scour and turbidity. Furoid macroalgae (brown seaweeds) are confined to rocky substrata and are thus uncommon in estuaries, but green macroalgae, such as species of *Enteromorpha*, *Cladophora* and *Chaetomorpha*, may produce dense growths on the sediments of those eutrophic estuaries that receive a high nutrient input, especially of nitrogen and phosphorus (McComb & Lukatelich, 1995; McGlathery, 2001). In some highly eutrophic situations, the macroalgae can smother and replace seagrasses by blocking available light (McGlathery, 2001; Duarte, 2002). Macroalgae also have high rates of primary production and, as with seagrasses, are favoured in areas where hydrodynamic energy is relatively low (McLusky & Elliott, 2004).

While relatively few of the fish species found in estuaries consume predominantly plant material throughout their life (Blaber, 2000), some, such as several in the family Hemiramphidae feed on plankton when young but almost entirely on macrophytes as adults (Blaber, 2000). Moreover, one species of hemiramphid, *Hyporhamphus melanochir*, is a herbivore during the day and a carnivore at night (Klumpp & Nichols, 1983). Some species that ingest large amount of macrophytes, however, do not possess the cellulase in their gut that is required to digest such plant material and it thus passes through the gut undigested (Blaber, 1974; De Wet & Marais, 1990; Sheppard *et al.*, 2012).

PHYTOPLANKTON AND ZOOPLANKTON

Although phytoplankton is an important primary producer in estuaries, that role is typically less important than in marine and freshwater ecosystems (McLusky & Elliott, 2004). Furthermore its

contribution varies markedly, being least in highly turbid estuaries where photosynthesis is inhibited. In less turbid situations, it makes an important contribution to the food of zooplankton, fish larvae and suspension-feeding macrobenthic invertebrates (Cloern, 1982; Lewitus *et al.*, 1998). The number of fish species that feed on phytoplankton is restricted, however, because the gill rakers of only a few species, such as *Hilsa kelee*, have the structure and arrangement required to filter phytoplankton (Blaber, 1979; Blaber & Cyrus, 1981).

Permanent members of the zooplankton (holoplankton) range upwards in size from that of small protozoans to that of crustaceans, such as calanoid copepods and mysids, while the temporary zooplankton (meroplankton) are represented by the planktonic larvae of macrobenthic animals, such as certain fish species of polychaetes and crabs. Zooplankton forms an important component of the diets of certain species and particularly of clupeids such as *Sprattus sprattus*, *C. harengus*, *G. aestuaria* and *Tenualosa toil* (Blaber, 1979; Blaber *et al.*, 1996; Casini *et al.*, 2004). While zooplankton is the most important component of the diet of the vast majority of larval fishes found in estuaries (Whitfield, 1985; Gaughan & Potter, 1997), it contributes far less to the total biomass of invertebrates than the benthic fauna of estuaries and particularly in those that are turbid (McLusky & Elliott, 2004).

BENTHIC INVERTEBRATES

Invertebrates living in and on the bottom sediments of estuaries constitute a major food source for the juveniles and adults of fish species in estuaries (Whitfield, 1998; Elliott *et al.*, 2002; West *et al.*, 2003; Platell *et al.*, 2006). Such organisms vary greatly in size and thus also provide food for a large size range of fishes. These invertebrates are traditionally divided by size into two groups, the smaller meiofauna and the larger macrofauna. In fresh water, the size spectrum tends to be continuous and the division between these groups is thus rather arbitrary (Strayer, 1986; Stead *et al.*, 2005). As in the sea, however, the situation in estuaries is very different, with the animals in the meiofauna and macrofauna each being represented by discrete modes in the distributions of their biomasses and body sizes and by differences in their ecological and evolutionary traits (Schwinghamer, 1981; Warwick & Clarke, 1984; Warwick, 1989, 2007). In estuaries, the

macroinvertebrates produce planktonic larvae that settle to the bottom when they have reached a larger size than the members of the meiobenthos, thereby reducing the potential for competition with and predation by those members of the meiobenthos that are resident in and on the substratum. In contrast, a major component of the macrobenthos in fresh water is the larvae of flying insects that effect aerial dispersal, the early benthic instars of which are of similar size to the permanent meiobenthos and with which they are thus more likely to interact.

Meiofaunal species diversity is remarkably high in brackish water since, in contrast to macrofauna, many marine or freshwater meiofaunal species are highly tolerant of the stresses imposed by such environments (Giere, 1993). Although meiofauna have a lower standing stock biomass than the macrofauna, their high turnover rates may result in a high secondary production. On a mudflat in Cornwall, U.K., for example, the annual production of meiofauna was $16.8 \text{ g carbon.m}^{-2}.\text{year}^{-1}$ compared with $5.5 \text{ g carbon.m}^{-2}.\text{year}^{-1}$ for the macrofauna (Warwick *et al.*, 1979). In a comprehensive review, Gee (1989) showed that meiofauna are an important food source for the small (30-60 mm) juveniles of many commercially important fishes (flatfishes and salmonids) and for certain others that are fed on by commercial species. Fishes have been shown to feed preferentially on a few species of harpacticoid copepod, rather than on the numerically dominant meiofaunal taxa, and notably nematodes, due to their being more available as a result of their active movement on or near the sediment surface and their energetic efficiency as food (Gee, 1989). The supply of meiofaunal food for juvenile fishes was considered unlikely to be limiting.

The taxonomic composition of the benthic invertebrate fauna in estuaries is also quite different from that in fresh water. In estuaries, the macrobenthos comprises the whole diverse spectrum of phyla that occur in the sea, recognizing that echinoderms are not tolerant of low salinities and thus tend to be found only in the lower reaches of estuaries (Pagett, 1981). The number of species in a typical estuarine assemblage is, however, less than in fully marine or freshwater environments. On the other hand, the macrobenthos in fresh water essentially comprises only three phyla, *i.e.* annelids, molluscs and arthropods, the most abundant and diverse being a group of arthropods, the insects, the majority of which, as noted above, are represented by the larvae of flying adults (Macan & Worthington, 1959).

FISHES

The larger fish species found in estuaries tend to belong to the piscivore guild, but sometimes only shift towards piscivory as they increase in size (Blaber, 2000). Piscivorous fishes are particularly abundant in tropical estuaries and include sharks belonging to the Carcharhinidae and teleosts representing families such as the Belonidae, Carangidae and Sciaenidae.

On the basis of a dietary study, West *et al.* (2003) concluded the food web in the Tijuana Estuary on south-western coast of the United States consisted of the following three major trophic levels: (1) primary consumers that consumed substantial amounts of plant material and detritus, (2) benthic carnivores, which consumed large numbers of calanoid copepods and amphipods and (3) piscivores that often preyed on small gobiid species. The results of Akin & Winemiller (2006) emphasized that most of the consumers in an estuary discharging into the Gulf of Mexico fed low in the food web and that the abundant detritivorous fish species *M. cephalus* and *Brevortia patronum* and benthic macroinvertebrates played an important role in linking detritus to top predators *via* short food chains, which is consistent with the food webs constructed for other estuaries (Elliott *et al.*, 2002).

REPRODUCTIVE MODE

Most marine estuarine-opportunist species are serial spawners that release large numbers of pelagic eggs into the water column of their marine environment, where they are fertilized, after which the resultant postflexion larvae and juveniles migrate onshore (Elliott *et al.*, 2007). The production of pelagic eggs and larvae by species that breed in macrotidal estuaries potentially exposes those earliest life cycle stages to being flushed out into the marine environment during strong tidal water movements (Elliott *et al.*, 2007). This accounts for the few species that spawn successfully in macrotidal estuaries possessing adaptations that greatly reduce the likelihood of their eggs and larvae undergoing to such flushing. These adaptations include the production of demersal, adhesive eggs, as with many species of goby and atherinid (Leis & Rennis, 1983; Miller, 1984; White *et al.*, 1984). The males of another goby, *Gobius niger*, one of the few estuarine resident species in the large Severn

Estuary (Claridge *et al.*, 1986), construct nests using either shells or rocks, digging a hole underneath into which the female deposits her eggs that are then fanned and guarded by the males (Vaas *et al.*, 1975; Miller, 1984). Other retention mechanisms include parental care, such as provided by pouch-brooding as with syngnathids, which enable the young to be protected until they reach a size and stage of development that enables them to combat the effects of flushing (Elliott *et al.*, 2007).

The potential problems of flushing to the eggs and larvae of estuarine residents are far less in microtidal estuaries in regions such as south-western Australia, because, during the dry late spring to early autumn period, when most estuarine residents spawn (Potter & Hyndes, 1999), tidal water movement through most of those systems is very restricted and freshwater discharge is typically small. The environment during that dry period is thus benign and thereby accounts for the substantial number of species that are capable of spawning within the microtidal estuaries of this region and for some of these being particularly abundant. Yet, most of these estuarine resident species still possess adaptations that would aid retention within the estuary. These include the production of demersal, adhesive eggs, which characterize gobies (Miller, 1984; Hoese, 1994), epibenthic schooling by their flexion and postflexion larvae, as with the atherinid *L. presbyteroides* (Steffe, 1990), the construction of nests in which the eggs and larvae are protected, *e.g.* the estuary cobbler *C. macrocephalus* (Laurenson *et al.*, 1993b), or oral-brooding as by the male of the cardinal fish *Apogon rueppellii* (Neira, 1991) or pouch-brooding as with *Urocampus carinirostris* and other syngnathids (Fritzsche, 1984; Neira *et al.*, 1992). Such mechanisms would facilitate retention during the brief surges of freshwater discharge that accompany the brief cyclonic events that occur in some years in this region (Hodgkin & Hesp, 1998).

In studies of *A. rueppellii*, which is abundant in the two largest estuaries on the lower-west coast of Australia (Loneragan *et al.*, 1986; Loneragan *et al.*, 1989), the mean number of eggs brooded in the mouths of males ranged from *c.* 70 in fish of 45-49 mm to 345 in those of 90-94 mm (Chrystal *et al.*, 1985) and their larvae are released at an advanced post-flexion stage that is followed by a short planktonic life (Neira, 1991). *Cnidoglanis macrocephalus*, a plotosid catfish that is abundant in certain estuaries, produces eggs that can exceed 7 mm in diameter, which are guarded in nests

excavated by the males (Laurenson *et al.*, 1993b). The yolk sac larvae, of which *c.* 100 were observed in one nest, do not hatch until they have reached standard lengths as great as 27-29 mm.

Species representing other reproductive modes such as ovoviviparity, involving the production of egg cases in which the young develop, and viviparity, where the female produces live young, are not prevalent in estuaries. A conspicuous example is provided by the viviparous blenny *Zoarces viviparous* (Elliott *et al.*, 2007).

HISTORY OF ESTUARINE FISHING

Archaeological studies demonstrate that invertebrates and fishes collected from rivers, estuaries and nearshore coastal environments have long been an important food resource for humans (Blaber, 2000, 2011; Blaber *et al.*, 2000; Lackey, 2005). The methods of capture probably involved beach combing and wading to collect sedentary species and clubs and spears to catch fishes in nearshore waters (Watson *et al.*, 2004). Fishing methods subsequently evolved to include hooks, nets, fish traps and fishing weirs and the use of small water craft to access the waters where fishes were most abundant (Watson *et al.*, 2004). Remnants of fish traps and fishing weirs are still present in certain estuaries in Europe (such as the Thames), North America and Australia (Godbold, 2001; O'Sullivan, 2003).

In addition to acting as a source of fishes, estuaries have also provided an important docking point for ships for importing and exporting trade, accounting for why so many cities have been built around their mouths. Indeed, seven of 10 of the world's largest megacities are located on or close to estuaries. Tokyo, originally a small fishing village called Edo, which means estuary, was located at the mouth of the river of that name (Jansen, 1989). Guangzhou is on the delta of the Pearl River in China, Jakarta at the mouth of the Ciliwung River in Indonesia, New York City on the Hudson River estuary, Seoul on the Han River close to its estuary, while Shanghai is at the mouth of the Yangtze River in China and Karachi at the mouths of the Lyari and Malir Rivers in Pakistan. Estuaries were thus able to act as conduits for the transportation of a wide range of products from the coast to inland settlements, with fords and bridges being constructed at the heads of many estuaries to facilitate and

control this transport and resultant trade (Wilson, 1988, 2002). This led to the growth of communities and settlements along the shores of estuaries and thus to an increased demand for fishes.

In the middle ages, subsistence and artisanal fisheries provided the main source of food and an important income for people living along many coasts (Blaber, 2000; Blaber *et al.*, 2000; O'Sullivan, 2003). By the tenth and eleventh centuries, the increased demand for fishes by growing urban populations in Britain, coupled with the development of improved methods of preservation and transportation, led to commercial fishing becoming more significant economically and thus to better boat design and the construction and development of more efficient fishing gears (Jarvis, 1988; Lackey, 2005).

The fourteenth century saw the introduction in the Thames Estuary of a wooden beam trawl, the wondyrchoun, which, because of its impact on the environment and the excessive amounts of bycatch of small fishes that it caught, resulted in a petition to King Edward III for its use to be banned (Kennelly & Broadhurst, 2002). While the commissioners appointed to deal with this petition decided that this gear should be restricted to deeper water, and not be employed in bays or estuaries, no law was passed to this effect (Kennelly & Broadhurst, 2002; Roberts, 2007). Trawling continued to spread slowly and, by the late seventeenth century, was in common use around Brixham in the English Channel and around the mouth of the Thames Estuary, but the fishing boats then in use were capable of towing only small trawls (Roberts, 2007).

By the seventeenth century, the fish resources of estuaries elsewhere in Europe were also being subjected to increasing levels of recreational exploitation. Recreational fishing was not new, however, as it had been enjoyed by the Egyptian aristocracy over 4 000 years ago (Lackey, 2005). The publication of the *The Compleat Angler* by Izaak Walton in 1653 reflected a growing participation in recreational fishing during the Renaissance, with such activity becoming an important and common pastime in Western society by the mid-1800s (Lackey, 2005).

The detrimental changes that occurred in many estuaries in Europe as a result of anthropogenic activities during the nineteenth and twentieth centuries, and which led to a decline in their fish faunas and thus their fisheries, are illustrated by the history of the Thames Estuary.

THE THAMES ESTUARY, A CASE HISTORY OF ANTHROPOGENIC CHANGES

In England, in 1086, river water provided the power to drive *c.* 6 000 water-mills, a number of which diverted water through constricted, artificial channels (Wheeler, 1979), and thus, even by that early period, such man-made constructions impeded the migration of anadromous and catadromous species. During the middle ages, fulling, dyeing, paper and copper mills and tanneries and foundries had been established, using power provided by water mills. Such mills continued to be used until the nineteenth century when they began to be superseded by steam-powered machinery (Wheeler, 1979). Pound locks to aid river traffic were also constructed in Europe during the middle ages, with the result that, by 1809, 26 such locks were present on the Thames, with a further six being added a few years later.

The growth of various industries led to a great increase in the amount of industrial effluent discharged into rivers and from there into estuaries, as well as directly into the estuaries themselves. In the case of the Thames, particularly large volumes of sewage were also discharged into both its riverine and estuarine reaches. By 1502, the Fleet River, a tributary of the Thames had become 'so choked with silt and rubbish that navigation was impossible' and thus required dredging, a process that needed to be repeated in 1606 and 1652 (Wheeler, 1979). Disposal of industrial effluent, sewage and waste into the Thames and other European rivers in the eighteenth and nineteenth centuries led to very high loads of sediments, pathogens, nutrients and toxins entering estuaries and, as a consequence, the catches of many fish species had begun to decline by the nineteenth century. Indeed, Tinsley (1998) reports that the decline in water quality was so severe that, by the middle of the nineteenth century, stretches of the River Thames were experiencing such extreme anoxic conditions that they required extensive remedial action. This involved the construction of interceptor sewers to divert sewage from central London to reservoirs east of the city, where it was stored until it could be discharged into the lower reaches of the estuary on the ebb tide.

The Atlantic salmon *Salmo salar* and the anadromous brown trout (sea trout) *Salmo trutta*, which had previously been common in the Thames, had become scarce by 1836 and were virtually non-existent by 1861 (Wheeler, 1979; Andrews, 1984). These declines in abundances were related to the construction of dams, weirs and locks, which acted as barriers to the upstream migration of these

anadromous species and reduced their gravel spawning habitats by slowing water movement behind weirs, and also to the removal of those habitats by dredging to improve navigation (Fig. 2.4.8; Wheeler, 1979). In addition, large numbers of *S. salar* were being removed by the development of traps for catching them at weirs and by recreational fishing in the rivers. The use of similar traps at weirs to catch the catadromous *A. anguilla*, together with the negative impact of barriers to migration and an increase in pollution, hastened the decline in the abundance of this eel species (Fig. 2.4.8). Populations of the anadromous *L. fluviatilis* and *A. fallax* also declined as the number of barriers increased. Other targets of fisheries in the Thames Estuary included fishes such as whitebait (juvenile *C. harengus* and *S. sprattus*) and the flounder *Platichthys flesus* and invertebrates such as the starfish *Asterias rubens* and the brown shrimp *Crangon crangon*. Wheeler (1979) notes that, in 1797, commercial catches of the smelt *Osmerus eperlanus*, a marine species that was probably the main target species for fishers in the Thames, were still high. As water quality, *e.g.* dissolved oxygen levels, however, declined over the next 40 years, the commercial catches of this osmerid, which is very sensitive to such declines as was demonstrated by data for the Forth Estuary (Costa *et al.*, 2002), fell markedly. By the beginning of the twentieth century, this species was being caught only at the mouth of the Thames Estuary. Declining water quality had also affected certain species of shellfish, which, because they are filter feeders and thus accumulate pathogens in the water, were later implicated as agents of transmission of cholera and typhoid (Wilson *et al.*, 1998).

From 1884, various chemical precipitation methods were introduced to treat London's sewage during sedimentation and before discharge to the estuary, and further interceptor sewers were constructed (Tinsley, 1998). By 1900, *O. eperlanus*, *P. flesus* and whitebait were returning to the Thames (Wheeler, 1979). Water quality remained satisfactory until about 1915, when increasing volumes of sewage, arising from the large growth in London's population and the decision to discontinue chemical treatment, saw anoxic conditions return to the stretches of water within 10 km of the sewage outfalls (Wheeler, 1979; Tinsley, 1998). Between 1935 and 1950, further population growth and the discharge of sewage into tributaries from the small sewage works constructed to service new suburbs that had developed, led to a larger stretch of estuarine waters becoming anoxic (Tinsley, 1998). As a result, from *c.* 1920 to 1960, no fishes other than *A. anguilla* were apparently

present in the stretch of the lower Thames from *c.* 26 km upstream to *c.* 40 km downstream from London Bridge (Wheeler, 1958, 1969). Major efforts were made from the 1960s onwards to treat sewage and thus increase dissolved oxygen concentrations (Tinsley, 1998). Records of fishes caught on the cooling water screens of power stations in the late 1960s and early 1970s demonstrated that the rise in oxygen levels was accompanied by a return in fish species that had not been recorded in the Thames for many years (Wheeler, 1979; Andrews, 1984). Indeed, the increase in the number of species and abundance of fish recorded since the 1960s has led to the conclusion that the formerly very polluted Thames Estuary has become far cleaner (Andrews, 1984; McLusky & Elliott, 2004), with Thomas (1998) observing that ‘the fish community has now reached a state of fragile equilibrium which can be perturbed by extremes in environmental parameters’.

EXAMPLES OF COMMERCIAL AND RECREATIONAL SPECIES OF THE DIFFERENT LIFE CYCLE GUILDS

MARINE ESTUARINE-OPPORTUNISTS

As mentioned earlier, the species belonging to the marine estuarine-opportunist guild typically use estuaries mainly as a nursery area and thus do not usually contribute significantly to estuarine fisheries. Although it has not been quantified, however, estuaries clearly provide a very important nursery habitat for a number of these species, several of which, such as the bass *Dicentrarchus labrax*, the whiting *Merlangus merlangus* and *P. saltatrix*, are caught commercially later in life in the marine environment (Claridge *et al.*, 1986; Elliott & Dewailly, 1995; Able & Fahay, 2010). The juveniles of a few species, such *C. harengus* and *B. tyrannus*, have also been caught, however, in substantial numbers in estuaries.

The juveniles of *C. harengus* and of another clupeid, *S. sprattus*, which is likewise a marine estuarine-opportunist, are now by far the most important components of the whitebait fishery in England (Walmsley & Pawson, 2007). The quintessential dish whitebait has been on London’s menus since at least 1612 and became highly fashionable in the seventeenth and eighteenth centuries, with diners travelling to the taverns of Blackwall and Greenwich to enjoy a meal of these freshly-caught, small fishes (Timbs, 1866). These fishes, which swim near the surface, were carried upstream in large

numbers in July by the flood tide and became concentrated where the estuary of the River Thames narrows and curves at Greenwich, thus becoming readily accessible to fishers, before being carried downstream on the ebb tide (Wheeler, 1979). The whitebait nets, which had mouths of about three feet by three feet (91 x 91 cm), were positioned to face the oncoming tide (Parnell, 1838). While there is no longer a whitebait fishery within the main body of the Thames Estuary, that estuary and nearshore coastal waters constitute important nursery areas for individuals of the *C. harengus* stock that spawn in the marine waters in the vicinity of that estuary (Wood, 1981).

Brevoortia tyrannus is distributed along the eastern coast of North America, where it spawns in nearshore coastal waters (Able & Fahay, 2010). Large numbers of its larvae enter estuaries, where the 0+ year age class remains until temperatures start to decline, when many emigrate from the estuary to join the adult population. Some individuals return to the estuary in the warmer months of the year and form the basis of the fishery for this species in estuaries (Able & Fahay, 2010).

The purse seine fishery for *B. tyrannus*, which represents one of the oldest and largest commercial fisheries in the United States, supplies fish for reduction to oil and its subsequent refinement into margarine or cooking oil, and for incorporation into animal feeds and particularly for poultry (Smith, 1991, 1999; ASMFC, 2011; Blaber, 2011). A far smaller catch is also taken by a variety of fishing gears for use as bait (ASMFC, 2011; Blaber, 2011). The total catches of this clupeid have oscillated markedly. They thus rose markedly from c. 200 000 t in the early 1940s to reach peaks in excess of 500 000 t in the late 1950s and then declined precipitously to c. 200 000 t in the late 1960s, before showing an overall rise to reach typical annual levels in excess of 300 000 t in the mid-1970s to mid-1990s and then declining to < 200 000 t after 2002 (Anonymous, 2011; Blaber, 2011). The importance of the fishery for *B. tyrannus* in Chesapeake Bay is illustrated by the fact that > 50% of the total catch of this species now comes from that system and, since 1980, the catch of this clupeid has constituted > 40% of the total commercial landings of all finfish species from the Atlantic coast of North America (Blaber, 2011; Churnside *et al.*, 2011).

The white steenbras *Lithognathus lithognathus*, which is highly-prized by shore-based anglers in South Africa and important for commercial beach seine fishers, spawns on the Transkei and Eastern Cape coasts and its juveniles enter and remain within estuaries on the Cape coast during their

first year of life (Bennett, 1993a). On leaving estuaries, the juveniles occupy the surf zone until they mature, when they undertake an annual migration between their spawning grounds and the south-western Cape (Bennett, 1993b). Heavy over-exploitation both within and outside estuaries and the deleterious effects of estuarine degradation have led to the stock of this sparid declining and ultimately collapsing in 2002 (Bennett, 1993b; Heemstra & Heemstra, 2004).

POPULATIONS IN WHICH INDIVIDUALS COMPLETE THEIR LIFE CYCLE IN ESTUARIES

As explained earlier, the species confined to estuaries and the estuarine populations of species represented in both estuaries and marine environments are particularly prevalent in the benign environment provided by microtidal estuaries in regions where freshwater discharge is limited during summer when fishes typically spawn in those regions. These species are particularly well represented by *A. butcheri* and *C. macrocephalus* in the estuaries of southern Australia.

Acanthopagrus butcheri is endemic to southern Australia, where it is an iconic recreational species in many estuaries and supports a commercial fishery in some of these systems (Kailola *et al.*, 1993). The results of genetic studies, together with the absence of this species in coastal marine waters, imply that, in Western Australia, the populations in the various estuaries are discrete, *i.e.* their individuals spend their entire life cycle in their natal estuary (Chaplin *et al.*, 1998). As freshwater discharge declines during spring in south-western Australia, this sparid moves into the saline lower reaches of the rivers, *i.e.* upper estuary, where it spawns and the adults and resultant juveniles remain during the subsequent months of low freshwater discharge (Sarre & Potter, 1999; Sakabe & Lyle, 2010). Many juveniles and adults are then flushed from the rivers into the estuary basins by strong freshwater discharge during winter and early spring. In south-western Australia, commercial gillnet fishers target the fish during this concerted movement, which makes this species potentially susceptible to high exploitation at this time (Potter *et al.*, 2008).

Despite the above potential for excessive exploitation by commercial fishers and the numerous anglers who target *A. butcheri*, this species is very abundant in many south-western Australian estuaries. This success can be attributed to the plasticity of its life cycle traits. For example, it is capable of opportunistically feeding on very different food sources in different estuaries,

according to the relative availability of those sources (Sarre *et al.*, 2000; Chuwen *et al.*, 2007). Although the very marked differences in the composition of the food consumed by *A. butcheri* in two nearby estuaries were accompanied by very pronounced differences in growth, the growth, under identical conditions, of the progeny cultured from brood stock obtained from each of those estuaries was essentially the same (Partridge *et al.*, 2004). This implies that the growth of this species is highly plastic and related to environmental conditions rather than to any potential genetic differences. Furthermore, episodic recruitment of this sparid in the estuarine environment comprising the Gippsland Lakes in eastern Australia has been shown to be related to inter-annual differences in the environment, and particularly the extent of salinity stratification and freshwater flow, with the interface between the salt and freshwater providing a particularly productive environment for the planktonic invertebrate prey of the larvae of *A. butcheri* (Jenkins *et al.*, 2010; Williams *et al.*, 2012). While such episodic recruitment will lead to variations in the annual commercial catches of this species, the long-term trends exhibited by the catches of this species in the above estuarine environment (Fig. 2.4.9) have been attributed mainly to other factors. Thus, the decline in catches from the mid-1930s to the mid-1960s for *A. butcheri* in the Gippsland Lakes was attributed to a loss of seagrass habitat, while the decline from the early 1980s onwards was due, in part, to management initiatives, involving a change in the minimum legal length for retention and the introduction of closed areas (Department of Primary Industry, 2010).

Because each population of *A. butcheri* is confined to its natal estuary, this species is an excellent candidate for restocking those estuaries in which its abundance has declined markedly. As the population of *A. butcheri* in the Blackwood River estuary in south-western Australia was atypical in apparently suffering such a decline, an experiment was undertaken in which juvenile *A. butcheri* cultured in the laboratory from brood stock obtained from the Blackwood River estuary were marked, using alizarin complexone to stain their otoliths, and released into that estuary at 3 to 6 months of age (Potter *et al.*, 2008). The fact that 62-74% of the *A. butcheri* caught by a commercial fisher 6 to 8 years later were cultured fish demonstrates restocking is a viable proposition for replenishing the stocks of this species in the estuary (Gardner *et al.*, 2013).

Cnidoglanis macrocephalus is endemic to south-western Australia, where it has been exploited and particularly by commercial fishers (Chuwen *et al.*, 2011). The estuarine and marine assemblages of this plotosid are represented by genetically-distinct populations, which implies that individuals complete their life cycles in either estuaries or the sea (Laurenson *et al.*, 1993b; Ayvazian *et al.*, 1994). The commercial catches of this species declined in a number of estuaries between the 1960s and 1980s, a trend attributed to high levels of exploitation (Steckis *et al.*, 1995; Blaber *et al.*, 2000). The conclusion that this species is susceptible to over-exploitation is supported by detailed comparisons of fishery independent data for 1987-1989 and 2005-2008 in Wilson Inlet, the estuary which is the main commercial source of this species (Chuwen *et al.*, 2011). The latter study also demonstrated that the decline in abundance in that seasonally-open estuary was accompanied by marked reductions in the age and size at maturity, but not by a change in growth. The results indicated that the changes in maturity were the consequence of fishery-induced evolution rather than compensatory responses to a reduction in fish density.

The maintenance of a viable population of *C. macrocephalus* in Wilson Inlet, in the face of considerable fishing pressure, can be attributed to the following three factors: (1) the acquisition of biological data that led to the minimum legal length for capture being increased markedly so that it aligned with the size at maturation (Laurenson *et al.*, 1993a; Laurenson *et al.*, 1993b; Chuwen *et al.*, 2011), (2) the establishment of an area at the seaward end of the estuary that is closed to commercial net fishing (Laurenson *et al.*, 1993a) and (3) the production of very large eggs that are guarded in nests by males and the delay of hatching until a large size has been attained.

The total catches of the tropical shad *Tenuulosa toli*, which is the most important commercially-exploited fish in the estuaries of Sarawak on the island of Borneo, have declined since the 1980s and, by the mid-1990s, significant catches were being obtained only from two fast-flowing, turbid estuaries in Sarawak (Blaber *et al.*, 1996; Milton *et al.*, 1997). The results of those studies imply that *T. toli* is a protandrous hermaphrodite, the first such example in the Clupeiformes, and that spawning occurs in the middle reaches of the estuary (Fig. 2.4.10). The larvae and juveniles move to the upper, saline reaches of the estuary, where they develop as males. Males spread throughout the estuary during the spawning period and, following spawning, move to the middle and lower reaches

of the river, where they become females. While individuals can complete the whole of their life cycle in the estuary, some males enter local coastal waters where salinities are reduced and they become females, after which they re-enter the estuary (Fig. 2.4.10). Blaber *et al.* (1996) concluded that the *T. toli* populations in the above two estuaries exhibited little interchange, suggesting that, if any population was overfished, it would receive little recruitment from adjacent estuaries to replenish its numbers, which might explain the disappearance of this species from some small estuaries in Sarawak.

The natural environment of the white perch *Morone americana* comprises the estuaries and lower tidal reaches of rivers on the east coast of North America (Beck, 1995). This species lives in the deep, highly saline areas of estuaries during winter and then, between early spring and late summer, migrates to shallow, brackish or tidal freshwater habitats, where it spawns. While most of the resultant juveniles typically migrate downstream into more saline areas (Kraus & Secor, 2004), a proportion remain in fresh water during the first year of life, with this proportion depending on water flow and thus presumably on salinity (Kerr *et al.*, 2009). This percichthyid is among the most important commercial and recreational fish species in Chesapeake Bay (Butowski, 2005).

The ability of some individuals of *M. americana* to spawn in fresh water accounts for the success of this species when introduced, either accidentally or intentionally, into numerous inland reservoirs and rivers throughout a large inland region of North America (Able & Fahay, 2010). Such introductions, however, may prove a competitor for the yellow perch *Perca flavescens* as both species have a similar diet (Schaeffer & Margaf, 1986).

ANADROMOUS SPECIES

Eggs of the iteroparous *S. salar* and of the various species of the semelparous Pacific (*Oncorhynchus*) salmon are deposited in redds (nests), which have been excavated by these species in the gravel substratum of rivers and tributaries. They are then fertilized by males and covered by gravel, which affords protection while still providing an adequate flow of water and oxygen to the eggs (Kondolf, 2000). All adults of the Pacific salmon die after spawning, whereas some of the Atlantic salmon survive and return to the ocean, subsequently returning to rivers to spawn in one or

more subsequent years (Thorstad *et al.*, 2010). After hatching, and depending on type and species of salmon, the young fishes spend varying amounts of time in riverine, lacustrine or estuarine habitats before migrating to the ocean. For example, while fry of the chum salmon *Oncorhynchus keta* typically begin their migration to the ocean soon after emergence from their eggs (Pauley *et al.*, 1988), ocean type Chinook salmon, *Oncorhynchus tshawytscha*, migrate to the ocean after a few months in their riverine nursery habitat, while stream type Chinook salmon may remain in the freshwater environment for 1 to 2 years (Heard *et al.*, 2007). The fish grow in the ocean environment for a number of years and eventually start to become mature, at which time they return to the river to spawn and thus complete the cycle.

Traditionally, fisheries for salmonids developed in rivers, in which certain species are still iconic for recreational and indigenous fishers, with commercial fishing subsequently expanding into coastal and oceanic waters (Gresh *et al.*, 2000; Eggers *et al.*, 2005). Although wild stocks of *S. salar* in the northern part of their geographic range in both Europe and North America appear stable, many of those further south have declined or been extirpated (Parrish *et al.*, 1998). These and similar declines in the wild stocks of Pacific salmon in the north-west of North America over the past century have been attributed to the barriers posed to the upstream migration by the construction of dams, which have impeded migration, increased pollution and reduced stream water flow, and to the effects of overfishing and changes in oceanic environment, and to the genetic and competitive impacts of individuals produced by aquaculture that were released or escaped into the natural environment (Gross, 1998; Parrish *et al.*, 1998; Lackey, 2003; Ford & Myers, 2008). Artificial culture, which contributes *c.* 98% of the total biomass, has maintained, however, the overall abundance of *S. salar* at a high level (Parrish *et al.*, 1998). Similarly, catches of wild individuals of the sockeye salmon *Oncorhynchus nerka*, the pink salmon *Oncorhynchus gorbuscha* and *Oncorhynchus keta* have been supplemented through stock enhancement *via* hatchery releases, artificial spawning channels and lake fertilization programmes, which, in British Columbia for example, account for *c.* 85% of total production (Noakes *et al.*, 2000). Beamish *et al.* (1997) report, however, that, despite large hatchery releases, the abundances of *O. kisutch* and *O. tshawytscha* off the western coast of the United States

and Canada continue to decline, suggesting that this might be due to limitations of the marine carrying capacity.

As with all 41 lamprey species, the 18 anadromous species of this agnathan (jawless) group spend a protracted period in fresh water as blind and toothless larvae (ammocoetes), which live in the soft substrata of rivers and filter detritus and unicellular algae from the overlying water for food (Potter, 1980). The ammocoetes eventually undergo a radical metamorphosis, during which they develop eyes, prominent dorsal fins and a tooth-bearing suctorial disc. After migrating downstream and through the estuary to the sea, the young adults use their oral disc to attach to their hosts, which comprise predominantly teleosts and from which they then extract blood and flesh (Renaud *et al.*, 2009). The damage caused by particularly the flesh-feeding species is so severe that it frequently leads to the death of the host (Bahr, 1933; Beamish, 1980).

The large numbers (*c.* 667 000) of the young adults of the river lamprey *Lampetra ayresii*, which congregated in 1975 in the Straits of Georgia (eastern Canada) immediately after entering salt water, were estimated, to have killed within 90 days a total of *c.* 60 million juvenile fish, comprising small individuals of mainly *C. harengus* and the sockeye salmon *Oncorhynchus nerka* (Beamish, 1980).

The young adults of the Pacific lamprey *Lampetra tridentata* can feed while on their migration from their riverine natal environment through the estuary into the sea (Beamish, 1980). They then move into water with depths greater than 20-70 m and are present in all major fishing ground in Canada's west coast. Numerous attacks by this species have been observed on *O. nerka* and *O. gorbuscha* as these salmonids aggregate prior to entering rivers on their spawning runs.

One of the largest of the anadromous species of lampreys, *P. marinus*, has become landlocked in North America and subsequently passed from Lake Ontario into the upper Great Lakes, where it has thrived and, through the damaging effects of its feeding habits, produced a massive decline in certain fish stocks (Smith & Tibbles, 1980). The methods used in attempts to control this invader have proved very costly.

The very high price attracted by the roe of sturgeon accounts for the fact that 'of the various species of sturgeon, world-wide, all but two are classified as threatened, six are critically endangered,

eight endangered and a further six classified as vulnerable' (Wilson, 2002). Indeed, the IUCN states that 85% of the sturgeon species are now at risk of extinction, making this anadromous taxon the most threatened group of animals on its red list (IUCN, 2010). The marked decline that has occurred since the 1980s in the landings of sturgeons caught during their upstream migration is probably due to a combination of reduced abundance and regulations to restrict the capture of endangered sturgeon stocks. Increased aquaculture since c. 2000 has seen cultured production of sturgeon rise to a level in 2010 that exceeds the maximum value reported between 1950 and 2010.

CATADROMOUS SPECIES

The decline of global landings of *A. rostrata*, *A. anguilla* and *A. japonica* since the mid-1980s led Wilson (2002) to state that eel stocks were threatened and to comment that there were still gaps in our knowledge of the life cycle of these species. Since the mid-1970s, however, aquaculture production of *A. anguilla* had increased such that by 2010 it was approximately of the same magnitude as the catch of its wild fish. Culture of *A. japonica* had also commenced at about the same time and, in 2010, aquaculture production of this species was 720 times greater than its maximum annual catch in the years between 1950 and 2010. It is important to recognize, however, that the glass eels that form the basis of this culture had been harvested from the wild population (Pillay, 1990; Masuda *et al.*, 2012). The spawning area of *A. japonica* has now been located and Masuda *et al.* (2012) have succeeded in replicating the full life cycle of this species in an aquaculture environment.

ANTHROPOGENIC CHANGES TO ESTUARIES AND THEIR IMPLICATIONS

It is worth reiterating the statement of Jackson *et al.* (2001a) that temperate estuaries are the most degraded of all marine ecosystems. The impacts and threats of anthropogenic influences on estuaries and their faunas have been reviewed by Kennish (2002), McLusky & Elliott (2004), Whitfield & Cowley (2010) and by authors in the chapters in Elliott & Kennish (2011), the most notable of which are now briefly outlined with a few selected examples.

Certain habitats within many estuaries, particularly in areas of rapid population growth and uncontrolled development, have either been lost or altered through anthropogenic activities (Kennish, 2002). The numerous examples include the removal of 50% of the tidal saltmarsh habitat in the United States by a variety of activities such as dredging, spoil dumping, canal cutting and reclamation of land for agriculture (Kennish, 2001).

Eutrophication, brought about by the input of large amounts of nutrients from surrounding agricultural land, urban development and sewage, can have a variety of effects in estuaries. For example, the resultant production of massive exotic and toxic algal blooms and localized hypoxic and anoxic conditions has frequently led to an increase in the death of fishes and benthic invertebrates, alterations in fish structure and reductions in seagrass and water quality (Kennish, 2002; Landsberg, 2002; Kemp *et al.*, 2005; Anderson *et al.*, 2008; Breitburg *et al.*, 2009). Eutrophication can lead, however, to increases in, for example, the amount of macroalgae and its associated fauna and thus to an increase in abundance of fishes, including those of recreational and commercial importance (Steckis *et al.*, 1995; Kemp *et al.*, 2005). The effects of eutrophication on fish communities have been conceptualized, however, as following a three step process (Caddy, 1993; 2000) as reported by Kemp *et al.* (2005): '(1) nutrient-enhanced production of demersal and pelagic species (more food), (2) decline of demersal fish but continued increase in pelagic fish species (benthic habitat loss), and (3) a general decline in total fish production under conditions of broadly deteriorating water and habitat quality'. Ultimately, extreme eutrophication over a protracted period can result in the almost total extirpation of the fish fauna, as occurred in the Thames Estuary in the middle part of the last century (Wheeler, 1958; Tinsley, 1998).

Some fish stocks in estuaries have declined as a result of overfishing (Kennish, 2002), examples of which are provided by *L. lithognathus* in southern Africa and *C. macrocephalus* in southwestern Australia. Blaber (2011) has recognized that fishing in estuaries has direct and indirect effects on target and non-target species, habitat and water quality, and the nursery functions of the estuary for some species. The impacts of these effects may adversely alter the trophic structures of the estuarine ecosystems and, in extreme circumstances, may lead to the extinctions of the estuarine assemblages of some species. Blaber (2011) also noted that the objectives of different groups of fishes and other

human users of the estuary may differ, leading to conflict among those different groups. Other potential threats to estuarine fish faunas include the effects of freshwater diversions on the hydrology of the estuary, the introduction of exotic species and sea level rises (Kennish, 2002).

During recent decades, substantial fish kills have been recorded in many estuaries throughout the world. These mortalities are typically attributable to one or more of the following: (1) hypoxic and anoxic events caused by massive blooms of unicellular algae, such as the dinoflagellates *Prorocentrum minimum* and *Karlodinium micrum*, which have caused heavy mortalities of fishes and crustaceans in Chesapeake Bay (Goshorn *et al.*, 2004; Tango *et al.*, 2005), (2) highly elevated salinities, such as those produced in estuaries that are closed during very dry periods (Whitfield, 1999; Hoeksema *et al.*, 2006), (3) greatly reduced salinities due to atypically heavy freshwater discharge (Bennett, 1985; Steffe *et al.*, 2007) and (4) pronounced changes in water temperatures, such as occurred during a cold snap in a South African estuary and led to the mortality of very large numbers of predominantly small tropical species (Forbes & Cyrus, 1993). The environmental effects of climate change on estuaries and resultant changes in productivity will be superimposed on the effects of anthropogenic stresses (Scavia *et al.*, 2002).

Effective management of the fishes that use estuaries and of their associated fisheries, both within and outside the estuarine environment, depends on recognizing that anthropogenic activity is often having a marked impact on the physico-chemical characteristics of estuaries and thus a pronounced influence on certain species. Thus, while the impact of exploitation of each stock at different stages of its life cycle stages must be recognized, consideration should also be given to the effect on fishes of a loss or degradation of crucial estuarine habitat, diversions of water from rivers and thus disruption of flow into estuaries, declining water quality, environmental pollution, and the impacts of introduced aquatic species and climate change. These, in turn, can result in considerable changes to a range of biological characteristics of the various species and to modifications of the structure of the estuarine food web (Whitfield & Cowley, 2010). Such changes are likely to modify the productivity of the targeted fish species, with the result that historical or current rates of exploitation of those species may become less sustainable (Rice, 1995).

Although Whitfield & Cowley (2010) consider that there is increasing evidence that stocks of certain ‘estuary-dependent’ fish species are overexploited or have collapsed, Blaber (2000) has pointed out that it is difficult to separate the effects of fishing in estuaries from other sources of variability. An integrated approach, which constrains the exploitation of the various fish stocks to an appropriate level and maintains or restores the quality of estuarine habitats, is essential if estuaries are to continue to provide the ecosystem services necessary to support their biota (Blaber *et al.*, 2000; Whitfield & Cowley, 2010; Barrbier *et al.*, 2011). Such an approach to the management of estuaries requires methods that can identify where there are environmental problems and the development of indicators, which enable the health of the estuarine environment to be monitored (Blaber *et al.*, 2000). These indicators have sometimes been based on the abundance of the various fish species in samples collected from the estuary (Whitfield & Elliott, 2002; Harrison & Whitfield, 2004; Hallett *et al.*, 2012; Pérez-Domínguez *et al.*, 2012), while others employ data on the benthic macroinvertebrates, which, because they are typically less mobile and have relatively short life cycles, can provide finer spatial resolution and reflect a more immediate response to environmental change (Weisberg *et al.*, 1997; Borja *et al.*, 2000; Tweedley *et al.*, 2012).

The anthropogenic activities that have led to the current degraded state of many of the world’s estuaries have been implemented incrementally over a number of decades, if not centuries, and the cumulative effects on estuarine ecosystems have often been indirect. While there is an increasing awareness by the community of the impacts of anthropogenic activity on estuarine habitats and their faunas, action to restore degraded estuaries and to adopt integrated management approaches to maintain the fish faunas and associated fisheries will require political will & community acceptance.

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Tables

TABLE 2.4.1. Differences between the main physico-chemical and biotic characteristics of macrotidal and microtidal estuaries

Macrotidal estuaries	Microtidal estuaries
1. Strong and typically diurnal tidal water movements, with a very marked flood and ebb flow during each tidal cycle. Provides a mechanism for upstream tidal transport of the larvae of marine fish species.	Conspicuous tidal water movements restricted to the lower reaches and even then are small. No tidal mechanism for rapid transport of larvae.
2. As a result of 1, there is, at any one point, a marked diurnal increase and then decline in salinity.	Tidally-induced changes in salinity are limited and essentially confined to the lower estuary. Marked salinity changes are caused by discharge of large volumes of fresh water following periods of heavy rainfall and subsequent progressive reductions in that discharge.
3. Extensive intertidal areas.	Intertidal areas virtually non-existent in the main body of the estuary.
4. Primary production due to microphytobenthos, <i>e.g.</i> diatoms, on the bare sediment surface of the intertidal region in temperate areas is particularly important. High tidal scour inhibits development of seagrasses and macroalgae. Substantial densities of macroinvertebrates in both intertidal and shallow subtidal areas.	Microphytobenthos abundant in shallow, unvegetated subtidal areas, supporting substantial populations of invertebrates. Seagrass tends to be more prevalent. Compared to macrotidal estuaries, the prevalence of eutrophication is greater when nutrient input is large.
5. High turbidity due to suspension of fine bottom sediments by tidal motion and wave action, with a turbidity maximum in the middle or upper reaches.	Low turbidity apart from during periods of high freshwater discharge; fine sediment settles and is not kept in suspension.
6. Phytoplankton production limited due to high turbidity.	Phytoplankton production more prevalent due to greater water clarity.
7. Allochthonous detrital input derived from the catchment (rivers and surrounding land) and sea.	Allochthonous detrital input derived predominantly from the catchment.

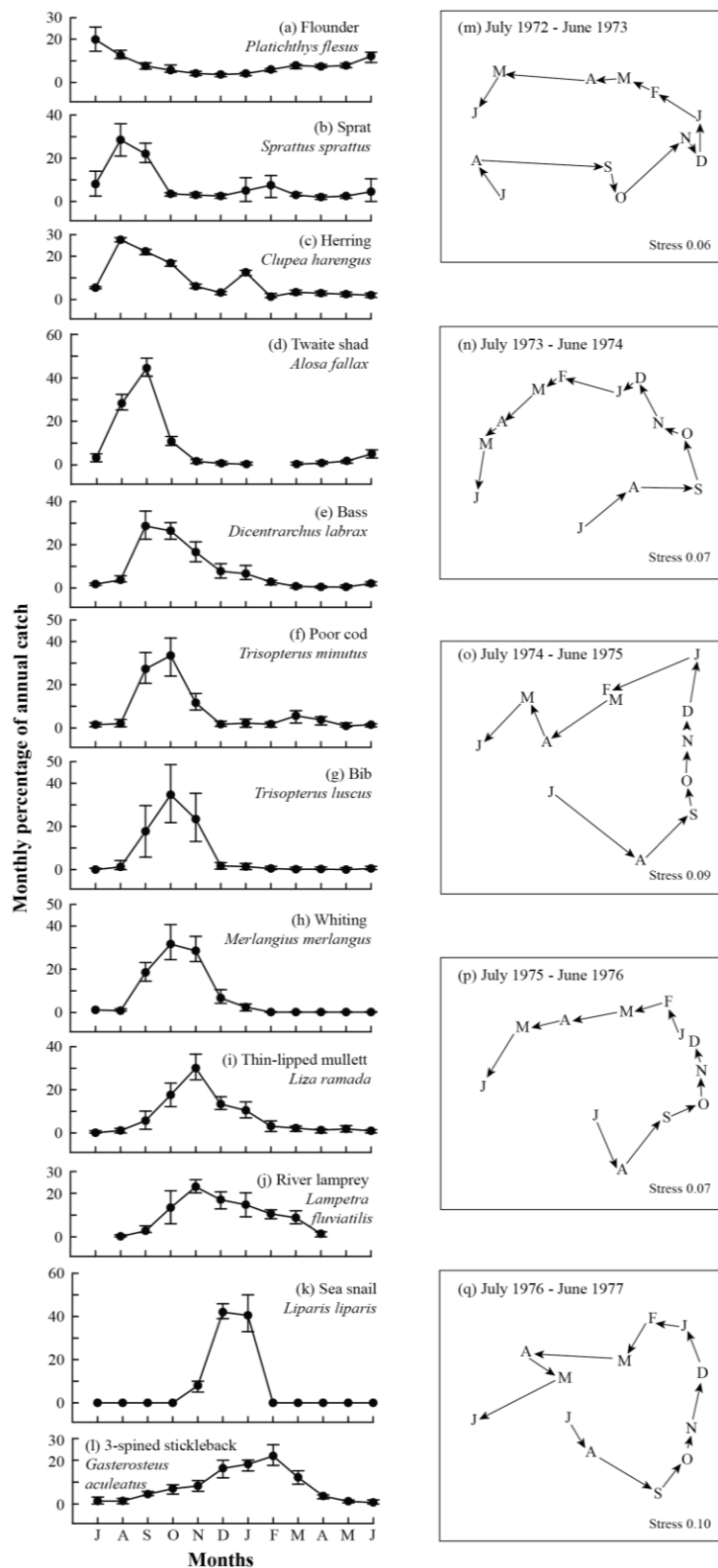


Fig. 2.4.1. Numbers of nine abundant marine species of teleost (a – c, e – i & k), two anadromous species (d & j) and *Gasterosteus aculeatus* (l) caught at Oldbury in the Severn Estuary, U.K. in each month of the calendar year, expressed as a mean \pm 95% of the total catch of the respective species obtained in weekly sampling between July 1972 and June 1977. m-q represent non-metric multidimensional scaling ordination plots, derived from the percentage compositions of all species in each month in each of the five years between July 1972 and June 1977. Redrawn from Claridge *et al.* (1986) and Potter *et al.* (1997).

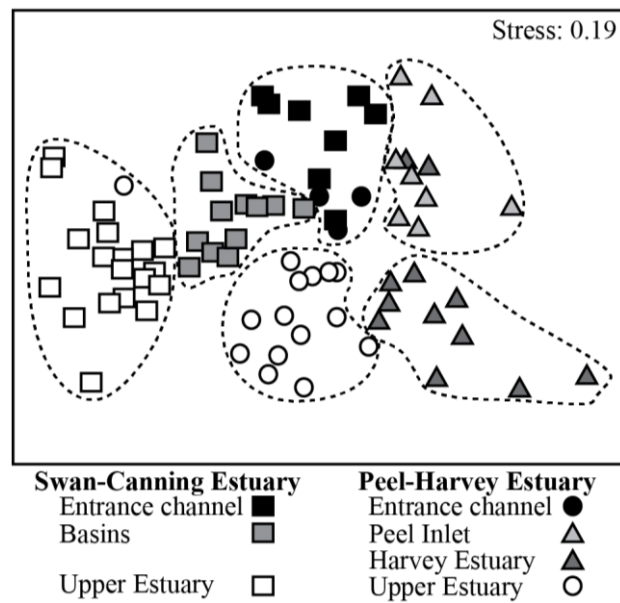


Fig. 2.4.2. Non-metric multidimensional scaling ordination plot, derived from the densities of the different fish species caught in the various regions of the Swan-Canning and Peel-Harvey estuaries in 1979 and 1980. Redrawn from Potter & Hyndes (1999).



Fig. 2.4.3. Photograph of numerous dead *Acanthopagrus butcheri* that were deposited on the banks of Culham Inlet following their death after a very marked rise in salinities. From Hoeksema *et al.* (2006).

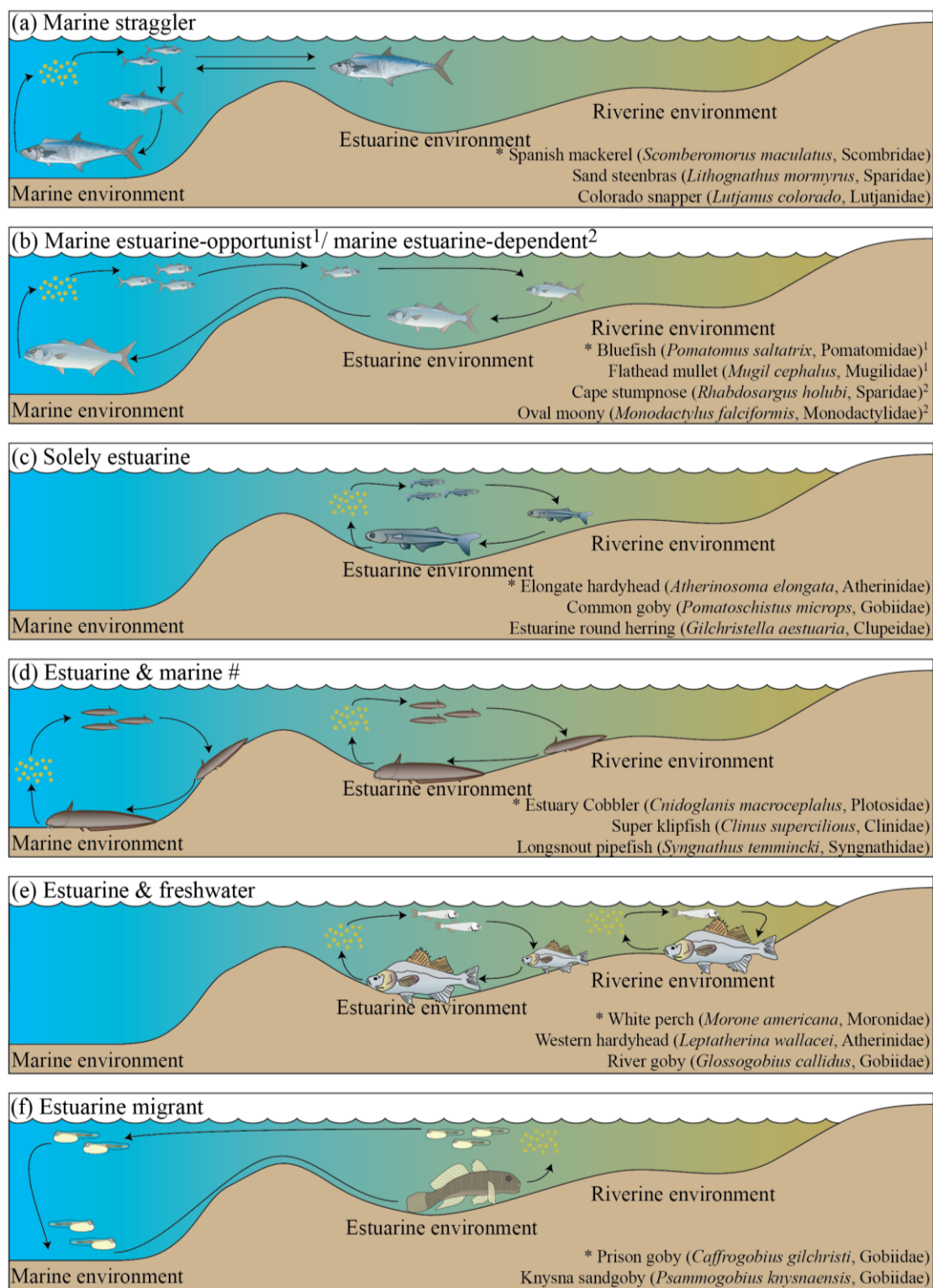


Fig. 2.4.4. Life cycle categories of fishes found in estuaries: (a) marine straggler, (b) marine estuarine-opportunist/marine estuarine-dependent, (c) solely estuarine, (d) estuarine & marine, (e) estuarine & freshwater and (f) estuarine migrant. * Denotes the species displayed in the figures. # Refers only to the estuarine populations of the guild. Modified from Potter *et al.* (2013).

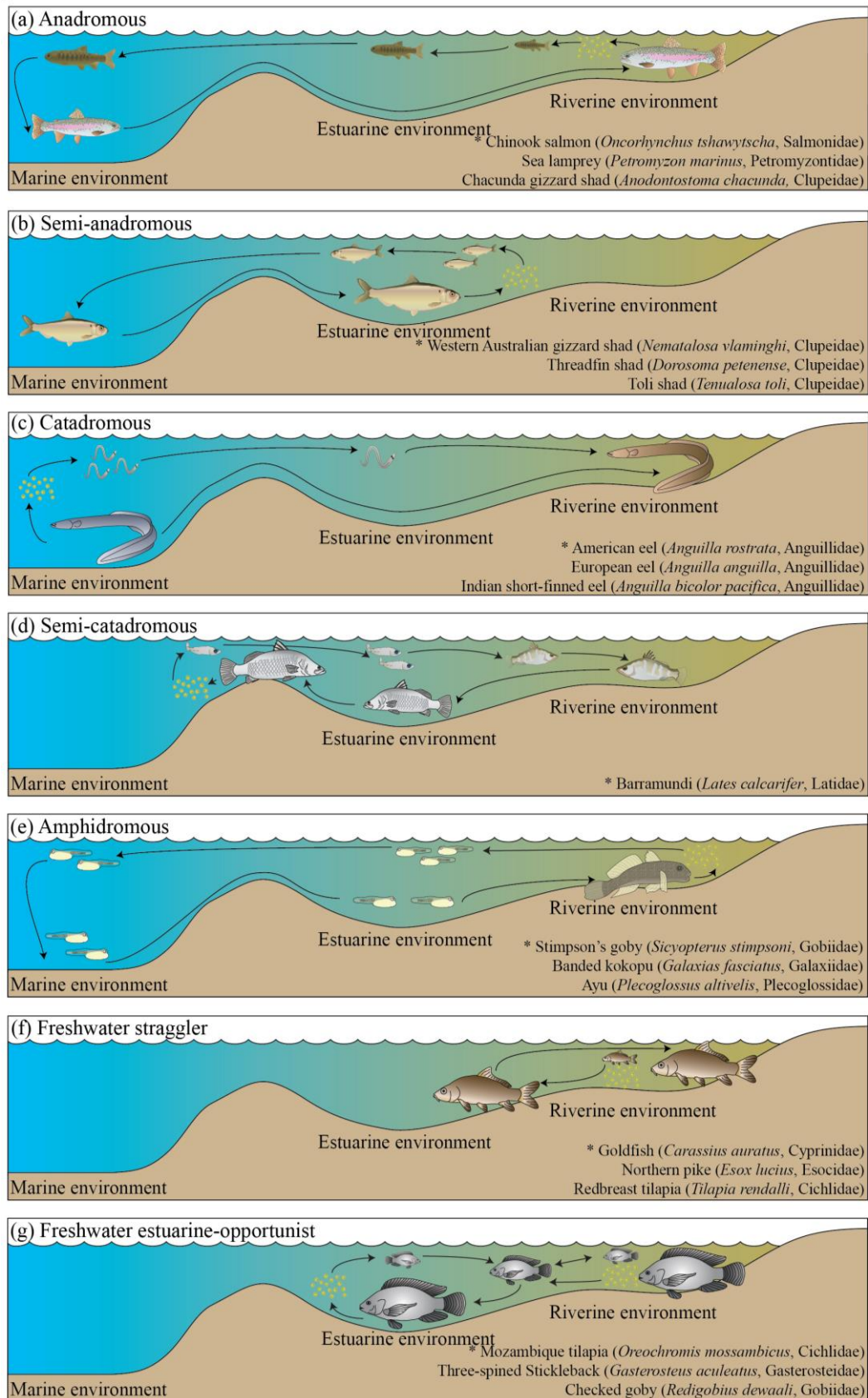


Fig. 2.4.5. Life cycle categories of fishes found in estuaries continued: (a) anadromous and (b) semi-anadromous, (c) catadromous, (d) semi-catadromous, (e) amphidromous, (f) freshwater straggler and (g) freshwater estuarine-opportunist. * Denotes the species displayed in the figure. Modified from Potter *et al.* (2013).

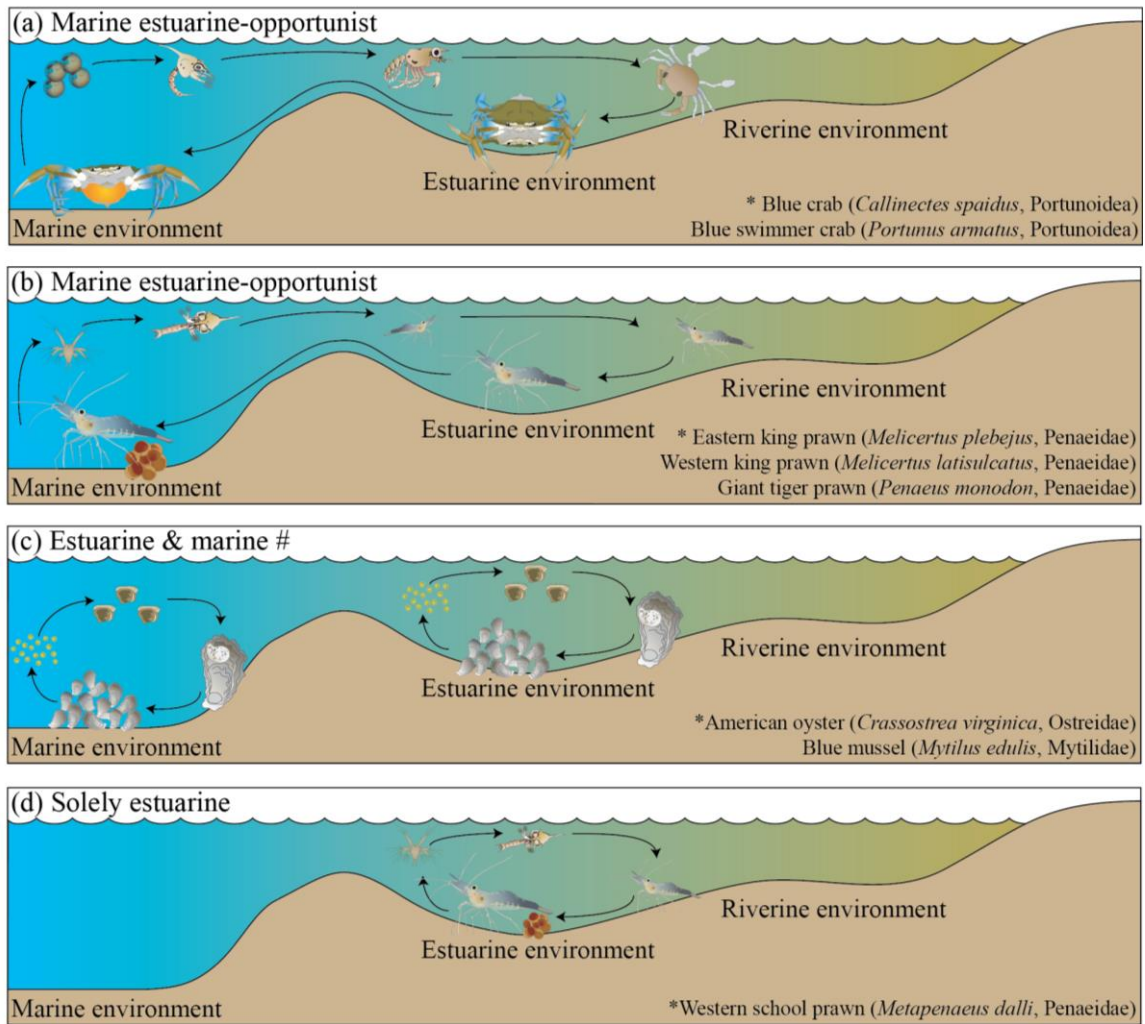


Fig. 2.4.6. Life cycle categories of selected invertebrates in estuaries: (a), (b) marine estuarine-opportunist, (c) estuarine & marine and (d) solely estuarine. * Denotes the species displayed in the figure. # Refers only to the estuarine populations of the guild.

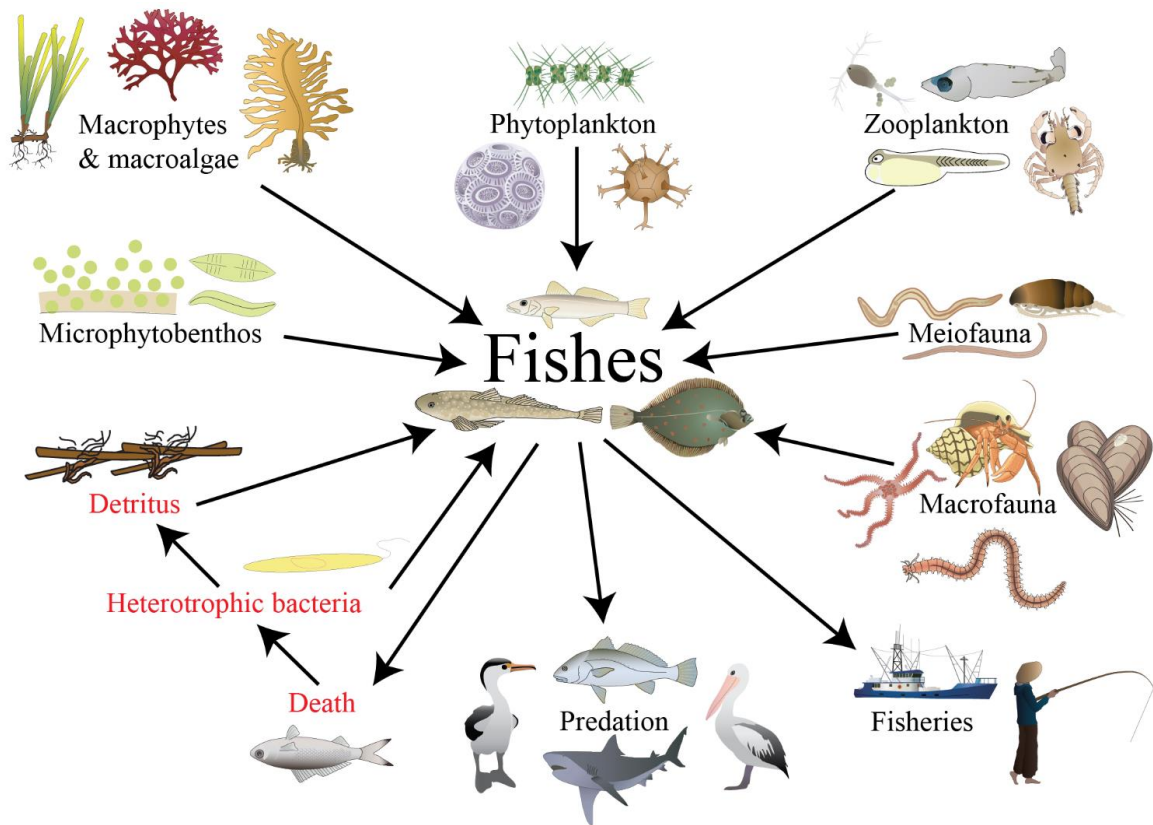


Fig. 2.4.7. The biota of estuaries, denoting their relationships to the diets of fishes.

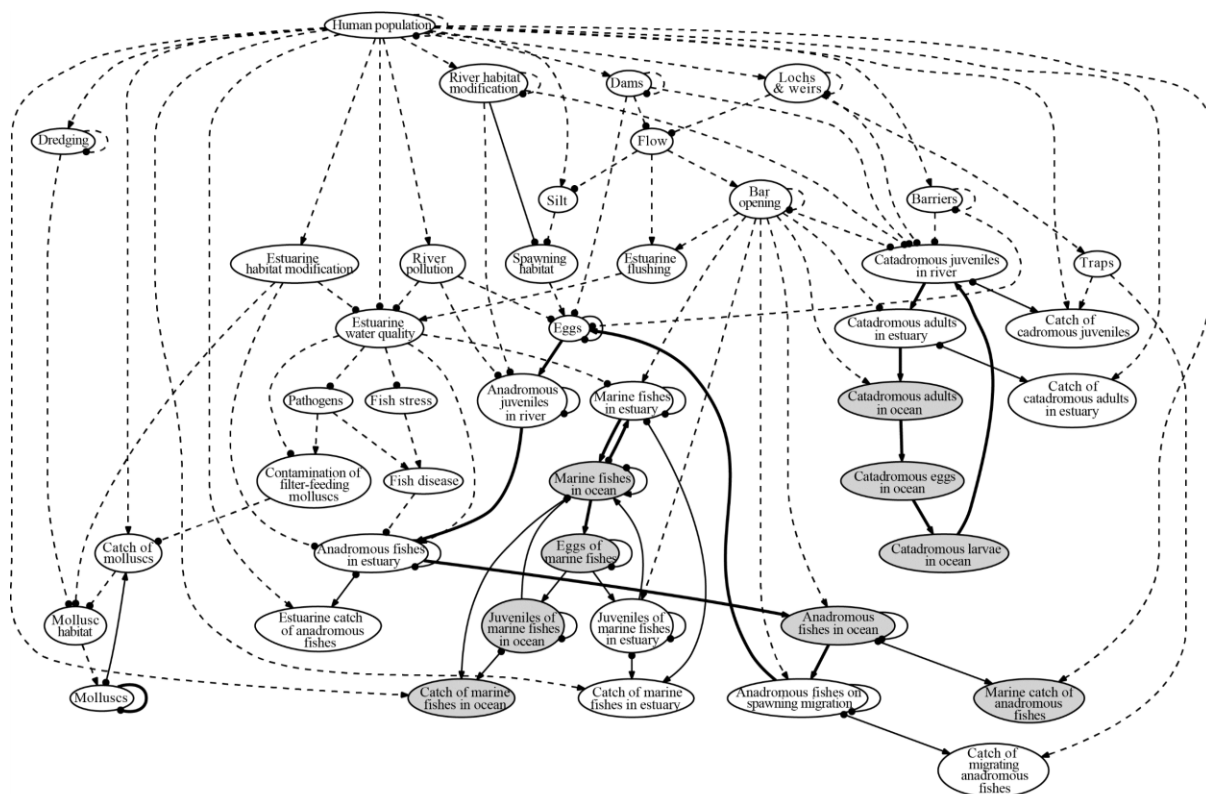


Fig. 2.4.8. Conceptual model showing the positive (\longrightarrow) and negative ($\longrightarrow \bullet$) factors that affect fishes in estuaries. Bold lines represent connections between the different life cycle stages of the species that use estuaries and the dashed lines represent the direction of the effect of anthropogenic effects.

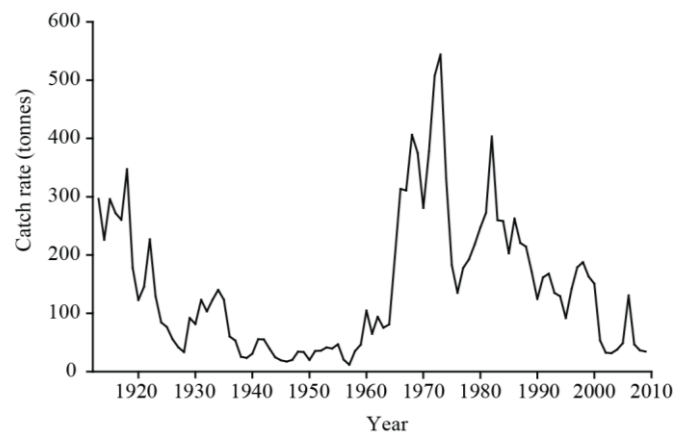


Fig. 2.4.9. Annual commercial catch of *Acanthopagrus butcheri* in the Gippsland Lakes in south-eastern Australia between 1914 and 2009 - 2010. Redrawn from fisheries status report of the Department of Primary Industry in Victoria 2010.

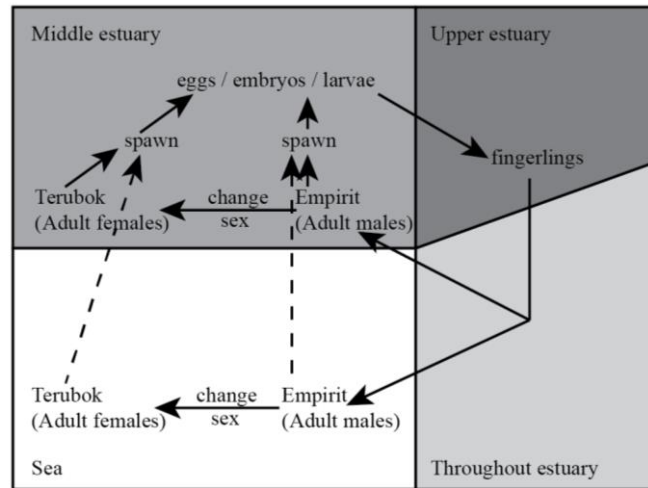


Fig. 2.4.10. Schematic diagram of the life cycle of the tropical shad *Tenuulosa toli*. Redrawn from Blaber *et al.* (1996).