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# THE CONTRASTING ECOLOGY OF TEMPERATE MACROTIDAL AND MICROTIDAL ESTUARIES

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## Abstract

Tidal range is a master factor governing the differences in physico-chemical and biological characteristics between microtidal (<2 m) and macrotidal (>2 m) estuaries, which, for convenience, thus include mesotidal estuaries (2–4 m). Microtidal estuaries differ from macrotidal estuaries in geomorphology, tidal water movements, salinity regimes, residence times, turbidity, sedimentology and intertidal area. Consequently, their phytoplankton, microphytobenthos and macrophytes communities differ in biomass and production, areal extent, distribution patterns and composition. Mesozooplankton comprise predominantly autochthonous species in microtidal estuaries and allochthonous species in macrotidal estuaries. Meiobenthos in microtidal estuaries have greater densities in subtidal than intertidal areas and species persist along the estuary. Macrobenthos is dominated by small deposit-feeding species in microtidal estuaries, whereas macrotidal estuaries contain some larger species and suspension feeders. Species richness and abundance of estuarine-resident fish species and the contributions of diving piscivorous birds and wading invertebrate-feeding birds are greater in microtidal estuaries. As paradigms regarding estuarine ecology have been based mainly on northern hemisphere macrotidal systems, this review has redressed this imbalance by detailing the extent of differences between microtidal and macrotidal estuaries. In particular, it uses data and case studies for southern hemisphere microtidal systems to demonstrate that the physico-chemical characteristics and ecology of the main flora and fauna of microtidal estuaries are frequently not consistent with those paradigms.

## Introduction

There is an increasing awareness of the profound differences in the biota and ecology of temperate estuaries in the upper and lower parts of the tidal range; i.e. in macrotidal and microtidal systems. These biotic differences reflect differences in the hydrographical regime and associated physico-chemical conditions in these systems. Awareness of the extent of such differences in biotic characteristics developed, in particular, from on-going discussions of the implications of studies by the present authors, which have encompassed systems at essentially the extreme ends of the tidal range in temperate estuaries, e.g. macrotidal systems such as the Severn Estuary in the United Kingdom, and of microtidal systems in south-western Australia, as well of those of other research workers in various regions of the world.

The results of numerous studies have established general paradigms regarding estuarine ecology that have typically been based on macrotidal systems in the northern hemisphere (e.g., Heip et al. 1995, Elliott & Hemingway 2002, McLusky & Elliott 2004, Day et al. 2012). This review aims to redress this imbalance by considering the ways in which the characteristics and ecology of microtidal estuaries are not always consistent with these paradigms, drawing, in particular, from data and case studies for microtidal systems in the southern hemisphere. In the case of fishes, the data now available for microtidal systems enable more detailed comparisons of the ways in which the various species of fish use estuaries.

This review focuses on differences, rather than similarities, between macrotidal and microtidal estuaries. Groups of organisms, such as chemoautotrophic bacteria and heterotrophic microbenthos, for which differences between these two categories of estuary cannot readily be discerned, and mammals, reptiles and amphibians, which play only a limited ecological role in estuaries, are not covered in this review and nor, generally, are aspects of ecology that apply equally to both types of system.

As this review focuses on the implications of different tidal regimes on the ecology of estuaries, it is important to understand the categorization scheme, based on tidal range, which will be used for these systems. Many scientists have followed Davies (1964) in classifying estuaries with a large tidal range (i.e. >4 m) as macrotidal, those with a tidal range of 2–4 m as mesotidal and those with a tidal range <2 m as microtidal (Boothroyd 1978, Pethick 1984, Cooper 2001, Archer 2013). For the sake of simplicity, and as many environmental and biotic characteristics change at a tidal range of ~2 m, we have followed Monbet (1992) in considering estuaries as representing two broad categories of tidal range, i.e. microtidal (<2 m) and macrotidal (>2 m), both of which are widely distributed throughout the world (Perillo et al. 1999, Whitfield & Elliott 2011).

In recent years, the estuaries in Europe have been considered, for legislative purposes, to be just one of the types of water body listed under the term "transitional waters" as part of the Water Framework Directive (European Parliament and Council of the European Union 2000). Transitional waters were defined by the directive as "bodies of surface water in the vicinity of river mouths which are partially saline in character as a result of their proximity to coastal waters but which are substantially influenced by fresh water flows" (European Commission 2003). Although transitional waters were considered to include brackish non-tidal lagoons, the input of freshwater is restricted to seepage from the land or seasonal riverine input (McLusky & Elliott, 2007). Furthermore, the term lagoon is restricted by Davis (1994) to bodies of water with little or no freshwater inflow and little or no tidal flow and are thus not considered estuaries for this review (see 'Definition of an estuary' section).

Furthermore, as pointed out by McLusky & Elliott (2007), there are a number of problems in using this term across Europe, when it does not distinguish clearly between transitional and coastal waters, and when interpretation of that term is not always consistent among countries. Moreover, the term "transitional waters", as envisaged by the Water

Framework Directive, has not been adopted outside Europe. Because an estuary is considered by the present authors to constitute a bona fide ecosystem, the characteristic features of what is regarded as an estuary have initially been carefully defined. As descriptions of the characteristics of estuaries have often been based on typical temperate systems in the northern hemisphere (e.g. Pritchard 1967b), it did not recognise that some estuaries in other temperate regions, such as southern Australia and southern Africa, can become markedly hypersaline and closed periodically from the sea (Day, 1980, Potter et al. 2010).

Having established the diagnostic characteristics and importance of estuaries, the different ways of categorizing these systems on the basis of tidal range and salinity gradient are described. An account is given of how tidal range influences, in an inter-related way, the geomorphological, hydrological and sedimentological characteristics of these systems. The ways in which differences in the extent of tidal range and its associated effects influence the characteristics of the flora and fauna are then outlined. For example, unlike estuaries with a small tidal range, those with a large tidal range expose, during each tidal cycle, a wide intertidal area, on which microphytobenthos flourishes and thus helps fuel the food chain. Furthermore, the strong tidal water movements that characterize macrotidal systems provide a mechanism for transporting fauna rapidly from marine waters into and through estuaries. Differences in tidal range are also reflected in variations in turbidity and residence time, which, in turn, influence the composition of the flora and fauna and the extent to which certain taxa, such as fish and zooplankton, reproduce and complete their life cycles within the estuary.

## Definition of an estuary

Numerous attempts have been made to define the features that are common to all estuaries that encapsulate their range and complexity (e.g. Dionne, 1963, Pritchard, 1967b, Day 1981, Perillo 1995, Hume et al. 2007, Potter et al. 2010). Recognition of the need to develop a better understanding of the physico-chemical and biotic characteristics of estuaries led to 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 seawater is measurably diluted with fresh water derived from land drainage" (Pritchard, 1967b). Although this definition generally applies to estuaries with a large tidal range, it does not encompass the following two important characteristics of many estuaries in southern Africa and southern Australia, which have a small tidal range (Day, 1980, 1981). First, it did not recognize that some of these estuaries become isolated from the sea through the formation of sand bars at their mouths during the dry period of the year. Second, it did not take into account that certain regions in some of these southern hemisphere estuaries become hypersaline during the drier months. The modification of the definition by Day (1980, 1981), which took into account these differences, has recently been refined by Potter et al. (2010) to read as follows: "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"

The above definition excludes those intermittently closed and open lakes and lagoons (ICOLLs) that do not receive freshwater water input via a well-defined river. Some systems termed ICOLLs along the east coast of Australia (Bird 1967, 1994, Adlam 2014) are morphologically similar to the seasonally and normally-closed estuaries on the south coasts of Australia and Africa, except that they do not receive freshwater input from one or more clearly defined rivers (Harris 2008, Flemming 2011).Thus, ICOLLs are also not considered estuaries.

There has not been universal agreement as to what constitutes the upper (i.e. landward) and lower (i.e. seaward) limits of estuaries in general (Elliott & McLusky 2002, Wolanski 2007). Pritchard (1967b) defined the upper limit as the point beyond which salinity declined to <0.1. While this definition is usually appropriate for macrotidal systems, it does not take into account that regions within the main body of certain other estuaries can become markedly hypersaline through evaporation during the hot and dry summer months and a lack of or limited input of freshwater and/or intrusion of marine water (Whitfield & Bruton 1989, Chuwen et al. 2009b, Perissinotto et al. 2010b). This problem is particularly prevalent in certain microtidal estuaries in southern Africa and Australia and especially in those that become cut off from the sea either intermittently, seasonally or for most of the time (Young et al. 1997, Hodgkin & Hesp 1998, Whitfield et al. 2006, Webster 2010). This primary salinization contrasts with secondary salinization, in which salts, originating from anthropogenic activities, accumulate in the upper estuary and/or tributary rivers (Cañedo-Argüelles et al. 2013). The range of activities that can lead to secondary salinization include the clearing of deep-rooted native vegetation, which brings saline ground water to the surface and thus leads to salts entering the estuary and its tributary rivers (Morrissy 1974, Allison et al. 1990, Halse et al. 2003). Certain mining and industrial activities can also produce secondary salinization (Johnson et al. 2010, Coring & Bäthe 2011).

In contrast to Pritchard (1967b), Fairbridge (1980) regarded an estuary as extending as far as the "upper limit of tidal rise". He recognized, however, that this point will change during the year as a consequence of variations in the strength of the tide and volume of freshwater discharge. Furthermore, the extent of tidal penetration in a macrotidal estuary, in which its water and those of the tributary rivers have not been regulated through, for example the building of dams or weirs, exceeds the point to which salt water, derived from marine waters, declines to a salinity of 0.1 (Pritchard 1967b, Elliott & McLusky 2002). Thus, Fairbridge’s definition includes freshwater tidal areas, which are regarded by Elliott & Hemingway (2002) as important components of estuaries. The use of tidal extension to define the upper limit of estuaries is adopted in the present review because it includes freshwater tidal areas and avoids problems arising from secondary salinization of tributary rivers.

The lower limit of estuaries is also difficult to define (Elliott & McLusky 2002, Wolanski 2007). This is particularly the case in macrotidal estuaries, which typically have wide funnel-shaped mouths gradually opening in to the marine environment. In such systems, there is thus no clear morphological demarcation, such as prominent headlands, between the estuary and neighbouring coastal marine waters (Wolanski 2007). In the case of the large macrotidal, funnel-shaped Severn Estuary, in the UK, it was decided to define the lower limit of the estuary as the seaward boundary of the zone where salinity is less than 95% of the adjacent offshore seawater for 95% of the time (Dyer 1996), an approach implicitly adopted in this review, recognizing that, for many estuaries, this is likely to be an approximation. Furthermore, the volume of freshwater entering certain estuaries is so large, at certain times of the year, that it sometimes forces a plume of estuarine water extending many kilometres outwards from the coastline (McHugh 1967, Kjerfve 1989, Blaber 1997). Thus, some authors consider the outer limit of the estuary to include all waters within the seaward edge of the plume in the open ocean (Kjerfve 1989, Blaber 1997, Wolanski 2007). Extreme examples of this phenomenon are found in tropical estuaries which are outside the scope of this review.

The well-defined narrow mouth of the entrance channel of many microtidal estuaries is typically considered to represent the outer limit of such systems (Potter et al. 1990, Cooper 2001). However, in terms of salinity, the entrance channel of microtidal estuaries is essentially marine for the drier months of the year and thus, in this respect, corresponds to the coastal marine waters to which these estuaries are connected.

## Formation and types of estuary

Estuaries have been formed mainly as a result of climatic events that influence eustatic sea level changes, such as glaciation and deglaciation (Schubel & Hirschberg 1978). They are thus ephemeral features on a geological time scale, with life spans of thousands to tens of thousands of years. In their current form, they are very young geologically, having commenced formation ~15,000 years ago as the sea level began to rise rapidly, reaching their current level ~5,000 years ago (Emery & Uchupi 1972). The life span of an estuary is prolonged by a rise in sea level and shortened by a decline in that level.

If sea level remains relatively constant, the life span of estuaries will be influenced by the rates of sedimentation (Schubel & Hirschberg 1978). This is exemplified particularly well by the estimation that, if sea level remained constant, all of the sediment discharged into the lagoons and estuaries of the Atlantic and Gulf coasts of the United States by rivers other than the Mississippi would fill these basins within 9500 years (Emery & Uchupi 1972). Sedimentation by fine-grained silty particles, derived from terrestrial runoff, occurs along the banks and at the mouths of estuaries. The former reduces the width of the estuary, while the latter, in the presence of low wave energy, produces deltas at their mouths (Davies 1973, Day et al. 2012). Sedimentation was regarded by Hodgkin (1998) as the principal long-term process that threatens the existence of microtidal estuaries in south-western Australia and urged managers to consider its impact on the functioning of these systems.

Estuaries have frequently been classified on the basis of their morphology, among which the categorizations of Fairbridge (1980) are particularly useful for biologists because of their simplicity (Flemming 2011). That classification comprises eight categories, two of which, i.e. fjords and fjärds, are drowned glacial troughs in coastal areas of high and low relief, respectively. Although falling within Fairbridge's definition of estuaries, they are not typical of traditional estuaries in several respects. Thus, for example, while they are macrotidal, their steep sides preclude the existence of extensive intertidal areas and, when present, freshwater inflow is generally insufficient to appreciably dilute the large volume of seawater they contain, with any such dilution usually confined to the surface layers, thus producing a stratified water column (Follum & Moe, 1988; Nordic Council of Ministers, 2006). Consequently, their fauna and flora are not estuarine in character as evidenced, for example, by the benthic macrofauna of Lochs Linnhe and Eil in Scotland (Pearson, 1975) and Frierfjord and Langesunfjord in Norway (Gray et al. 1988). For these reasons, fjord and fjärds have not been included in this review. The following brief descriptions of the characteristics of the six types of estuary considered in the current review, which are illustrated in Figures 1 and 2, are taken from Fairbridge (1980), Perillo, (1995), Davidson et al. (1991), Bianchi and Allison, (2009) and Snedden et al. (2012).

Rias and coastal plain (or funnel-shaped) estuaries, which are both V-shaped in profile, were formed during the Holocene transgression by flooding from the sea of pre-existing river valleys. Rias are found on high relief coasts and have relatively deep and narrow, well-defined channels (Figure 1A and 2A). In contrast, coastal plain estuaries are found on low relief coasts, and are generally shallower (<20 m) and bordered by broad, shallow flats (Figure 1B and 2B).

The majority of bar-built estuaries were formed by flooding of river valleys by the sea, on very low relief coasts in microtidal areas and where river discharge is low. The transport of marine sediments into the mouths of these estuaries produces a sand barrier (bar), which reduces the size of the mouth (Figure 1C and 2C). The bar sometimes extends across the entire estuary mouth and thus cuts it off from the ocean, creating what is termed a ‘blind estuary’ (Figure 1D and 2D).

Delta front estuaries, which are typically found in tropical areas and thus outside the scope of this review, are formed in large river systems through the accumulation of river-derived sediments at their mouths (Figure 1E and 2E). The final category, the tectonic estuaries, which vary markedly in their characteristics, were produced by neotectonic processes, such as faulting, graben formation, landslide or volcanic eruption (Figure 1F and 2F).

## Importance of estuaries

Estuaries are among the most productive of all aquatic ecosystems (Schelske & Odum 1961, Whittaker & Likens 1975, Bianchi 2006). They are typically nutrient-rich, receiving organic carbon via a range of routes, including discharge from rivers, runoff from surrounding land, tidal water movements, the atmosphere and waste inputs (Cloern 1987, McLusky & Elliott 2004). These allochthonous inputs are supplemented by autochthonous primary production from macroaglae, phytoplankton, microphytobenthos and vascular plants, e.g. salt marsh vegetation, seagrass and mangroves (Schelske & Odum 1961, Cloern 1987). Estuaries can thus be considered as sources and sinks for nutrients and organic material derived from autochthonous production and typically receive, to an even greater extent, input of allochthonous material (Elliott & Whitfield 2011). They are also frequently regarded as a trap for detritus (Baird & Ulanowicz 1993), which is derived mainly through decomposition of plant and faecal material. Organic detritus constitutes an important food source, particularly for benthic invertebrates (Fauchald & Jumars 1979, Giere 2009) and plays a crucial role in biogeochemical cycling (Rice 1982, Mann 1988).

The high productivity of estuaries provides an abundant food source for numerous taxa, including marine species of fish and crustacean that use these systems as nursery areas, and for the relatively few species of these taxa that complete their life cycle in estuaries (Beck et al. 2001, Sheaves et al. 2014). Furthermore, the visibility of such species to avian and piscivorous predators is reduced by the high turbidity in estuaries with a strong tidal influence, or by macrophytes, e.g. seagrass in the clearer waters of microtidal estuaries (Odum & Heald 1972, Blaber & Blaber 1980, Robertson & Blaber 1992, Jackson et al. 2001a). The extensive use of estuaries by the juveniles of marine species has often been regarded as facilitating more rapid growth and thus increasing survival beyond that which could be achieved by remaining in their natal environment (Sogard 1992, Le Pape et al. 2003, Yamashita et al. 2003, Veale et al. 2015).

Several of the fish and shellfish species that use estuaries as a nursery area make a major contribution to fisheries in the marine environment. Lellis-Dibble et al. (2008) estimated that what they termed “estuarine-resident species”, i.e. those that use estuaries during some stage of their life cycle, contributed 46% by mass and 68% by value to commercial fish and shellfish landings in the United States between 2000 and 2004. Moreover, such species contribute >75% of commercial fish catch in Australia, and in some regions up to 90% of all recreational angling catch (Creighton et al. 2015). Note, however, that the term ‘estuarine resident’ is used in a more restricted sense in the present review, i.e. it is confined to species that complete their life cycle in the estuary (see ‘Categorization of the ways that fish use estuaries’ section). Estuaries also play a crucial role in the life cycle of diadromous fish species as they provide a route for anadromous species to migrate between their spawning grounds in fresh water and main feeding areas at sea, as with several species of salmonids, and for the reverse migration by catadromous species such as anguillid eels (McDowall 1988). Many of these species constitute the basis of important fisheries in rivers and sometimes estuaries, e.g. the Atlantic salmon *Salmo salar* and the European eel *Anguilla anguilla* (Churchward & Hickley 1991, Dekker 2003, Potter et al. 2015b).

Despite the importance of estuaries from an ecological and fisheries perspective, those in temperate regions are regarded as the most degraded of all marine ecosystems (Jackson et al. 2001b). Most of this degradation has resulted from anthropogenic effects that have arisen as a direct result of the human colonization and development of the areas surrounding estuaries. Estuaries were initially attractive to humans as they provided an abundant food source, both within their waters and through the development of agriculture on the surrounding fertile land (Wilson 1988). These characteristics, and the convenience of estuaries in providing a sheltered harbour for ships, and thus the potential for importation and exportation of produce and a route to more inland areas, led to the establishment of permanent settlements around their shores (Wilson 1988, 2002). This, in turn, resulted in the development of various industries around estuaries (McLusky & Elliott 2004). Inevitably, estuaries increasingly became a reservoir for human and industrial waste, some of which was toxic, and for nutrients from run-off from farm land (Kennish 1992, Tweedley et al. 2015b).

### Tidal regimes

As mentioned earlier, Davies (1964) and many other scientists have classified estuaries with a tidal range >4 m as macrotidal, 2–4 m as mesotidal and <2 m as microtidal (Boothroyd 1978, Pethick 1984, Cooper 2001, Archer 2013). Hayes (1975) emphasised that as “tidal range had the broadest effect in determining large-scale differences in morphology of sand accumulation … a classification of estuaries could be best based on tidal range”. He retained the classification of Davies (1964), apart from separating the macrotidal into macrotidal (4–6 m) and hypertidal (>6 m) categories. A more finely divided scheme was subsequently developed by Hayes (1979), which recognised upper and lower sub-divisions of both the macrotidal and mesotidal categories, which has been followed by other sedimentologists such as Flemming (2012).

While the complex scheme of Hayes (1979) is valuable when considering the influence of tides on sediment accumulation and scouring, it is less relevant to the ecology of estuaries, which cannot be partitioned in such a finely-dissected way. As pointed out earlier, for the purposes of the present review, estuaries are considered to comprise just two categories, i.e. microtidal (<2 m) and macrotidal (>2 m). Physical processes in microtidal estuaries are typically wave-dominated, whereas those in macrotidal estuaries are tide-dominated. However, estuaries at the upper end of the microtidal range and lower end of the macrotidal range are a mixture of wave- and tide-dominated energy regimes, with the contribution by wave action greater in the former and tidal action greater in the latter (Flemming 2012). The present review focuses on regions to the north of the Tropic of Cancer, but south of the Arctic Circle, and southwards of the Tropic of Capricorn. It thus includes temperate estuaries towards the upper limit of macrotidal, e.g. some of those in north-western Europe and north-eastern North America, and those towards the lower end of microtidal, e.g. southern Australia and southern Africa.

## Hydrology and sedimentology

### *Water circulation and salinity*

The salinity gradient in estuaries varies both vertically in the water column and longitudinally along the estuary. This reflects differences in the patterns of water circulation and the extent to which tidal flow and freshwater discharge interact (e.g. Pritchard 1955, Dyer 1973, 1997, Savenije 2005, Valle-Levinson 2011, Geyer & MacCready 2014). In the vertical dimension, estuaries comprise three broad categories, i.e. well mixed, partially mixed and highly stratified or salt wedge, which represent a gradation in the degree of stratification. The precise pattern of circulation can also be influenced by wind and the bathymetry of the estuary and, in wide estuaries, the Coriolis force.

Well-mixed estuaries are those in which tidal flow has a far greater influence than freshwater discharge and there is extensive mixing of salt and fresh water and no conspicuous vertical change in salinity, i.e. no halocline (Savenije 2012). In partially-mixed estuaries, tidal flow and freshwater flow are more similar. There is, however, a net upstream flow of seawater at the bottom and net downstream flow of fresh water at the surface and substantial mixing of water from the two layers at intermediate depths, constituting a two-way gravitational circulation. Highly-stratified or salt-wedge estuaries are those in which there is usually little or no mixing between the fresh water on the surface and the salt water below, resulting in the production of a halocline. Wind-induced vertical mixing can occur, however, in these estuaries when they are particularly shallow and subjected to strong prevailing winds (Kjerfve & Magill 1989).

Well-mixed and partially-mixed estuaries are most numerous in macrotidal regions, with the latter systems tending to be deeper, whereas highly-stratified/salt-wedge estuaries are most common in microtidal regions. For example, the Severn Estuary, which is at the upper end of the macrotidal range, is well-mixed (Langston et al. 2003b), while the microtidal Río de la Plata Estuary is highly-stratified (Marcelo Acha et al. 2008) and systems such as the macrotidal Tamar and Thames estuaries, which have intermediate tidal ranges, are partially mixed (Uncles et al. 1983, Savenije 2005).

It should be recognized, however, that the extent of mixing can differ between regions within an estuary and temporally within a region of an estuary in response to marked changes in freshwater discharge and thus reflect different types of estuary. A good example of such seasonal differences is provided by the microtidal Swan River Estuary in south-western Australia, where 80% of discharge occurs between June and October, i.e. late autumn to early spring (Hodgkin & Hesp 1998). When large volumes of freshwater discharge enter the upper estuary during those months, the water column becomes essentially fresh from top to bottom (Figure 3A). As freshwater discharge declines, a saltwater wedge penetrates progressively upstream over the substratum and beneath the fresh water, producing a well-defined halocline (Figure 3B). During the dry summer and early autumn months, the upper estuary becomes well mixed (Figure 3C). Freshwater discharge increases sharply in late autumn and early winter and flows rapidly over the saline water, leading to marked stratification of the water column and thus a pronounced halocline (Figure 3D). While some authors have distinguished between a salt wedge and highly-stratified estuaries (Chester 1990), the crucial point, from a faunal perspective, is that, in both, the velocity of river flow is greater than tidal flow and this results in a two layered stratification (Wright et al. 1999, Twomey & John 2001, Watanabe et al. 2014).

Strong salinity stratification encourages high rates of sediment deposition (e.g. Traykovski et al. 2004, Ralston et al. 2012), thus enhancing nutrient recycling (Hopkinson et al. 1999, Watanabe et al. 2014) and can lead to conditions that produce hypoxia and even anoxia (Douglas et al. 1997, Paerl et al. 1998, Kurup & Hamilton 2002), which can dramatically influence the distribution of species and faunal composition (Cottingham et al. 2014, Tweedley et al. 2015a).

The turbulent mixing that occurs in macrotidal estuaries is a two-way process, whereby fresh water is mixed downward and saline water upward (Figure 4a). During each tide, the volume of fresh water leaving the estuary, mixed with marine water from below, must be equivalent to river inflow. There is thus a mean outflow of water at the surface and a mean inflow of more saline water directly above the estuary bed, i.e. a two layered gravitational circulation (Dyer 2001, Valle-Levinson 2010). In the stratified region of microtidal estuaries, the two layers are mixed by friction and velocity shear, producing small waves on the halocline that inject small amounts of more saline water from the lower to upper layer (Figure 4b). Although this is equivalent to an upward flow of salt water in macrotidal estuaries, the mixing is less pronounced (Dyer 2001).

In a longitudinal context, the trends exhibited by salinity gradients (e.g. McLusky & Elliott 2004, Valle-Levinson 2010, 2011, Savenije 2012) can be used to categorize estuaries in the following manner. Positive estuaries are those in which salinity declines progressively in an upstream direction as the influence of tide decreases, while that of freshwater flow increases (Figure 5A and 5B). Positive estuaries are numerous in both macrotidal and microtidal areas throughout temperate regions of the world (Figure 5A and 5B). In contrast, estuaries are termed ‘negative’ or ‘reverse’ when the salinity gradient increases in an upstream direction, which occurs when the loss of water by evaporation exceeds freshwater input from all sources (Figure 5C). Estuaries with these characteristics are typically shallow and occur in microtidal regions in Mediterranean climates, such as the Tomales, San Diego and Mission estuaries in California and the Coorong, Leschenault and Vasse-Wonnerup estuaries in southern Australia (Largier et al. 1997, Webster 2010, Tweedley et al. 2014a, Veale et al. 2014). As rainfall is highly seasonal in these regions, the inverse salinity trends are most pronounced during the warm and dry summer months and some of these estuaries can become positive in the wet season, i.e. salinity then declines in an upstream direction (Figure 5A). Inverse or reverse salinity gradients are developed in estuaries, either through their associated river(s) discharging little or no water during the warm dry summer months (Figure 5C) or because those river(s) discharge only into the lowermost reaches of the estuary (Figure 5D; Webster 2010, Veale et al. 2014).

The term ‘salt-plug estuary’ was coined by Wolanski (1986) when some region of the estuary becomes hypersaline and salinity thus increases from the mouth to that region and then declines progressively upstream (Figure 5E; Valle-Levinson 2011). Examples of such estuaries in temperate areas are provided by Guaymans Bay in the Gulf of California (Valle-Levinson 2011) and the Peel-Harvey Estuary in south-western Australia (Loneragan et al. 1987).

In some microtidal estuaries in regions of low rainfall, the volume of freshwater inflow is so low that a sand bar forms at the mouth of the estuary, which prevents the exchange of water between the estuary and the ocean (see ‘Sand bar dynamics’ section). Freshwater inflow can subsequently be insufficiently strong to breach that bar for protracted periods, and even years. As a consequence, the waters in the shallow basins of these normally-closed estuaries can become markedly hypersaline through evaporation and very limited freshwater inflow. In this respect, this type of estuary equates most closely with the salt plug estuary (Figure 5F). Examples of this type of estuary include the St Lucia Estuary in South Africa and the Hamersely, Stokes and Culham inlets in south-western Australia (Figure 5F; Whitfield et al. 2006, Chuwen et al. 2009b). The last of those estuaries provides an extreme example of this type of estuary, with salinities reaching as high as 296, when the bar had not opened for at least three years (Chuwen et al. 2009b), and thereby causing the death of 1.3 million individuals of the sparid *Acanthopagrus butcheri* (Hoeksema et al. 2006b).

Due to the pronounced tidal water movements, the salinity at any location in the middle region of macrotidal estuaries changes markedly during each tidal cycle (Uncles 1984, Damme et al. 2005). In contrast, the changes in salinity during a tidal cycle in microtidal systems are small. Marked salinity changes do occur, however, in microtidal estuaries, following discharge of large volumes of fresh water following periods of heavy rainfall (e.g. Whitfield & Paterson 1995, Kanandjembo et al. 2001).

### *Residence and flushing times*

The health and water quality of an estuary are regulated by its physical, chemical and biological processes (Arega et al. 2008). One of the physical processes that indicates whether an estuary is susceptible to degradation is the rate at which water, and its constituents, is exchanged with the open ocean. Indeed, estuaries are often regarded in the context of time scales, based on the mixing, transport and escape of estuarine water, i.e. flushing time, residence time and/or age, of which the first two are the most frequently employed (e.g. Zimmerman 1976, Takeoka 1984, Zimmerman 1988, Nixon et al. 1996, Jay et al. 2000, Monsen et al. 2002, Uncles et al. 2002, Sheldon & Alber 2006, Wolanski 2007). A combination of the various definitions of the above three transport time scales has been used to provide definitions that are readily interpretable to biologists for each of those time scales, recognizing that “to avoid misunderstandings and even erroneous conclusions it is important to introduce precise definitions and to use them with care” (Bolin & Rodhe 1973). This is particularly important in the case of flushing and residence times of an estuary because, although they represent different concepts, they are often confused (Monsen et al. 2002, Sheldon & Alber 2002)

- Flushing time. Time required for freshwater inflow to replace the amount of fresh water present in the estuary, i.e. volume of fresh water in the estuary divided by river flow rate.
- Residence time. Time required for a water parcel to escape from the estuary from a specified location.
- Age. Time required for a water parcel to travel from a boundary to a specified location within the estuary, i.e. the time a particle has spent in the estuary.

The crucial point, however, is that, when comparing the ecology of biota in macrotidal and microtidal estuaries in the context of residence time, a long residence time corresponds to both a long flushing time and long age and vice versa. While, at a sophisticated level, the concept of a single residence time (or flushing time or age) per estuary can be regarded as an oversimplification, it is convenient from both broad ecological and engineering viewpoints (Oliveira & Baptista 1997). It is also important to recognize that the residence time within an estuary can vary markedly, both spatially and temporally (e.g. Oliveira & Baptista 1997, Yuan et al. 2007).

The flushing times given by Uncles et al. (2002) for a wide range of macrotidal and microtidal estuaries in Europe and North America were calculated during spring tides and at times when freshwater discharge was relatively low. They demonstrated that flushing time is strongly related to tidal length and tidal range (Figure 6). Indeed, these two variables were shown by multiple regression analyses to explain 91% of the variability in flushing time, with tidal length the most influential.

The flushing time, among the above macrotidal and microtidal estuaries, increases progressively with tidal length, i.e. it is greater in longer than shorter estuaries, and is inversely related to tidal range. Consequently, flushing time is typically least in macrotidal estuaries at the upper end of the tidal range and greatest in microtidal estuaries. Thus, for example, the flushing times in macrotidal estuaries with a large tidal range are frequently less than three days, whereas those in microtidal estuaries lie between 40 and 230 days (Figure 6; Uncles et al. 2002).

The flushing time and residence time of 12 macrotidal estuaries on the northern coast of Spain were estimated by Borja et al. (2006), using the mean annual freshwater discharges and other data given for those estuaries in Valencia et al. (2004). The flushing times were less than three days in 11 of those estuaries and less than one day in eight, which is consistent with the trends described by Uncles et al. (2002). Furthermore, residence time was also less than one day in the latter eight estuaries and the three shortest residence times were recorded for the same estuaries as the three highest flushing times (Borja et al. 2006).

The flushing times recorded by Uncles et al. (2002) for the Elbe, Weser and Humber, which were at the upper end of those times for the macrotidal estuaries they analysed, did not differ markedly from those estimated by Vandenbruwaene et al. (2013), which were likewise measured under low flow conditions. The mean and minimum flushing times (under maximum flow) estimated for those three estuaries by the latter authors were ~40–45% and

~20–25%, respectively, of those under low flow conditions. These comparisons emphasize that, in large macrotidal estuaries, and particularly in those with relatively long flushing times for such systems, freshwater discharge does have a significant impact on flushing time, although not as pronounced as in microtidal systems. While residence time in the macrotidal Mersey Estuary, on the north-west coast of England, is typically related more to tidal range than to freshwater discharge during spring tides (9–10 m), it can be significantly affected by freshwater discharge when the tidal range is small, i.e. during neap tides (3–4 m; Yuan et al. 2007).

Models produced by Liu et al. (2008) for the Danshuei River Estuary (Taiwan), which is at the lower end of the macrotidal range, and by Huang et al. (2011) for the microtidal Little Manatee Estuary, Florida, USA, demonstrated that residence time decreases with increasing freshwater inflow (Figure 7). These trends were described effectively by an exponential regression equation ($r^2 = 0.93$) and power-law function ($r^2 = 0.98$), respectively. The latter model emphasized that residence time began to increase markedly as flow decreased to low levels, i.e. $<4\ \text{m}^3\ \text{s}^{-1}$, a trend exhibited in other microtidal estuaries (e.g. Shen & Haas 2004, Wan et al. 2013).

The values for residence time can vary appreciably during the year, and particularly in microtidal estuaries, whose characteristics are influenced, to a greater extent, by variations in seasonal freshwater flow than is generally the case in macrotidal estuaries. Thus, on the basis of measurements over 78 years, the mean monthly freshwater discharge in the microtidal Chesapeake Bay in March and April was ~3.5 times greater than the minima in July to September (U.S. Geological Survey 2015), which is reflected in differences of approximately four times between the maximum and minimum flushing times of 365 and 90 days, respectively (de Jonge et al. 1994).

Intra-annual differences in residence time are even more pronounced in microtidal estuaries in Mediterranean climates, where rainfall and thus freshwater discharge is highly seasonal. For example, in south-western Australia, 80% of rainfall on average occurs between May and September, i.e. from late autumn to early spring (Hodgkin & Hesp 1998). Thus, in the upper reaches of the permanently-open Swan River Estuary in 1996, the residence time ranged from as short as 1 day in winter to as long as 235 days in summer (Kalnejais et al. 1999). In seasonally-open estuaries in the same region, e.g. Wilson Inlet, where a bar (sand barrier) forms a temporary barrier from the ocean, the modelling study of Ranasinghe & Pattiaratchi (1998) showed that freshwater inflow was the overwhelming factor governing the flushing of that estuary. However, residence time in such estuaries will clearly be infinite when the estuary mouth is closed by a sand bar in the warm summer months and moderate to low during the wet winter months. Obviously, residence times in normally-closed estuaries, which are not flushed for periods of up to several years, will be infinite for those very protracted periods (Young & Potter 2002, Brearley 2005).

The rate at which water in the estuary is exchanged with the ocean is greater in macrotidal systems, which typically have a wider mouth than microtidal systems and a tidal prism (i.e. the volume of water between mean high tide and mean low tide) that can be several orders of magnitude greater than the volume of freshwater discharge (Ryan et al. 2003).

In summary, macrotidal estuaries are typically funnel shaped, which, together with the strong tidal action and freshwater input, facilitates efficient flushing (Figure 4A). In contrast, microtidal estuaries typically have narrow entrance channels, which restrict exchange with the ocean and thus limit flushing, with only a small proportion of the water body in the estuary exchanged during each tidal cycle (Figure 4B and 4C).

### *Turbidity*

The amount of suspended particulate matter (SPM) within the water column of estuaries depends on a number of factors, including estuarine circulation patterns, the quantity of sediment in the freshwater discharge and marine waters and the settling velocity of that suspended material (McLusky & Elliott 2004). Among these factors, tidally-generated sediment re-suspension, sediment deposition and/or longitudinal advection of a horizontal gradient in SPM are the main mechanisms that govern SPM variability within and among estuaries (e.g. Schubel 1971, Allen et al. 1980, Nichols & Biggs 1985, Van de Kreeke et al. 1997, Uncles et al. 2002). Thus, given the large differences in their tidal water movements, the levels of suspended particulate matter, and thus turbidity, will clearly differ between macrotidal and microtidal estuaries.

As estuaries are dynamic environments, the levels of SPM within any given estuary can change markedly over a range of spatial and temporal scales. The concentrations of SPM are highest at the point where riverine discharge and tidal currents meet, i.e. the turbidity maximum (McLusky & Elliott 2004, Flemming 2011). In macrotidal estuaries, the concentration and location of the turbidity maximum is influenced mainly by tidal processes on short time-scales and by gravitational circulation at longer time-scales, whereas in microtidal estuaries the turbidity maximum is typically greatest during high freshwater discharge (Jay & Musiak 1994, Uncles et al. 2002). A particularly good example of how tidal strength within an estuary can influence SPM is provided by the estimate that, in the macrotidal Severn Estuary in the UK, 30 Mt of sediment are suspended in the water column during spring tides, compared with only 4 Mt on a neap tide just seven days later (Kirby et al. 2004). The remaining 26 Mt settle on the bottom of the estuary, forming extensive layers of fluid mud. In contrast to the influence of tidal strength in macrotidal estuaries, SPM concentrations in microtidal estuaries, which are typically shallow, can increase markedly during storms as the rate of sediment re-suspension increases due to wind-generated waves. In the Thermaikos Gulf, in Greece, for example, SPM concentrations increased 15-fold from 1–2 mg $l^{-1}$ during normal condition to 35 mg $l^{-1}$ during storms (Paphitis & Collins 2005).

The marked differences between the SPM concentrations of macrotidal and microtidal estuaries is illustrated by analyses of data from 44 estuaries in Europe and North America, measured in the region of maximum turbidity, within approximately an hour of local high water at spring tides and during relatively low freshwater flow (Uncles et al. 2002). The results indicate that 74% of the differences in SPM concentrations were explained by mean spring tidal range (at the estuary mouth) and tidal length in estuary, with the former the more influential (Figure 8). Similar results were recorded by Hughes et al. (1998), who collated data for SPM concentrations at the bottom of the water column (where SPM concentrations are typically greatest; e.g. Schubel 1968) in the middle of the turbidity maximum for a smaller suite of microtidal and macrotidal estuaries (Table 1).

### *Sediment dynamics*

Estuaries lie at the land-sea interface and are subjected to unidirectional riverine hydrodynamics and also a bidirectional process regime driven by tides and waves (Spencer & Reed 2010). The changing axial balance between these processes results in a tripartite longitudinal zonation (Dionne 1963, Dalrymple et al. 1992). Marine processes dominate in the lower region where sediment is typically coarse, and, although the upper region is dominated by riverine inputs, the sediments there are also coarse, comprising sand and gravel. In contrast, the sediments of the middle region are muddy as a result of flocculation, coagulation and aggregation of suspended material due to the mixing of salt water and fresh water. While this tripartite longitudinal zonation is broadly independent of tidal range

(Flemming 2011), there are some differences between the sediment dynamics of macrotidal and microtidal estuaries.

In the case of both macrotidal and microtidal estuaries, fine and coarse sediments enter from the catchment, with the sediment load depending on the geological characteristics of the catchment and climatic differences, particularly in relation to rainfall (McLusky & Elliott 2004, Gray & Elliott 2009). In macrotidal systems, the coarse sediment, transported into the estuary from rivers is deposited at the point where riverine and tidal currents converge due to the marked decrease in velocity (Ryan et al. 2003). Once deposited, the sediment is regularly redistributed by the strong tidal currents, often forming mobile sandbanks (Figure 9A; Connor et al. 2004). In contrast, the absence of strong tidal currents in microtidal estuaries enables the coarser sediments to be carried downstream by rivers from the catchment to form fluvial (tidal fresh water) deltas at the junction of the rivers and estuary basin (Figure 2C; Pasternack & Brush 1998, 2002).

During flood and ebb tides, fine sediments in the middle reaches of macrotidal estuaries are resuspended, aggregated and transported, although the higher settling velocities of the flocs and aggregates increases their rates of deposition (Figure 9A). These particles are thus deposited during slack tides, usually within the upper and lower bounds of the turbidity maximum (Flemming 2011). In microtidal estuaries, the finer sediments are deposited in the deeper water of the basin, where current velocity is typically low and the higher salinities aid in flocculation and deposition (Figure 9B; Ryan et al. 2003). Indeed, the low energy environments of the basin, combined with their relatively large size results in up to 80% of the fine sediments that are transported into the estuary becoming ‘trapped’ there (Patchineelam et al. 1999, Roy et al. 2001), constituting a very effective sink for this terrigenous material. Moreover, the presence of microphytobenthos and seagrasses stabilize the sediment by reducing water velocity and thus also thier resuspension (Ward et al. 1984, Murray et al. 2002, Tweedley et al. 2008).

Fine sediment is also deposited in the extensive intertidal areas present in macrotidal estuaries by tidal water movement, resulting in the seaward development of these areas (Figure 9A; Green et al. 2000). In microtidal estuaries, the deposition of fine sediments on the fringes of the central basin is governed predominantly by internally-generated waves (Ryan et al. 2003).

The lower reaches of macrotidal and microtidal estuaries are both characterized by relatively coarse sediments that are carried into the systems by tidal action, a mechanism that is more effective in the former type of estuary due to its larger tidal range, a two-layer gravitational circulation and a wide mouth. For example, in the macrotidal Tay Estuary in Scotland, a lack of river-derived sediment has led to the substratum throughout the estuary becoming dominated by marine-derived sediments (Buller & McManus 1975). Sediment entering macrotidal coastal plain estuaries also forms elongated mid-channel sand bars, which can extend the intertidal areas in a seaward direction (Dalrymple et al. 1992, Wells 1995).

Rather than forming mid-channel sand bars as in macrotidal estuaries, the landward transport of marine-derived sand in microtidal estuaries extends only into the lower-most parts of the estuary where it forms flood and ebb tide deltas (Roy 1984, Green et al. 2000). Coastal transport of sediment along and onshore can also lead to the formation of a bar (berm or sand beach barrier) across the mouths of microtidal estuaries, which reduces the width of the mouth and can become so large that it closes the estuary off from the ocean (Cooper 2001, Roy et al. 2001, Chuwen et al. 2009b, Rich & Keller 2013). During storms, sediment can be transported over this bar by large waves, forming washover deposits that may extend into the estuary (Boyd et al. 1992, Ryan et al. 2003).

Relatively smaller volumes of sediment are exported from microtidal than macrotidal systems, because of their trapping efficiency (Figure 9; Ryan et al. 2003). In both types of estuary, the export of sediment increases during river floods.

Organic detritus, which forms an important component of the food chain in estuaries (e.g. Odum 1968, Heinle et al. 1977, Fauchald & Jumars 1979, Giere 2009), constitutes a variable proportion of the fine sediments of estuaries. In macrotidal estuaries, detritus is derived from both the catchment (rivers and surrounding land) and the sea, whereas in microtidal estuaries it enters predominantly from the catchment. The role of detritus and its associated bacteria in the nutrition of estuarine organisms, which does not apparently differ between macrotidal and microtidal estuaries, has been reviewed in detail by Heip et al. (1995).

### *Sand bar dynamics*

Sand bars (see above) are formed by sediment transport resulting from either the interaction between the longshore current, which carries sediment, and the inlet current or by the onshore transport of sediment during periods of low freshwater flow (Ranasinghe et al. 1999). In regions where freshwater discharge is highly seasonal, such as California, southern Australia and southern Africa, sand bars sometimes form a barrier sufficiently large to prevent exchange with the sea (Figure 10; Elwany et al. 1998, Hodgkin & Hesp 1998, Ranasinghe & Pattiaratchi 1999, Cooper 2001, Rich & Keller 2013). These estuaries thus become either seasonally or normally-closed or even permanently-closed when freshwater discharge is particularly low, when they could be regarded as salt lakes or lagoons (Hodgkin & Hesp 1998, Cooper 2001, Chuwen et al. 2009b).

The amount of freshwater inflow from rivers is the most important factor in maintaining an open connection between microtidal estuaries and the ocean (Reddering 1988, Elwany et al. 1998, Whitfield et al. 2008, Rich & Keller 2013). For example, the probability of the Carmel Estuary in California being open increases 10-fold as mean daily river flow increases from 0.2 to 1.0 $m^3 s^{-1}$, and is open on 98.5% of the days when river flow is greater than 0.5 $m^3 s^{-1}$ (Rich & Keller 2013). However, the tidal prism and magnitude of wave energy play a supporting role (Elwany et al. 1998). Thus, in South Africa, the amount of flow required to maintain an open mouth to an estuary ranged from 1 $m^3 s^{-1}$to 2 $m^3 s^{-1}$ on the lower energy south-western Cape coast to 5–10 $m^3 s^{-1}$ on the high energy KwaZulua Natal coast (Whitfield & Bate 2007).

In south-western Australia, the sand bars at the mouths of seasonally-open estuaries are typically breached in the winter or spring as the volume of water in the estuary increases as a result of the heavy rainfall that occurs in that region during those seasons (e.g. Ranasinghe & Pattiaratchi 1999). The extent to which freshwater discharge influences whether an estuary becomes closed is illustrated by the fact that, in south-western Australia, the mean discharge of ~14 $m^3 s^{-1}$ for permanently-open estuaries is far greater than the ~2 $m^3 s^{-1}$ for seasonally-open estuaries, which, in turn, is substantially greater than the 0.10 $m^3 s^{-1}$ and 0.13 $m^3 s^{-1}$ for normally and permanently-closed estuaries, respectively (Figure 11). This trend largely reflects a sequential decline in rainfall from the west, where the estuaries tend to be permanently-open, to the east, where estuaries are often normally closed (Hodgkin & Hesp 1998).

The breaching of the bar at estuary mouths is mainly brought about by the physical pressure from marked increases in freshwater discharge, but overwashing from the coastal environment immediately outside the estuary can also result in breaching (Figure 10E). This is achieved either by incision of the bar by overtopping waves or by landward erosion of the seaward side of the bar due to back wash (Rich & Keller 2013). During a 14 year period in the East Kleinemonde Estuary in southern Africa, short periods of overwash (<3 h), which are usually associated with a specific high tide, occurred on 14% of the days, whereas longer periods (>3 h), which are primarily driven by storms, occurred on 2% of days (Whitfield et al. 2008). The effects of overwash, however, are not always sufficient to breach the bar and beaching due to overtopping alone is never protracted (Rich & Keller 2013). The frequency and magnitude of overtopping is essentially inversely related to bar height, with a low height requiring a lesser volume of freshwater discharge required to breach the bar.

A few estuaries, such as the Moore River Estuary in south-western Australia, become intermittently-open to the ocean for a few hours to 18 days as a result of the effects of a substantial input from artesian springs, rather than of freshwater discharge derived from rivers (Young et al. 1997). Some other estuaries are intermittently-open through artificial breaching of the bar at irregular intervals (Brearley 2005).

Estuaries that become closed from the sea, either seasonally, intermittently or normally, constitute 80% of the ~50 estuaries in south-western Australia (Potter & Hyndes 1999). Likewise, 75% of the total number of ~250 estuaries in southern Africa fall into this category (Whitfield 1998).

### *Intertidal region*

The pronounced changes in tidal height within a tidal cycle, which occur in macrotidal estuaries, result in extensive intertidal areas becoming exposed at low tide. In macrotidal estuaries in the UK, it has been estimated, for example, that the percentage contribution of the intertidal area to the total area of the estuary is ~55% in rias and coastal plain estuaries and 72% in bar-built estuaries (Figure 12; Davidson et al. 1991). These values are all far greater than the 3.5% recorded for bar-built estuaries in south-western Australia, which are microtidal (OzCoasts 2015). Tidal range also influences the morphology of these areas, with their slopes increasing with increasing tidal range (Kirby 2000, Pritchard et al. 2002).

## Phytoplankton

The production, biomass and community composition of phytoplankton in estuaries are determined by the interplay between hydrodynamic and sedimentary processes, light penetration, nutrients and salinity, and by grazing pressure, principally from zooplankton and benthic suspension-feeding invertebrates (Lancelot & Muylaert 2011, Cloern et al. 2014). Each of these factors differs markedly between macrotidal and microtidal estuaries.

Light is essential for phytoplankton growth, with the ratio between the euphotic depth and degree of vertical mixing of the water column determining the amount of light available to facilitate phytoplankton development (Kromkamp & Peene 1995, Irigoien & Castel 1997, Desmit et al. 2005). Freshwater inflow into estuaries results in stratification of the water column, which promotes the rapid production of phytoplankton blooms, whereas tidal stresses break down stratification and maintain sediments in suspension, thereby attenuating light and constraining phytoplankton production. Variability of phytoplankton production is therefore tied to both the seasonal discharge of fresh water and the input of tidal energy (Figure 13; Lancelot & Muylaert 2011, Cloern et al. 2014).

Macrotidal estuaries are usually very turbid because strong tidal scour re-suspends bottom sediments, producing local accumulations of suspended particles at the turbidity maximum, which, together with river inputs of terrestrial material and irrespective of nutrient concentrations, inhibits light penetration and phytoplankton development (Cloern 1987, Fichez et al. 1992, Heip et al. 1995). Maximum turbidity zones are common in relatively long macrotidal estuaries (Uncles et al. 2002) and primary production is strongly light-limited in these regions (e.g. Soetaert et al. 1994a, Radke et al. 2010). Turbidity is typically greater in macrotidal than microtidal estuaries (Monbet 1992), and phytoplankton growth is predominantly light-limited by high turbidity in those with very large tidal ranges, such as the

San Francisco Bay Estuary (Cloern 1987), the Schelde Estuary (Soetaert et al. 1994a), the Gironde Estuary (Irigoien & Castel 1997) and the Severn Estuary (Joint 1984, Underwood 2010).

Phytoplankton biomass is affected not only by turbidity but also by tidal flow and residence time. If phytoplankton growth is faster than loss through grazing and sedimentation, its biomass will be greater in microtidal estuaries, which are characterized by longer residence times (Lucas et al. 2009). This relationship between phytoplankton biomass and residence time may be reflected seasonally in a single estuary. For example, the short residence time in the lower reaches of the Hudson River Estuary usually inhibits phytoplankton blooms, whereas, in years of low river discharge, residence time increases and phytoplankton blooms can develop (Howarth et al. 2000). In general, phytoplankton biomass in macrotidal estuaries tends to be greater during dry than wet summers (Lionard et al. 2008).

As a result of the interplay of riverine inputs and tidal stress, and even when nutrient concentrations are equal, the mean chlorophyll *a* concentrations in low-energy microtidal estuaries are greater than in high-energy macrotidal estuaries, which is reflected in a 10-fold greater yield of chlorophyll *a* per unit nitrogen (Figure 14; Monbet 1992). Indeed, in terms of annual phytoplankton production, many of the highest ranking estuaries in the world are microtidal, such as Chesapeake Bay on the eastern coast of the USA and the Swan River Estuary in south-western Australia (Figure 15).

In turbid conditions, typical of macrotidal estuaries, tidal flows largely determine phytoplankton dynamics and diatoms tend to dominate the phytoplankton community throughout the year when nutrients are sufficient (Schuchardt & Schirmer 1991, Muylaert et al. 2000). Seasonal changes in the composition of phytoplankton largely reflect that of adjacent marine waters. On the other hand, seasonality and the horizontal distribution of phytoplankton in microtidal estuaries, which often occur in regions with Mediterranean climates, are determined largely by seasonal variation in rainfall in the catchment and the resultant river inflows. For example, in the Swan River Estuary, the highly seasonal discharge of fresh water affects salinity, nutrient concentrations and the residence time available for the growth of phytoplankton taxa, which determines the seasonal succession of marine, estuarine and freshwater phytoplankton taxa and their spatial separation along the estuary (Thompson & Hosja 1996, Chan & Hamilton 2001). The greater phytoplankton biomass found in the upper estuary is correlated with the degree of stratification and mixing depth (Karandonis 2004).

Unusual patterns of rainfall can result in unpredictable effects on the phytoplankton in the Swan River Estuary, such as occurred in January 2000 when there was record maximum rainfall throughout much of the catchment of the estuary, followed within three weeks by a large, mono-specific bloom of the cyanobacterium *Microcystis aeruginosa,* with cell counts peaking at over 100,000 $\mathrm{ml}^{-1}$ (Robson & Hamilton 2004). Furthermore, the changes in the amount of freshwater discharge into Australian estuaries, due to anthropogenic effects and associated increases in nutrient loadings, have a significant impact on the composition and biomass of the phytoplankton communities (Chan & Hamilton 2001, Chan et al. 2002). Similar seasonal effects of river flows and nutrient concentrations have also occurred in the Wilson Inlet in Australia (Twomey & Thompson 2001, Haese & Pronk 2011), the Sundays Estuary (Kotsedi et al. 2012), Berg Estuary (Snow & Bate 2009) and Kowie Estuary (Dalu et al. 2014) in South Africa, the Patos Lagoon Estuary in Brazil (Abreu et al. 2010).

Variation in freshwater inflows also influences the dynamics and composition of the phytoplankton in the microtidal Río de la Plata Estuary on the east coast of South America, although this estuary is funnel shaped rather than having the typical geomorphological form of microtidal estuaries elsewhere, and is consequently also influenced by tides, however small (Gómez et al. 2004, Calliari et al. 2005, Licursi et al. 2006, Silva et al. 2014). A subset of microtidal estuaries is seasonally or intermittently open to the ocean by a sand-bar, and the biomass, production and taxonomic composition of the phytoplankton differ substantially between the open and closed phases. For example, in the Mdloti estuary, South Africa, phytoplankton biomass, primary production and the production:biomass ratio peaked during the open phase, which was attributed to a favourable combination of optimum light conditions, high influx of macronutrients and high water temperatures (Anandraj et al. 2008). Similarly, the productivity of phytoplankton in the intermittently-open Smiths Lake in eastern Australia increases during the open phases (Everett et al. 2007). However, this association is not consistent. For example, in two other South Africa estuaries, the Mhlanga and Mdloti, chlorophyll *a* concentrations were greatest when these estuaries were closed.

As pointed out earlier (see ‘Water circulation and salinity’ section) the intermittent connection to the ocean and highly seasonal rainfall, which often characterize microtidal estuaries, can result in regions of these estuaries becoming hypersaline. In one such system, Lake St Lucia in South Africa, the salinity in 2010/11 ranged from 5–158 and the composition of the phytoplankton community changed markedly along a reverse salinity gradient (Nche-Fambo et al. 2015). Under low salinity conditions chlorophytes and cryophytes comprised the majority of the phytoplankton, whereas in high salinities and hypersaline conditions diatoms and dinoflagellates and then cyanobacteria dominated the community. A shift in phytoplankton community from chlorophytes and cryophytes to diatoms and dinoflagellates was also recorded along a reverse salinity gradient in the Coorong Estuary in South Australia (Jendyk et al. 2014).

Macrotidal estuaries, in which phytoplankton production is strongly limited, rarely become eutrophic and the incidence of toxic algal blooms is minimal. In these estuaries, only a small proportion of the nutrients supplied by the rivers is used by the phytoplankton, whereas eutrophication and toxic algal blooms frequently manifest themselves in microtidal estuaries where turbidity is lower and residence time longer. As a large proportion of the nutrients is utilized by the phytoplankton in microtidal estuaries these systems are much more sensitive to increases in nutrient input that might lead to excessively high phytoplankton biomass (Monbet 1992). Here, diatoms tend to dominate in spring when light levels are relatively low and stratification does not occur, as for example in Chesapeake Bay (Marshall et al. 2006), but dinoflagellates and cyanobacteria are usually more abundant in summer when residence times are long and turbidity is low, as in the Neuse–Pamlico Estuary, North Carolina (Valdes-Weaver et al. 2006). Elevated concentrations of dinoflagellates and cyanobacteria are symptomatic of eutrophication in microtidal estuaries and may result in serious environmental problems since many species in these two taxa are toxic and mainly responsible for the harmful algal blooms that frequently occur in microtidal estuaries throughout the world. These blooms have serious consequences, including large fish kills, as for example in the Peel-Harvey Estuary in south-western Australia (Potter et al. 1983b, Lenanton et al. 1985), and an increased danger to human health through diarrhetic and paralytic shellfish poisoning, as for example in Alfacs Bay on the Mediterranean coast of Spain (Artigas et al. 2014).

The amount of grazing on estuarine phytoplankton by zooplankton is relatively low in macrotidal estuaries. Due to the relatively long generation time of the dominant calanoid copepods, their biomass is limited by the low residence time of the water (Pace et al. 1992). These copepods are very sensitive to anoxic conditions and may thus be absent in extremely polluted estuaries with low oxygen concentrations (Appeltans et al. 2003), which are particularly prevalent in microtidal estuaries. Although zooplankton feed on phytoplankton, even in turbid macrotidal estuaries (Tackx et al. 1989, Tackx et al. 1990), the grazing pressure of mesozooplankton on phytoplankton in estuaries is generally less than in other ecosystems, even in microtidal ones such as Chesapeake Bay (White & Roman 1992). The inability of larger zooplankton to feed efficiently on the small constituents that constitute the microphytoplankton could account for the lower grazing pressure in a microtidal South African Estuary (Froneman 2006).

Grazing on phytoplankton by suspension feeding benthic macroinvertebrates is precluded in extremely turbid macrotidal systems, such as the Severn Estuary in the UK, because their filtering mechanisms cannot cope with clogging by dense suspensions of inert particles (Warwick 1984, Warwick et al. 1991, Warwick & Somerfield 2010) and, in any case, very little phytoplankton is present under these conditions. However, the potential for these suspension feeders to control phytoplankton biomass under less turbid conditions is staggering. For example, it is estimated that the entire volume of water in the Oosterschelde Estuary, the Netherlands, is filtered by benthic suspension feeders, principally cockles (*Cerastoderma edule*) and mussels (*Mytilus edulis*), in only 3.7 days (Smaal et al. 1986, Dame et al. 1991, Dame & Prins 1997). Since the residence time of water in this estuary is between one and three months (Wollast 1988), these organisms clear phytoplankton from each litre of water many times. Not surprisingly, the Scheldt was the only estuary in a review of 131 estuarine systems that had negative net annual phytoplankton production (Cloern et al. 2014). In the Bay of Brest, the assemblage of suspension feeding bivalves, ascidians, barnacles, sponges, polychaetes, etc. filters the total volume of the Bay in just three days (Hily 1991). Dame & Prins (1997) reviewed phytoplankton production in eleven relatively large, open estuaries, which were bivalve-dominated or contained bivalve mariculture. They found that successful populations of filter-feeding bivalves were characterised by short volume clearance times and tended to be found in systems with relatively short residence times and high rates of phytoplankton production in relation to standing crop. This allowed a high bivalve biomass to be sustained. The situation in smaller microtidal systems with restricted access to the open sea is not known, and would be a worthwhile topic for future study.

A comparison of the factors influencing phytoplankton production in macrotidal and microtidal estuaries is depicted in Figure 16. The large tidal water movements in macrotidal estuaries result in scour and re-suspension of sediment particles into the water column, thereby increasing turbidity and decreasing light penetration (Figure 16). Phytoplankton production thus becomes light-limited and the community dominated by diatoms. In contrast, when discharge is low in microtidal estuaries, turbidity is also low and light penetration is relatively high, resulting in large densities of phytoplankton, which, in turn, can support communities of filter-feeding invertebrates (Figure 16). While the composition of phytoplankton in these systems varies seasonally, in response to temporal variations in rainfall, it is typically dominated by dinoflagellates and cyanobacteria during summer when residence times are longer. Finally, the far longer residence times of water in microtidal estuaries, combined with their low turbidity, can result in the production of large blooms of phytoplankton, some of which can be toxic.

### Microphytobenthos

The microphytobenthos comprises diverse assemblages of photosynthetic diatoms, cyanobacteria, flagellates and green algae, which, when light penetrates, form biofilms on sediment surfaces (Underwood 2001). Despite their abundance on intertidal mud and sand flats and in shallow subtidal regions, the microphytobenthos has been studied far less than phytoplankton, which occurs in all aquatic environments. This is probably due to their inconspicuousness and to a lack of interest from oceanographers, who do not include them in marine food webs. MacIntyre et al. (1996) and Miller et al. (1996) have referred to microphytobenthos as the “Secret Garden”.

Fine cohesive sediments are dominated by motile microphytobenthic species that are termed ‘epipelic’ biofilms, whereas, in coarser non-cohesive silty sands and sands, the microalgae are attached to individual sand and silt particles and are termed ‘epipsammic’. Epispammic assemblages also usually contain a substantial proportion of epipelic taxa (Underwood 2001).

In turbid macrotidal estuaries, the microphytobenthos inhabits large intertidal areas of unvegetated tidal flats and fringing salt-marshes and their ecology is relatively well understood and comprehensively reviewed (e.g. Underwood & Kromkamp 1999, Underwood 2001). The majority of photosynthesis in fine cohesive sediments occurs within the top 200–400 µm, although in sandy sediments, where light penetration can be greater, photosynthesis can occur down to approximately 2 mm (Underwood 2001). Photo-inhibition of microphytobenthos at high irradiances is avoided by a combination of physiological strategies, which overcome the effects of high light intensities, while vertical migrations within the sediment maximize exposure to light and avoid the risk of overexposure (Underwood & Paterson 1993, Kromkamp et al. 1998, Perkins et al. 2001, Serôdio et al. 2001, Underwood et al. 2005).

The epipelic microalgae on mudflats only photosynthesize during diurnal tidal exposures of the surficial photic layer of the sediment (Joint 1978, Guarini et al. 2000) and photosynthesis ceases when the flats are inundated by turbid water and at night. As much as 50% of the microphytobenthos in the upper millimetres of the sediment has been estimated to migrate downwards during the flood tide, thus avoiding the effects of scouring associated with large tidal water movements (Pinckney et al. 1994, Smith & Underwood 1998). The microbial community of the microphytobenthos is remarkably resistant and resilient to relatively long-term desiccation and rewetting, a feature essential for success in the intertidal areas of macrotidal estuaries (McKew et al. 2011).

Although the biomass and production of the epipelic microphytobenthos are not considered nutrient limited (Admiraal et al. 1982, Underwood et al. 1998), nutrient regimes may influence the taxonomic composition, with certain taxa affected differentially by levels of specific nutrients (Underwood & Kromkamp 1999, Underwood 2001). Epipelic diatoms exude copious amounts of extracellular polymeric substances that may help increase the stability of the sediment by gluing and binding its particles, thereby reducing the likelihood of resuspension of diatoms and sediment (Underwood & Paterson 1993, Paterson & Black 1999, Perkins et al. 2001, Stal 2010). However, 30 to 50% of the epipelic microphytobenthic biomass can be resuspended in the water column (de Jonge & van Beusekom 1995, Irigoien & Castel 1997). The energy of tidal flow that causes resuspension of sediments tends to be greater toward the lower shore, where sediments are intrinsically less stable due to their higher water content. Consequently, the biomass and production of microphytobenthos tend to be greater toward the upper shore, which also has a longer photoperiod.

Epipelic biofilms provide a major food source for deposit-feeding macrobenthos, and particularly of those that feed at the surface of the substratum, such as the bivalve *Scrobicularia plana* (Figure 17; Hughes 1969), and some fish species, such as the Thick-lipped Grey Mullet *Chelon labrosus*, which use their gill-rakers to filter epipelic biofilms from the sediment they have ‘sucked in’ (De Silva 1980, Romer & McLachlan 1986). Microphytobenthos is also an important component of the diet of species in the meiobenthos, but the degree to which the meiobenthic grazers regulate microphytobenthic biomass has not been quantified. Resuspended microphytobenthos will also be grazed in the same way as phytoplankton (see above). Primary production by the microphytobenthos in macrotidal estuaries is at least equivalent to and often greater than that of phytoplankton (Underwood & Kromkamp 1999). For example, in the Lynher Estuary, UK, the net carbon production of microphytobenthos of 143 g $m^{-2}$ $y^{-1}$ is substantially greater than the 81.7 g $m^{-2}$ $y^{-1}$ produced by phytoplankton (Joint 1978).

The ecology of microphytobenthos in microtidal estuaries is less well understood than in macrotidal systems, with the microtidal estuaries of southern Africa being the most studied. Although intertidal flats and fringing marshes are far less extensive in microtidal than macrotidal estuaries, the water in microtidal systems is typically clear rather than turbid and thus the majority of microphytobenthic production occurs in submerged sediments.

The productivity of microphytobenthic algae in many microtidal estuaries is exceptionally high as a result of the positive ratio of euphotic depth to total depth (Adams et al. 1999, Perissinotto et al. 2000). In the large St. Lucia Estuary, South Africa, the average concentration of microphytobenthic chlorophyll *a* was 201 mg $m^{-2}$, with a maximum value of 2576 mg $m^{-2}$ (Perissinotto et al. 2010a), both of which are among the highest reported for any estuarine ecosystem, including those impacted by eutrophication (McLusky & Elliott 2004). In many estuaries in South Africa, the biomass of microphytobenthic algae is 1–3 orders of magnitude greater than the biomass of phytoplankton in the water column (Adams et al. 1999, Nozais et al. 2001, Perissinotto et al. 2002, Perissinotto et al. 2003). In South Africa, the microphytobenthic biomass in temporarily-open systems, which represent 73% of all estuaries (Nozais et al. 2001), is generally greater than in permanently-open estuaries (Adams et al. 1999, Snow et al. 2000a, 2000b). Major changes in microphytobenthic standing stocks are related to the alternation of open and closed phases, generally being highest during closed phases (Nozais et al. 2001, Froneman 2002, Perissinotto et al. 2002, Mundree et al. 2003, Perissinotto et al. 2003). A study in the Mdloti Estuary indicated that the community of microphytobenthos was physiologically healthier during the open than closed phase, when the phaeopigment to chlorophyll *a* ratio indicated a “stressed” community (Mundree et al. 2003).

Similar trends have been observed in the microtidal estuaries of Australia. In Wilson Inlet, in south-western Australia, the microphytobenthos makes the largest overall contribution to primary production, with its dominance greatest in summer when the estuary is closed (Figure 18; Haese & Pronk 2011). Microphytobenthos is also the dominant primary producer in Lake Illawarra, New South Wales, Australia, where the coastal tidal range is 1.8 m, but, because of the narrow entrance, the range in this estuary is only 3–4 cm and the residence time is as long as 60 days (Webster et al. 2002).

There are, however, exceptions to the above trends. In contrast to other seasonally-open estuaries in South Africa, the microphytobenthic biomass in the Van Stadens Estuary was greater during open than closed periods (Skinner et al. 2006). This uniquely oligotrophic intermittently-open estuary is sand dominated, with the mouth breaching at irregular intervals. Microphytobenthic biomass was most affected by the concentration of soluble reactive phosphorus introduced from the catchment. In the more normal situation, as for example in the Mdloti Estuary in South Africa, nutrients in the overlying water do not apparently have a significant impact on the microphytobenthic biomass (Nozais et al. 2001, Mundree et al. 2003).

Despite weak tidal currents, benthic microalgae in microtidal estuaries frequently become resuspended into the water column. In the Venice Lagoon many benthic taxa, such as *Amphora*, *Cocconeis*, *Navicula*, *Nitzschia*, *Pleurosigma* and *Thalassiosira*, were more abundant in the water column than exclusively planktonic diatoms (Facca et al. 2002). Similarly, Hosja and Deeley (2000) found a high proportion of normally benthic species in surface waters of the Leschenault Estuary in south-western Australia, consistent with very shallow depths and significant wind mixing for much of the year. In South African estuaries, benthic microalgae constitute the staple food item of the mysid *Gastrosaccus brevifissura,* and results of stable isotope analysis suggest that other major pelagic grazers, such as calanoid copepods, are also able to utilize this rich food source; their energetic demands could not be sustained by phytoplankton alone (Perissinotto et al. 2003).

## Macrophytes

### *Vascular plants*

Salt marshes and seagrass beds are of major ecological importance in estuaries, acting as sources of food and habitats for a variety of other organisms. Salt marshes, comprising, for example, glassworts (*Salicornia* spp.) and cordgrass (*Spartina* spp.), are very extensive in the intertidal region of macrotidal estuaries and are recognized as one of the most productive ecosystems in the world (Valiela & Teal 1979, Montague & Wiegert 1990, Heip et al. 1995), with net production increasing as tidal range increases (Figure 19; Steever et al. 1976). On the other hand, seagrasses, which cannot tolerate long periods of exposure to the air, undergo maximum development in the sandy sediments of the shallow waters of microtidal estuaries, in which there is little tidal scour and low turbidity. This environment thus provides suitable substrata for seagrasses and favourable light conditions for photosynthesis (Larkum et al. 2006). The relative development of these two groups of vascular plants in macrotidal and microtidal estuaries is, however, a matter of degree rather than mutual exclusivity. For example, a small seagrass (*Zostera*) bed is present in the Severn Estuary, UK, near the turbidity maximum, in probably the most turbid estuary in the UK and with the second highest tidal range in the world (Langston et al. 2003b), while small areas of salt marsh fringe several of the permanently-open microtidal estuaries in south-western Australia (e.g. Backshall & Bridgewater 1981, Pen 1987, Pen et al. 2000, Svensson et al. 2007), and even some seasonally-open estuaries in South Africa (e.g. Riddin & Adams 2008, Tabot & Adams 2013).

### *Salt marshes*

Salt marshes in macrotidal estuaries exhibit considerable geographic variation. In the northern hemisphere, very extensive salt marshes of *Spartina alterniflora* occur in the lower intertidal zone of macrotidal estuaries on the Atlantic and Gulf coasts of North America (Ibanez et al. 2012). These are highly productive, with a net carbon production of up to 1 kg $m^{-2}$ $y^{-1}$ which can be exported to the estuary and adjacent waters (Heip et al. 1995). In contrast, salt marshes on the Atlantic coast of Europe lack vascular plants in the lower intertidal zone (Beeftink 1977). Instead, they are typically confined to the upper intertidal area, above the point of the lowest neap high tides, where a serial change in species composition with tidal height is found (McLusky & Elliott 2004). These marshes do not appear to export significant amounts of particulate organic matter to the estuary (Hemminga et al. 1992, Hemminga et al. 1993) and may even import such material (Dankers et al. 1984). However, in European salt marshes, there is a net export of dissolved nitrogen (Boorman et al. 1994). Nutrient outwelling from salt marshes enhances estuarine phytoplankton and zooplankton production, which, in turn, support commercial fisheries. Intertidal salt marshes also play a role in the physical dynamics of macrotidal estuaries. Water is stored temporarily at tidal frequency in these marshes, which increases the local residence time (Wolanski 2007). Saltmarsh plants also play a key role in enhancing sedimentation from the turbid estuarine waters when the vegetation is greater than 8 cm in height (Boorman et al. 1998).

It is a sine qua non that intertidal salt marshes are less extensive and of less ecological importance in microtidal than macrotidal estuaries (Ibanez et al. 2012). Early maps of the global distribution of salt marshes (Chapman 1977), which was reproduced in Ibanez et al. (2012), indicate that such marshes are not present from the microtidal regions of South Africa and south-western Australia. However, although small in area, salt marshes are present in these latter two regions. In South Africa they are found only in the estuaries of the Cape

Coast and, while they occur in about 70 of the Cape's 155 estuaries, three quarters of South Africa's total saltmarsh area is concentrated in just four places: the Langebaan Lagoon (5700 ha), the Knysna Estuary (1800 ha), the Olifants River Estuary (200 ha) and the Swartkops Estuary (170 ha), all of which are permanently open (Adams et al. 2008). As Langebaan receives no freshwater inflow, it is a lagoon rather than an estuary, and the extent of truly estuarine salt marsh is very small.

Although salt marshes are better developed in estuaries with regular tidal exchange, they do occur in some seasonally-open estuaries. The frequency and duration of an open mouth in an estuary determines whether a salt marsh is present and the distribution of salt marsh species is determined mainly by specific environmental habitats associated with periods of tidal inundation and salinity (Adams et al. 1999). The large supratidal salt marsh areas in the Ncizele Estuary in the Eastern Cape of South Africa may have resulted from seawater overwash creating high salinity conditions, and the extensive salt marsh in the Cefane Estuary also in the Eastern Cape may be due to this seasonally-open system being open relatively frequently, and having an average salinity of 21 (Walker 2004).

In permanently-open estuaries, in which there is a relatively large tidal range for a microtidal system, zonation tends to be better developed, e.g. in the Knysna Estuary. Where small tidal ranges occur, vegetation forms mosaic patterns rather than well-defined zonation bands (Adams et al. 2008). O'Callaghan (1990) identified two types of saltmarsh communities in Cape estuaries, namely those associated with permanently-open estuaries where tidal exchange predominates and those associated with estuaries that are predominantly closed. Salt marsh tends to cover the whole of the intertidal area. *Spartina maritima*, which occurs in 18 of the larger permanently-open estuaries from MSL (Mean Sea Level) to MHWNT (Mean High Water of Neap Tides), is now beginning to invade some seasonally-open estuaries (e.g. Adams et al. 2012), although it is absent from most of the latter type of estuaries because it requires an adequate tidal exchange (Adams & Bate 1995).

Tidal levels from MHWNT to MHWST (Mean High Water of Spring Tides) are characterised by *Sarcocornia perennis* and numerous other species. As elsewhere, the above microtidal estuaries are susceptible to summer drought, salt stress and irregular flooding. Glassworts, such as *Sarcocornia* and *Salicornia*, are succulent and salt-tolerant and, because of their ability to withstand desiccation and salinity stress, are widely distributed in microtidal marshes and in the upper intertidal zone of macrotidal estuaries throughout the world (Ibanez et al. 2012). In marshes associated with seasonally-open estuaries, e.g. Kleinmond Lagoon, *Cotula coronopifolia* is present in the lower reaches, while *Sporobolus virginicus*, *Juncus kraussii* and *Samolus* sp. occur further up the system.

The pattern of distribution of *Spartina maritima* and *Sarcocornia perennis* on the shores of microtidal regions of southern Brazil, Uruguay and Argentina (Isacch et al. 2006) is similar to that of permanently-open estuaries in South Africa. Indeed, Adam (1990) has argued that there is an overall similarity of flora and vegetation in salt marshes in the estuaries of South Africa, south-western and south-eastern Australia, New Zealand and temperate South America, which are mainly microtidal, and that they differ from the flora of typical macrotidal estuaries in the northern hemisphere.

Salt marshes are also not extensive in the microtidal estuaries of south-western Australia. Relatively small areas of fringing vegetation are found in several of the permanently-open estuaries, such as the Peel-Harvey (Backshall & Bridgewater 1981) and Swan-Canning (Pen 1987), but are essentially absent from seasonally-open estuaries such as the Broke and Wilson inlets (Hodgkin & Clark 1988b, 1989, Haese & Pronk 2011). Although *Spartina* does not occur naturally in these estuaries, *Sarcocornia* is found in the higher salinity regions near the mouth of some that are permanently-open, e.g. the Blackwood estuary (Congdon 1981).

*Seagrasses*

As the biology and ecological role of seagrasses has been comprehensively described by Larkum et al. (2006), the present review only considers the characteristics that distinguish macrotidal from microtidal estuaries. The distribution of seagrasses is controlled by turbidity, water velocity, salinity, substratum, nutrient availability, temperature and water depth, with light availability and substratum considered the most important controlling factors (Howard-Williams 1979, Howard-Williams & Allanson 1981, Spence 1982, Weisser et al. 1992). In estuarine areas where the sediment is constantly being modified by dynamic processes, seagrasses are absent. Ideal conditions favouring their establishment in estuaries are high water clarity, limited sedimentation, low water velocity (characteristics of microtidal estuaries) and a suitable salinity range for each species. The light requirements for seagrasses are greater than those of other marine plants, presumably because of the high photosynthetic demand to survive in rooted anoxic conditions (Adams & Riddin 2007). Although turbid events (floods or storm events) may be tolerated for short periods, they have the potential to affect the distribution and abundance of seagrasses (Larkum et al. 2006).

Of the four genera of seagrasses typical of temperate estuaries (*Zostera*, *Ruppia*, *Potamogeton* and *Zannichellia*), *Zostera* is the most common in macrotidal estuaries, where it occurs to a depth of up to 1 m and may also be found on the lowest levels of the shore where it may be exposed briefly to air during low spring tides (McLusky & Elliott 2004). Generally, current speeds greater than 1 m $s^{-1}$ result in the removal of submerged plants (Adams et al. 1999), and *Zostera* appears to be more resistant than other genera to physical disturbance. In the microtidal estuaries of South Africa and south-western Australia, *Ruppia* spp. are the most frequent seagrasses (Congdon 1981, Adams & Riddin 2007, Haese & Pronk 2011) and may be the only angiosperms in some seasonally-open estuaries, such as Wilson Inlet in south-western Australia (Haese & Pronk 2011). They are physiologically well adapted to the microtidal environment, particularly in the case of seasonally-open estuaries. *Ruppia* species are found in highly diluted, almost fresh waters and in hypersaline waters where they can tolerate salinities up to three times the concentration of seawater, as well as in continental saltwater lakes and ponds completely isolated from the sea (Tyler-Walters 2001, Den Hartog & Kuo 2006).

The salinity tolerance of each seagrass species varies, with some able to survive rapid salinity fluctuations (Kantrud 1991, Murphy et al. 2003). *Ruppia* spp. are poor competitors with other more vigorous aquatic plants and, therefore, occur most frequently in environments of variable salinity and temperature that other species cannot tolerate (Verhoeven 1979). However, they appear to be more sensitive to physical disturbance than *Zostera* spp. For example, in the Swartvlei Estuary in South Africa, where mixed stands of *Ruppia* and *Zostera* occur, *Zostera* was found at the channel edges and *Ruppia* in the more sheltered sections (Howard-Williams 1980). *Ruppia* has a very delicate, shallow root system that makes it susceptible to turbulence, with currents of approximately 0.5 m $s^{-1}$ resulting in mechanical damage, while those of less than 0.1 m $s^{-1}$ favour its growth and establishment (Kantrud 1991). However, the leaf base detaches easily in turbulent water, which helps prevent damage to the root system (Verhoeven 1979). In the case of *Ruppia* spp., an increase in suspended sediment of 100 mg $l^{-1}$ is likely to have a significant effect (Tyler-Walters 2001) and a 40% reduction in light intensity can result in a 50% reduction in the standing crop (Congdon & McComb 1979).

High nutrient concentrations in the water column generally have an adverse effect through reducing light availability due to increased epiphyte and macroalgal growth and phytoplankton blooms. Twilley et al. (1985) found that epiphyte growth in nutrient-enriched conditions reduced the light incident on *Ruppia* leaves by >80%, resulting in significant decreases in biomass. *Ruppia* spp. generally occurs in water depths greater than 0.5 m and can be found down to 10 m in very clear water (Adams & Riddin 2007). They occur at shallow depths (<1.5 m) on fine, clay sediments, but at 2 m or more on sand or shell substrata (Tyler-Walters 2001). The resistance of *Ruppia* spp. to aerial exposure is very low and after desiccation, all plant parts, except ripe seeds, die within a few days (Verhoeven 1979). Similarly, Tyler-Walters (2001) reported that exposure for one hour will result in a loss of *Ruppia* stands. This duration of exposure also influences seed germination, and *Ruppia* seeds will not germinate in moist soil, but need to be covered with water (Kantrud 1991).

### *Macroalgae*

Brown seaweeds, such as *Fucus* and *Ascophyllum* play a relatively minor role in the ecology of estuaries, being confined to hard substrata, such as rock outcrops, quays and piers, which cover a very small proportion of the total estuarine area (McLusky & Elliott 2004). Such habitats are found in macrotidal estuaries where tidal currents scour sediment from hard surfaces, and some larger permanently-open microtidal estuaries that are open to shipping. They are virtually absent in seasonally-open microtidal estuaries. On the other hand, green algae such as *Ulva* and *Cladophora* colonize soft substrata and are common intertidally in macrotidal estuaries and subtidally in microtidal estuaries that receive high inputs of nutrients, particularly nitrogen. An increase in eutrophication over the last five decades has resulted in increased macroalgal production (Soulsby et al. 1985), being greatest where, as in microtidal estuaries, tidal scour is relatively low (Heip et al. 1995). In macrotidal estuaries, strong tidal currents may dislodge algae and wash them out to sea. For example, water currents of 1.22 m $s^{-1}$ in Langstone Harbour, UK, washed out *Ulva* (=*Enteromorpha*) (Lowthion et al. 1985), and currents of 1.4 m $s^{-1}$ in the Mondego Estuary in Portugal had the same effect (Martins et al. 2001). The macroalgal species in the microtidal seasonally-open estuaries of South Africa are opportunistic, being able to tolerate fluctuating salinity, proliferating when the estuary mouth is closed and being washed out to sea when open (Adams et al. 1999). Nevertheless, biomass and production in macrotidal estuaries can be high. For example, the maximum biomass of *Ulva* (=*Enteromorpha*) spp. on a mudflat in the Coos Bay Estuary, Oregon, USA, reaches 1050 g $m^{-2}$ (dry weight) with an annual carbon production of 1060 g $m^{-2}$ $y^{-1}$ and, unlike the microphytobenthos, nearly all photosynthesis appears to take place during submersion rather than aerial exposure (Pregnall & Rudy 1985, Heip et al. 1995).

*Ulva* (=*Enteromorpha*) and *Cladophora* grow more rapidly than thicker algae due to their distromatic structure and higher nutrient uptake rates (Fletcher 1996, Raffaelli et al. 1998), resulting in accumulations that can reduce the water quality of estuaries. Upon decomposition, oxygen in the water column may become depleted and sediments may become anoxic when large floating mats settle to the bottom under low flow conditions (Sfriso et al. 1987, Sfriso et al. 1992, Valiela et al. 1992). In the microtidal Venice Lagoon in Italy, this has caused mortalities among fish and invertebrates (Sfriso et al. 1992). A shift to anoxic sediment can lead to a change in the structure of the infaunal community (Raffaelli et al. 1991, Ahern et al. 1995) and subsequently affect bird populations (Raffaelli et al. 1989). In the microtidal estuaries of South Africa, extensive rotting growths of *Ulva* produce noxious sulphidic odours, affecting recreational activities, as occurs for example in the Swartvlei Estuary during summer (Howard-Williams 1979). Decaying mats of *Cladophora* and *Ulva* also adversely impact the social acceptability of water in the Great Brak and Kleinemonde estuaries and are often the reason for manipulating the opening of the mouth (Adams et al. 1999). Even more severe problems have been encountered in the microtidal estuaries of south-western Australia, and particularly in the Peel-Harvey Estuary, the largest estuary in the region. During the 1960s, this estuary started to become highly eutrophic through the input of nutrients from surrounding agricultural land and other sources such as piggeries (McComb & Lukatelich 1995). This eutrophication was reflected in the development of massive growths of *Cladophora*, *Chaetomorpha* and *Ulva* species, particularly in Peel Inlet, which was accompanied by an increase in the biomass of commercial fish species (Steckis et al. 1995). Although permanently open prior to 1994, the natural entrance channel was narrow and thus restricted the amount of the exchange of water with the sea. To ameliorate the problems associated with eutrophication, an additional artificial channel to the sea was constructed some distance from the natural entrance channel to increase tidal exchange between the estuary and the ocean. This helped flush nutrients out of the estuary and, as a consequence, the extent of macroalgal growths in this system declined (Water and Rivers Commission 1998). This was accompanied by a decline in the overall abundance of fishes and a change in their species composition (Young & Potter 2003a,b; Potter et al. 2016).

## Zooplankton

### *Microzooplankton*

Microzooplankton, comprising mainly heterotrophic flagellates and ciliates, are ecologically important in estuaries as they provide a link between bacterial production and higher trophic levels. Heip et al. (1995) summarize their distribution and trophic role in estuaries, but information on their ecology in microtidal estuaries is insufficient to draw generalities concerning differences from macrotidal estuaries. The few studies in the microtidal Nyara and Kasouga seasonally-open estuaries in South Africa (Walker et al. 2001, Froneman 2002, Froneman 2004b) suggest that the abundances of microheterotrophs are typically greatest during the closed phase of the estuary and lowest after breaching events. Froneman (2006) suggests that the elevated abundances during the closed phase can probably be attributed to the increased residence time of water and the low concentrations of macronutrients, which promote the establishment of the microbial loop. This suggests that, in general, microzooplankton are more abundant and play a greater ecological role in microtidal than macrotidal estuaries as a result of their having longer residence times.

### *Mesozooplankton*

Mesozooplankton species are categorized as either autochthonous, i.e. undergoing their whole life in estuaries, or allochthonous, i.e. do not originate in the estuary but are advected into the estuary from either the river or the sea. Differences in the relative proportions of autochthonous and allochthonous species and their relative salinity tolerances constitute major differences between macrotidal and microtidal estuaries (Figure 20). The three estuarine usage groups are analogous to the estuarine usage functional group of fishes (Potter et al. 2015a,b; see 'Categorisation of the ways that fish use estuaries' section). Unlike fishes, however, the spatial and temporal distributions of these groups depend, throughout life, on passive transport in the water body, rather than active swimming, and will depend more on tidal currents, the strength of which distinguishes macrotidal from microtidal estuaries.

There is insufficient information to allocate each mesozooplankton species to a single group. For example, individual species of *Acartia* and *Centropages* may belong to either the estuarine autochthonous or the marine allochthonus group. As very few freshwater species are able to tolerate even small amounts of salt, allochthonous freshwater plankton is generally unimportant in estuaries (Grindley 1981). The relative proportions of the other two groups vary considerably between macrotidal and microtidal estuaries. At one extreme, as in some small strongly tidal estuaries such as the Mundaka and Adour opening into the Bay of Biscay, autochthonous zooplankton is completely absent (D'Elbee & Castel 1982, Villate 1991) whereas, at the other extreme, the zooplankton in some microtidal seasonally-open estuaries in South Africa are almost exclusively autochthonous (Froneman 2006).

The relatively few species of estuarine autochthonous mesozooplankton belong mainly to the calanoid copepod genera *Eurytemora* and *Acartia* in Europe and North America, to *Pseudodiaptomus* in North America and South Africa and to members of the Centropagidae in Australia (Grindley 1981, Miller 1983, Heip et al. 1995). These endemic species may be perennial or, as with species of *Acartia* and *Eurytemora*, may endure periods of environmental adversity as resting eggs in the bottom sediment (Grice & Marcus 1981, Næss 1991). In turbid macrotidal estuaries, where primary production is limited, the diet of mesozooplankton may be supplemented with detritus and associated bacteria, and thus enable high population densities to be maintained throughout the year (Heip et al. 1995 and references therein). In these macrotidal estuaries, the potential problem for autochthonous mesozooplankton of being continuously lost to the sea is ameliorated by mechanisms such as selective vertical migration during the ebb and flood of the tide, i.e. selective tidal stream transport (see later; Bosch & Taylor 1973, Miller 1983, Ueda et al. 2010). Although the strength of tidal currents is greatly reduced in microtidal estuaries, species of copepod and mysid maintain their position in the lower reaches of the Sundays River Estuary in South Africa by remaining in deeper water during flood and ebb tides or moving laterally into areas with slower currents (Wooldridge & Erasmus 1980).

The zooplankton of microtidal estuaries has been studied most intensively in southern Africa. Mesozooplankton in the seasonally-open microtidal estuaries in that region are almost exclusively autochthonous, comprising mainly copepods of the euryhaline genera *Acartia* and *Pseudodiaptomus* which can account for >85% of total zooplankton abundance and biomass (Coetzee 1981, 1985, Perissinotto et al. 2000, Froneman 2001, 2002, 2004a, 2006). Here, relatively low levels of taxonomic diversity are generally associated with prolonged periods of mouth closure, reflecting the poor representation of marine- and freshwater-breeding species (Froneman 2004a, Perissinotto et al. 2004, Froneman 2006). In permanently-open microtidal estuaries, mesozooplankton diversity is greater, due to an increased contribution to total diversity by allochthonous marine-breeding species and, particularly in those estuaries with sustained freshwater inflow, by allochthonous freshwater species (Wooldridge 1999). In freshwater-deprived systems, the phytoplankton, because of their small size, cannot be fed on directly by the few dominant species of large zooplankton and thus phytoplankton production is made available to higher trophic levels through the trophic intermediary of heterotrophic microzooplankton (Froneman 2002, 2004c, 2006).

The breaching of many seasonally-open estuaries in South Africa is accompanied by a considerable decline in both the total abundance and biomass of zooplankton (Froneman 2004a, Bernard & Froneman 2005). This is by no means a consistent phenomenon, since the productivity of phytoplankton and zooplankton increases during the open phase in the microtidal Smiths Lake in eastern Australia. The microtidal estuaries of south-western Australia have been less intensively studied, but in the seasonally-open Wilson Inlet, which is breached each year, the main taxa of zooplankton are allochthonous marine species rather than autochthonous estuarine species (Gaughan & Potter 1995). Worldwide, copepods also dominate the allochthonous marine component of the estuarine mesozooplankton, typically the calanoid genera *Acartia*, *Centropages*, *Paracalanus*, *Pseudocalanus* and *Temora* and the cyclopid genus *Oithona* (Heip et al. 1995 and references therein). For example, the zooplankton of the lower region of the permanently-open Swan River Estuary is dominated by species of *Acartia*, *Centropages*, *Paracalanus*, *Temora* and *Oithona* (Gaughan & Potter 1994). Although this suggests that there is a strong allochthonous marine component, there is also a small allochthonous freshwater component in winter, represented by the cladoceran *Daphnia*.

In macrotidal estuaries, there is some debate as to whether allochthonous marine mesozooplankton thrive or suffer. Mortality may result from salinity stress or poor feeding conditions. In the Westerschelde Estuary in northern Europe, for example, Soetart & Herman (1994) estimated that some 1500 t dry weight of zooplankton entered, died and decomposed in the estuary annually. In such estuaries, there is considerable seasonal variation in the abundance and biomass of the predominant allochthonous marine mesozooplankton, since they depend on the seasonal primary production in the sea. For example, in the Severn, Neuse and Westerschelde estuaries, biomass may be one to several orders of magnitude greater in spring and summer than in winter (Collins & Williams 1982, Mallin et al. 1991, Soetaert & Van Rijswijk 1993), contrasting with the much less pronounced variation in the autochthonous estuarine mesozooplankton of microtidal estuaries, and particularly in those that are periodically closed. There is some indirect evidence that microtidal estuaries, with their greater water clarity, higher phytoplankton production and longer residence times support a greater biomass of zooplankton than macrotidal estuaries. It is thus relevant that, in the Oosterschelde Estuary in northern Europe, zooplankton biomass rose after the construction of an artificial barrier that increased both residence time and water clarity (Bakker & van Rijswijk 1994). However, due to the lack of strictly comparable data, it is not possible, at present, to make generalizations regarding differences in zooplankton biomasses in macrotidal and microtidal estuaries.

## Benthic invertebrates

### *Meiobenthos*

The comprehensive review of the ecology of estuarine meiobenthos by Heip et al. (1995) focused mainly on macrotidal estuaries, as there was a paucity of observational or experimental data for microtidal estuaries available at that time. Although, some research has been undertaken on the meiobenthos of estuaries of southern Africa and southern Australia in the last two decades, the data are still too sparse to make unequivocal statements about the effects of tidal regimes.

The most abundant meiobenthic taxa in most estuaries, irrespective of tidal regime, are free-living nematodes, followed usually by harpacticoid copepods and then an assortment of taxa, including turbellarians, gastrotrichs and kinorhynchs. In contrast to the marine and freshwater macrofauna, many species of the marine and freshwater meiofauna have a greater tolerance to the salinity stresses of brackish water (Giere 2009), and consequently this group has a far higher species diversity in estuaries than the macrobenthos. The feeding relationships of meiofauna are very complex, with their species capable of feeding on detritus, bacteria, diatoms and other members of the meiobenthos or by absorbing dissolved nutrients (Chia & Warwick 1969, Coull 1988, Feller & Warwick 1988), and they may often feed discriminately and selectively on items of a particular size, shape and quality (Alongi & Tietjen 1980, Warwick 1981, Schiemer 1984). Food is generally derived from the sediment, and very few meiobenthic species filter feed on phytoplankton from the water column.

Species diversity is maintained by the partitioning of food resources in the microscopically-structured sedimentary environment, and is not as dependent on sediment stability as the macrobenthos, which relies on spatial segregation on a macro-scale (Warwick et al. 1990). Intuitively, then, the relatively high species diversity would be expected to be maintained, even in the unstable sediments of tidally-scoured macrotidal estuaries, as well as in the more stable sediments of microtidal estuaries. Furthermore, meiofaunal densities are greater in the intertidal areas of macrotidal estuaries where microphytobenthos production and biomass are greater than in the subtidal (Smol et al. 1994, Soetaert et al. 1994b), whereas the reverse is true in microtidal estuaries where the subtidal areas are rich in microphytobenthos due to high water clarity and sediment stability (Rosa & Bemvenuti 2005).

Very little information is available on the ecology of meiofauna in the microtidal estuaries of southern Africa (Perissinotto et al. 2010b). In the seasonally-open Mdloti Estuary, South Africa, meiofaunal abundance was substantially greater when the estuary mouth was closed than when open (Nozais et al. 2005). This is consistent with the microphytobenthic standing stocks in seasonally-open South African estuaries generally being greatest in the closed phase (Nozais et al. 2001, Perissinotto et al. 2002). During the closed phase, meiobenthic abundances in the seasonally-open Mdloti Estuary are comparable with those in permanently-open estuaries in southern Africa (e.g. Dye & Furstenberg 1981, Nozais et al. 2005). In contrast, the densities of meiobenthos in the intermittently open/closed “coastal lakes” (ICOLLs) in south-eastern Australia were generally higher in open than in closed lakes (Dye 2005). Here, the abundance of meiobenthos generally decreased with increasing distance from the sea, and nematodes, copepods and turbellarians were characteristic of assemblages near the mouths of the lakes, while polychaetes and oligochaetes (arguably true meiobenthos) characterized more isolated areas (Dye & Barros 2005).

Meiobenthic densities can remain high even in the hypersaline conditions that may develop in microtidal estuaries after long periods of closure. For example, after a long period of closure, the inner areas of the St. Lucia Estuary in South Africa became hypersaline, and although taxonomic diversity in these areas decreased, with an overwhelming dominance of nematodes and harpacticoids, the total meiofaunal density did not differ significantly from outer areas that had not become hypersaline (Pillay & Perissinotto 2009).

For the most part, taxonomic studies of estuarine meiobenthos have been conducted at coarse levels of taxonomic resolution (phylum, class and order), and there is little comparative information regarding the way in which tidal regimes influence species distributions. However, comparison of the nematode species composition (the dominant component of the meiobenthos) in the macrotidal Exe Estuary in south-western England (Warwick 1971, Field et al. 1982) with that of the microtidal Swan River Estuary in south-western Australia (Hourston et al. 2005, 2009, 2011) may serve as an exemplar of the kinds of differences to be expected. The former has a mean tidal range of 3.8 m at spring tides (Langston et al. 2003a), compared with only ~0.4 m in the latter (Hodgkin & Hesp 1998). The great differences in the extent and sediment characteristics of the intertidal regions in those two estuaries necessitated the use of different sampling designs. In the Exe, the majority of the estuarine area (64%) is exposed at low tide, and sediment characteristics and salinity both vary along the longitudinal axis of the estuary and from the upper to lower shore (Davidson et al. 1991). Sampling was therefore conducted along four intertidal transects in the upper, middle and lower reaches of the estuary and on the adjacent fully marine coast. Sampling was undertaken at MHWST, MHWNT, MTL (Mean Tide Level), MLWNT and MLWST except in the upper estuary where the MHWST level could not be sampled due to the presence of a sea wall (Figure 21A). In the Swan River Estuary, the intertidal area is extremely small (4%) and thus nematodes were sampled at 12 shallow subtidal (<2 m deep) sites located at intervals throughout the length of the estuary and at a marine coastal site just outside its mouth (Figure 21B).

Shade plots (Clarke et al. 2014b) have been constructed to compare the patterns of distribution of species within the Exe and Swan River estuaries and their adjacent coastal areas (Figure 22). For this purpose, the abundances of each species in each sample were fourth-root transformed and averaged across replicates and seasons to provide a single value for each site. The transformed data for each species at each site in each estuary were then standardized by calculating their percentage contribution to the total number of individuals at that site and estuary. The standardized data for the sites in each estuary were used to produce a shade plot for each estuary. The columns in each shade plot, which represent a site, are ordered in a sequence from coastal marine waters (left) to the upper reaches of the estuary (right). The species, each representing a single row, are ordered using a constrained seriation procedure to give the closest possible correlation with a serial sequence (Clarke et al. 2014a). The magnitude of the shading in the plot thus provides a simple way of visualizing the contribution of each species at each site in each estuary, ranging from white, when that species was absent, through various shades of grey and then to black when it reached maximum contribution (Clarke et al. 2014b).

The patterns of distribution of species along the two estuaries vary markedly. Thus, species present in the Exe Estuary gradually change in a serial manner from the fully marine transect (sites 15–19) through to the upper estuarine transect (sites 1–4), with some species disappearing and others appearing along that axis (Figure 22A). Many of the species found in the Exe Estuary are also found outside this estuary. In contrast, the various species recorded in the Swan River Estuary are found at sites throughout this system and differ markedly from those in nearby coastal waters (Figure 22B). However, the percentage contributions of certain species differed between sites 1-6 downstream and 7-12 upstream in the Swan River Estuary (see also Hourston et al. 2011).

The above differences in the patterns of distribution of nematode species in the Exe and Swan River estuaries are commensurate with the effects of the marked differences in the tidal range in the two systems. Thus, the strong tidal currents in the Exe Estuary result in longitudinal and lateral habitat heterogeneity in terms of sediment granulometry and interstitial salinity in the estuary, with individual nematode assemblages having specific habitat requirements. The strong tidal exchange permits transport of resuspended meiofauna between the open sea and the lower reaches of the estuary, with a gradual change species composition in habitat type and across this interface. Coarse well-oxygenated sands are found both outside the estuary and inside its mouth and many species are found in both regions. The trend in the Swan River Estuary results from limited tidal exchange between the coast and estuary, with an abrupt change in species composition between these two environments, and a similar suite of species, albeit with different percentage contributions, throughout the estuary itself. This lack of intra-estuarine habitat heterogeneity reflects the lower overall species richness recorded in the Swan River than Exe estuaries.

### *Macrobenthos*

Although omnivory is a general strategy for survival of estuarine macrobenthos, and caution must thus be exercized in categorizing this fauna into narrow feeding groups (Herman et al. 1999), the main general distinction between suspension feeders and deposit feeders is important when comparing the dynamics of macrotidal and microtidal estuaries. Suspension feeders filter their food directly from the water column, while deposit feeders feed on organic material produced on or physically deposited onto the sediment surface (surface-deposit feeders). This organic material is subsequently incorporated deeper into the sediment by physical and biological processes and consumed by deep-deposit feeders.

The biomass of suspension feeders in estuaries is generally food limited, and is highest in well-flushed estuaries with short residence times where the food supply is continuously replenished with new seawater (Smaal & Prins 1993, Heip et al. 1995, Dame & Prins 1997). The biomass of suspension feeders per unit water volume is closely related to the residence time of the water (Figure 23). The data used to compile this graph do not include, however, any microtidal estuaries and the form of the graph is substantially affected by both the very high biomass and short residence time (0.5 days) at the island of Sylt in the Wadden Sea, and the very low biomass and long residence time (10,000 days) in the Askö area of the Baltic

Sea, both of which are coastal rather than true estuarine locations. Furthermore, hydrodynamical constraints on a local scale almost invariably result in the patchy occurrence of suspension feeders, and their highest levels of biomass, production and filtration capacity are generally found in only a small fraction of the total area of an estuary (Heip et al. 1995, McLusky & Elliott 2004). Thus, extrapolation of data from mussel or oyster beds, for example, over whole estuaries should be treated with caution. However, sites with low current velocities are intrinsically unfavourable for suspension feeders (Sanders 1958, Heip et al. 1995) and, if the relationship holds for microtidal estuaries with long residence times, they would be predicted to have a relatively low biomass of suspension feeders. This may be at least partially compensated for by the generally higher levels of phytoplankton production in microtidal than macrotidal estuaries (see ‘Phytoplankton’ section).

In highly turbid macrotidal systems, such as the Severn Estuary, suspension feeding macrobenthos are virtually absent because their filtering mechanisms cannot cope with clogging by dense suspensions of inert particles (Warwick 1984, Warwick et al. 1991, Warwick & Somerfield 2010), and, in any case, very little phytoplankton is present under these conditions. Suspension feeding standing stocks will thus be greatest in estuaries with both a strong tidal flow and relatively clear water in which living phytoplankton of high nutritional quality is continually replenished. In such estuaries, as for example the Schelde and Ems estuaries in northern Europe, the biomass of macrobenthos is highest in that part of the estuary nearest the sea, due to the high abundance of suspension feeders (Meire et al. 1991, Ysebaert et al. 2003).

The food of macrobenthic deposit feeders is of generally of poorer quality than that of suspension feeders, often comprising over 95% inorganic material (Heip et al. 1995). This poses a particular sorting problem for deep deposit feeders but less so for surface deposit feeders in which the edible fraction is more concentrated as microphytobenthos and freshly deposited phytoplankton. Although large quantities of organic material may be present in the sediment, an inability to process sufficient amounts of sediment to meet their dietary requirements may limit the growth of deposit feeders. They also face the problem of low oxygen concentrations. This is particularly true for microtidal estuaries in which physical diffusion of oxygenated water into the sediment is minimal, and biologically mediated diffusion is also reduced due to the small body size of the biota. In the upper reaches of the microtidal Swan River Estuary in south-western Australia, for example, oxygen penetrated only to a depth of 1.0–1.5 mm (Norlem et al. 2013), as it does in most shallow productive estuaries (Heip et al. 1995). On the other hand, suspension feeders can maintain a flow of oxygenated surface water via siphonal or tentacular mechanisms while living in sediments low in oxygen.

It is difficult to allocate many macrobenthic species to a particular feeding mode because they may be facultative deposit/suspension or deposit/predatory feeders. Nevertheless, despite the disadvantages of deposit-feeding life, it is clear that the macrobenthos of both macrotidal and microtidal estuaries is generally dominated by deposit-feeding species, with isolated dense beds of suspension feeders being found in some macrotidal situations. For example, in the microtidal Peel-Harvey Estuary in south-western Australia, species that can be unequivocally allocated to a single feeding mode numerically comprised 61.9% deposit feeders and 1.2% suspension feeders in 1986–7 and subsequently 71.8 and 0.2%, respectively, in 2003–4 after radical attempts to ameliorate the effects of extreme eutrophication (Wildsmith et al. 2009). In both the upper and lower reaches of the macrotidal Tamar Estuary, UK, deposit feeders were overwhelmingly dominant, both numerically and in terms of biomass (Figure 24; Warwick & Gee 1984).

The experience of the present authors with the macrobenthic faunas of macrotidal estuaries in the UK and microtidal estuaries in south-western Australia gives the subjective impression that the average body size in the latter estuaries is much less, although it has not been possible to substantiate or generalize this observation with strictly comparative data. Several explanations for this possible phenomenon can be invoked. The south-western Australian estuaries are numerically dominated by taxa that are tolerant to environmental degradation, i.e. with high AMBI (a marine biotic index in which high scores denote high levels of disturbance) scores, probably due to the detrimental effects of natural accumulations of organic material in estuaries with long residence times (Tweedley et al. 2014b and references therein). The sediment trapping efficiency in such estuaries is very high and up to 80% of the organic material from the catchment and marine sources may be trapped in the low energy central basin (Patchineelam et al. 1999, Roy et al. 2001). It is well known that small *r*-selected species are stimulated by high organic loads, and deep-dwelling species are replaced by surface or sub-surface deposit feeders (Pearson & Rosenberg 1978, Weston 1990, Herman et al. 1999). On the other hand, although almost constant in concentration, organic material derived predominantly from eucalypt leaves in the catchment would be of poor nutritive value and slow to decay (Bunn & Davies 1990), resulting in a low assimilation efficiency and precluding high rates of respiration, growth and reproduction in the predominantly deposit-feeding assemblage. Heip et al. (1995) have argued that such factors would favour the development of *K*-selected species with large body size. However, such high organic loadings may result in severe and frequent hypoxia (Cottingham et al. 2014, Tweedley et al. 2015a), with insufficient time between hypoxic events for animals to grow to an appreciable size. Also, the benthic fauna in these estuaries is restricted to the surface layer of sediment, no deeper, for example, than 10 cm in the Swan River Estuary (Rose 1994), offering no protection from predation and little opportunity for animals to reach their physiological lifespan.

In macrotidal estuaries the pattern of macrobenthic species richness follows the generalized model of Remane & Schlieper (1971), with high diversity of oligohaline species at the freshwater end (salinity 0.5–5) and stenohaline marine species near the mouth (salinity >25), with a lower diversity of obligate estuarine and euryhaline species in the brackish middle reaches (salinity 5–18). This trend is not apparent in the microtidal estuaries of southern Africa where, in both marine- and freshwater-dominated permanently-open estuaries, species richness declines progressively in an upstream direction (Branch & Grindley 1979, Hodgson 1987, Schlacher & Wooldridge 1996). There is a more uniform distribution of species in seasonally-open estuaries (e.g. Koop et al. 1983) and freshwater-deprived permanently-open estuaries, which could be related to the predominance of euryhaline species and the virtual absence of any horizontal patterns in physico-chemical variables (Henninger et al. 2011). Species richness and diversity are nevertheless highest in these freshwater-deprived permanently-open systems (Teske & Wooldridge 2001). Although fewer species are usually present in seasonally-open estuaries, the density of the macrobenthos can be higher than in permanently-open systems (Teske & Wooldridge 2001). River-dominated permanently-open estuaries tend to have lower macrobenthic densities, species richness and diversity than estuaries in the other categories (Teske & Wooldridge 2001). Although data for macrobenthic species in south-western Australian estuaries are limited, the species richness of this fauna in the permanently-open Swan River Estuary and the seasonally-open Broke Inlet both have a uniform distribution with no longitudinal gradient (Valesini et al. 2009, Tweedley 2011).

## Fish

### *Categorization of the ways that fish use estuaries*

Any attempt to compare the ecology of the fishes in macrotidal and microtidal estuaries requires a thorough understanding of the ways in which the various species use these systems. Indeed, it has long been recognized that such species can be categorised using such criteria (e.g. Cronin & Mansueti 1971, Haedrich 1983, Potter et al. 1990, Elliott & Dewailly 1995, Potter & Hyndes 1999, Whitfield 1999). Those early studies led to the development by Elliott et al. (2007) of the Estuarine Usage Functional Group (EUFG), which was recently refined by Potter et al. (2015a). This scheme recognizes that, irrespective of estuary type, the species in these systems can be assigned to one of four main categories, i.e. marine, estuarine, diadromous and freshwater (Figure 25 and 26). Marine species are those that spawn at sea, estuarine-resident species comprise those that complete their life cycle within the estuary, diadromous species constitute those that feed at sea and migrate into fresh water to spawn or undergo the reverse migration, and freshwater species are those that spawn in fresh water. Each of the above four categories are subdivided into a number of guilds (Figure 25 and 26).

In terms of number of species, the fish faunas of estuaries are dominated by marine species and particularly so in macrotidal systems (see ‘Contributions of the numbers and abundances of species to the EUFG’ section). Many of these species can be regarded as adventitious visitors, as they are typically in low abundance in estuaries and are usually found in their lower reaches. These species thus represent the ‘marine straggler’ guild, which includes stenohaline species, such as most sharks, skates and rays (Figure 25a). Occasionally, however, such species may be relatively abundant in the main body of both macrotidal and microtidal estuaries, when the salinities there are close to that of seawater (Potter & Hyndes 1994).

Many of the most abundant species in particularly macrotidal estuaries are ‘marine estuarine-opportunists’, which typically enter estuaries as larvae or young juveniles and spend variable amounts of time in this environment before returning to the sea (Figure 25B). The estuary thus acts as a nursery area for these species (Blaber & Blaber 1980, Beck et al. 2001), with the abundant food available in these systems facilitating rapid growth and thereby a reduction in their susceptibility to predation (Le Pape et al. 2003, Yamashita et al. 2003, Potter et al. 2011, Veale et al. 2015). Numerous marine estuarine-opportunists also use sheltered nearshore marine environments as well as estuaries as nursery areas, with the relative use of these two environments varying among species and according to the extent that one or both of those environments are present in the area (Lenanton & Potter 1987, Gillanders et al. 2003, Able 2005, Able & Fahay 2010).

The third guild within the marine category, 'marine estuarine-dependent' (Figure 25B), comprises a few species whose juveniles require the protected environment of estuaries for survival (Blaber 1981, Wallace et al. 1984, Bennett et al. 1985, Whitfield 1999). Such species are found in southern Africa, where the coast lacks the sheltered nearshore areas that would reduce exposure to the turbulent wave action that characterizes those waters (Whitfield & Elliott 2011). The term 'estuarine-dependent' is often used less explicitly and its meaning may vary according to how an estuary is defined (Able 2005).

The estuarine category contains fewer species than the marine category, which is largely attributable to the problems posed to eggs and larvae by the turbid conditions and salinity fluctuations found in estuaries, and particularly those in macrotidal areas (see 'Adaptations for spawning in estuaries' section). Those species that complete their life cycle within the estuary constitute the 'solely estuarine' guild (Figure 25C). A number of species spawn, however, in both estuaries and marine waters outside those systems. While some of these species are represented by discrete populations in estuaries and coastal waters, as with *Cnidoglanis macrocephalus* (Ayvazian et al. 1994), and thus constitute the 'estuarine & marine' guild (Figure 25D), other species are represented by contiguous populations that cross the barrier between the estuary and the ocean (Able & Fahay 2010). A few species spawn in tributary rivers and estuaries and thus constitute the 'estuarine & freshwater' guild (Figure 25E). However, the extent to which the assemblages of such species in these two environments are discrete has generally not been established. The fourth guild within the estuarine category, i.e. ‘estuarine migrant’ (Figure 25F), comprises species whose larvae are sometimes flushed out to sea and often return to the estuary on flood tides (Whitfield 1989, Neira & Potter 1992a). Note that, because distinctions have not always been made between the different guilds of the estuarine category, and as a main thrust of the section on fishes in this review is whether the individuals of a species found in estuaries complete their life cycles in these systems, such species are, for convenience, all included under the umbrella term ‘estuarine residents’.

Estuaries act as a crucial route through which species of the diadromous category migrate between fresh water and the sea. This category comprises species that spawn in rivers and migrate to the sea where most of their growth takes place, i.e. the ‘anadromous’ guild (Figure 26A), and those that spawn in the sea and migrate to rivers where growth occurs, i.e. the ‘catadromous’ guild (Figure 26B). Although there are few diadromous species, this category does contains some important taxa, such as the anadromous species of salmonids and lampreys and the catadromous eels. The upstream migration of a few ‘anadromous’ species only extends as far as the upper estuary and they constitute the ‘semi-anadromous’ guild (Figure 26C), and the downstream migration of a few catadromous species only progresses as far as the mouth of the estuary and therefore constitute the ‘semi-catadromous’ guild (Figure 26D). The fifth guild of the diadromous category, i.e. ‘amphidromous’, is represented by species that spawn in fresh water and/or the estuary and whose larvae are consistently flushed out to sea, where they grow and then later return to an estuary and/or river, where the majority of growth occurs (Figure 26E; McDowall 2007, Tweedley et al. 2013).

The ‘freshwater’ category comprises species that spawn in fresh water, but are found in estuaries. It contains those species that essentially stray into the low-salinity upper reaches of the estuary, i.e. the ‘freshwater straggler’ guild (Figure 26F), and the ‘freshwater estuarine-opportunist’ guild (Figure 26G), which contains species that are found regularly downstream of the oligohaline reaches of estuaries.

*Composite studies on the ichthyofaunas of eastern North America and Europe*

Nordlie (2003) used data for the ichthyofaunas of 20 estuaries on the eastern seaboard of North America to quantify the number of species that represented a particular group on the basis of how they used the estuary, thus employing essentially the approach used later in the Estuarine Usage Functional Group (EUFG) scheme (Elliott et al. 2007, Potter et al. 2015a). Marine species were found to contribute as much as 70% to the total number of species, with marine estuarine-opportunists and marine stragglers comprising 17.7 and 52.3 %, respectively. Estuarine-resident species and diadromous species contributed only 9.3 and 5.5%, respectively, with freshwater species constituting the remainder. The contribution made by marine species declined with latitude, whereas that of diadromous species (in this case anadromous species) increased. Those trends thus followed a gradient from low to high tidal ranges, i.e. microtidal to macrotidal. The pronounced tendency for anadromous species to occur most frequently in the northern subpolar/cool-temperate and thus macrotidal estuaries of the Northern Hemisphere was noted previously by McDowall (1988).

Franco et al. (2008) adopted a similar approach to that of Nordlie (2003), using ichthyofaunal data from 38 estuaries throughout Europe to elucidate the overall structure of fish communities in this region. As in eastern North America, European estuarine faunas, in terms of number of species, were dominated by marine species (58%) and the contributions by estuarine residents (19%) and diadromous species (9%) were low, with the remainder comprising freshwater species. Following a detailed study of the biological characteristics of fish species in the Severn Estuary, which has a particularly high tidal range, Claridge et al.

(1986) concluded that the vast majority of species were marine and that few completed their life cycle within this estuary.

In their analyses of feeding strategies of fishes in European estuaries, using the guilds in the EUFG, Franco et al. (2008) demonstrated that marine estuarine-opportunist species feed on the hyperbenthos, shifting, as they increase in size, from small to large benthic prey and/or to fish. The food of estuarine-resident species consists predominantly of small benthic, epibenthic and hyperbenthic prey, such as mysids, shrimps and fish larvae. There is a strong tendency for fish species in estuaries to feed on detritivorous invertebrates and, while detritus is a crucial component of estuarine food webs, fish, in general, do not feed directly on this material (Franco et al. 2008), an exception being provided by mugilids (Odum 1968, Eggold & Motta 1992). Some estuarine and marine species feed, however, on zooplankton, phytoplankton, resuspended microphytobenthos and organic particulate material, especially in the highly productive estuaries entering the Baltic and North seas, which accounts for the large numbers of planktotrophic pelagic species, such as clupeoids, in those waters.

When likewise adopting a guild approach for reproductive modes, the results of Franco et al. (2008) demonstrated that most of the marine species found in European estuaries produce pelagic eggs, whereas the vast majority of estuarine residents have adaptations that facilitate retention of their eggs and larvae within the estuary, thereby reducing the likelihood of being flushed out to sea. These adaptations, which include the production of eggs that are benthic and often adhesive and mechanisms for parental care, are described in the section entitled ‘Adaptations for spawning in estuaries’.

### *Transport and retention of the larvae of marine fish and crustacean species*

Most marine estuarine-opportunist species of teleost produce large numbers of pelagic eggs, which, after fertilization, are transported towards the shore where they typically enter estuaries as larvae (e.g. Boehlert & Mundy 1988, Elliott et al. 2007, Franco et al. 2008, Able

& Fahay 2010). Since, in permanently-open estuaries, there is typically a net outflow of water into the ocean and current speeds frequently exceed larval swimming speeds, such immigration by teleosts and also certain crustaceans requires behavioural adaptations that enable the larvae to exploit, for this purpose, particular characteristics of the circulation patterns in the estuary (Forward et al. 1999).

In estuaries with a two-layer gravitational circulation, the outflow near the surface is partially balanced by a net inflow at the bottom of the water column (Pritchard 1967a, McLusky & Elliott 2004). The larvae of many marine species of teleost and certain species of mollusc and crustacean utilize this pattern of circulation (residual bottom inflow) in macrotidal estuaries to move upstream by remaining in bottom waters (Fortier & Leggett 1982, Chen et al. 1997, Jenkins et al. 1999, Roegner 2000, Schultz et al. 2003, Hare et al. 2005). This type of passive movement is often enhanced by employing selective tidal stream transport (STST), in which the larvae remain in the bottom waters during ebb tides and move towards the surface during flood tides (Figure 27), thereby enabling the larvae of some species to be transported several kilometres upstream through the estuary on a single tide and large distances over several tides or to disperse on reaching upstream areas (Geer Walker et al. 1978, Weinstein et al. 1980, Fortier & Leggett 1983, Jager & Mulder 1999). This is particularly advantageous as larvae have weak swimming ability and it greatly reduces the amount of energy that would otherwise be required to reach nursery habitats.

From flux calculations for the larvae of three fish species at the mouth of Chesapeake Bay, Hare et al. (2005) concluded that wind forcing, as well as residual bottom inflow and STST, are responsible for the ingress of larvae into this microtidal estuary. The larval stages of catadromous species, such as the eels *Anguilla rostrata* and *A. anguilla*, also employ STST to move through estuaries and then employ counter-current swimming to penetrate upstream in rivers (McCleave & Kleckner 1982, Trancart et al. 2014).

When invertebrates (represented predominantly by crustaceans) undergo a vertical migration, this movement typically occurs nocturnally and almost invariably so when individuals have reached the post-larval and juvenile stages (Forward & Tankersley 2001). The vertical migrations of larval fish also typically occur at night (Norcross & Shaw 1984, Islam et al. 2007). An avoidance of well-lit areas of the water column during the day reduces the susceptibility of those stages to predation as they become larger and thus more vulnerable to detection by visual predators (Forward & Tankersley 2001, Gibson 2003, Islam et al. 2007). While the larvae of the puffer fishes *Takifugu rubripes* and *T. xanthopterus* migrate vertically at night in the macrotidal Ariake Estuary, this movement is independent of tidal phase (Yamaguchi & Kume 2008).

Selective Tidal Stream Transport is also used to move downstream in an estuary (Forward & Tankersley 2001). For example, the larvae (zoeae) of several species of fiddler crab in the genus *Uca* are released within estuaries at around high tide at night and are then exported offshore on the ebb tide, where they develop through to the post-larval (megalopae) stage (Morgan & Christy 1995, Christy & Morgan 1998, Petrone et al. 2005). This behaviour is mediated by a circatidal rhythm that involves an upward vertical migration during ebb tides, and a converse descending migration during flood tides, thereby ensuring that the larvae are not swept back upstream during such tides (López-Duarte & Tankersley 2007a,b). The juveniles of many species of penaeid prawns also use ebb tide transport to migrate downstream in estuaries to their spawning grounds in coastal marine waters (Dall et al. 1990).

Some species of crustacean employ both ebb and flood tide transport at different stages in their life cycle. For example, once the zoeae of *Uca* spp. have metamorphosed into megalopae in coastal waters, they employ nocturnal flood tide transport to reach their nursery habitats in the estuary (Tankersley & Forward 1994).

STST is used not only for upstream and downstream movement in estuaries but also for retention within certain regions of these systems (Weinstein et al. 1980, Boehlert & Mundy 1988). Larvae can also be retained within estuaries by moving laterally into areas of low current flow (Wooldridge & Erasmus 1980) or passively accumulating in such areas (Morgan et al. 1997).

Although the two-layered circulation of estuaries in macrotidal regions and of those toward the upper end of the microtidal range provides an effective mechanism (STST) for fish and crustacean larvae to move rapidly many kilometres upstream, this is not the case in estuaries at the lower end of the microtidal range (Whitfield 1989). In the microtidal estuaries of south-western Australia and southern Africa, which typically contain a narrow and relatively shallow entrance channel, the tidal effect becomes rapidly attenuated in an upstream direction from the mouth (Spencer 1956, Hodgkin & Hesp 1998). The upstream flow in the middle and upper reaches during a tidal cycle in microtidal estuaries is thus very limited and does not therefore provide an effective mechanism for transporting larvae rapidly upstream through these systems.

Marine estuarine-opportunist species, such as the sparid *Rhabdosargus holubi*, the monodactylid *Monodactylus falciformis* and the mugillid *Liza richardsoni*, enter the microtidal estuaries of southern Africa nocturnally on flood tides and mainly as post-larvae and thus after they have developed fins and an increased swimming ability (Beckley 1985, Whitfield 1989). They then move to the banks, where tidal flow is reduced, and subsequently travel slowly upstream.

The use of conical plankton nets at night in the entrance channel of two estuaries in south-western Australia, a microtidal region, yielded the larvae of few marine estuarine-opportunist species that are abundant as juveniles in the basins of these systems (Gaughan et al. 1990, Neira & Potter 1992a). As the larvae of these species were also not abundant in the oblique plankton tows conducted in the entrance channel of one of those estuaries, these species may enter these systems predominantly as juveniles (Gaughan et al. 1990). This point requires verification by sampling for fish larvae and young juveniles along the shoreline of the entrance channels, as has been done in South Africa (Beckley 1985).

As mentioned earlier, wind can assist the ingress of the larvae of marine estuarine-opportunist fish species into microtidal estuaries, such as Chesapeake Bay (Hare et al. 2005). Likewise, in the permanently-open microtidal Mar Chiquita Estuary in Argentina, strong prevailing onshore winds (>10 m $s^{-1}$) in summer are more influential than tidal effects in facilitating the recruitment of larval and juvenile fishes through the narrow entrance channel (Bruno et al. 2014, Bruno & Acha 2015).

When microtidal estuaries become closed by a bar at their mouth, the larvae of marine estuarine-opportunists, such as *Rhabdosargus holubi*, *Monodactylus falciformis* and mugilid species, can exploit overwash of the bar from coastal waters for recruitment into these systems (Figures 10e, 28; Cowley et al. 2001). The importance of this recruitment mechanism in estuaries, such as the East Kleinemonde in South Africa, is demonstrated by the fact that, between March 1993 and August 1997, the mouth of this system was open for only 43 days, i.e. 2.6% of that period, whereas overwashing occurred on 421 days, i.e. 25.5% of that period (Cowley 1998).

### *Ichthyoplankton within estuaries*

Emphasis on fish larvae, thus far, has been mainly placed on the mechanisms by which the larvae of marine estuarine-opportunist species enter and are transported through estuaries to their nursery habitats in these systems. However, some species use estuaries in other ways; i.e., as residents or as a migratory route (Figure 25 and 26).

Most of the studies which have considered, in detail, the contributions made by the larvae of species belonging to the different EUFGs described earlier, have been undertaken in microtidal estuaries. Whitfield (1989) separated the species found as larvae in the microtidal estuaries of southern Africa into four groups; 1) marine immigrants, 2) marine transients, 3) estuarine and 4) estuarine migrants. These groups correspond to the following guilds in the EUFG, 1) marine estuarine-opportunist, 2) marine straggler, 3) solely estuarine or estuarine & marine, and 4) estuarine-migrant (Figures 25, 26). As pointed out earlier, the last two groups are combined under the term ‘estuarine resident’ because individuals representing these species in estuaries would be expected to complete their life cycle within these systems. In south-western Australia, the semi-anadromous guild must also be added as a fourth group, because, although it is only represented by the clupeid *Nematalosa vlaminghi,* that species is very abundant in estuaries such as the Swan River (Chubb & Potter 1984).

The numbers of species, recorded as larvae in permanently-open estuaries along the microtidal coasts of south-western Australia and southern Africa, far exceeds those in seasonally-open estuaries, which is attributable to a greater number of marine species and particularly of marine stragglers in those permanently-open systems (Neira & Potter 1992a, b, 1994, Strydom 2003). This difference clearly reflects the fact that, unlike permanently-open systems, seasonally-open estuaries are often closed during the summer months when many marine species spawn.

Although the percentage contributions of estuarine-resident species to the overall number of species of fish larvae in the permanently-open Swan River and Walpole-Nornalup estuaries were only 16 and 28%, respectively, their contributions to the total abundance of fish larvae were as high as 92 and 98%, respectively (Neira et al. 1992, Neira & Potter 1994). The contribution of the larvae of estuarine-resident species to the number of species in the ichthyoplankton of the seasonally-open Wilson Inlet was greater (64%) and such larvae represented over 99% of all individuals (Neira & Potter 1992b). In terms of abundance, the ichthyoplankton communities of permanently- and seasonally-open southern African estuaries are also dominated by estuarine-resident species (Strydom 2003, Pattrick et al. 2007, Strydom 2015). The above trends demonstrate that, irrespective of whether the mouth of an estuary remains permanently open or seasonally open, certain estuarine-resident species are very successful in the microtidal estuaries of south-western Australia and southern Africa.

Remarkably, the dominance of the ichthyoplankton in estuaries in cool-temperate, warm-temperate and temperate/subtropical regions of southern Africa is due to exceptional numbers of one species, i.e. the clupeid *Gilchristella aestuaria*, with mean contributions as high as 77, 63 and 74% in those regions respectively (Strydom 2015). Estuarine-resident species of gobiid also made a substantial contribution to the ichthyoplankton of these estuaries. Gobiids made an overwhelming contribution to the ichthyoplankton of south-western Australian estuaries, in which, in terms of abundance, this family contributed between 40 and 88% in the Swan River Estuary, Walpole-Nornalup Estuary and Wilson Inlet (Neira & Potter 1992b, Neira et al. 1992, Neira & Potter 1994). While certain species of goby, such as *Caffrogobius gilchristi* and *Psammogobius knysnaensis* in southern Africa and *Favonigobius lateralis* in south-western Australia, spawn in estuaries, many individuals of these species leave these systems as preflexion larvae on ebb tides and return as postflexion larvae on flood tides (Whitfield 1989, Neira & Potter 1992a).

Gobiids of the genus *Pomatoschistus*, which are considered estuarine residents, are abundant in the ichthyoplankton of several European macrotidal estuaries (Faria et al. 2006, Marques et al. 2006, Ramos et al. 2006, Primo et al. 2011). The success of the Gobiidae in estuaries is related to this family possessing adaptations, e.g. demersal, adhesive eggs, which facilitate retention in these systems (Miller, 1984; Ramos et al. 2006). Although several species of atherinid are very abundant as juveniles and adults in south-western Australian estuaries, and the same is true for one species of atherinid in southern African estuaries (Potter & Hyndes 1999, James et al. 2007), this family is poorly represented in plankton tows from those systems, which is attributable to their larvae being out of range of those tows as a result of their epibenthic schooling behaviour (Steffe 1990).

A cluster dendrogram, derived from plankton sampling throughout the year emphasizes that the species composition of the ichthyoplankton in the Swan River Estuary changes markedly and progressively in an upstream direction from the morphologically distinct narrow entrance channel, i.e. the lower estuary, to the wide basins of the middle estuary and then to riverine upper estuary, which is characterised by reduced salinities (Figure 29; Neira et al. 1992). This reflected inter alia a progressive decline in marine species (marine stragglers and marine estuarine-opportunists) from 89% to 9.5% to <0.1%, whereas those of estuarine-resident species increased from 15% to 90.5% to 98% in the lower, middle and upper estuary, respectively (Neira et al. 1992). Even within the 8 km long entrance channel of this estuary, the contributions by the main marine species decreased sequentially in an upstream direction, whereas the reverse trend was true for the most abundant estuarine-resident species (Gaughan et al. 1990). The above consistent trends reflect the very small tidal range and thus absence of an effective mechanism for relatively rapid tidal transport through the estuary.

In certain south-eastern Australian microtidal estuaries, the larvae of the estuarine resident *Acanthopagrus butcheri* congregate in the immediate vicinity of the pronounced halocline that often forms in the upper (riverine) part in spring as freshwater discharge is declining, but still appreciable (Williams et al. 2012, 2013). This enables these larvae to exploit the zooplankton that likewise aggregate around the halocline. The larvae of *Morone americana* and *M. saxatilis* also congregate in the vicinity of the less pronounced halocline in Chesapeake Bay and particularly where estuarine turbidity and thus prey are greatest (North & Houde 2003).

### *Juvenile and adult fish*

#### *Contributions of the numbers and abundances of species to the EUFG*

The catches of the juveniles and adults of species in the different guilds in the EUFG have been collated for 11 macrotidal and 24 microtidal estuaries for which such data are available. This has enabled the number of species and number of individuals (abundance), which represent either one of three categories (estuarine, diadromous and freshwater) or one of two guilds (marine straggler and marine estuarine-opportunist) to be calculated. The data for the various estuaries represented either by shallow, nearshore and deep, offshore waters separately or collectively are represented in Figures 30–32. As the assignment of a few species to a particular category or guild sometimes differed between authors, the classification in Franco et al. (2008) is largely followed in this review.

In terms of number of species, the contribution of the two main marine guilds in macrotidal estuaries collectively ranged from 53% in the Elbe Estuary to 81% in the Forth Estuary (Figure 30). However, the numbers of marine straggler species and their contributions ranged widely from two (14%) in the Canche Estuary and four (20%) in the Authie Estuary to 32 (56%) in the Tagus Estuary and 38 (52%) at Oldbury in the Severn Estuary. This wide range largely reflects differences in the amount of sampling as the number of marine stragglers, in particular, increases with sampling effort (Vasconcelos et al. 2015). The number of marine estuarine-opportunist species ranged from nine to 16 in all but two of the 11 macrotidal estuaries in which 22 and 29 such species were recorded. Six of those 11 macrotidal estuaries contained only two estuarine-resident species, typically comprising a single species of gobiid and syngnathid.

Many authors have pointed out that the strong tidal action and turbidity in macrotidal estuaries provide a hostile environment for the successful development of the eggs and early life cycle stages of fishes and also make those stages susceptible to being flushed out to sea

(Haedrich 1983, Elliott et al. 2007). This hostile environment accounts for only a few species capable of breeding successfully in macrotidal estuaries (Claridge et al. 1986, Lobry et al. 2003, Franco et al. 2008). In this context, it is relevant that the numbers of estuarine-resident species in the three Portuguese estuaries (7–10) were greater than in the other macrotidal estuaries (2–3) and that the former estuaries are at the lower end of the macrotidal range (i.e. mesotidal) and thus subjected to less turbulent conditions. These estuarine residents comprised multiple species of gobiid, syngnathid and atherinid (Thiel et al. 2003, Pombo et al. 2007, Nyitrai et al. 2012).

In terms of abundance, marine estuarine-opportunists dominated the ichthyofauna of six of the nine macrotidal estuaries for which there were data, constituting 55 to 91% of the total number of fish recorded. The low contribution of this guild in the Elbe Estuary is due to the domination of the catches by *Osmerus eperlanus* (86%), an anadromous species that is found throughout the estuary and spawns in riverine areas, which have not suffered from anthropogenic changes and contain an abundance of the zooplankton prey of *O. eperlanus* (Thiel & Potter 2001). Estuarine-resident species contributed less than 35% to the total number of fish in seven of the nine macrotidal estuaries and made a particularly small contribution in the Severn Estuary (Figure 30), which has by far the greatest tidal range. The exceptional contribution by estuarine-resident species to the ichthyofauna in the Tagus Estuary (68%) was due very largely to the contribution by gobies, *Pomatoschistus* spp. (61%), recognizing that this would almost certainly have included *Pomatoschistus minutus*, which was considered a marine estuarine-opportunist in the Severn Estuary (Potter et al. 2001).

As with macrotidal estuaries, the habitats in the nearshore, shallow and offshore, deeper waters of microtidal systems in various temperate regions of the world are used as a nursery area by a range of marine estuarine-opportunist species (Figures 31, 32). However, the extent of the contributions by such species to the number of species and overall abundance varies markedly according to water depth and proximity to shore and with the extent to which the estuary mouth remains open to the ocean.

In the microtidal estuaries of south-western Australia and the microtidal Elkhorn Estuary in California, the contributions made by the number of marine estuarine-opportunist species and, to a far greater extent, by their overall abundance (Figures 31, 32), are greater in the deeper, offshore than in the corresponding nearshore, shallow waters. In nearshore waters in south-western Australia, the number of marine estuarine-opportunist species declines sequentially from 13-20 in permanently-open estuaries (e.g. Swan-Canning, Peel-Harvey estuaries) to six in seasonally-open estuaries (e.g. Broke and Wilson inlets) and 0–3 in normally-closed estuaries (e.g. Wellstead Estuary and Culham Inlet). The numbers of marine estuarine-opportunists in intermittently-open estuaries (e.g. Moore and Vasse-Wonnerup estuaries) lie at the lower end of the range in permanently-open estuaries. However, when expressed as percentage contributions, the values for marine estuarine-opportunists are greater in intermittently-open than permanently-open estuaries, because the number of marine stragglers is low (i.e. two versus 16–26) and thus the overall number of species is less. The small number of marine stragglers in intermittently-open estuaries is due to the closure of these estuaries for periods and their low salinities. In terms of overall abundance, the contributions of marine estuarine-opportunists decline from 17–47% in permanently-open estuaries to 2–5% in intermittently-open estuaries, to <1% seasonally-open and essentially zero in normally-closed estuaries (Figure 32).

Although the contribution by the number of marine estuarine-opportunist species in nearshore, shallow waters of estuaries in the cool temperate region of South Africa did not exhibit a pronounced trend with respect to estuary type, the contributions, in terms of abundance, clearly declined sequentially from the permanently-open to seasonally-open to normally-closed estuaries (Figure 31). Based on pooled data for the abundances in nearshore and offshore waters or solely for nearshore waters, marine estuarine-opportunists make relatively small contributions to the ichthyofaunas of estuaries in the Mediterranean and South America and in the Keiskamma, East Kleinmonde, Mgwalana and Bot estuaries in southern Africa (Figure 31).

The numbers and contributions of estuarine-resident species, throughout temperate regions of the world, are typically greater in microtidal than macrotidal estuaries (cf. Figures 30, 31, 32). The disparity is far more marked with abundance, with, for example, the contributions by such species to the ichthyofaunas of nearshore waters in microtidal estuaries typically ranging from 80 to 99% (Figure 31 and 32). Estuarine residents make a larger contribution, however, to the total number of species and, to an even greater extent, overall abundance of the ichthyofauna in the shallow, nearshore environment than in the deeper, offshore environment (Figure 32). Furthermore, and not surprisingly, estuarine residents dominate, to a greater extent, the overall abundance of fishes in estuaries that become closed to the sea for a period than in estuaries whose mouths remain permanently open (Figure 31 and 32).

As in macrotidal estuaries, the estuarine residents of microtidal estuaries include gobiids, with as many as four or five species being abundant and completing their life cycle within the estuaries of south-western Australia and southern Africa (Potter & Hyndes 1999, James et al. 2007, Valesini et al. 2014). The syngnathidae, which was frequently represented by a single species of estuarine resident in macrotidal estuaries, contains one or two such species in both south-western Australia and southern Africa (James et al. 2007, Valesini et al. 2014). The Atherinidae are far better represented as estuarine residents in microtidal than macrotidal estuaries, with the numbers of a single species (*Atherina boyeri*) comprising 95% of all fish recorded in the Acquatina Estuary in Italy and four species being abundant in estuaries along the south-west coast of Australia (Prince & Potter 1983,Potter et al. 1990, Hoeksema et al. 2009, Veale et al. 2014). In contrast to estuaries elsewhere, the ichthyofauna of those in southern Africa is dominated to a remarkable degree by an estuarine resident, the clupeid *Gilchristella aestuaria* (James et al. 2007, Strydom 2015). Other abundant estuarine-resident species in south-western Australia include an apogonid, sparid and plotosid (Potter & Hyndes 1999). The greater diversity of estuarine-resident species in south-western Australia than at a similar latitude in southern Africa may have resulted from selection pressures for adaptations that would ameliorate the problems posed by the more extensive land-locking of estuaries in this region (Potter et al. 1993, James et al. 2007).

Although the number of diadromous species that migrate through macrotidal estuaries is relatively small, some of these can be relatively abundant, as shown by the data for 11 estuaries (Figure 30). The catadromous eel *Anguilla anguilla* is the most frequently caught diadromous species in those estuaries. Even so the abundance of *A. anguilla* would have been underestimated, however, because of the difficulty in obtaining a representative sample of the small, thin and translucent “glass eel” stage. Although the Atlantic Salmon, *Salmo salar*, uses estuaries as a migratory route in Europe, anadromous salmonids are far more numerous in estuaries in the cool environments of the north-eastern and north-western coasts of North America (Lackey 2003, Nordlie 2003).

The number of diadromous species recorded in microtidal estuaries is lower than in macrotidal estuaries and the same is true for their abundance (Figures 31, 32). In terms of abundance, the diadromous species in microtidal estuaries are dominated by anguillids, with four species recorded in southern Africa, two in eastern Australia and one in the Mediterranean (Potter et al. 1990, McDowall 1996, Maci & Basset 2009). However, the clupeid *Nematalosa vlaminghi*, which is regarded as semi-anadromous, does form large spawning aggregations in the upper reaches of some estuaries in south-western Australia

(Chubb & Potter 1984). While the lamprey *Geotria australis* migrates through estuaries in south-western Australia (Potter et al. 1983a), it is rarely caught by the traditional methods used for catching fish in estuaries, i.e. seine net, gill net and trawling.

The numbers and contributions of freshwater species vary in relation to the extent to which sampling extends towards and includes riverine reaches.

### *Adaptations for spawning in estuaries*

An analysis of the egg types of fish species in estuaries in the central region of the Middle Atlantic Bight estimated that ~85% of the species that spawn within those estuaries produced demersal eggs, compared with only ~2% that were pelagic, whereas the reverse trend applied to species that spawned in marine waters outside the estuary, i.e. ~14% versus ~68%, respectively (Able & Fahay 2010). Although as many as ~75% of the ≥ 20 species that spawn in the microtidal Río de la Plata Estuary produce pelagic eggs, strong onshore winds during spring and summer, when these species spawn, minimize the advective loss of eggs to the ocean (Berasategui et al. 2004). The relatively large number of estuarine-resident species has been further facilitated by the benefits of the small tidal range (0.3–1.0 m; Gómez et al. 2009), which reduce the potential for eggs and larvae to be flushed out of the estuary.

As demonstrated earlier, the number of estuarine-resident species, and more particularly their overall relative abundance, are greater in microtidal than macrotidal estuaries and especially in their nearshore waters. Indeed, in terms of abundance, these estuarine residents, which comprise, in particular, small species such as those of the Atherinidae and Gobiidae, dominate the nearshore ichthyofauna of estuaries in south-western Australia, a region that lies at the lower end of the microtidal range (Potter & Hyndes 1999, Hoeksema et al. 2009). It is thus relevant that estuarine-resident species typically spawn in the dry mid-spring to mid-autumn months (Potter et al. 1986b, Potter et al. 1986c, Gill et al.

1996). During this period, water movement and turbulence are restricted because freshwater discharge and tidal action (as throughout the year) are limited, the salinity and temperature remain elevated and primary and secondary productivity are high. The environment of these microtidal estuaries is therefore benign and productive during this period and thus ideal for successful spawning, development and growth.

The small number of estuarine-residents found in microtidal estuaries possess some of the same types of adaptations for retention as those in the far more turbulent macrotidal estuaries. Gobies and atherinids such as *Atherina breviceps* thus likewise possess demersal eggs with adhesive filaments (Neira et al. 1988, Hoese 1994, Neira et al. 1998) and the flexion and post-flexion larvae of atherinids exhibit epibenthic schooling (Steffe 1990). The eggs of the plotosid *Cnidoglanis macrocephalus* are very large and laid in nests constructed by the males, who guard the larvae between their pelvic fins (Laurenson et al. 1993), while those of the apogonid *Ostorhinchus rueppelliii* are brooded in the mouths of males (Chrystal et al. 1985, Neira 1991), and those of the syngnathid *Urocampus carinirostris* in pouches (Neira et al. 1992). Although the clupeids *Gilchristella aestuaria* and *Nematalosa vlaminghi* produce pelagic eggs, they both spawn in the upper reaches of microtidal estuaries in southern Africa and south-western Australia, which reduces the likelihood of their eggs and larvae being flushed out of the estuary (Talbot 1982, Chubb & Potter 1984). Estuarine-resident species frequently have extended spawning periods, including some with repeated spawning, which increases the potential for such species to encounter favourable conditions for successful spawning and egg and larval development (Nordlie 2003). These species are also typically able to tolerate a wide range of salinities (Young & Potter 2002, Veale et al. 2014).

The few species that breed in macrotidal estuaries have similar adaptations for retention within the estuary as those of estuarine-resident species in microtidal estuaries. They include the production of demersal, adhesive eggs, e.g. atherinids and most goby species (Leis & Rennis 1983, Dando 1984, Miller 1984, White et al. 1984), construction of nests e.g. certain goby species (Vaas et al. 1975, Miller 1984) and pouch brooding e.g. syngnathids (Fritzsche 1984, Wilson et al. 2003, Bolland & Boettcher 2005).

*Seasonality and regionality*

Analysis of samples collected over five years from intake screens of a power station on the Severn Estuary demonstrated that, each year, the abundances of the main fish species, which were almost exclusively marine estuarine-opportunist and diadromous species, peaked in a time-staggered manner in this large macrotidal system (Figure 33; Claridge et al. 1986, Potter et al. 2015b). Differences in the timing of immigration of the various marine estuarine-opportunist species into macrotidal estuaries reflect differences in spawning times and/or in the distance between spawning areas and that estuary (Allen & Barker 1990, Potter et al. 1997, Witting et al. 1999, Maes et al. 2005). A particularly good example of how the time of spawning by those marine species that typically use estuaries vary in a sequential manner is reflected in the trends shown by the abundances of larvae of such species in tows from the Middle Atlantic Bight (Figure 34).

The sequential immigration and emigration of fish species in the Severn Estuary results in very pronounced annual cyclical changes in the composition of the ichthyofauna (Figure 33). These trends are paralleled by those in the Scheldt Estuary over ten years (Maes et al. 2005) and are consistent with those recorded in other macrotidal estuaries (e.g. van den Broek 1979, Araújo et al. 1998, 1999, Thiel & Potter 2001). Although the composition of the ichthyofauna of the Severn Estuary underwent similar cyclical changes each year, the amount of intra-annual variation differed between years. While this reflected inter-annual variations in the recruitment strengths of particularly the 0+ age class of marine estuarine-opportunist species (Potter et al. 1997), these variations were not correlated strongly with either salinity or temperature, as was also the case with the ichthyofauna of the Scheldt Estuary (Maes et al. 2005). However, the pattern of cyclical changes can be modified by extreme environmental conditions, such as very dry or very wet winters (Potter et al. 1986a).

The composition of the ichthyofauna in the macrotidal Elbe Estuary was shown by nMDS (non-metric multi-dimensional scaling) ordination of data for five sites distributed along the system to change progressively in an upstream direction as salinity declined (Thiel & Potter 2001). This reflected a sequential decline in the number and abundance of marine species (but with the extent of penetration varying among those species) and an increase in the number of freshwater species. Thus, for example, species such as the gadoid *Merlangius merlangus* did not penetrate beyond the lower two sampling sites, whereas the clupeid *Clupea harengus* was recorded at all five sites but in low numbers at the uppermost site. These differences presumably represent differences in the salinity tolerance of the various species. Indeed, salinity was shown to be the most important of 19 abiotic and biotic factors in influencing the composition of the ichthyofauna along the axis of three macrotidal estuaries in France (Selleslagh et al. 2009).

Although the species composition of the ichthyofauna in both nearshore and offshore waters of microtidal estuaries is related to season, it is influenced to a greater extent by region within the estuary (Loneragan et al. 1987, Loneragan et al. 1989). The greater influence of region reflects the marked differences between the morphological and thus hydrological characteristics of the different regions of particularly the larger and permanently-open estuaries. Thus, at a family level, the species belonging to the Atherinidae and Gobiidae are largely partitioned between the entrance channel (lower estuary), basins (middle estuary) and saline reaches of the tributary rivers (upper estuary) of the Swan River Estuary (Figure 35) (Prince & Potter 1983, Gill & Potter 1993). The lesser influence of season than region in microtidal than macrotidal estuaries is considered to be related to their far less pronounced tidal water movements.

*Elevated salinities and temperatures*

Shallow microtidal estuaries, and particularly those in Mediterranean climates with hot and dry summers, are highly susceptible to becoming hypersaline (Largier et al. 1997, Whitfield et al. 2006, Chuwen et al. 2009b). This is due not only to the absence of freshwater input, but also to the lack of penetration of marine water from the sea. The problem is most severe when the estuary mouth becomes closed by a bar during the dry summer months and even more so when that bar remains a barrier for one or more years (Figure 5F). It can be further exacerbated by salt run-off after the clearing of vegetation in the catchment and, under extreme circumstances, salinities can rise to ~300 (Hoeksema et al. 2006a, Chuwen et al. 2009a). As salinities increased over three years in Culham Inlet in south-western Australia, during which it remained closed, the various fish species in that system progressively ceased to be caught during regular sampling (Hoeksema et al. 2006a). Thus, for example, the sparid *Acanthopagrus butcheri* declined markedly in abundance at a salinity of 65 and was no longer caught above 85, with a massive mortality of ~1.3 million individuals occurring at intermediate salinities in that range (Hoeksema et al. 2006b). The only species present when salinities reached 136 was the atherinid *Atherinosoma elongata*, which has been recorded previously in salinities of 122 in a nearby estuary (Young & Potter 2002). Furthermore, the congener *A. microstoma* was the only species to survive in the highly elevated salinities in the uppermost region of an estuary with a reverse salinity gradient (Zampatti et al. 2010) and has been shown by laboratory studies to tolerate salinities up to 108 and to osomoregulate in salinities up to at least 85 (Lui 1969, Wedderburn et al. 2008). The ability of atherinids, in particular, to survive when salinities become elevated in microtidal estuaries is further emphasised by the fact that three species in this family, *A. elongata*, *Craterocephalus* *mugiloides* and *Atherinomorus vaigiensis*, represented 90% of the total number of fishes caught in the apex of an estuary with a reverse salinity gradient (Veale et al. 2014).

Studies in southern Africa demonstrated that, as salinities reached 65 in the St Lucia Estuary during a period of closure, marine estuarine-opportunists declined by more than 40% in terms of number of species and 50% by abundance (Whitfield et al. 2006). The sole surviving species, when salinities reached 110 in one part of this system, was the cichlid *Oreochromis mossambicus* (Vivier et al. 2010). Mortalities of more than 6000 fish, representing at least 11 species, were recorded in the Seekoei Estuary in South Africa as salinities rose above 90 during a period when this system was closed (Whitfield 1999).

### Birds

In estuaries, birds are important consumers of animals, plants and algae both intertidally and subtidally. The most intuitively obvious difference between macrotidal and microtidal estuaries for birds is the extent of intertidal areas available for feeding. The extensive and productive intertidal mud and sand flats in the macrotidal estuaries of northern Europe (see earlier) support huge numbers of wading birds (“Charadrii”), particularly in autumn when they arrive on migration from their Palaearctic breeding grounds in northern Canada, Greenland, Arctic Europe and Siberia. Some of these individuals remain in these northern estuaries for the winter, while others migrate southwards during the Austral summer to the microtidal estuaries of South Africa, Australia and South America (Serventy 1938, Siegfried 1981, Suazo et al. 2012). Other taxa that do not make this long-distance migration, such as some species of ducks, geese and gulls, may also be present in large numbers in northern European estuaries, feeding on both invertebrate and plant material on the highly productive intertidal flats.

Birds that feed subtidally will be less successful in macrotidal than microtidal estuaries. Herbivores, such as swans that feed by head-dipping and locating their food by “feel”, may be successful in the turbid waters of these macrotidal estuaries. In contrast, visually-feeding carnivorous waders, such as herons, storks and flamingos and diving piscivores, such as cormorants, pelicans and members of the falconiformes, would find it difficult to locate their food (Bell-Cross 1974). Diving ducks are also unable to operate in turbid, fast flowing water, and are absent, for example, from the Severn Estuary, UK (Kirby et al. 2004). In microtidal estuaries, which contain only small areas of intertidal sediment, subtidal feeders predominate, with the clarity of the water promoting the success of visual predators. In southern African microtidal estuaries, for example, migrant waders accounted for only ~5% of the avian biomass in those estuaries at which all birds were counted in summer, while the resident pelicans, cormorants and flamingos together made up 85% of the biomass (Siegfried 1981).

In a detailed study of the seasonally-open East Kleinemonde Estuary in the Eastern Cape, Terörde and Turpie (2012) found that it was primarily utilised by resident piscivorous birds, not only for feeding, but also for resting purposes. Intertidal wading birds are also virtually or totally absent from the microtidal Walpole-Nornalup Estuary and Broke, Wilson, Irwin and Parry inlets in south-western Australia (Hodgkin & Clark 1988a,b, 1989), in which piscivorous subtidal feeders also predominate. These avian piscivores can be major predators of commercially important fish species. For example, Coutin & Reside (2007) found that the Great Cormorant *Phalacrocorax carbo* in the microtidal Gippsland Lakes of south-eastern Australia feeds mainly on the sparid *Acanthopagrus butcheri* and that the population of ~3,000 cormorants consumed 340 t of this fish annually (~3.3 million fish), more than the biomass of the recreational and commercial fishery catches combined (Coutin 2000).

In southern Africa, fish-eating birds may also, at times, have a considerable impact on the abundance of fish populations. For instance, during the closure of the mouth of the West Kleinemonde Estuary in the eastern Cape, the abundance of juveniles of another sparid, *Rhabdosargus holubi*, decreased by 80% in five months, mainly due to predation by the Grey

Heron *Ardea cinerea* and two species of cormorants, *Phalacrocorax tucidus* and *P. africanus* (Blaber 1973).

The foregoing figures, however, may be exceptional. For example, in the microtidal Patos Lagoon Estuary in southern Brazil an estimated 73.4–81.9 t of the White Croaker *Micropogonias furnieri* and catfish (species representing the Ariidae) were consumed per year by Neotropic Cormorants *Phalacrocorax brasilianus*, representing only 3.7–4.1% of the annual landings of these species by the artisanal fishery (Barquete et al. 2008). There was also no evidence that any of the three cormorant species in the microtidal Peel-Harvey Estuary in south-western Australia exerted a pronounced adverse effect on the abundance of the major commercial fish in the estuary or on the food of those teleosts (Trayler et al. 1989). Nevertheless, the biomass of piscivorous birds in microtidal estuaries is far higher than in macrotidal estuaries. For example, the biomass of White Pelicans (*Pelecanus onocrotalus*) alone in the microtidal St Lucia Estuary in South Africa is at least four times greater than estimates by Swennen (1976) for all piscivorous birds in the Dutch Wadden Sea, and Siegfried (1981) suggests that the ecological impact of fish-eating birds is greater in the estuaries of southern African than in those of northern Europe.

Reduction in tidal exchange in seasonally-open estuaries through mouth closure will lead to a reduction in the number of wading birds, as these species depend on regular daily inundation and exposure of tidal mud and sandflats. Clear water will favour fish-eating birds, especially those that actively pursue their prey underwater. For example, Blaber (1973) reported a "feeding bonanza" of fish-eating birds after the mouths of estuaries in the Eastern Cape had closed. Piscivorous birds, and especially diving species such as cormorants and pelicans, depend on relatively deep water for feeding. In the St Lucia Estuary, for example, Whitfield & Cyrus (1978) found that the avian community in newly-created backwaters was dominated initially by piscivorous birds, but, with a decrease in water levels due to drought, invertebrate-eating wading birds became abundant. Seasonal changes in the incidence of piscivorous birds are also expected to occur in estuaries such as St Lucia in response to wind-induced seasonal changes in turbidity (Siegfried 1981).

Baird et al. (1985) reviewed predation by shorebirds in intertidal areas and documented a number of case studies in the macrotidal systems in northern Europe and also the microtidal Langebaan Lagoon in South Africa. Although the latter is not strictly an estuary, it appears that there is little, if any, difference between the avifaunas of South African estuaries and coastal lagoons (Siegfried 1981). Shorebirds consume significant quantities of the invertebrate production in macrotidal estuaries, ranging from 43% in the Tess estuary, UK, to 6% in the Grevelingen Estuary in the Netherlands, with a value of 20% in the Langebaan Lagoon, which is similar to that in the macrotidal Ythan Estuary, UK, (21%, Baird et al. 1985). Intertidal areas are used not only as feeding grounds, but also as a refuge for resting and moulting birds. Species of shelduck (*Tadorna* spp.) in Europe, Australia and South Africa all move seasonally into estuaries after breeding where considerable numbers of flightless birds congregate while undergoing their annual moult (Coombes 1950, Frith 1967, Siegfried 1981).

The macrotidal Grevelingen Estuary was formerly in open connection with the rivers Rhine and Meuse and with the North Sea, but, in May 1971, the construction of upstream and downstream dams led to the formation of a brackish lake between these two structures, (Nienhuis 1978, Bannink et al. 1984). This constitutes a large-sale experimental manipulation of tidal regime, i.e. from macrotidal to microtidal, at a single geographical location with the same external environmental conditions. Comparisons of the situation in the estuary before the construction of the dam and in the lake afterwards can be used to support or refute inferences on the contrasting ecology of macrotidal and microtidal estuaries described elsewhere in this review based on data from geographically very different regions. In a comparative study of the trophic role of birds in the estuary and lake, Wolff et al. (1976) found that wading birds feeding on zoobenthos took about 6 and 3% of the total zoobenthos production in the estuary and lake respectively, i.e. tides contributed to the greater exploitation of the zoobenthos by waders in the estuary. They also found that the level of predation by piscivorous birds in the lake was greater than in the estuary, which was attributed to the greater clarity of the water in the lake as this would favour the capture of prey. These changes are consistent with the observations above, based on data from macrotidal and microtidal estuaries throughout the world, and provide some experimental confirmation that the presence or absence of tides greatly influences the way birds are able to exploit food resources in estuaries.

Birds migrating from the macrotidal estuaries of the northern hemisphere to the microtidal estuaries of the southern hemisphere constitute the only ecological link between the two systems. The more common species of Palaearctic migrants to southern African estuaries are represented mainly by populations drawn from Greenland, Scandinavia and Siberia. All of the long-distance migrants that visit the microtidal estuaries of southern Africa are carnivores, the two main groups being waders (“Charadrii”) and terns (Sternidae); there are no herbivorous long distance migratory species. Wading birds in the high Arctic may be forced to migrate south because, although there is no shortage of invertebrate food, the short days frequently do not provide enough hours for these visual feeders to obtain sufficient food to support the high metabolic requirement necessary to sustain body temperature in the extremely cold conditions. Thus, there are instances of mortality among those that have not migrated (McLusky & Elliott 2004).

Apart from the warm temperatures of the Austral summer, the paucity of intertidal habitat in microtidal estuaries in South Africa is far from ideal for waders that feed on benthic invertebrates (Siegfried 1981). Apparently, however, the waders do not depart for the north to escape adverse conditions in the south, and the advantages gained through breeding in the north must be considerable to offset the presumed hazards of a 30,000 km migration each year. The reason waders do not breed in southern Africa may be due to the requirements of their young, which are not fed by their parents and depend instead on an abundance of protein-rich insects as food. The young hatch with relatively short bills and, unlike their parents, are thus inefficient at probing the ground for food items. Very little is known about insects in southern African estuaries, particularly in salt marshes, but Puttick's (1977) studies at Langebaan Lagoon indicate that the above-ground insect biomass is relatively low.

The great abundance of insect food that becomes available in the short northern spring and summer on the breeding grounds of waders probably explains the basis for the evolution of this migratory behaviour (Baker & Baker 1973). The paucity of intertidal habitat accounts for the generally high densities of waders in the estuaries of South Africa, resulting in a high predation pressure on invertebrate prey, but this is compensated for by the high production of these invertebrates, the highest production coinciding with the highest energy requirement of the birds prior to their northward migration (Kalejta & Hockey 1991, Kalejta 1992, 1993). These waders spend at least a month 'fattening up' prior to their northern migration, and the smaller species are capable of doubling their body weight (Turpie 1996). The juveniles of many of these migrants do not return to the breeding grounds in the first or even second year, which is probably an adaptive response to the low probability of both breeding success and survival of a long-distance journey, estimated to be as low as 30% (Turpie 1996). The northward journey is generally made more rapidly than the southern migration, thereby ensuring timely arrival at the breeding grounds where the birds must compete for breeding territories and mates (Turpie 1996).

A very conspicuous component of the avifauna of microtidal estuaries (among other habitats such as coastal mudflats, lagoons and salt lakes) are flamingos. In South African estuaries, the Greater Flamingo (*Phoenicopterus roseus*) accounts for 90% of the biomass of all bird species that feed on invertebrates, in spite of the greater abundance of the smaller carnivorous migrants. In these estuaries, the Lesser Flamingo (*P. minor*) is a major component of the assemblage of species that feed on algae and aquatic macrophytes (Siegfried 1981). The Chilean Flamingo (*P. chilensis*) takes the place of these species in temperate South America and the American Flamingo (*P. ruber*) in the tropical Caribbean. Flamingos have a wide global distribution, particularly in microtidal coastal regions (the Caribbean, South America, South Africa, Mediterranean, Red Sea, Pakistan and India), but strangely not in Australia. At least four species were present in Australia, however, as recently as the Pleistocene (Miller 1963). Although the fossils were associated with the inland Lake Eyre area, it seems probable that they would also have frequented the microtidal estuaries. Since they play such an important ecological role in other microtidal estuaries in the warmer temperate and tropical regions of the world, particularly in South Africa, other species must have assumed this role after their extinction in Australia. Possible candidates are the Black Swan (*Cygnus atratus*), which is almost exclusively herbivorous, and the Musk Duck (*Biziura lobata*), which feeds on a range of aquatic invertebrates and plants. Both of these species are extremely abundant in the microtidal estuaries of south-western Australia (Hodgkin & Clark 1988a,b, 1989).

## Summary and conclusions

The major characteristics that distinguish microtidal from macrotidal estuaries in temperate regions are summarized in Table 2 and in pictorial form in Figure 36. These comparisons emphasize that the extent of tidal range and tidal water movements has a profound and widespread influence on the ecology of estuaries and demonstrate that it is not always appropriate to apply paradigms derived from research in estuaries in macrotidal regions to those in microtidal regions. The rapid attenuation of tidal water movement in an upstream direction in microtidal estuaries means that, unlike the situation in macrotidal estuaries, there is no tidal mechanism for transporting the larvae of marine species of fish and crustacean rapidly through the estuary. A combination of a small tidal action, limited freshwater discharge and warm temperatures, typically found in microtidal estuaries during the warm summer months, provide a benign environment for spawning and thus facilitated the success of a number of estuarine-resident fish species. The extent of the intertidal zone is far less in microtidal estuaries and thus, at low tide, does not provide a wide area for the development of microphytobenthos, which act as a food source for the meio- and macrobenthos that constitute a major component of the diet of wading birds.

The other natural features of microtidal estuaries include a long residence time, the retention of organic material through poor flushing, low turbidity and marked stratification during and following significant freshwater discharge. This results in natural environmental stress through encouraging the development of algal blooms and hypoxia. These effects often become exacerbated through anthropogenic influences, such as the input of nutrients from surrounding agricultural and urban developments, and can lead to massive algal blooms, some of which are toxic, and to anoxia. Furthermore, when a bar forms at the mouth of microtidal estuaries and remains as a barrier for a protracted period, these systems can become markedly hypersaline through evaporation and lead to large mortalities of fish and other fauna.

Microtidal estuaries are more sensitive to anthropogenic perturbation than their macrotidal counterparts, particularly with respect to the accumulation of nutrients and pollutants. Their fragility thus warrants conservation measures that recognize their special environmental characteristics.

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## Tables

**Table 1** Suspended particulate matter (SPM) concentrations, measured at the bottom of the turbidity maximum zone, and mean spring tidal range (STR) in five macrotidal and four microtidal estuaries. Table modified from Hughes et al. (1998).

*Permissions granted.*

**Table 2** Summary of the differences between the main characteristics of typical macrotidal and microtidal estuaries.

*No permissions needed.*

## Table 1

| Estuary | Location | SPM conc. (g $L^{-1}$) | STR (m) | Reference |
|---|---|---|---|---|
| ***Macrotidal*** | | | | |
| Weser | Germany | 1.5 | 3.8 | Grabemann & Krause (1989) |
| Fly* | Papua New Guinea | 5.0–30.0 | 4.0 | Wolanski et al. (1995) |
| Tamar | UK | 26.0 | 4.5 | Uncles & Stephens (1994) |
| Gironde | France | 10.0 | 5.0 | Allen & Castaing (1973) |
| Severn | UK | 20.0 | 12.3 | Kirby (1988) |
| | | | | |
| ***Microtidal*** | | | | |
| James | USA | 0.1–0.3 | 0.7 | Nichols (1993) |
| Hawkesbury | Australia | 0.2 | 1.3 | Hughes et al. (1998) |
| Varde | Denmark | 0.1–1.0 | 1.6 | Bartholdy (1984) |
| Cooper | USA | <0.1 | 2.0 | Althausen & Kjerfve (1992) |

* denotes estuary is located in the tropics.

## Table 2

| **Macrotidal** | **Microtidal** |
|---|---|
| ***Types of estuary*** | |
| Typically ria or coastal plain estuaries | Typically bar-built or blind estuaries |
| ***Tidal regime*** | |
| Mean tidal range >2 m (includes mesotidal) | Mean tidal range <2 m |
| Astronomical tides > meteorological tides | Astronomical tides < meteorological tides |
| ***Hydrology*** | |
| Tide-dominated | Wave-dominated |
| Typically partially or well-mixed | Typically highly-stratified (salt wedge) |
| Mixing driven by tides | Mixing driven by wind and waves |
| Net outflow of water | May have net outflow or inflow of water |
| Salinity declines upstream from the mouth; i.e. positive estuary | May have either a positive or reverse salinity gradient or a salt-plug |
| Salinity does not exceed that of fully marine waters | Can become markedly hypersaline |
| Salinity at a single point changes markedly during the tidal cycle | Salinity at a single point changes little during the tidal cycle, but can change markedly seasonally in response to changes in freshwater discharge |
| High turbidity, which varies according to tidal cycle | Low turbidity, except during heavy freshwater discharge |
| Residence time typically short (i.e. hours – days) and varies according to tidal cycle | Residence time typically long (i.e. weeks-months), but can last years if estuary remains closed |
| Residence time does not change markedly throughout the year | Residence time varies markedly throughout the year, responding to changes in freshwater discharge |
| ***Sedimentology*** | |
| Coarse sediment from catchment deposited at point where riverine and tidal current meet, forming mobile sandbanks that are redistributed by tides | Coarse sediment from catchment deposited at junction of river and basin forming fluvial deltas |
| Deposition of fine sediments regulated by mixing of fresh and salt water | Fine sediments deposited in middle reaches due to low current velocities |
| Marine sediments form elongated mid-channel sand bars and extend intertidal area seaward | Marine sediments form flood and ebb tide deltas |
| Wide mouth, which remains open to the sea | Narrow mouth, produced by coastal sediment deposition. Mouth can become closed for periods, when freshwater discharge is low |
| Large intertidal area | Small intertidal area |
| Moderate ability to trap sediment | Very effective sediment traps |
| Strong tidal action flushes organic material from the system and, together with vertical mixing tends to prevent hypoxia | Weak tidal action and a highly-stratified water column leads to accumulations of organic material, which can produce hypoxia and even anoxia in deeper waters |
| Allochthonous organic material,derived from both catchment (rivers and surrounding land) and sea | Allochthonous organic material derived predominantly from the catchment |
| ***Phytoplankton*** | |
| Phytoplankton production light-limited | Phytoplankton production not light-limited |
| Phytoplankton composition dominated by diatoms throughout the year | Phytoplankton composition dominated by diatoms in spring and dinoflagellates and cyanobacteria in summer |
| Short residence time and high turbidity restrict production of phytoplankton blooms | Long residence time and low turbidity can result in massive phytoplankton blooms, some of which are toxic |

## Table 2 continued

| Macrotidal | Microtidal |
|---|---|
| ***Microphytobenthos*** | |
| Inhabit unvegetated intertidal areas and fringing salt-marshes | Inhabit predominantly shallow subtidal waters |
| Primary production during exposure at low tide | Primary production continuous during daylight |
| Primary production from microphytobenthos exceeds phytoplankton | Primary production from microphytobenthos exceeds phytoplankton, but its contribution varies seasonally |
| | Amount of primary production varies depending on whether estuary is open or closed |
| ***Macrophytes*** | |
| Extensive salt marsh areas and productivity increase with increasing tidal range | Very small areas of salt marsh |
| Salt marshes occur on most estuaries | Occurrence of salt marsh related to frequency and duration of bar opening |
| Distinct zonation in salt marsh species distribution | Patchy mosaic of salt marsh species, particularly in seasonally-open estuaries. |
| Salt marsh flora dominated by *Spartina* spp. | *Spartina* spp. generally absent |
| Small areas of seagrass | Can be extensive seagrass beds |
| Seagrass flora dominated by *Zostera* spp. | Seagrass flora dominated by *Ruppia* spp. |
| Can tolerate brief periods of aerial exposure | Intolerant of aerial exposure |
| Tidal currents uproot seagrass | Stable populations not subjected to export by uprooting |
| Brown algae (e.g. *Fucus* and *Ascophyllum*) in areas where tidal currents expose hard substrata | Brown algal species rare |
| Green algae found in intertidal areas | Green algae found in subtidal areas |
| Biomass of green algae reduced by tidal scour | Biomass of green algae can increase markedly causing blooms |
| ***Zooplankton*** | |
| | Abundance of microheterotrophs greatest when estuary mouth is closed |
| Comprise predominantly allochthonous species | Comprise predominantly autochthonous species |
| Mesozooplankton may supplement their phytoplankton diet with detritus and associated bacteria | Mesozooplankton feed mainly on phytoplankton |
| Use of selective tidal stream transport avoids flushing of fauna from estuary | Species in lower reaches of estuaries move either into deeper waters or onto the banks thus preventing flushing from estuary |
| Marked seasonal variation in abundance and biomass of the predominantly allochthonous marine mesozooplankton | Less pronounced seasonal variation in abundance and biomass of autochthonous estuarine mesozooplankton |
| Short residence times and low phytoplankton biomass result in low zooplankton biomass | Long residence times and high phytoplankton biomass result in high zooplankton biomass |
| | Mesozooplankton diversity greater in permanently-open than seasonally-open estuaries |
| ***Meiobenthos*** | |
| Meiofaunal densities greater in intertidal than subtidal regions | Meiofaunal densities greater in subtidal than intertidal regions |
| Occurrence of meiofaunal species form a gradient from coast to upper estuary | Marked difference in species composition between coast and estuary and species widely distributed throughout estuary |

## Table 2 continued

| Macrotidal | Microtidal |
|---|---|
| ***Macrobenthos*** | |
| Areas of high densities of suspension feeders (e.g. mussel and oyster beds) near mouths | Very low contribution of suspension feeders throughout the estuary |
| Presence of some large macrobenthic species | Overwhelming abundance of small macrobenthic species |
| Species diversity greatest in marine and oligohaline reaches and lowest in middle 'estuarine' region | Species richness relatively consistent among regions of the estuary, particularly in seasonally-open estuaries |
| Species use tidal currents for movement through and retention within the estuary | |
| ***Fish*** | |
| Larvae of marine species use passive and selective tidal transport to move through and disperse and remain within estuaries | Tidal action insufficient to facilitate rapid transport upstream through the estuary |
| Hostile environment for spawning and survival of eggs and larvae | Benign environment for spawning and survival of eggs and larvae |
| Relatively few abundant estuarine-resident species | Greater number of estuarine-resident species, some of which are very abundant |
| | Number of species declines from permanently-open to seasonally-open to normally-closed estuaries. |
| Species composition undergoes pronounced cyclical changes each year due to time-staggered immigration and emigration of juveniles of marine species and of diadromous species | Seasonal immigration and emigration patterns are less pronounced |
| | Can become markedly hypersaline when closed from the ocean by a bar and result in massive fish mortalities |
| ***Birds*** | |
| Very large numbers of intertidal wading invertebrate feeders | Low abundance of wading invertebrate feeders due to small intertidal area |
| Low numbers of diving piscivorous birds due to high turbidity of water | Large numbers of diving piscivorous birds due to high water clarity |

## Figures

**Figure 1** Graphical representations of the six types of estuary that were classified by Fairbridge (1980) on the basis of their geomorphological characteristics and which form the basis of this review. Examples of each estuary type and their location are given.

*Permissions granted.*

**Figure 2** Satellite images of the six types of estuary that were classified by Fairbridge (1980) on the basis of their geomorphological characteristics and which form the basis of this review. Examples of each estuary type and their location are given. Satellite images provided by Google, TerraMetrics, Getmapping plc, Landsat, DigitalGlobe and CNES/Astrium.

*No permissions needed.*

**Figure 3** Salinities recorded throughout the water column of the microtidal Swan River Estuary in south-western Australia in (A) early spring (23 September 2013), (B) late spring (11 November 2013), (C) early autumn (17 March 2014) and (D) late autumn (26 May 2014). + denotes points in the water column where salinity was measured. Data provided by the Department of Water, Western Australia.

*No permissions needed.*

**Figure 4** Conceptual models of the hydrology of typical (A) macrotidal and (B and C) microtidal estuaries. Modified from Ryan et al. (2003).

*No permissions needed.*

**Figure 5** Stylized examples of (A) macrotidal coastal plain positive estuary and (B) permanently-open bar-built microtidal positive estuary, both with positive longitudinal salinity gradients, (C and D) permanently-open microtidal estuaries with reverse longitudinal salinity gradients, (E) permanently-open microtidal estuary with a salt-plug and (F) microtidal estuary that is seasonally closed to the ocean by a sand bar across its mouth (dotted box), with a hypersaline positive longitudinal salinity gradient. Modified from Potter et al. (2010).

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**Figure 6** Flushing times ($\log_{10}$ days) as functions of tidal length and mean tidal range at the mouths of 39 estuaries in the Northern Hemisphere. Tidal length and tidal range are given as $\log_{10}$ and after back transformation. Dashed line represents the boundary between microtidal and macrotidal estuaries. Flushing times interpolated using natural neighbours. From Uncles et al. (2002).

*Permissions granted.*

**Figure 7** Relationship between model predictions of residence time and freshwater inflow, showing power function fit by regression. From Huang et al. (2011).

*Permissions granted.*

**Figure 8** Maximum concentrations of suspended particulate matter (SPM, $\log_{10}$ mg $l^{-1}$), depth-averaged and recorded within ~1 h of local high water, as functions of tidal length and mean tidal range at the mouths of 44 estuaries in the Northern Hemisphere. Tidal length and tidal range are given as $\log_{10}$ and after back transformation. Dashed line represents the boundary between microtidal and macrotidal estuaries. SPM concentrations interpolated using natural neighbours. From Uncles et al. (2002).

*Permissions granted.*

**Figure 9** Conceptual models of the sediment dynamics of typical (A) macrotidal and (B) microtidal estuaries. Modified from Ryan et al. (2003).

*No permissions needed.*

**Figure 10** Photographs showing the major hydrodynamic phases and events in the microtidal Kleinemonde Estuary in South Africa as described by Whitfield et al. (2008), i.e. (A) Closed Phase, (B) Outflow Phase, (C) Tidal Phase, (D) Semi-closed Phase and (E) Overwash Event. © Paul Cowley, South African Institute for Aquatic Biodiversity.

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**Figure 11** Mean freshwater inflow ±1 SE in permanently-open (PO), intermittently-open (IO), seasonally-open (SO), normally-closed (NC) and permanently-closed (PC) estuaries in south-western Australia. Number of estuaries in each type is provided. Note that permanently-closed estuaries are not strictly estuaries as defined in this review. Data from Brearley (2005).

*No permissions needed.*

**Figure 12** Mean percentage contribution ±1 SE of the intertidal area to the total area of bar-built estuaries in microtidal areas of south-western Australia and to those of rias, coastal plain estuaries and bar-built estuaries in macrotidal areas of the UK. Number of estuaries in each type is provided. Data for Australian estuaries taken from OzCoasts (2015) and for UK estuaries, from Davidson et al. (1991).

*No permissions needed.*

**Figure 13** Conceptual diagram showing the influence of water residence time and light availability on phytoplankton biomass. Redrawn from Lancelot & Muylaert (2011).

*Permissions granted.*

**Figure 14** Relationship between the mean annual concentrations of chlorophyll *a* and dissolved organic nitrogen in samples from 40 microtidal and macrotidal estuaries. Redrawn from Monbet (1992).

*Permissions granted.*

**Figure 15** Ranked distribution of median annual phytoplankton primary production for 131 estuarine and coastal ecosystems. Two values are given for 30 systems because values were available for both gross and net primary carbon production. One negative value (105 g $m^{-2}$ $y^{-1}$) from the Scheldt Estuary is not shown. Grey squares show the ranked distribution of the measurements for annual phytoplankton primary production in 45 estuaries in Boynton et al. (1982). From Cloern et al. (2014).

*No permissions needed.*

**Figure 16** Conceptual model demonstrating the contrasting phytoplankton ecology of macrotidal and microtidal estuaries. See text for explanation.

*No permissions needed.*

**Figure 17** Photographs of (A) an intertidal mudflat and saltmarsh on the macrotidal Tamar Estuary in the UK and (B and C) the star-shaped marks produced by the siphons of the bivalve *Scrobicula plana* when feeding on the surface film of that intertidal mudflat.

*No permissions needed.*

**Figure 18** Proportions of seasonal primary production by large and small phytoplankton, microphytobenthos, seagrass and macroalgae in the microtidal Wilson Inlet in south-western Australia, during winter (W) June–August, spring (Sp) September–November, Summer (Su) December–February and autumn (A) March–May. Modified from Haese & Pronk (2011).

*No permissions needed.*

**Figure 19** Production of intertidal *Spartina alterniflora* in relation to mean tidal range for a suite of salt marshes on the Atlantic coast of the USA. From Steever et al. (1976).

*Permissions granted.*

**Figure 20** Conceptual diagrams showing changes in the proportions of allochthonous and autochthonous zooplankton along the salinity gradient in (A) macrotidal estuaries and (B) microtidal estuaries. Modified from Heip et al. (1995).

*No permissions needed.*

**Figure 21** Map showing the sites sampled for nematodes in the (A) macrotidal Exe Estuary in the UK and (B) microtidal Swan River Estuary in south-western Australia. ●, coastal sampling sites; ○, estuarine sampling sites. Numbers refer to sampling sites in Warwick (1971) and Hourston et al. (2011). Satellite images provided by Google, TerraMetrics, Getmapping plc and DigitalGlobe.

*No permissions needed.*

**Figure 22** Shade plot of the fourth-root transformed and standardised abundances (shown in grey scale) of free-living nematodes in the (A) macrotidal Exe Estuary in the UK and (B) microtidal Swan River Estuary in south-western Australia. ●, coastal sampling sites; ○, estuarine sampling sites. Sites are ordered from left to right in an upstream direction (see Figure 21). Data from Warwick (1971) and Hourston et al. (2011). Site numbers are the same as in those publications.

*No permissions needed.*

**Figure 23** Relationship between biomass (ash-free dry weight) of benthic suspension feeders and residence time. Data taken from Heip et al. (1995).

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**Figure 24** Photographic silhouettes of macrofauna from an area of 0.5 $m^2$ in the upper (Clifton) and lower (West Mud) reaches of the macrotidal Tamar Estuary in the UK. White bar denotes 10 cm. Modified from Warwick & Gee (1984).

*No permissions needed.*

**Figure 25** Life cycle categories and guilds of fishes found in estuaries: (A) marine straggler, (B) marine–estuarine opportunist/marine–estuarine dependent, (C) solely estuarine, (D) estuarine and marine, (E) estuarine and 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. (2015a).

*Permissions granted.*

**Figure 26** Life cycle categories and guilds of fishes found in estuaries: (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 figures. # Refers only to the estuarine populations of the guild. Modified from Potter et al. (2015a).

*Permissions granted.*

**Figure 27** Diagrammatic representations of typical vertical migratory behaviour resulting in (A) flood-tide, (B) ebb-tide, (C) nocturnal flood-tide or (D) nocturnal ebb-tide transport. Animals oscillate between residence in the water column and on/near the bottom at different phases of the tide. The diel cycle and direction and relative magnitude of the tidal currents are shown in the upper panel. ‘SW’ is slack water and the arrows in the panels indicate direction of transport. Expanded from Forward & Tankersley (2001).

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**Figure 28** Diagrammatic representation of the life cycle and proposed recruitment strategy of the marine estuarine-dependent *Rhabosargus holubi* into the East Kleinemonde Estuary when the estuary mouth was (A) open and (B) closed. From Cowley et al. (2001).

*Permissions granted.*

**Figure 29** Cluster dendrogram constructed from a Bray-Curtis resemblance matrix of the mean transformed abundances of each species of ichthyoplankton recorded at 13 sites in the Swan River Estuary in south-western Australia averaged over one year. From Neira et al. (1992).

*Permissions granted.*

**Figure 30** Percentage contributions made by the (A) number of species and (B) number of individuals representing the different categories and guilds of the Estuarine Usage Functional Group in macrotidal estuaries in Europe. n, nearshore waters; o, offshore waters; c, nearshore and offshore waters combined. Numbers in italics in (A) represent the total number of species recorded in that estuary. F, Forth (Elliott et al. 1990); O, Oldbury and B, Berkeley in the Severn (Claridge et al. 1986); C, Canche; A, Authie and So, Somme (Selleslagh et al. 2009); E, Elbe (Thiel & Potter 2001); Sc, Scheldt (Maes et al. 2005); G, Gironde (Lobry et al. 2003); R, Ria de Averiro (Pombo et al. 2007); M, Mondego (Nyitrai et al. 2012); T, Tagus (Thiel et al. 2003).

*No permissions needed.*

**Figure 31** Percentage contributions made by the (A) number of species and (B) number of individuals representing the different categories and guilds of the Estuarine Usage Functional Group waters of microtidal estuaries in Europe, North and South America and warm and cool temperate regions of southern Africa. n, nearshore waters; o, offshore waters; c, nearshore and offshore waters combined. Numbers in italics in (A) represent the total number of species recorded in that estuary. po, permanently-open; so, seasonally-open; nc, normally-closed. V, Venice Lagoon (Franco et al. 2006); A, Acquatina Lagoon (Maci & Basset 2009); PL, Porto-Lagos Lagoon (Koutrakis et al. 2005); Ek, Elkhorn Slough, (Yoklavich et al. 1991); P, Pando (Acuña Plavan et al. 2010); GF, Great Fish; K, Keiskamma; East Kleinmonde; S, Swartvlei; M, Mgwalan (all James et al. 2007); Ee, Eerste (Clark et al. 1994); Pa, Palmiet (Bennett 1989); Z, Zandvlei (Clark et al. 1994); Kl, Kleinmond (Bennett 1989) and B, Bot (Bennett 1989). *No permissions needed.*

**Figure 32** Percentage contributions made by the (A) number of species and (B) number of individuals representing the different categories and guilds of the Estuarine Usage Functional Group recorded in nearshore and offshore waters of microtidal estuaries in south-western Australia. Numbers in italics in (A) represent the total number of species recorded in that estuary. po, permanently-open; io, intermittently-open; so, seasonally-open; nc, normally-closed. SC, Swan-Canning Estuary (Loneragan et al. 1989, Valesini et al. 2009); PH, Peel-Harvey Estuary (Loneragan et al. 1987, Valesini et al. 2009); BW, Blackwood River Estuary (Valesini 1995, Valesini et al. 1997); M, Moore River Estuary (Young et al. 1997, J. Williams unpublished data); V, Vasse-Wonnerup Estuary (Tweedley et al. 2014a, Cottingham et al. 2015); Br, Broke Inlet (Tweedley 2011); Wi, Wilson Inlet (Chuwen et al. 2009a, Valesini et al. 2009); We, Wellstead Estuary (Chuwen et al. 2009a, Valesini et al. 2009) and C, Culham Inlet (Hoeksema et al. 2006a).

*No permissions needed.*

**Figure 33** Relative abundance of nine common marine fish species (A–C, E–I & K), two anadromous fish species (D & J) and *Gasterosteus aculeatus* (L.) in samples collected weekly from Oldbury in the Severn Estuary, UK, between July 1972 and June 1977. Number of each species in each calendar month are expressed as a mean ± 95% confidence limits of the total catch of that species in that month. 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, 2015b).

*Permissions granted.*

**Figure 34** Shade plot showing the ranking by abundance, in each month, of the larvae of different fish species in oceanic waters in the central part of the Middle Atlantic Bight. Data taken from Able & Fahay (2010) and restricted to species that use estuaries.

*No permissions needed.*

**Figure 35** Distribution of five atherinid species and five goby species in the Swan River Estuary in south-western Australia. The gradation from black to white for each species reflects their relative abundance, ranging from maximum to zero densities, respectively. Modified from Potter & Hyndes (1999).

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**Figure 36** Conceptual diagrams highlighting some of the major biotic differences between a typical (A) macrotidal and (B) microtidal estuary. See text for explanation.

*No permissions needed.*

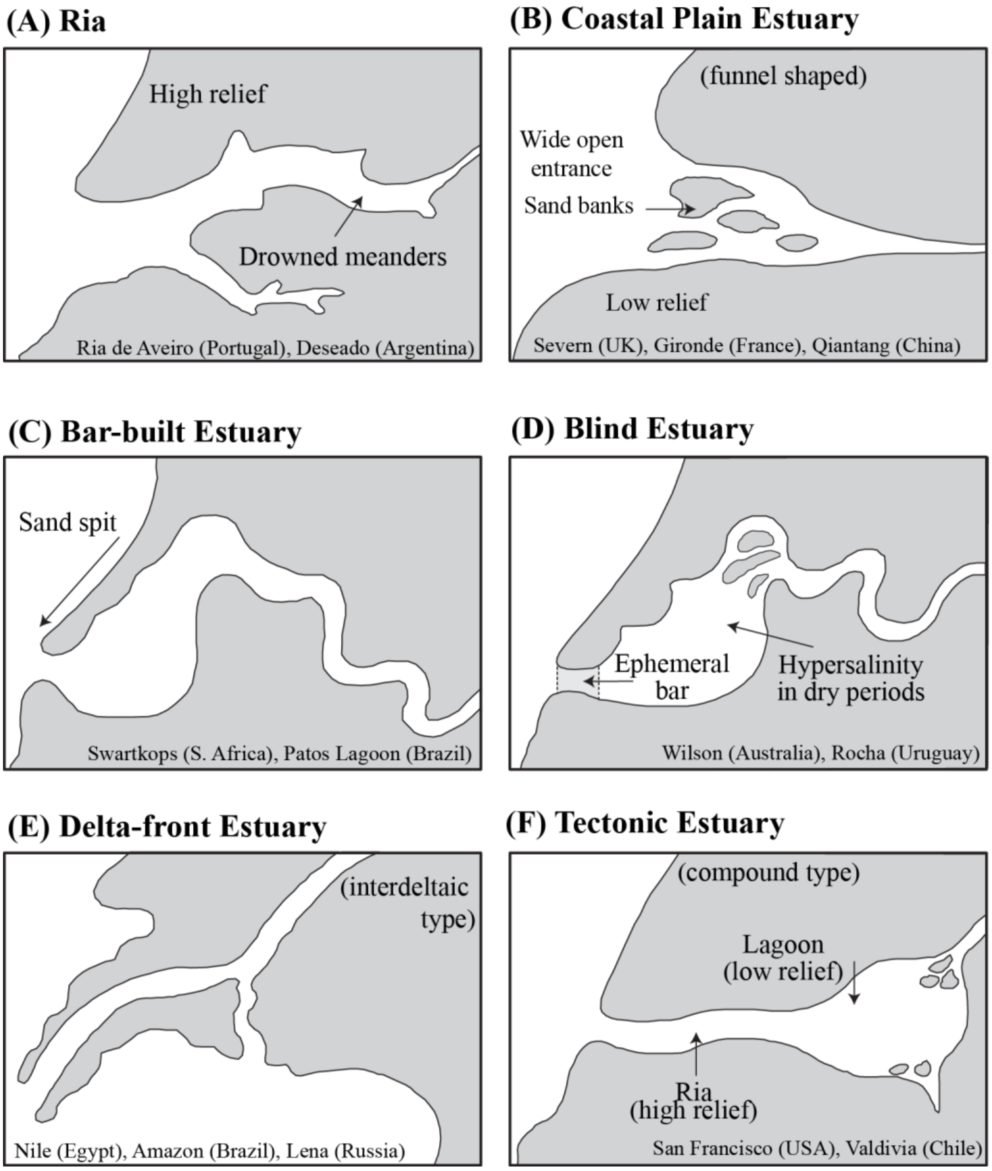

(A) Ria
High relief
Drowned meanders
Ria de Aveiro (Portugal), Deseado (Argentina)
(B) Coastal Plain Estuary
(funnel shaped)
Wide open entrance
Sand banks
Low relief
Severn (UK), Gironde (France), Qiantang (China)
(C) Bar-built Estuary
Sand spit
Swartkops (S. Africa), Patos Lagoon (Brazil)
(D) Blind Estuary
Ephemeral bar
Hypersalinity in dry periods
Wilson (Australia), Rocha (Uruguay)
(E) Delta-front Estuary
(interdeltaic type)
Nile (Egypt), Amazon (Brazil), Lena (Russia)
(F) Tectonic Estuary
(compound type)
Lagoon (low relief)
Ria (high relief)
San Francisco (USA), Valdivia (Chile)

**Figure 1**

**(A) Ria**
(Salcombe-Kingsbridge, UK)

**(B) Coastal Plain Estuary**
(Salmon, Canada)

**(C) Bar-built Estuary**
(Nornalup, Australia)

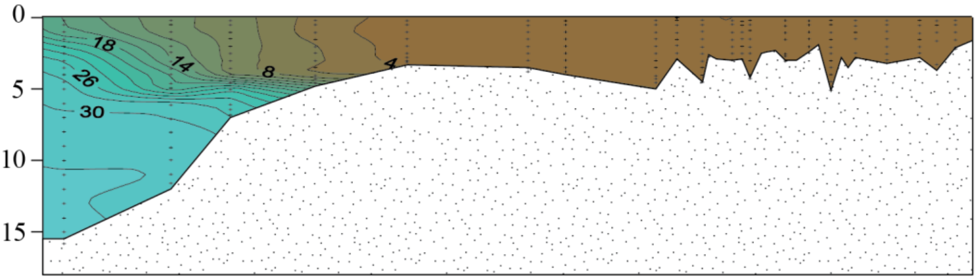
**(D) Blind Estuary**
(East & West Kleinemonde, South Africa)

**(E) Delta-front Estuary**
(Fly, Papua New Guinea)

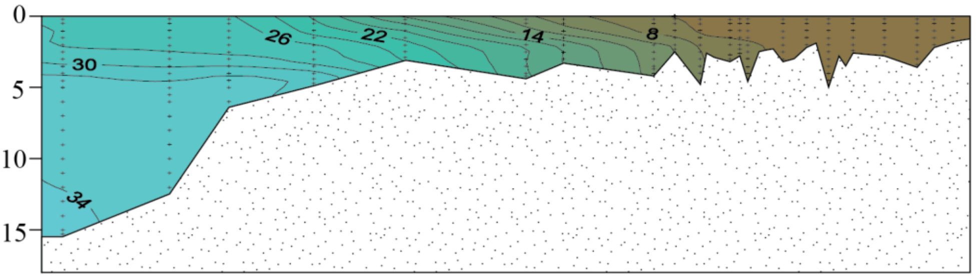
**(F) Tectonic Estuary**
(Lyttelton, New Zealand)

**Figure 2**

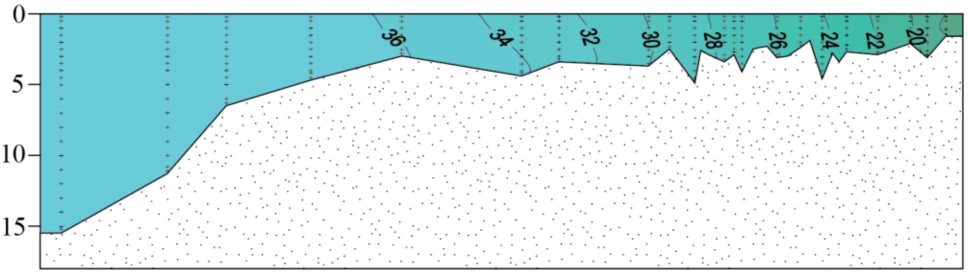
(A) Early spring



(B) Late spring



(C) Early autumn



(D) Late autumn

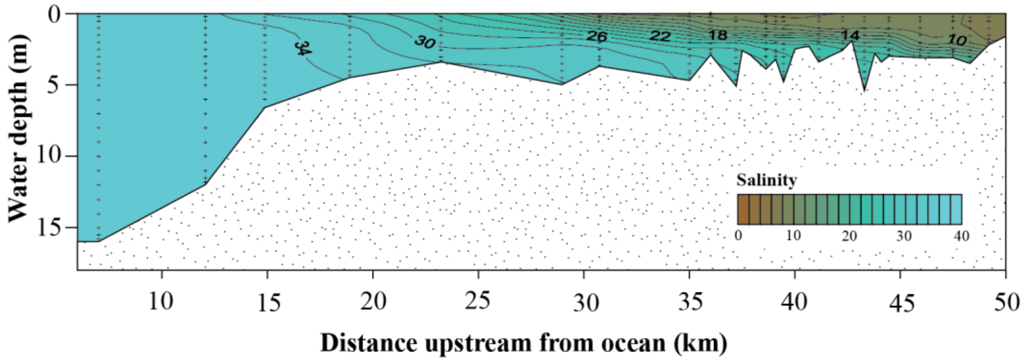


Figure 3

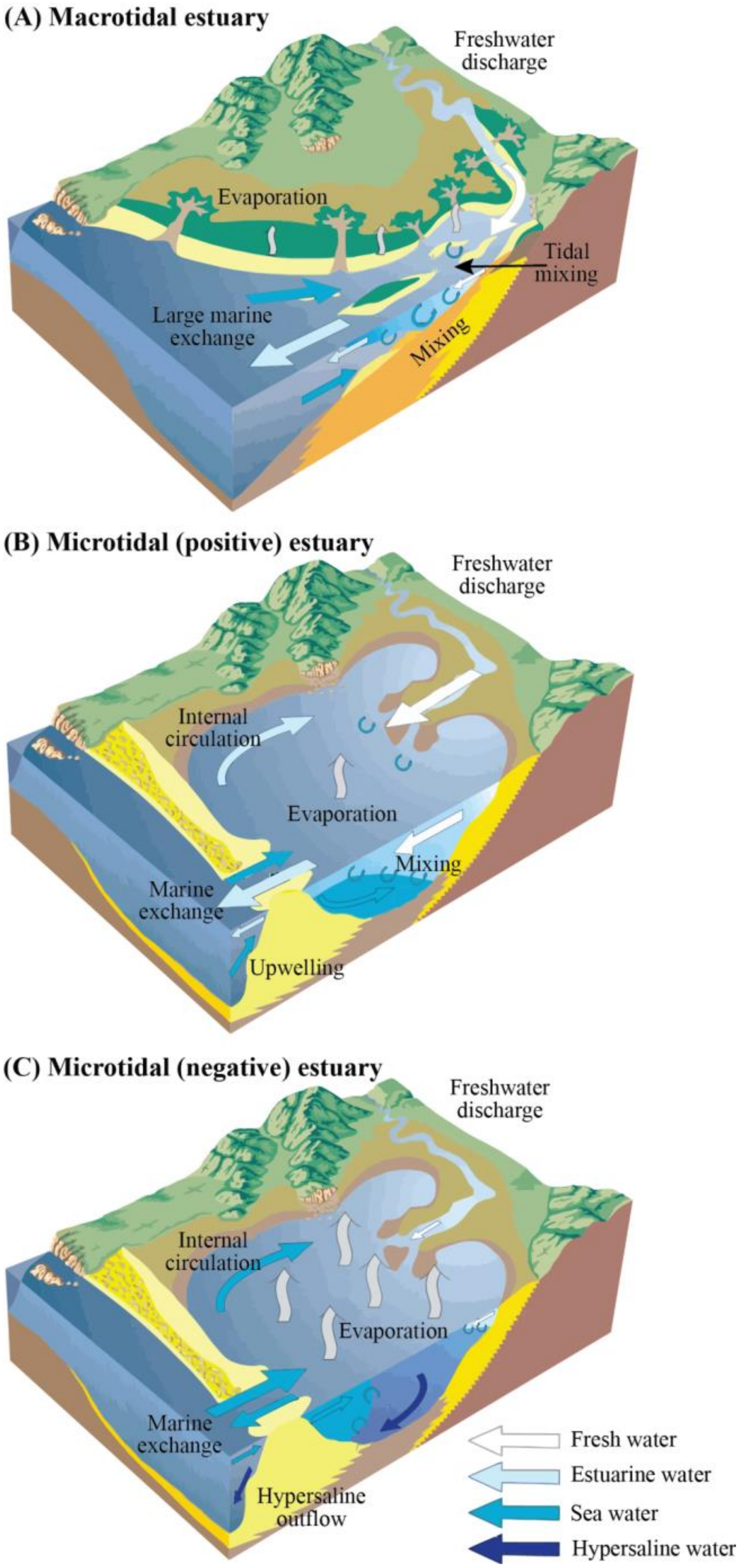

(A) Macrotidal estuary
Freshwater discharge
Evaporation
Tidal mixing
Large marine exchange
Mixing
(B) Microtidal (positive) estuary
Freshwater discharge
Internal circulation
Evaporation
Mixing
Marine exchange
Upwelling
(C) Microtidal (negative) estuary
Freshwater discharge
Internal circulation
Evaporation
Marine exchange
Hypersaline outflow
Fresh water
Estuarine water
Sea water
Hypersaline water

**Figure 4**

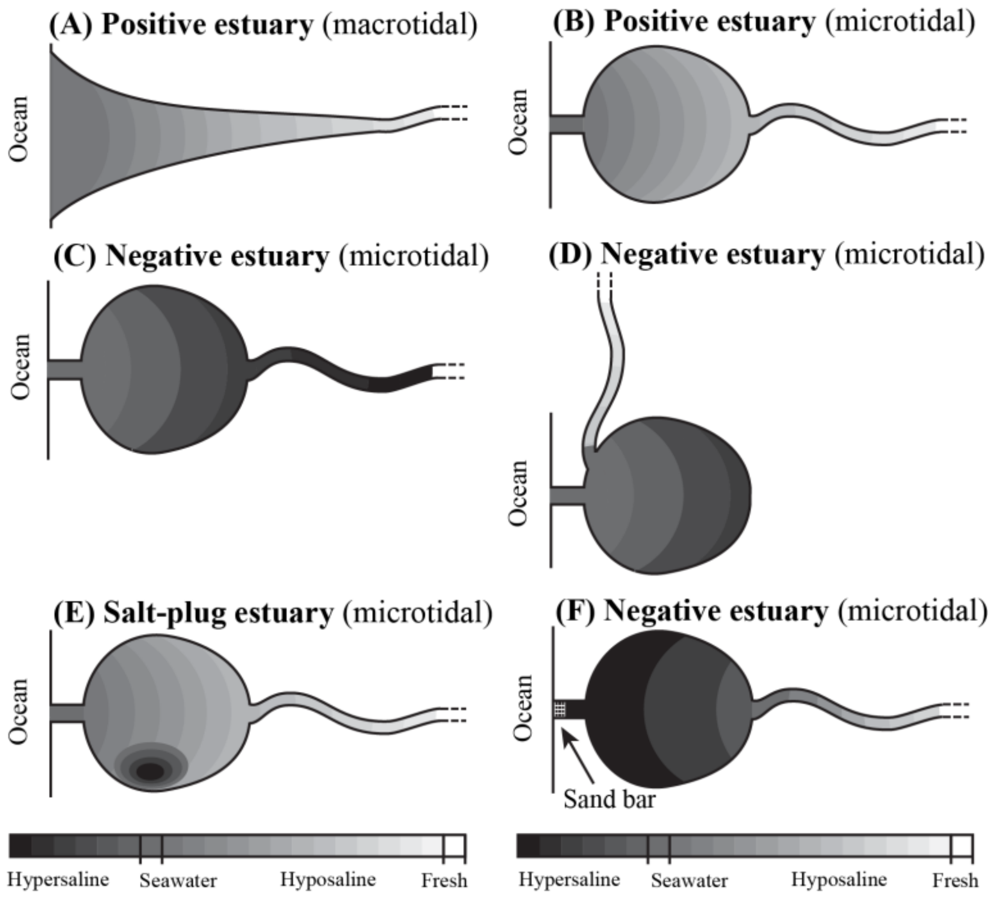

(A) Positive estuary (macrotidal)
(B) Positive estuary (microtidal)
(C) Negative estuary (microtidal)
(D) Negative estuary (microtidal)
(E) Salt-plug estuary (microtidal)
(F) Negative estuary (microtidal)
Ocean
Sand bar
Hypersaline
Seawater
Hyposaline
Fresh

**Figure 5**

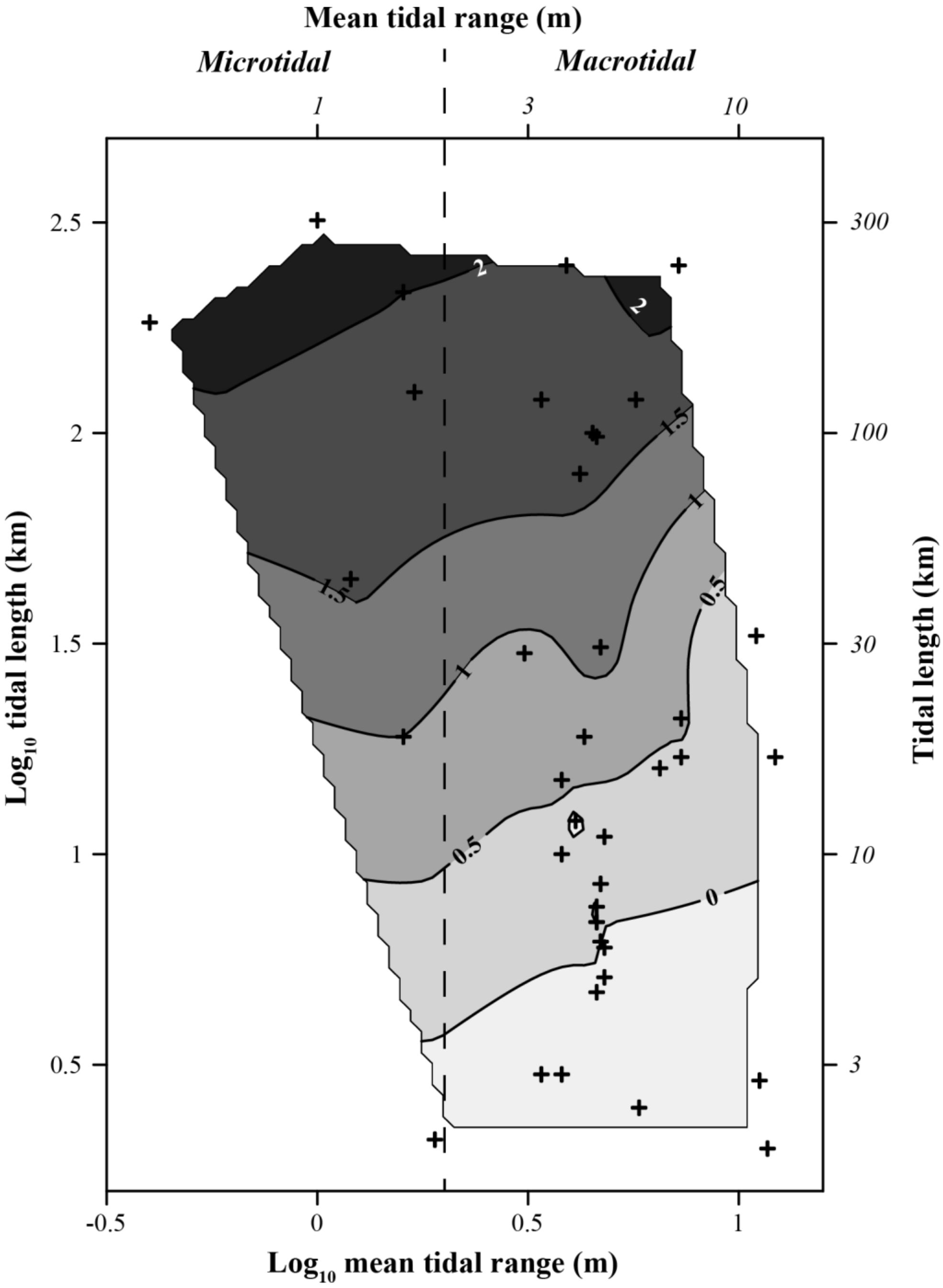

Mean tidal range (m)
Microtidal
Macrotidal
1
3
10
2.5
2
1.5
1
0.5
300
100
30
10
3
Log₁₀ tidal length (km)
Tidal length (km)
2
2
1.5
1.5
1
1
0.5
0.5
0
-0.5
0
0.5
1
Log₁₀ mean tidal range (m)

**Figure 6**

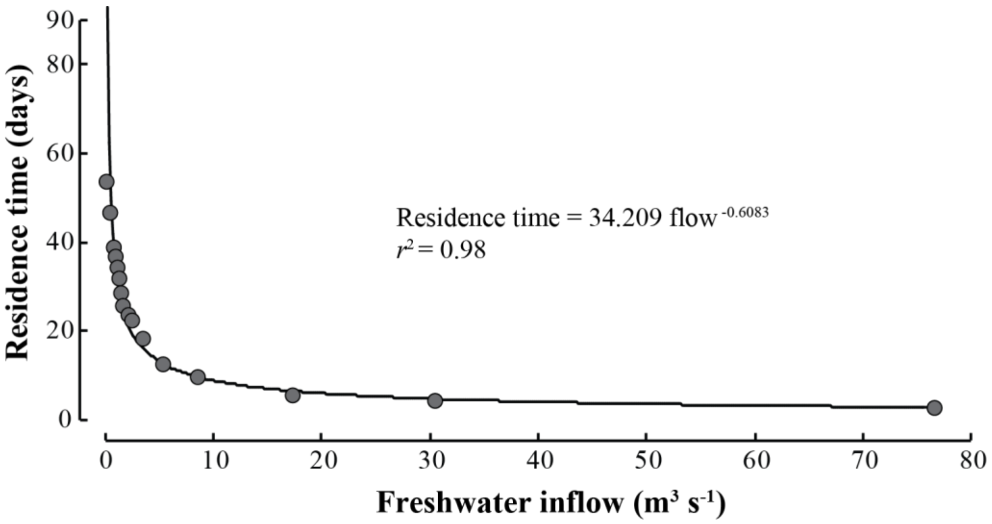

Residence time (days)
90
80
60
40
20
0
Residence time = 34.209 flow $^{-0.6083}$
$r^2 = 0.98$
0
10
20
30
40
50
60
70
80
Freshwater inflow ($m^3$ $s^{-1}$)

**Figure 7**

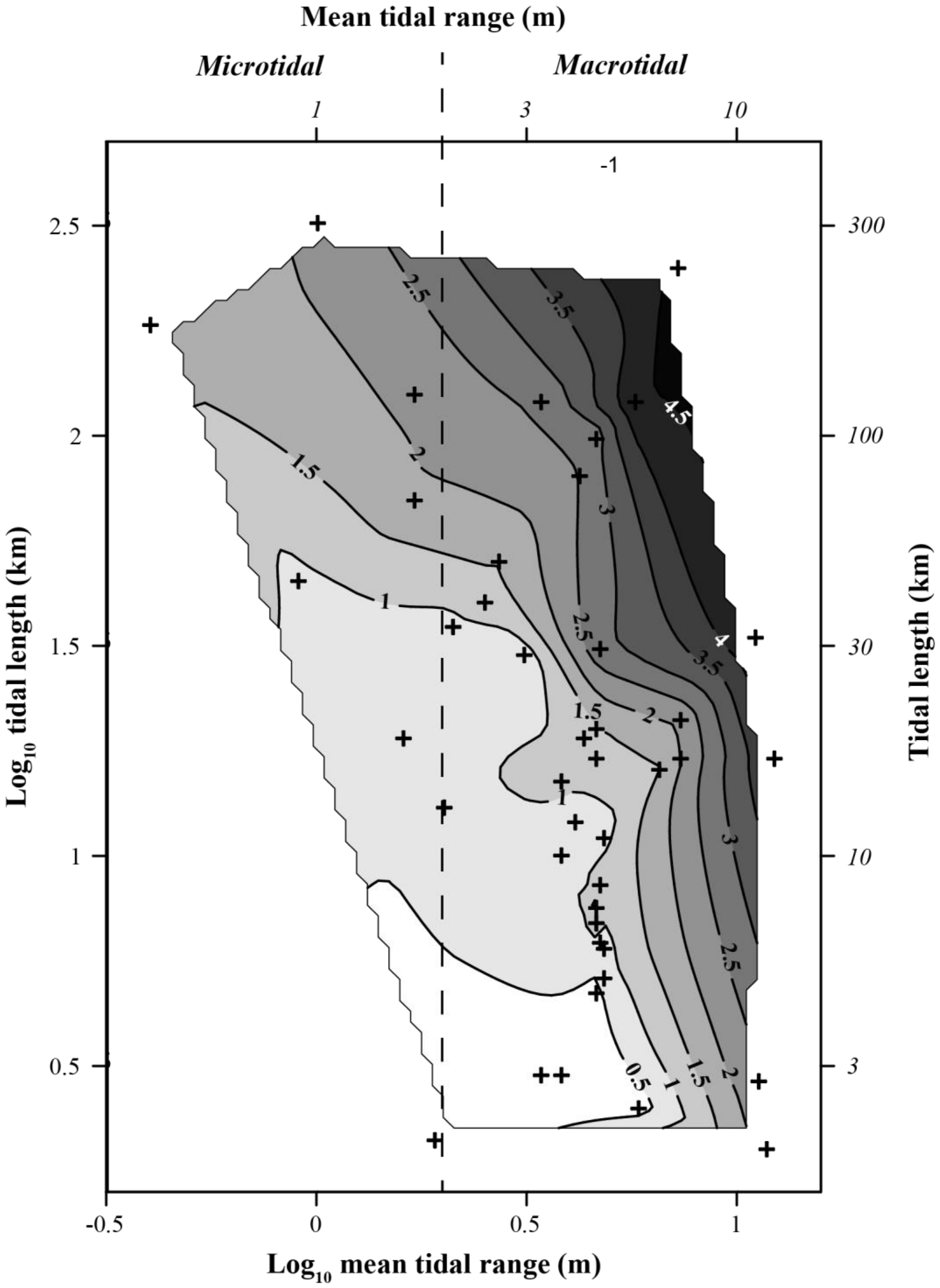
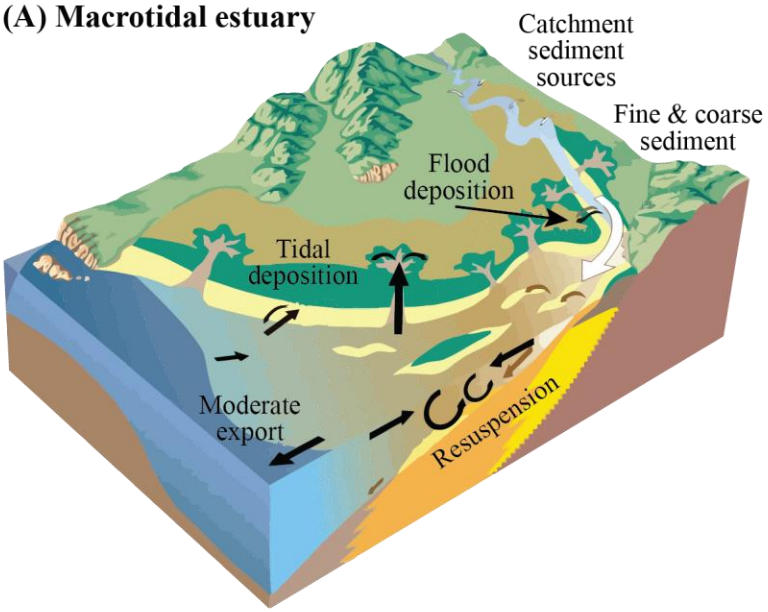

Mean tidal range (m)
Microtidal
Macrotidal
1
3
10
-1
2.5
3.5
4.5
2
1.5
3
1
2.5
4
3.5
1.5
2
1
3
2.5
0.5
1
1.5
2
Log10 tidal length (km)
Tidal length (km)
300
100
30
10
3
2.5
2
1.5
1
0.5
-0.5
0
0.5
1
Log10 mean tidal range (m)

Figure 8

**(A) Macrotidal estuary**



**(B) Microtidal estuary**

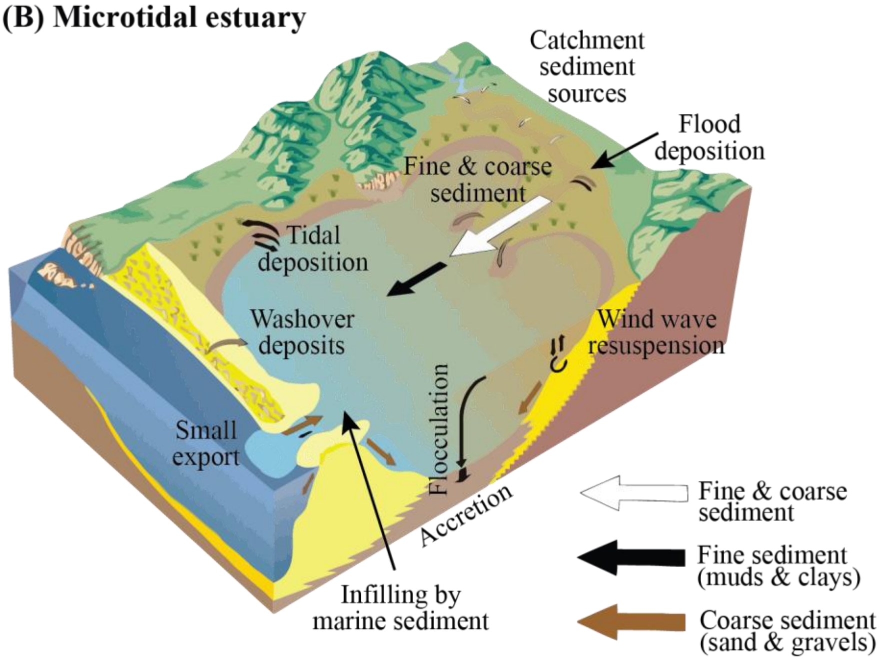


**Figure 9**

**Figure 10**

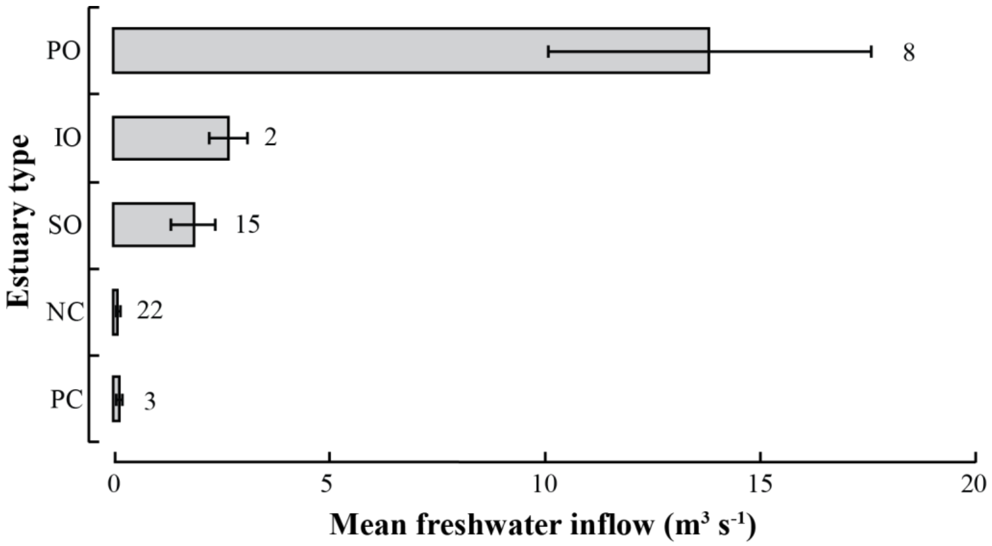

Estuary type
PO
IO
SO
NC
PC
8
2
15
22
3
0
5
10
15
20
Mean freshwater inflow (m³ s⁻¹)

Figure 11

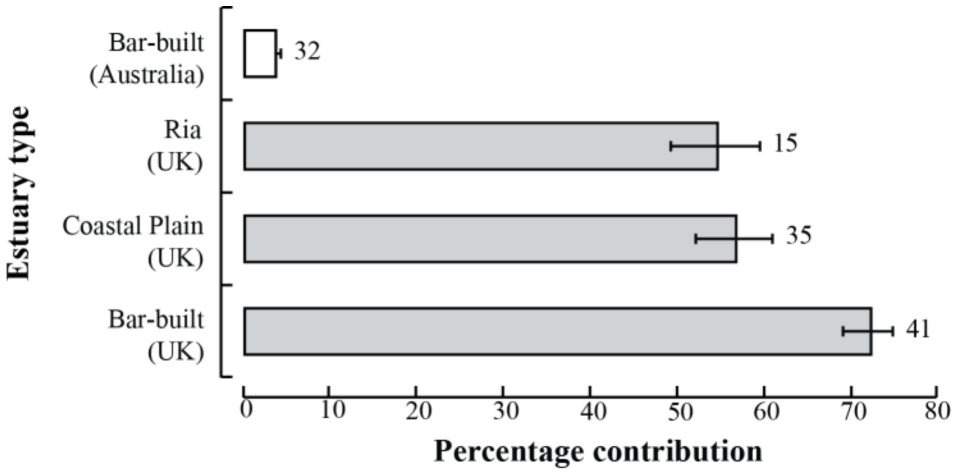

Estuary type
Bar-built (Australia)
Ria (UK)
Coastal Plain (UK)
Bar-built (UK)
32
15
35
41
0
10
20
30
40
50
60
70
80
Percentage contribution

**Figure 12**

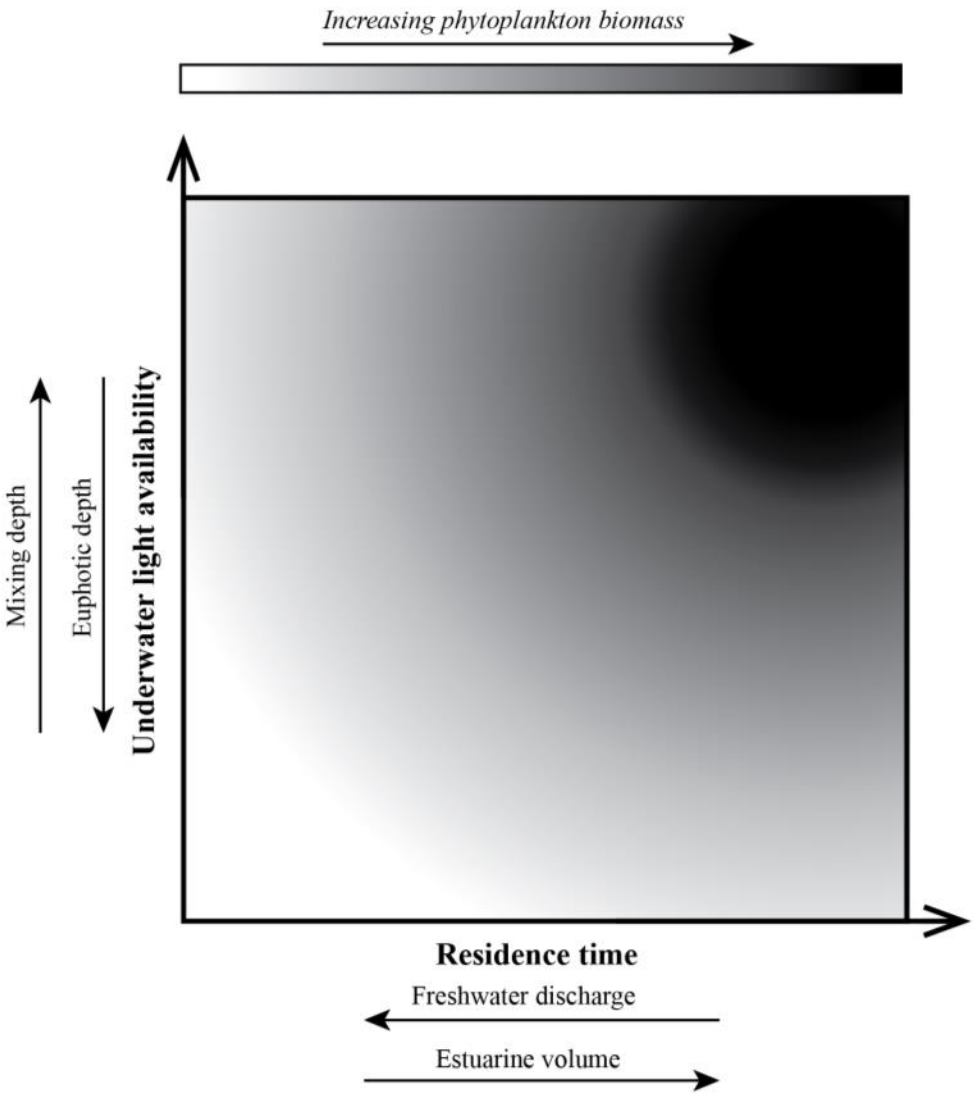

Increasing phytoplankton biomass
Mixing depth
Euphotic depth
Underwater light availability
Residence time
Freshwater discharge
Estuarine volume

**Figure 13**

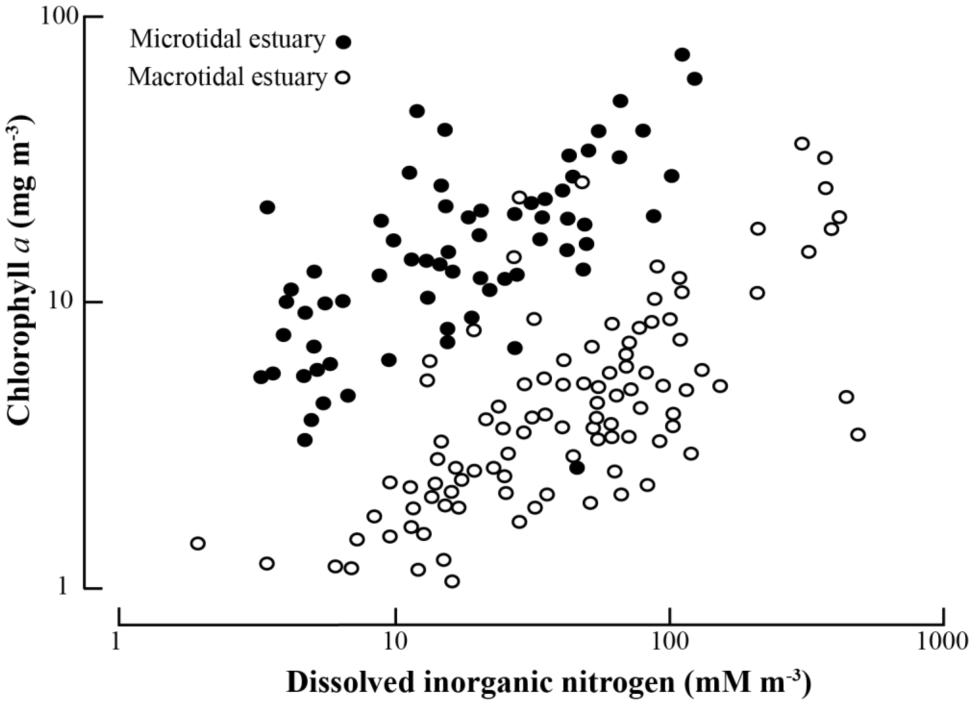

100
10
1
Chlorophyll a (mg m-3)
Microtidal estuary ●
Macrotidal estuary ○
1
10
100
1000
Dissolved inorganic nitrogen (mM m-3)

**Figure 14**

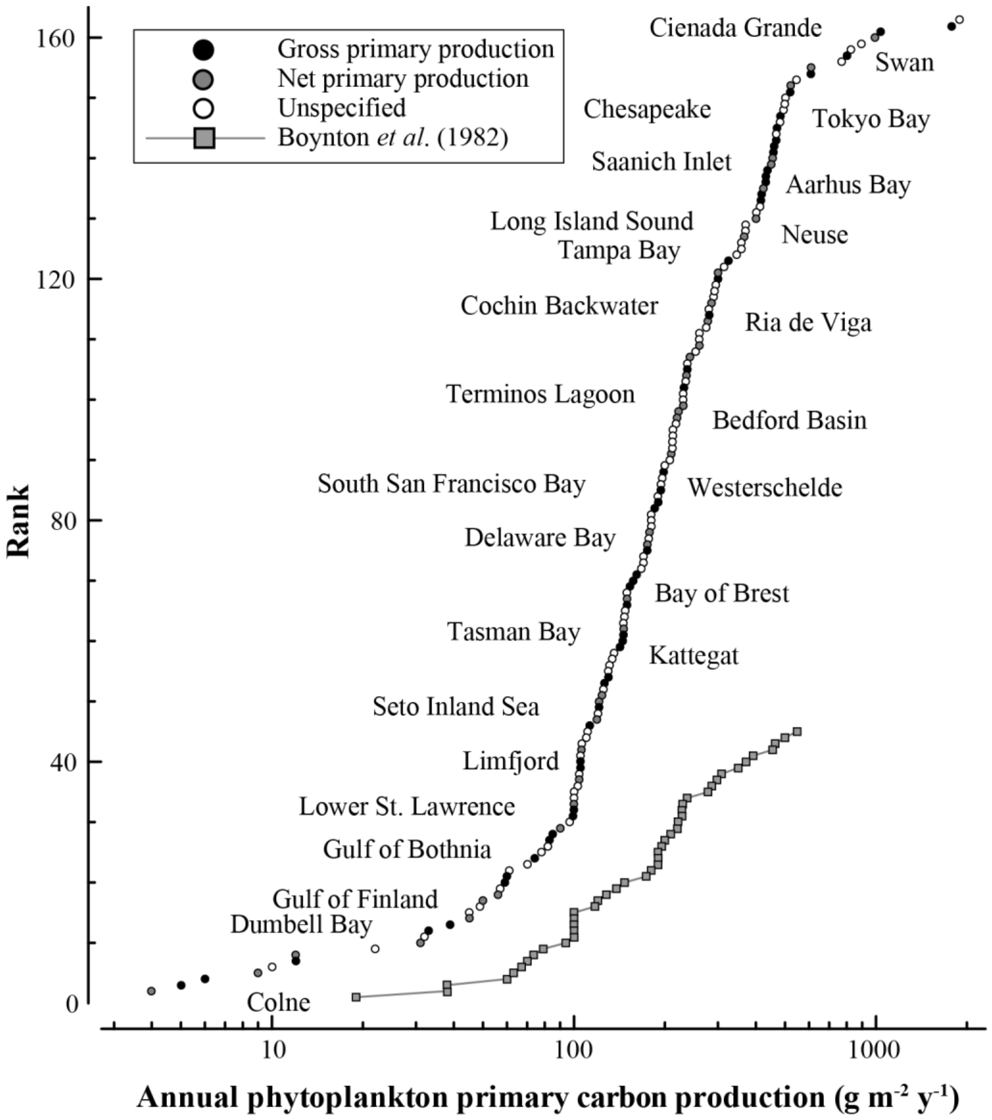

Gross primary production
Net primary production
Unspecified
Boynton et al. (1982)
Cienada Grande
Swan
Chesapeake
Tokyo Bay
Saanich Inlet
Aarhus Bay
Long Island Sound
Tampa Bay
Neuse
Cochin Backwater
Ria de Viga
Terminos Lagoon
Bedford Basin
South San Francisco Bay
Westerschelde
Delaware Bay
Bay of Brest
Tasman Bay
Kattegat
Seto Inland Sea
Limfjord
Lower St. Lawrence
Gulf of Bothnia
Gulf of Finland
Dumbell Bay
Colne
Rank
0
40
80
120
160
10
100
1000
Annual phytoplankton primary carbon production (g m-2 y-1)

**Figure 15**

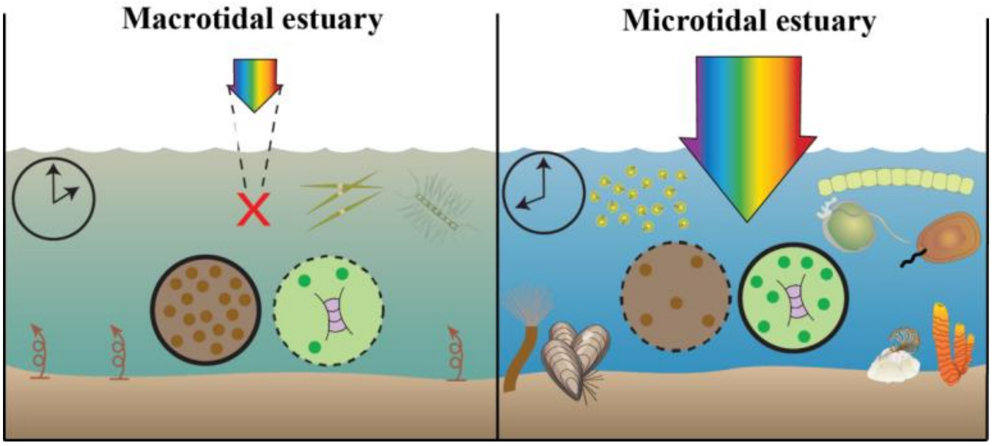


Figure 16

**Figure 17**

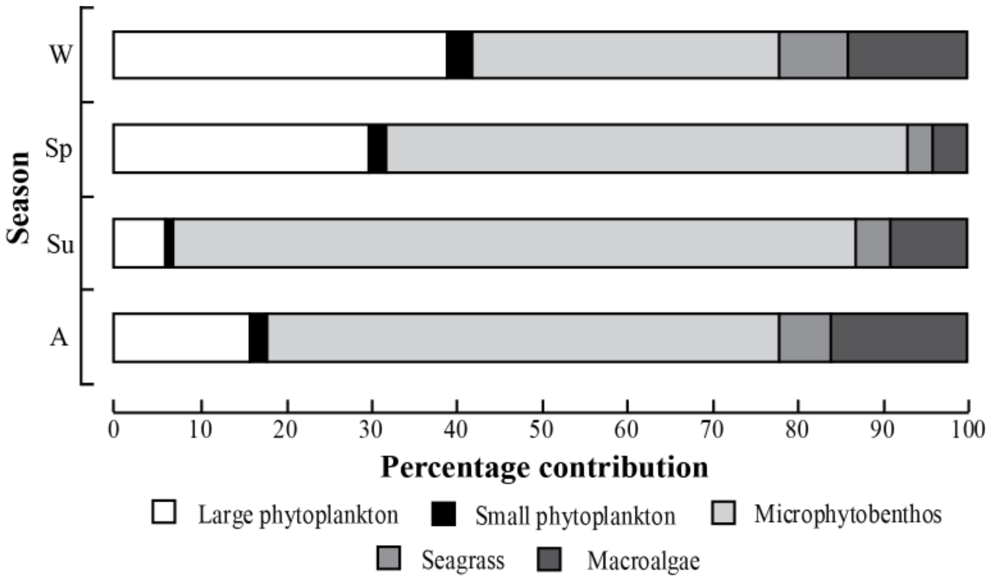

Season
W
Sp
Su
A
0
10
20
30
40
50
60
70
80
90
100
Percentage contribution
Large phytoplankton
Small phytoplankton
Microphytobenthos
Seagrass
Macroalgae

Figure 18

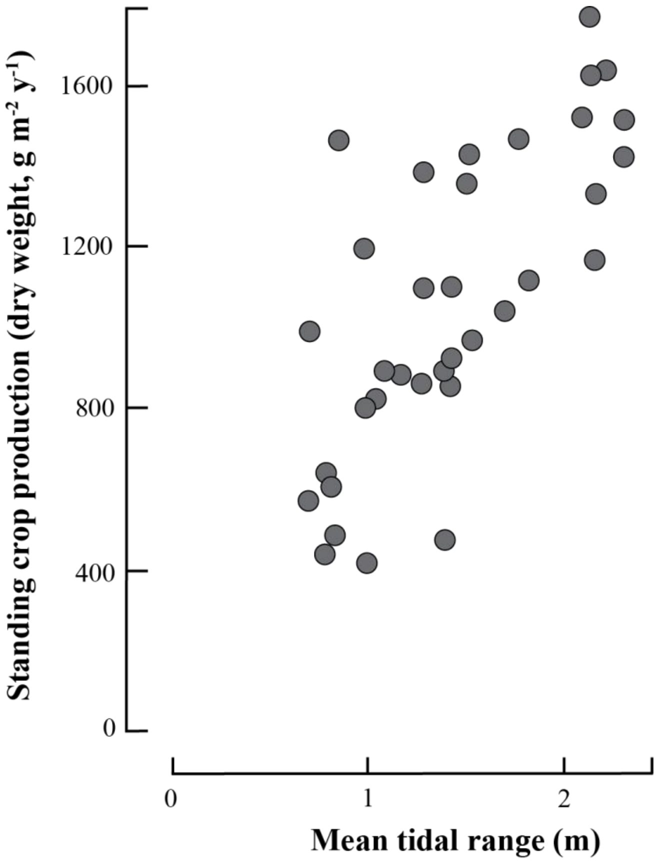

Standing crop production (dry weight, g m-2 y-1)
1600
1200
800
400
0
0
1
2
Mean tidal range (m)

Figure 19

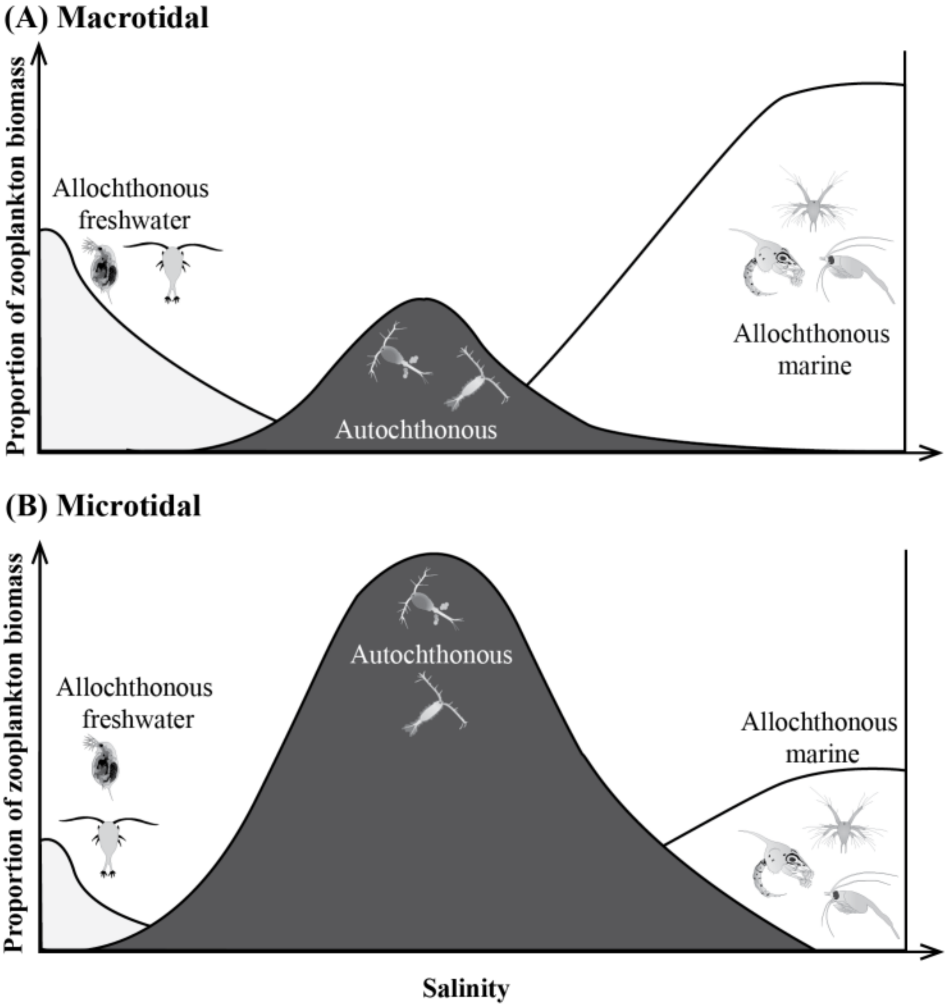

(A) Macrotidal
Proportion of zooplankton biomass
Allochthonous freshwater
Autochthonous
Allochthonous marine
(B) Microtidal
Proportion of zooplankton biomass
Allochthonous freshwater
Autochthonous
Allochthonous marine
Salinity

**Figure 20**


(A)
1-4
5-9
10-14
15-19
Google earth
4km
N
(B)
0
1
2
3
4
5
6
7
8
9
10
11
12
Google earth
9km
N

Figure 21

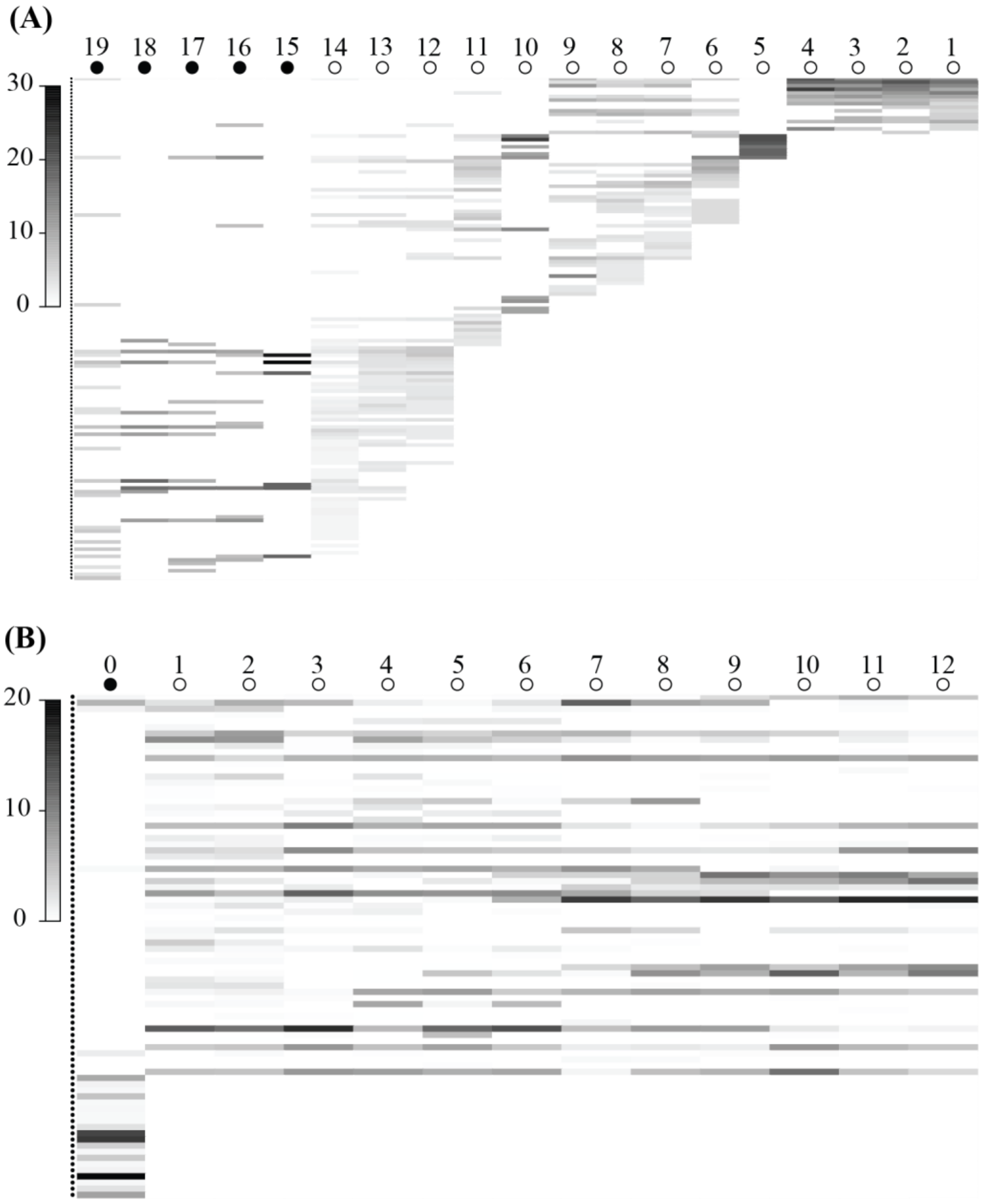

(A)
19
18
17
16
15
14
13
12
11
10
9
8
7
6
5
4
3
2
1
30
20
10
0
(B)
0
1
2
3
4
5
6
7
8
9
10
11
12
20
10
0

**Figure 22**

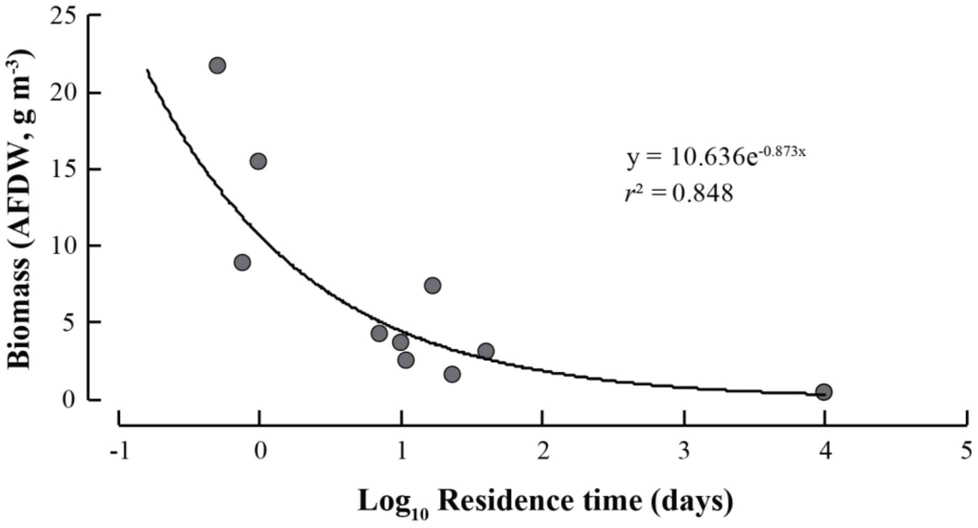
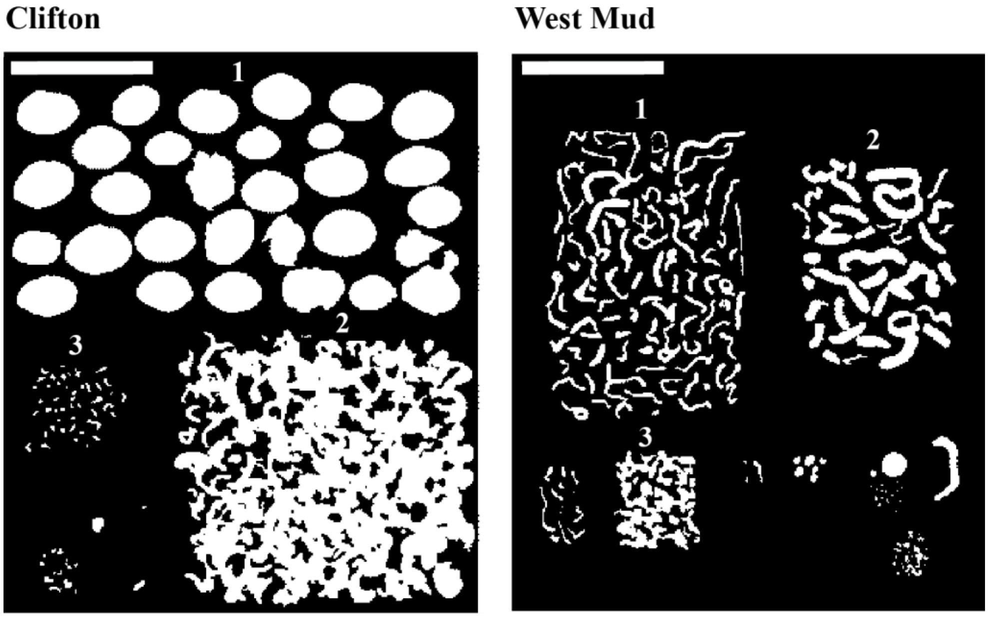

Biomass (AFDW, g m$^{-3}$)
25
20
15
10
5
0
y = 10.636e$^{-0.873x}$
$r^2$ = 0.848
-1
0
1
2
3
4
5
Log$_{10}$ Residence time (days)

**Figure 23**



**Clifton**

1) *Scrobicularia plana*
2) *Hediste (=Nereis) diversicolor*
3) *Corophium volutator*

**West Mud**

1) *Nephtys hombergi*
2) *Nereis diversicolor*
3) *Ampharete acutifrons*

**Figure 24**

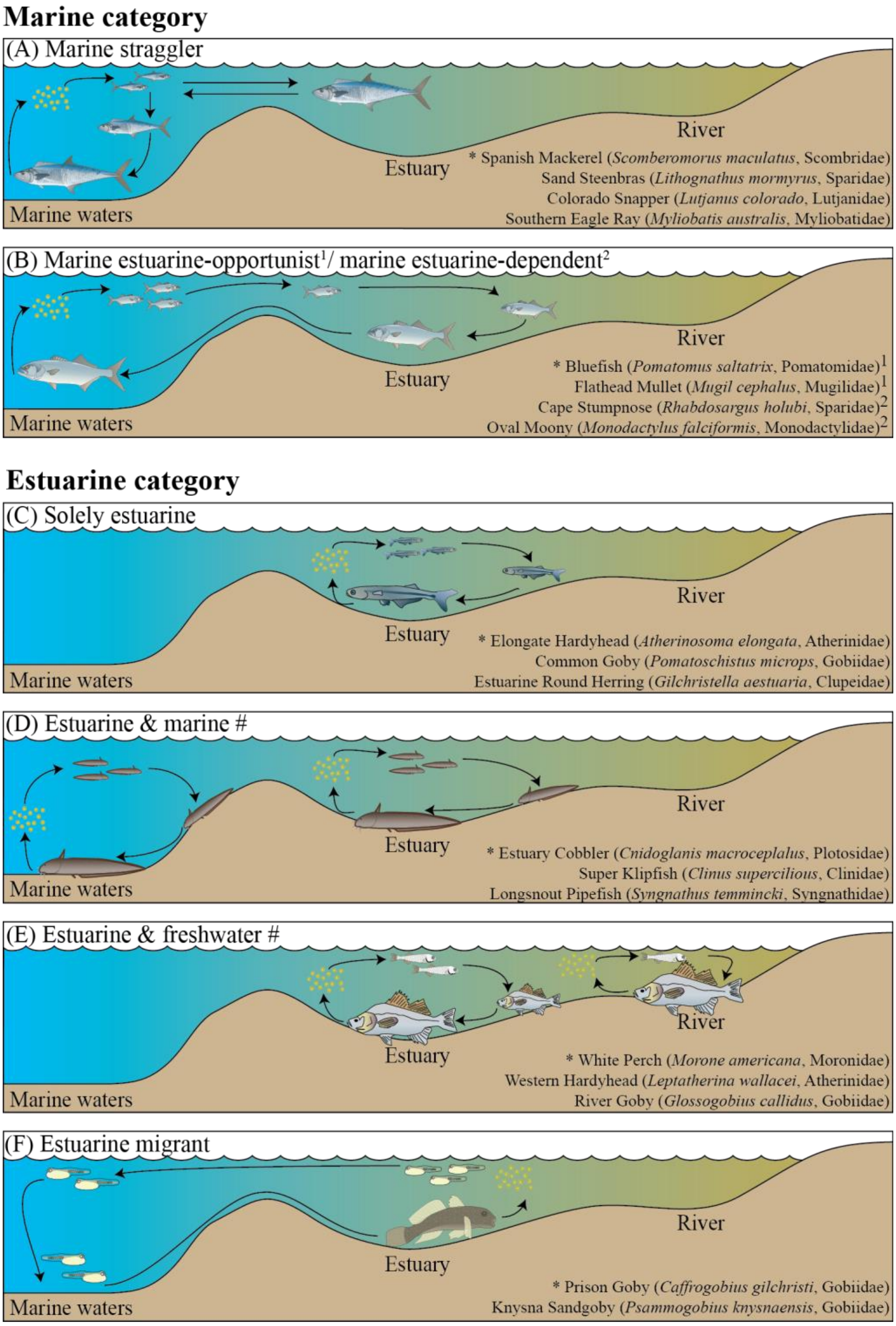

Marine category
(A) Marine straggler
River
Estuary
Marine waters
* Spanish Mackerel (*Scomberomorus maculatus*, Scombridae)
Sand Steenbras (*Lithognathus mormyrus*, Sparidae)
Colorado Snapper (*Lutjanus colorado*, Lutjanidae)
Southern Eagle Ray (*Myliobatis australis*, Myliobatidae)
(B) Marine estuarine-opportunist$^1$/ marine estuarine-dependent$^2$
River
Estuary
Marine waters
* Bluefish (*Pomatomus saltatrix*, Pomatomidae)$^1$
Flathead Mullet (*Mugil cephalus*, Mugilidae)$^1$
Cape Stumpnose (*Rhabdosargus holubi*, Sparidae)$^2$
Oval Moony (*Monodactylus falciformis*, Monodactylidae)$^2$
Estuarine category
(C) Solely estuarine
River
Estuary
Marine waters
* Elongate Hardyhead (*Atherinosoma elongata*, Atherinidae)
Common Goby (*Pomatoschistus microps*, Gobiidae)
Estuarine Round Herring (*Gilchristella aestuaria*, Clupeidae)
(D) Estuarine & marine #
River
Estuary
Marine waters
* Estuary Cobbler (*Cnidoglanis macroceplalus*, Plotosidae)
Super Klipfish (*Clinus supercilious*, Clinidae)
Longsnout Pipefish (*Syngnathus temmincki*, Syngnathidae)
(E) Estuarine & freshwater #
River
Estuary
Marine waters
* White Perch (*Morone americana*, Moronidae)
Western Hardyhead (*Leptatherina wallacei*, Atherinidae)
River Goby (*Glossogobius callidus*, Gobiidae)
(F) Estuarine migrant
River
Estuary
Marine waters
* Prison Goby (*Caffrogobius gilchristi*, Gobiidae)
Knysna Sandgoby (*Psammogobius knysnaensis*, Gobiidae)

**Figure 25**

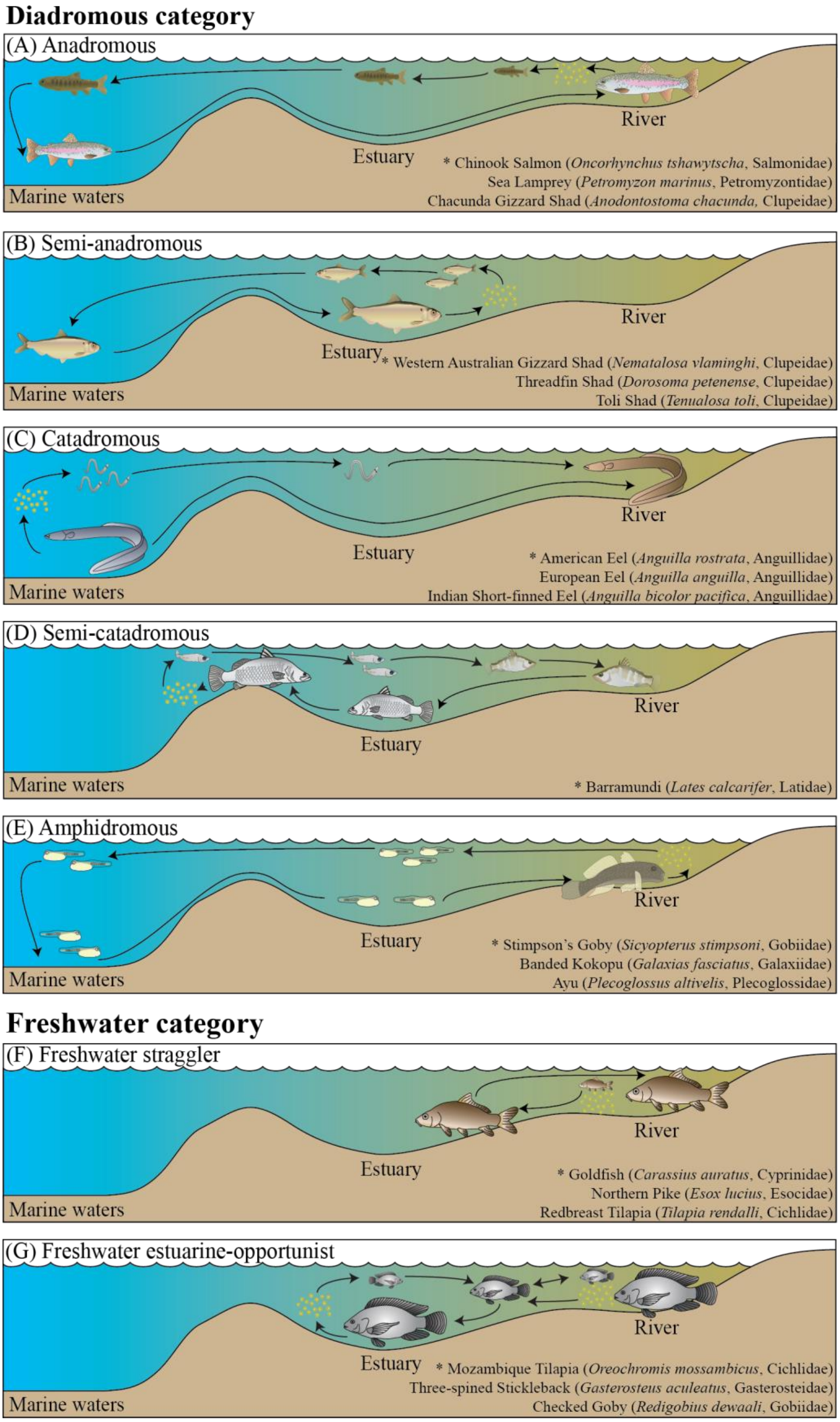

Diadromous category
(A) Anadromous
River
Estuary
Marine waters
* Chinook Salmon (*Oncorhynchus tshawytscha*, Salmonidae)
Sea Lamprey (*Petromyzon marinus*, Petromyzontidae)
Chacunda Gizzard Shad (*Anodontostoma chacunda*, Clupeidae)
(B) Semi-anadromous
River
Estuary
Marine waters
* Western Australian Gizzard Shad (*Nematalosa vlaminghi*, Clupeidae)
Threadfin Shad (*Dorosoma petenense*, Clupeidae)
Toli Shad (*Tenualosa toli*, Clupeidae)
(C) Catadromous
River
Estuary
Marine waters
* American Eel (*Anguilla rostrata*, Anguillidae)
European Eel (*Anguilla anguilla*, Anguillidae)
Indian Short-finned Eel (*Anguilla bicolor pacifica*, Anguillidae)
(D) Semi-catadromous
River
Estuary
Marine waters
* Barramundi (*Lates calcarifer*, Latidae)
(E) Amphidromous
River
Estuary
Marine waters
* Stimpson's Goby (*Sicyopterus stimpsoni*, Gobiidae)
Banded Kokopu (*Galaxias fasciatus*, Galaxiidae)
Ayu (*Plecoglossus altivelis*, Plecoglossidae)
Freshwater category
(F) Freshwater straggler
River
Estuary
Marine waters
* Goldfish (*Carassius auratus*, Cyprinidae)
Northern Pike (*Esox lucius*, Esocidae)
Redbreast Tilapia (*Tilapia rendalli*, Cichlidae)
(G) Freshwater estuarine-opportunist
River
Estuary
Marine waters
* Mozambique Tilapia (*Oreochromis mossambicus*, Cichlidae)
Three-spined Stickleback (*Gasterosteus aculeatus*, Gasterosteidae)
Checked Goby (*Redigobius dewaali*, Gobiidae)

**Figure 26**

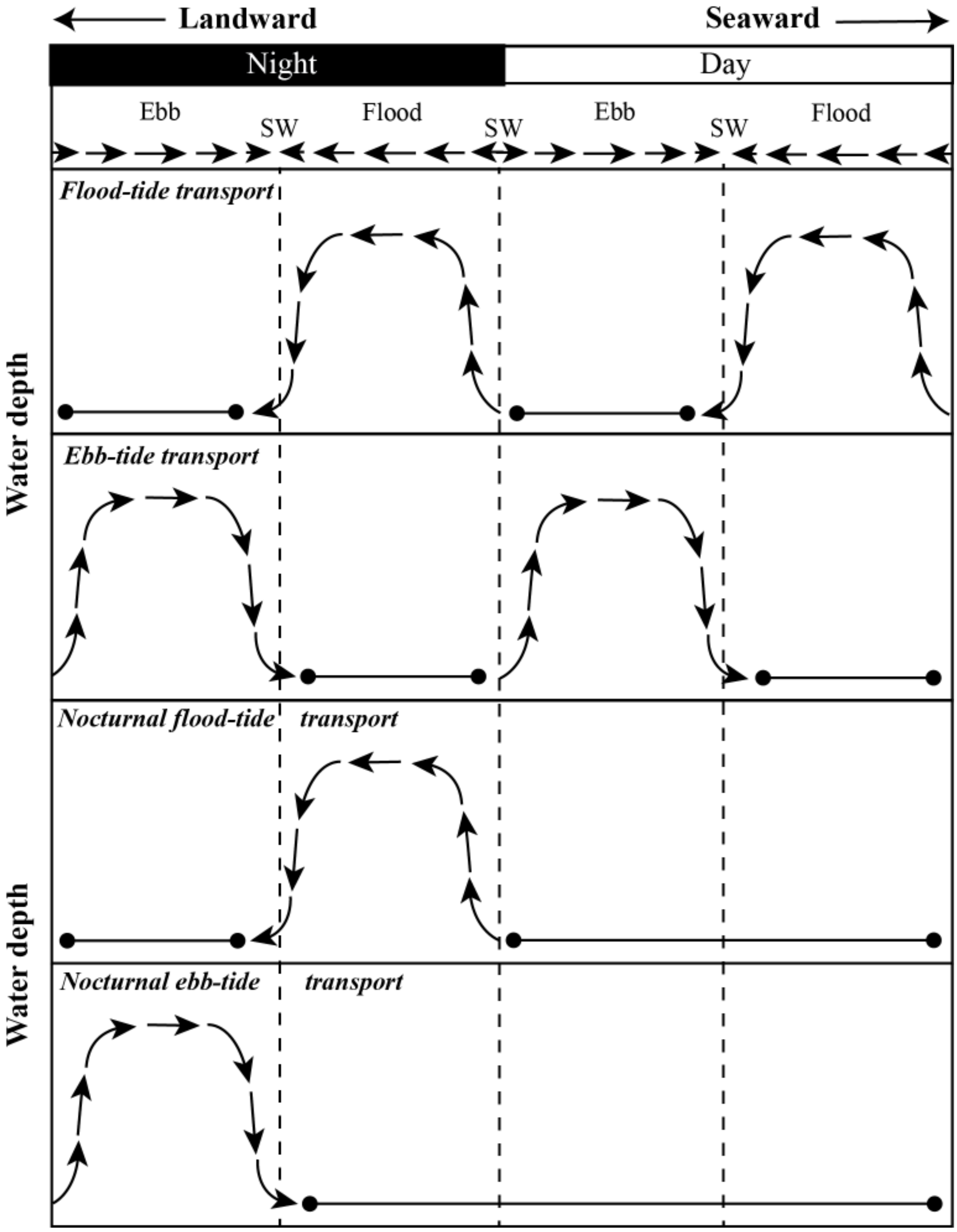

Landward
Seaward
Night
Day
Ebb
SW
Flood
SW
Ebb
SW
Flood
Flood-tide transport
Ebb-tide transport
Nocturnal flood-tide transport
Nocturnal ebb-tide transport
Water depth
Water depth

Figure 27

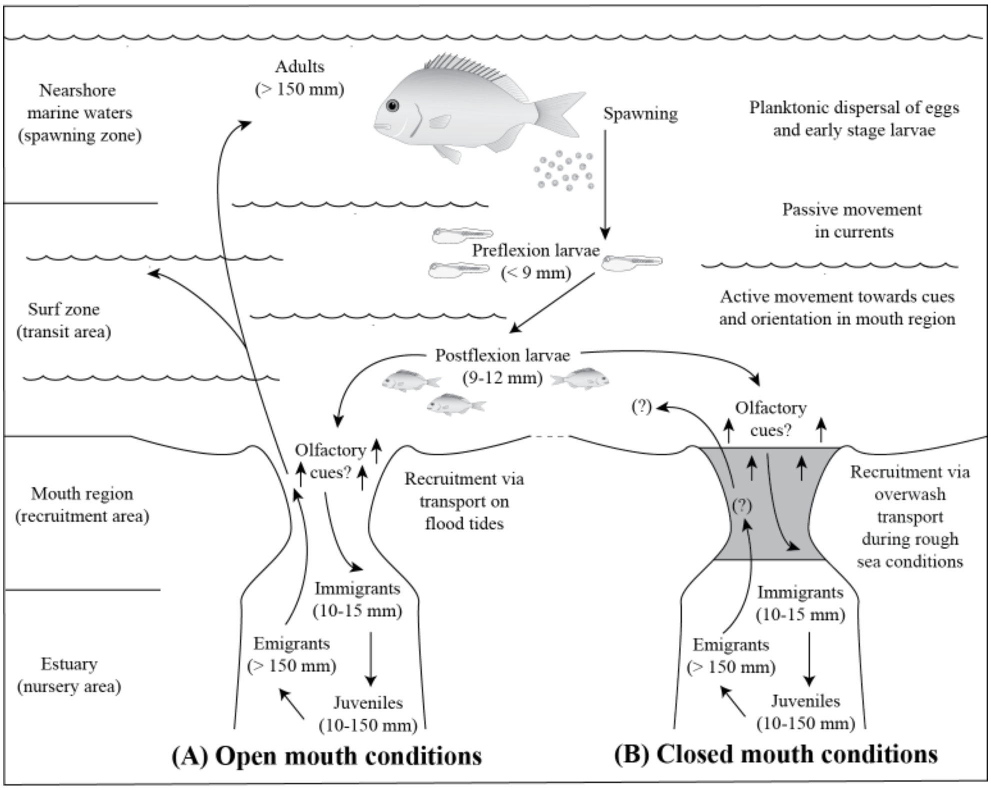

Nearshore marine waters (spawning zone)
Adults (> 150 mm)
Spawning
Planktonic dispersal of eggs and early stage larvae
Passive movement in currents
Preflexion larvae (< 9 mm)
Surf zone (transit area)
Active movement towards cues and orientation in mouth region
Postflexion larvae (9-12 mm)
(?)
Olfactory cues?
Mouth region (recruitment area)
Olfactory cues?
Recruitment via transport on flood tides
(?)
Recruitment via overwash transport during rough sea conditions
Immigrants (10-15 mm)
Immigrants (10-15 mm)
Estuary (nursery area)
Emigrants (> 150 mm)
Juveniles (10-150 mm)
Emigrants (> 150 mm)
Juveniles (10-150 mm)
(A) Open mouth conditions
(B) Closed mouth conditions

**Figure 28**

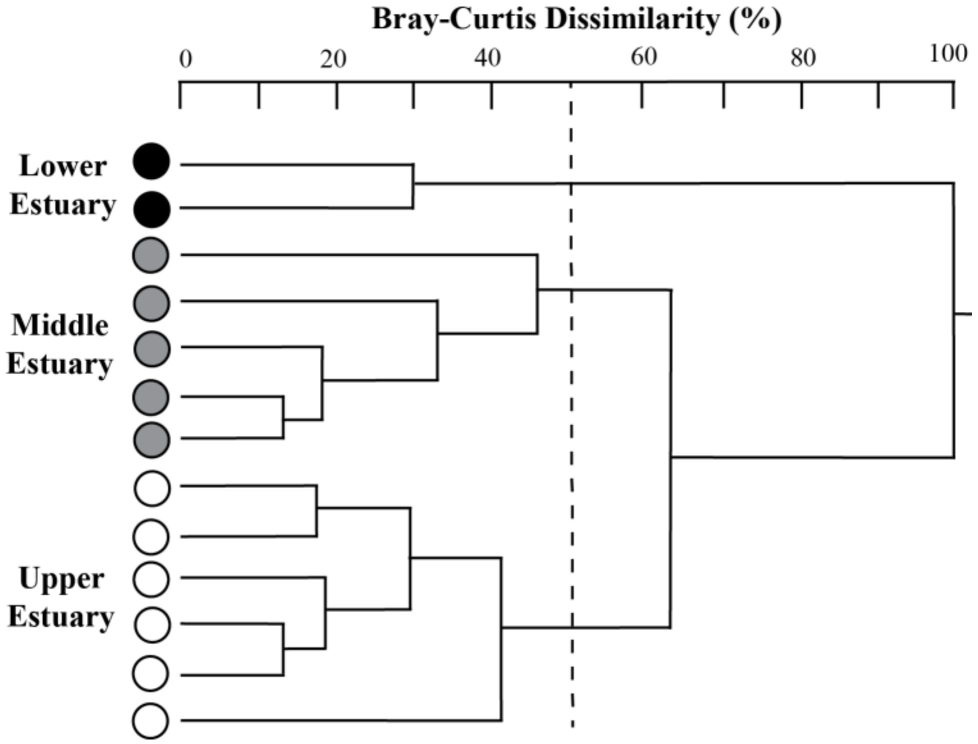
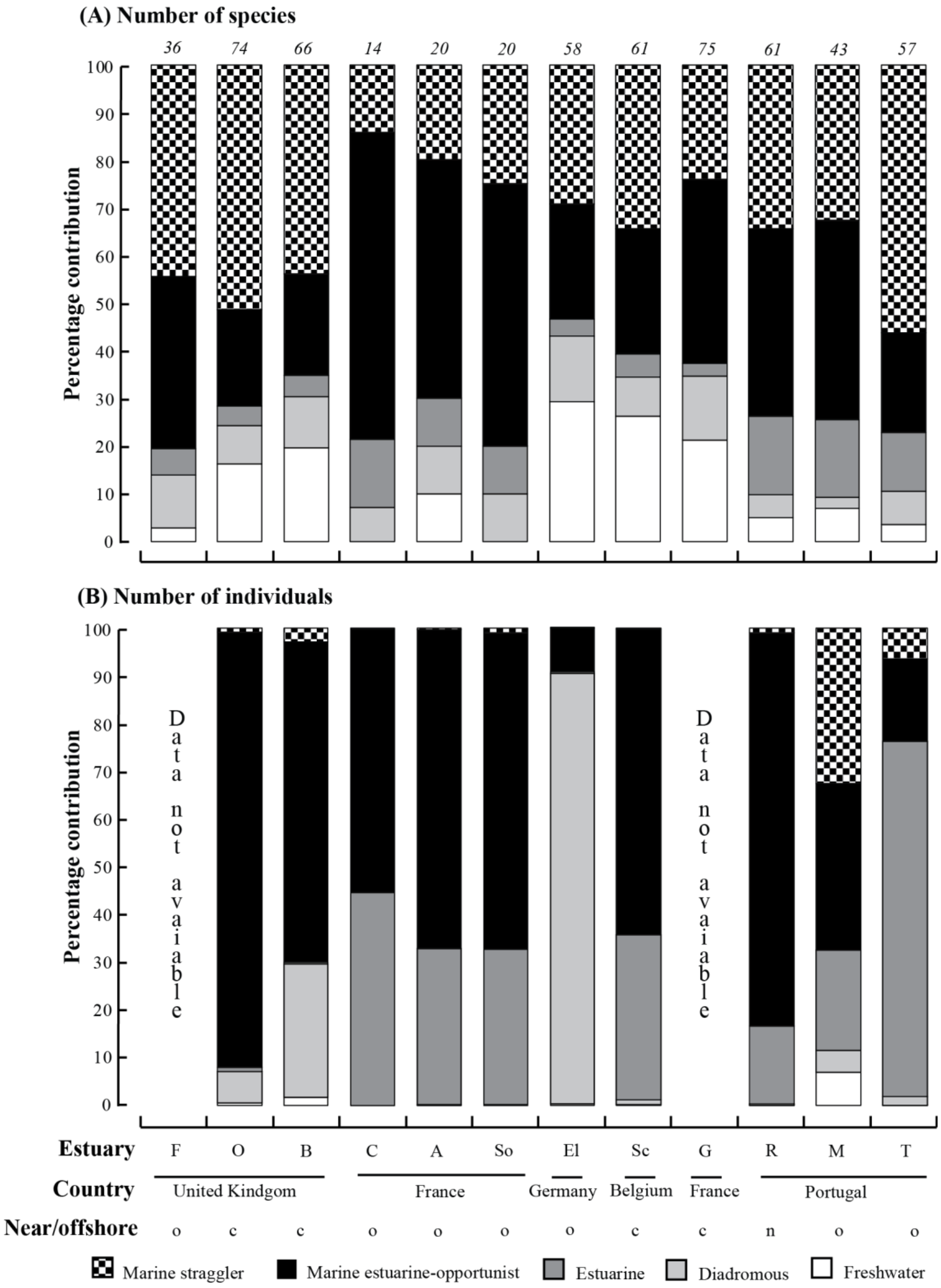

Bray-Curtis Dissimilarity (%)
0
20
40
60
80
100
Lower Estuary
Middle Estuary
Upper Estuary

**Figure 29**


(A) Number of species

(B) Number of individuals

**Figure 30**

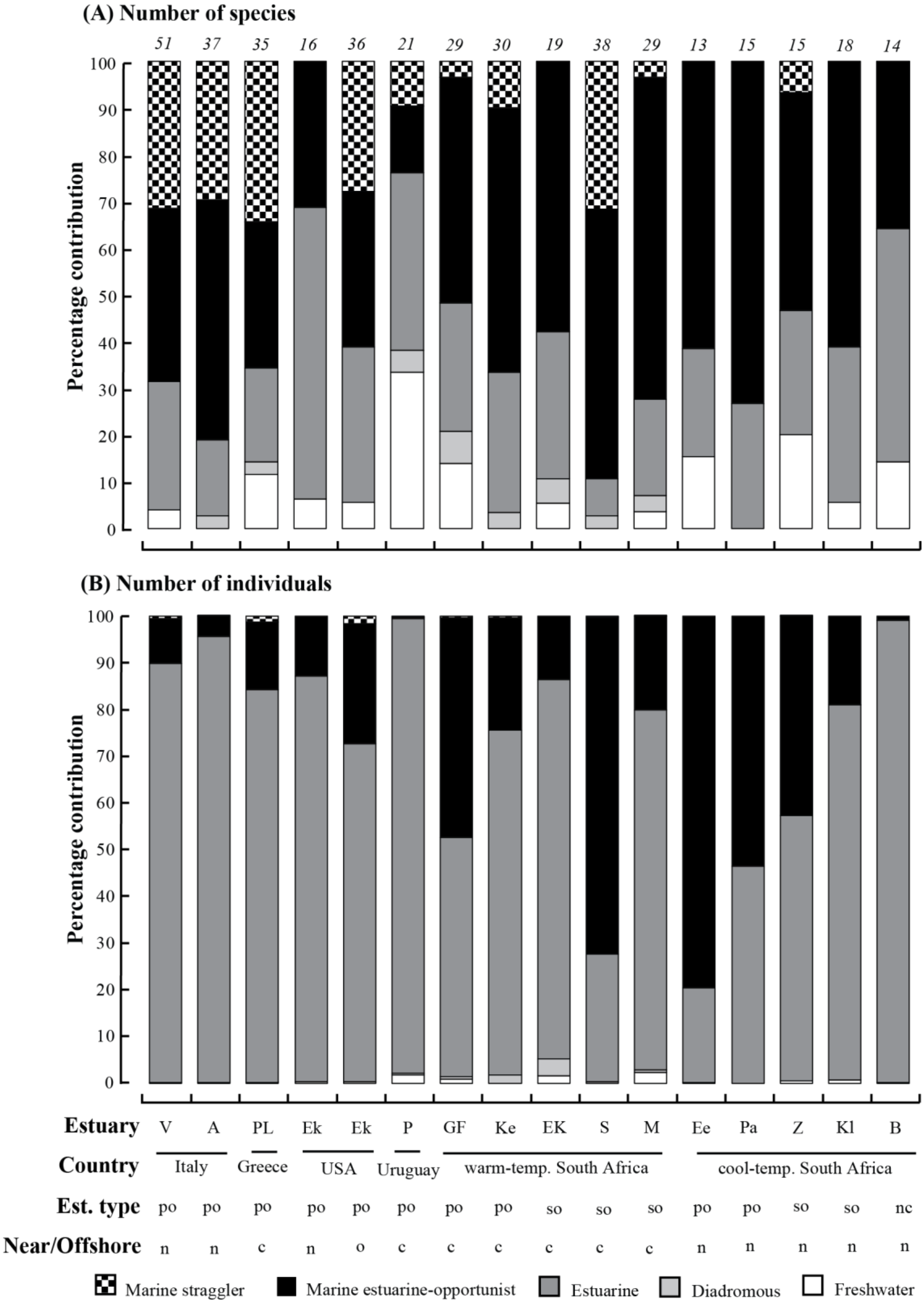
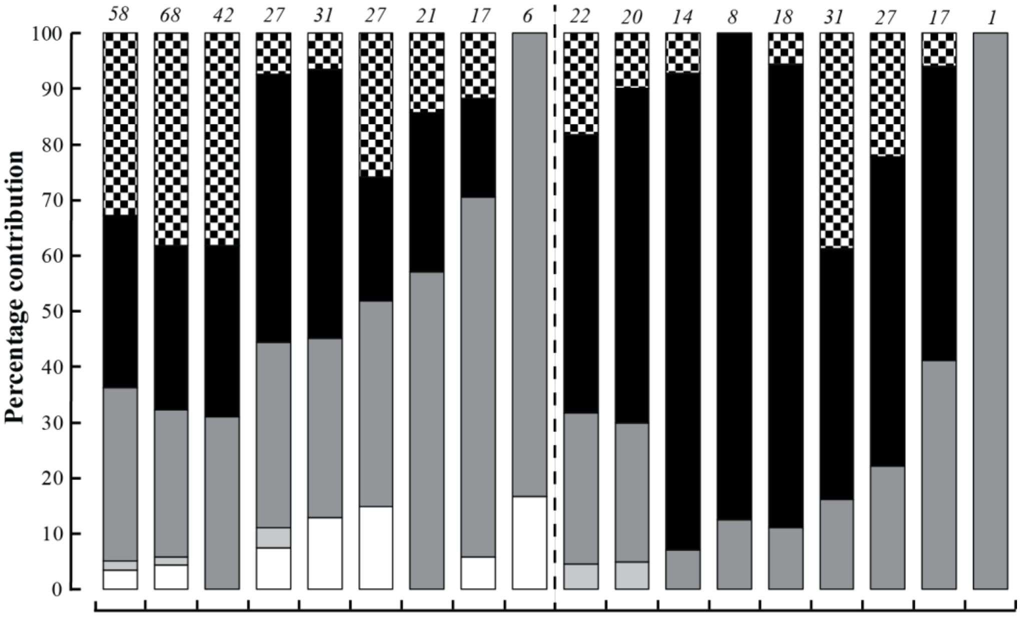

(A) Number of species
51 37 35 16 36 21 29 30 19 38 29 13 15 15 18 14
Percentage contribution
0 10 20 30 40 50 60 70 80 90 100
(B) Number of individuals
Percentage contribution
0 10 20 30 40 50 60 70 80 90 100
Estuary V A PL Ek Ek P GF Ke EK S M Ee Pa Z Kl B
Country Italy Greece USA Uruguay warm-temp. South Africa cool-temp. South Africa
Est. type po po po po po po po po so so so po po so so nc
Near/Offshore n n c n o c c c c c c n n n n n
Marine straggler
Marine estuarine-opportunist
Estuarine
Diadromous
Freshwater

Figure 31

(A) Number of species



(B) Number of individuals

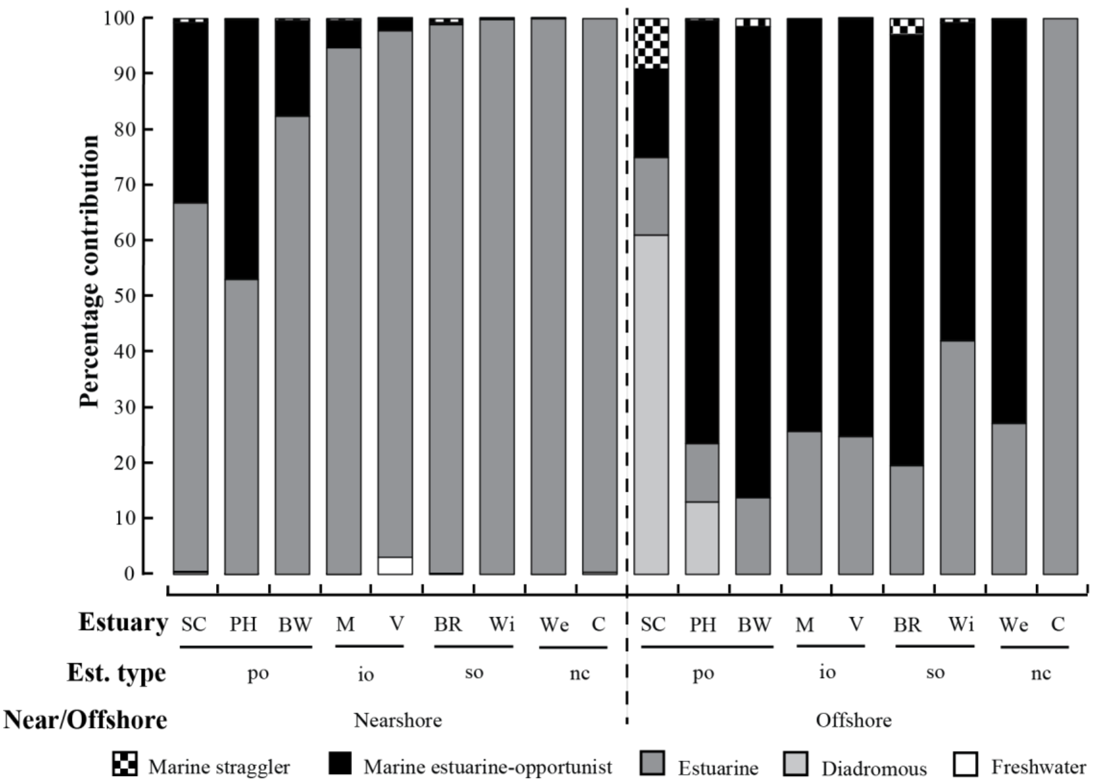


Figure 32

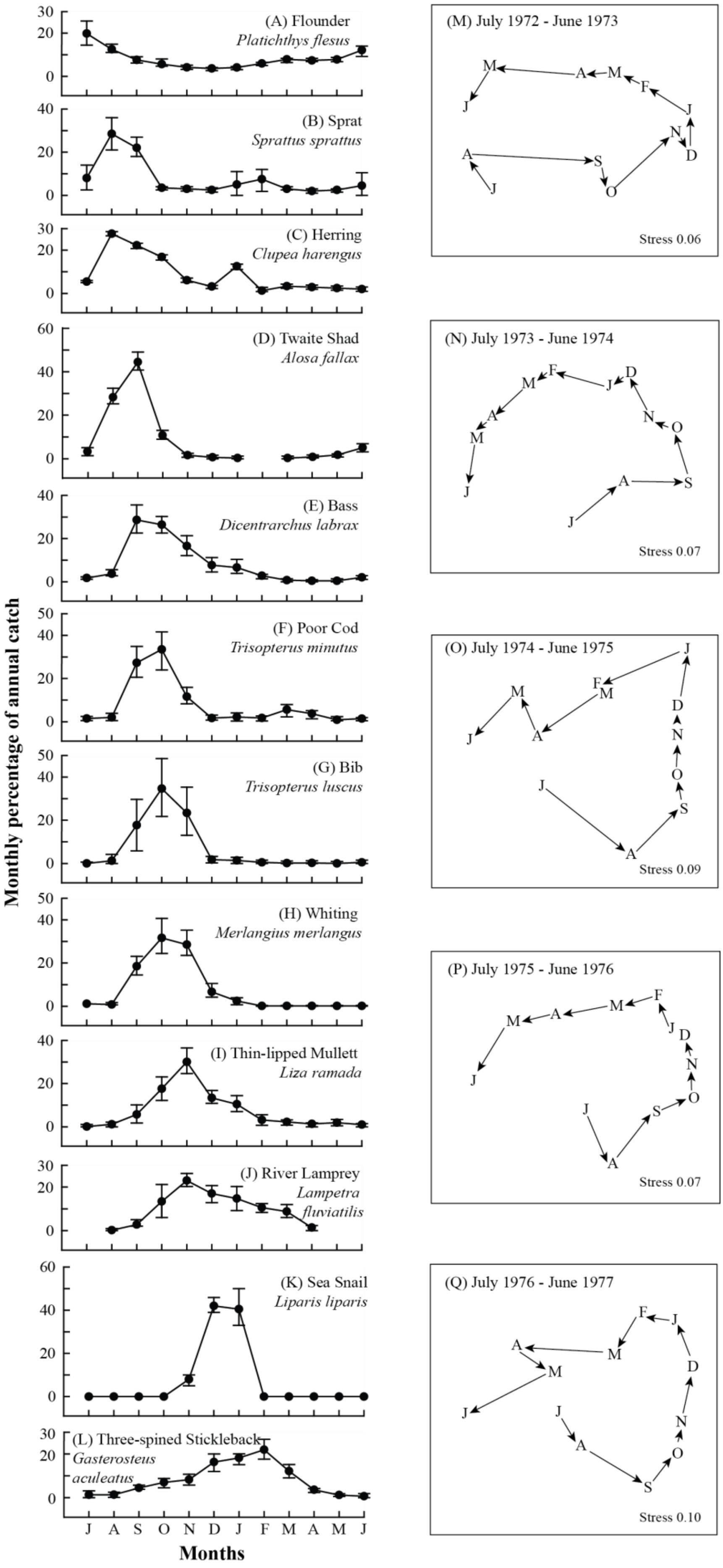

(A) Flounder
Platichthys flesus
(B) Sprat
Sprattus sprattus
(C) Herring
Clupea harengus
(D) Twaite Shad
Alosa fallax
(E) Bass
Dicentrarchus labrax
(F) Poor Cod
Trisopterus minutus
(G) Bib
Trisopterus luscus
(H) Whiting
Merlangius merlangus
(I) Thin-lipped Mullett
Liza ramada
(J) River Lamprey
Lampetra fluviatilis
(K) Sea Snail
Liparis liparis
(L) Three-spined Stickleback
Gasterosteus aculeatus
Monthly percentage of annual catch
J A S O N D J F M A M J
Months
(M) July 1972 - June 1973
Stress 0.06
(N) July 1973 - June 1974
Stress 0.07
(O) July 1974 - June 1975
Stress 0.09
(P) July 1975 - June 1976
Stress 0.07
(Q) July 1976 - June 1977
Stress 0.10

**Figure 33**

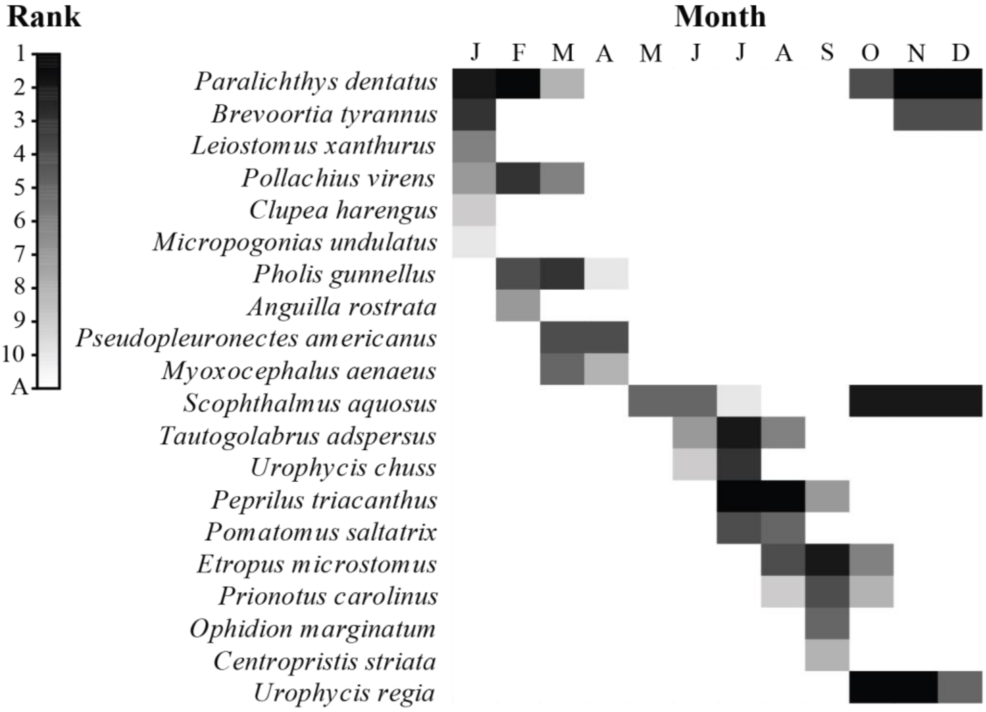
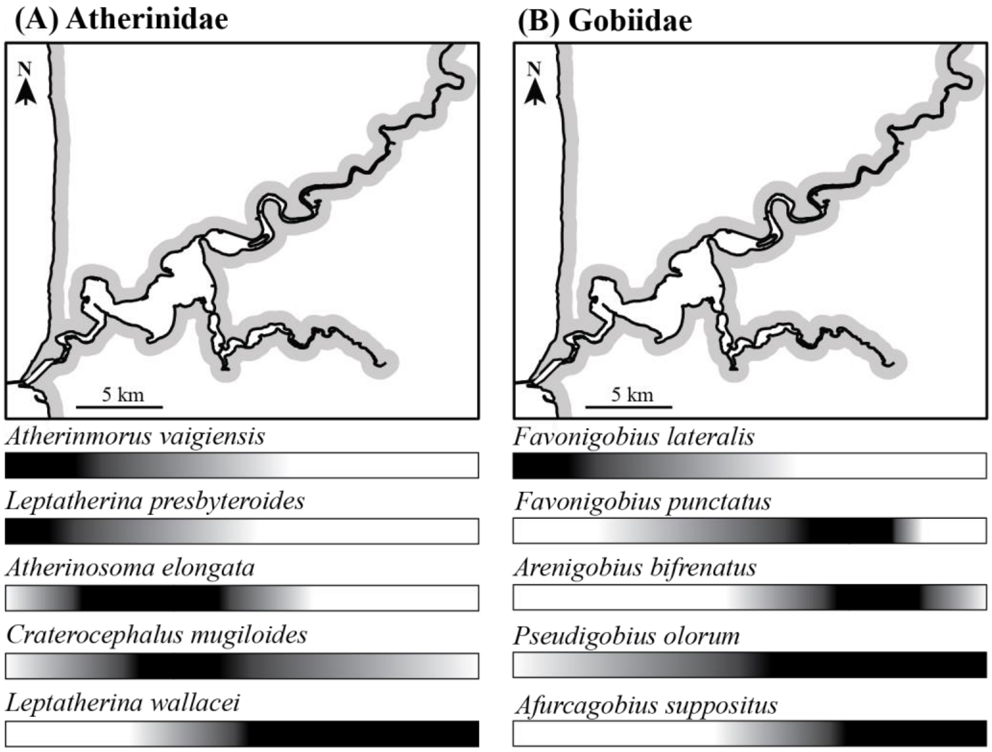


**Figure 34**

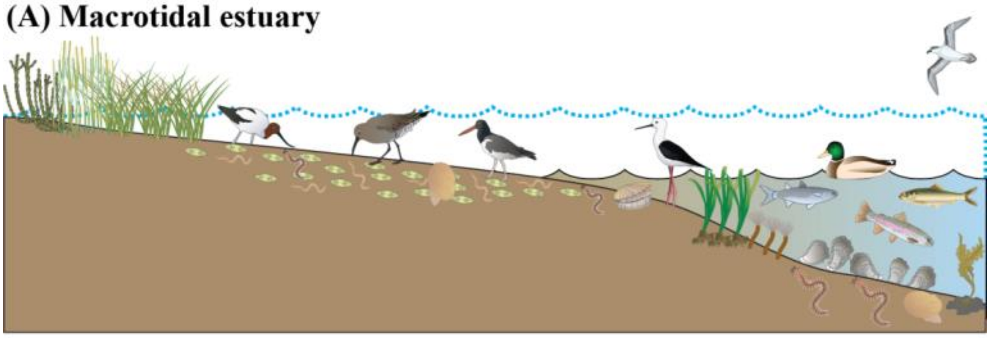


(A) Atherinidae

(B) Gobiidae

**Figure 35**

(A) Macrotidal estuary



(B) Microtidal estuary

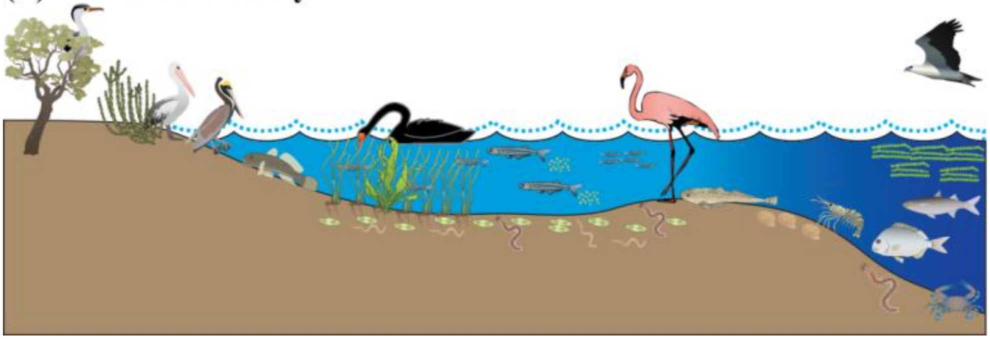


**Figure 36**