REVIEW

Littoral habitats as major nursery areas for fish species in estuaries: a reinforcement of the reduced predation paradigm

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ABSTRACT: For many decades, the role of estuaries as important nursery areas for fishes was accepted as fact by scientists and environmental managers. At the turn of the 21st century, a question mark was raised in relation to the reduced predation component of the nursery function, with some scientists contending that both large and small piscivorous fish species had access to the estuarine habitats that juvenile fishes in estuaries occupied. If true on a global scale, the nursery designation for these habitats would be compromised and the long-held paradigm that estuaries are important nursery areas for fishes would need to be revised. In this review, I examine the nature of fish nursery areas in estuarine littoral habitats from a mainly predation perspective and, based on a variety of ichthyofaunal and avifaunal studies, come to the conclusion that apart from a few selected estuarine systems, there is limited predation on juvenile fishes in these particular areas. This, coupled with the abundant suitable food resources for juvenile fish from different trophic categories, shelter from high-energy marine wave action and biological connectivity between a variety of submerged and emergent macrophyte communities, renders shallow estuarine littoral areas ideal nursery areas for the juveniles of mostly euryhaline marine fish species, the dominant component of estuarine ichthyofaunas globally. In addition, there are strong indications from the fossil record that these littoral estuarine nursery areas have been functioning since the Devonian, more than 350 million years ago.

KEY WORDS: Estuaries · Fish nurseries · Food · Shelter · Predation · Connectivity

1. INTRODUCTION

For many decades, the global paradigm relating to juvenile fish usage of shallow estuarine nursery areas has prevailed (e.g. Wallace & van der Elst 1975, Shenker & Dean 1979, Humphries et al. 1992, Gray et al. 1996, Heck et al. 1997, Hannan & Williams 1998, Able 1999, Minello et al. 2003, Nordlie 2003). This paradigm was based on documented evidence that juvenile fish were abundant in littoral estuarine waters that were usually turbid and sheltered from high-energy wave action (Cyrus & Blaber 1987, Cooper

2001), often had extensive submerged or emergent aquatic macrophytes (Heck et al. 2003, Whitfield 2017) and contained rich zoobenthic and microphytobenthic food resources (Wolff & de Wolf 1977, Barranguet & Kromkamp 2000). In addition, the evidence showed the structural complexity of macrophyte communities (e.g. seagrasses, mangroves, salt marshes and reed beds) provided shelter from piscivorous predators (Lubbers et al. 1990, Leslie et al. 2017).

A key factor underpinning the above paradigm was that large piscivorous fish were scarce or generally absent from estuarine littoral waters and that the

species richness of these piscivores was considerably lower in estuaries than in the adjacent marine environment. However, at the turn of the century, Sheaves (2001) questioned the reduced piscivory hypothesis pertaining to the nursery function provided by littoral estuarine areas. He indicated that the many predatory fish present in shallow tropical estuaries of north-eastern Australia and elsewhere were indeed piscivorous and therefore these nursery habitats were far from ideal for juveniles of estuary-associated taxa. Further evidence supporting this contention was subsequently provided by Baker & Sheaves (2006, 2009). Whilst numerous other factors play an important role in defining nursery ground value in estuaries (see Fig. 1), predator pressure constitutes one of the major components in determining the attractiveness of a particular habitat for juvenile fishes (McIvor & Odum 1988).

Early studies of fishes in estuaries (e.g. McHugh 1967, Wallace & van der Elst 1975) concluded that marine fish species found in estuaries were well-represented by juvenile life stages and that the dependence of these juveniles on estuaries as nursery areas varied according to the species (Miller et al. 1984). This view has not changed over the decades, and the opening statement by Able (2005, p. 5) captures this perspective, viz: 'Our understanding of the recruitment of estuarine fishes has been strongly influenced by two views: first, that estuaries are important nurseries and second, that many species are estuarine dependent'. Although the nursery function has been widely accepted by most estuarine ichthyologists, the estuarine-dependent status for many marine species in estuaries has been debated right up to the present. It also needs to be understood that, when viewing the evidence from virtually all fish sampling programmes in estuaries, these data are incomplete and, in many cases, biased depending on the type of gear(s) employed (Kjelson & Colby 1977).

The life cycles of fishes using estuaries as nursery areas are varied, and include a number of taxa that occupy estuaries during all or part of their juvenile life stages. According to Potter et al. (2015), the 4 fish guilds regarded as obligate users of estuaries include the marine estuarine-dependent guild, the solely estuarine and estuarine migrant guild, as well as diadromous species. Although the conduit function of estuaries for diadromous taxa has been widely cited, life-history plasticity also needs to be taken into account since some catadromous eels have been shown to reside mainly in brackish areas, even when inland river systems are available (Daverat et al. 2006, Arai et al. 2013). Furthermore, there are a number of anadromous species (e.g. various salmonids) that use estuaries as primary nursery areas prior to entering the sea for the remainder of their juvenile life stages (McDowall 1987), and there is a plasticity associated with the estuary phase (Volk et al. 2010).

In contrast, the members of the solely estuarine fish guild are completely dependent on estuaries as nursery areas, although some estuarine species exhibit pre-adaptive plasticity that enables them to occupy vacant niches in adjacent freshwater areas (Bamber & Henderson 1988). Indeed, *Gilchristella aestuaria* (Clupeidae) has both estuarine and freshwater populations in the freshwater lakes and lagoons of southern Africa (Whitfield 2019). The eggs and larvae of estuarine species are generally retained within the estuary due to benthic or epiphytic attachment (Neira et al. 1988, Wasserman et al. 2017), brooding or live bearing (Veith 1979, Mwale et al. 2014), pelagic eggs being released in the middle or upper reaches of many estuaries (Ré 1996, Strydom et al. 2002) or the presence of salt wedges or haloclines that retain fertilised ova within the estuary (Robichaud-LeBlanc et al. 1996, Acha et al. 1999).

Ingress of pelagic estuary-associated marine fish late larvae and early 0+ juveniles towards estuarine nursery areas has been summarized by Teodósio et al. (2016). These individuals may use flood tidal stream transport mechanisms or swim into estuaries against ebb tides, using hydrodynamically 'sheltered' littoral or bottom waters to gain access to an estuary (Whitfield 1989, Harrison & Cooper 1991, Teodósio et al. 2016). Retention within estuarine nursery areas is facilitated by either benthic access for demersal or bottom dwelling species (Strydom et al. 2015) or littoral occupation by other taxa such as sparids and mugilids (Beckley 1985). The larvae of pelagic clupeids spawned within estuaries may also attempt to remain within the estuarine nursery area using tidal hydrodynamic processes (Melville-Smith et al. 1981) and, in some cases, wind-driven water movements (Simionato et al. 2008). Although the embryos of certain estuarine-spawning gobies may be flushed out of the estuary into the marine environment at the preflexion larval stage (Beckley 1985), these taxa often return to the estuary as early juveniles (Whitfield 1994) and then remain there for the rest of their life cycle.

It has recently been proposed that the use of the littoral zone in estuaries as nursery areas for juvenile fishes has been in place for millions of years. A review by Gess & Whitfield (2020) described the similarities between southern African fish nursery areas

in a Devonian versus a Holocene estuarine lake. Indeed, these authors also proposed that the evolution of ancestral tetrapods from shallow coastal waters onto the land may well have been facilitated by marginal estuarine waters which were nursery areas for a variety of fish taxa and which attracted the early tetrapods into the littoral zone.

In this review, I examine the case pertaining to juvenile fish use of estuarine littoral areas and whether this nursery paradigm has validity or not. Although some small pelagic fish species mainly use channel and offshore estuarine waters as a nursery area (Blaber 1979), the focus of this review is on littoral waters <1 m in depth during all tidal levels. Global examples of estuarine nursery use are provided, with the focus of attention being placed on a small temporarily open/closed estuary, a medium-sized permanently open estuary and a large estuarine lake in South Africa. The reviewed material provides perspective on the use of these systems by the 0+ juveniles of marine fish species in particular, as well as the occurrence of piscivores in the littoral zone of these estuaries and the relative piscivorous fish species richness in estuaries compared to that in the adjacent marine neritic environment.

Piscivorous bird predation has been almost completely ignored in previous assessments of estuarine fish nursery function around the world. For the first time, bird predation on small fishes in selected South African estuarine environments is reviewed in order to gain a more complete picture of overall levels of predation from this source, particularly in the littoral zone where potential fish nursery habitats are most prevalent.

2. NURSERY AREA DEFINITION

Earlier considerations of fish nursery areas in estuaries tended to merely consider the availability of food and habitat for the juveniles utilizing these areas (e.g. Hoss & Thayer 1993). Little or no consideration was given to the presence or impact of piscivorous fishes or birds on these nursery habitats (e.g. Rozas & Minello 1998). Furthermore, the relative contribution of different types of habitat to adult fish populations also tended to be ignored (e.g. Heck & Thoman 1984). For the purposes of this review, the littoral zone in estuaries is defined as the <1 m depth contour that is not a static area but is dependent on tidal phase, i.e. moves towards the estuary channel or offshore waters at low tide and away from these zones at high tide.

Four main criteria need to be in place for a habitat to qualify as a nursery area: it must be physiologically suitable in terms of physical and chemical features, provide abundant suitable food for growth, afford a degree of protection from potential predators and have connectivity to allow colonisation by newly settled juveniles and the export of older fish to adult habitats. Additional criteria for fish nursery areas was provided by Beck et al. (2001), who went beyond proof of food utilization and protection from predators. They proposed that in order to qualify for nursery area status, a habitat also had to provide proof that a greater number of juveniles (on a per unit area basis) were contributed to the adult population of a particular species than was the case for other habitats.

This is not a comprehensive review of fish nursery areas in estuaries; instead, it is focused primarily on one aspect relating to nursery value, namely piscivorous fish and bird predation in the littoral zone of estuaries. To place this review into a larger estuarine nursery ground value context, the diagram compiled by Sheaves et al. (2015) is very appropriate (Fig. 1). Of the 10 drivers making up a logical sequence for the assessment of estuary nursery occupation, predation is only partially responsible for one of these.

3. LITTORAL ESTUARINE AREAS AS NURSERY HABITATS

3.1. Water depth, turbidity, tides and wave exposure

Water depth appears to be a key element in the lack of occupation of littoral areas by large piscivorous fishes. Shallow areas in the East Kleinemonde Estuary (South Africa) tend to be avoided by large fishes (Becker et al. 2017), and fish larger than 1 m have been found to seldom enter a littoral zone <0.7 m in depth (Becker et al. 2011). These findings were supported by a gill net study conducted by Paterson & Whitfield (2000) in the Kariega Estuary (South Africa) which documented that more than 6 of the 11 fish species sampled in deeper habitats adjacent to a salt marsh creek were piscivorous. None of these taxa entered the shallow creek (<1 m depth at high water spring tide) which was used as a refuge from these predators by the juveniles of a wide variety of marine fish species (Paterson & Whitfield 1996). Since fine mesh block nets were used to trap all fish on the salt marshes at spring high tide and collected from the nets at low tide (Paterson & Whitfield 2003),
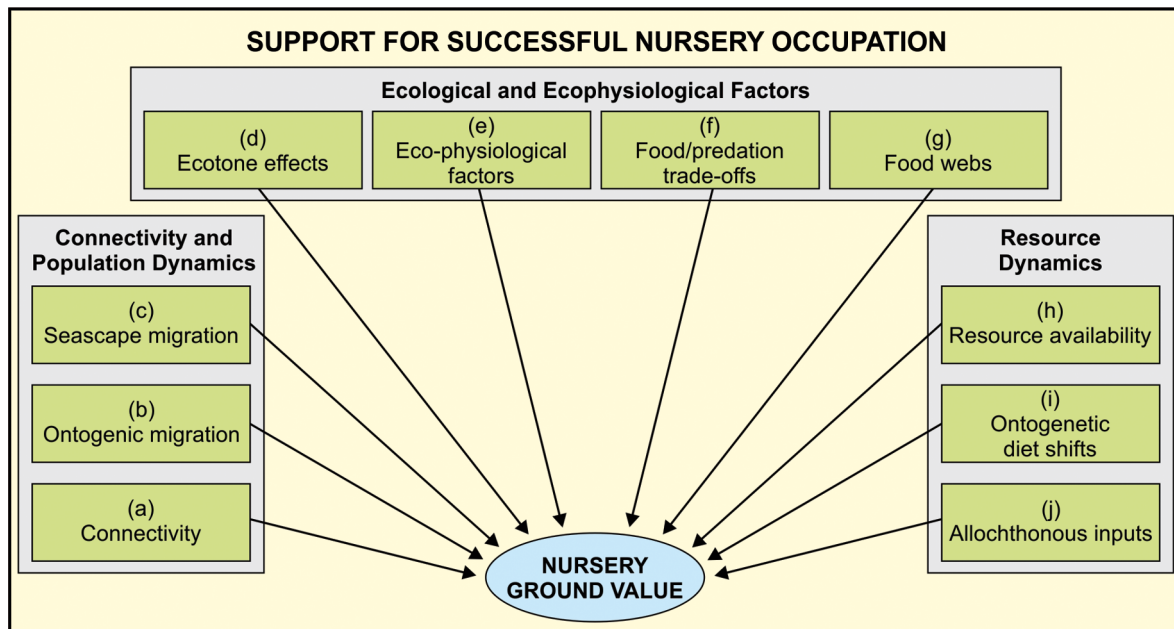
Fig. 1. Components influencing nursery ground value in estuaries (after Fig. 1 in Sheaves et al. 2015). Only compartment (f) is dealt with in this review

the absence of piscivorous fishes from these catches can be taken as confirmation that these predators were absent from the marshes at high tide.

Underwater observations support the contention that small juvenile fish are attracted to shallow estuarine nursery areas. A study by Munsch et al. (2016) found that smaller fish occupied shallow estuarine waters where large predators were less abundant than deeper waters. In addition, the smaller fish documented in that study were proportionally less abundant along deep shorelines that were created by intertidal armouring, thus reinforcing the value of shallow littoral areas as refuge for juvenile fish in estuarine nursery areas. The above authors concluded that estuarine nursery functions are mediated by a shallow depth gradient which may be compromised by steep littoral gradients created by shoreline infrastructure. A similar finding was arrived at by Manderson et al. (2004), who determined from tethering experiments on juvenile winter flounder *Pseudopleuronectes americanus* that predation risk for fish 30–35 mm standard length was low in shallow waters (<1 m deep) and increased rapidly with depth. They also concluded that winter flounder accumulate in littoral waters which act as predator refuges, regardless of whether complex physical habitats are present or not.

Sheaves (2001) and Baker & Sheaves (2006, 2009) presented convincing evidence that both large and small piscivorous fishes are present in estuarine water <2 m and that this negates, to a large extent, the hypothesis that shallow estuarine waters offer a refuge from these predators. The prime example of fish piscivory in shallow estuarine waters, and quoted extensively by Sheaves (2001), is provided by data from the Embley Estuary (Australia) (Haywood et al. 1998). Although 24 species were shown to have consumed fish in this system, only 6 species had a dietary percentage frequency of occurrence >50% (Table 3 in Sheaves 2001). Furthermore, water depths in the Embley Estuary always exceeded 2 m at high tide since the tidal amplitudes during the study ranged between 1.98 and 2.23 m (Haywood et al. 1998). Unfortunately, water depths of between 1 and 2 m can be easily accessed by large fish up to at least 1 m in length (Whitfield & Blaber 1978a) and therefore cannot be considered shallow.

The 31 000 ha Lake St Lucia estuarine system (South Africa) is a good example of what constitutes a littoral estuarine nursery area and what does not. The maximum depth of Lake St Lucia is only 3 m and the average depth is <2 m at mean sea level. Fish piscivory in the lake was studied by Whitfield & Blaber (1978a) using both gill and seine nets. Large marine piscivorous fishes were largely restricted to the lake basin and the juveniles of estuary-associated marine species to the shallow (<1 m) margins of the lake. Despite hundreds of thousands of juvenile mugilids and

sparids in the shallow littoral zone, the diet of the 2 large dominant piscivores, *Argyrosomus japonicus* (Sciaenidae) and *Elops machnata* (Elopidae), was overwhelmingly dominated by pelagic/open water zooplanktivores *Gilchristella aestuaria* (Clupeidae) and *Thryssa vitrirostris* (Engraulidae) (Whitfield & Blaber 1978a). The only partially piscivorous species located in any numbers in the shallow littoral waters of Lake St Lucia was *Terapon jarbua* (Terapontidae), and the diet of this species was found to be mainly fish scales (lepidophagy) and invertebrates (Whitfield & Blaber 1978b). Although *Glossogobius giuris* did occur in the St Lucia littoral, and the adults are known to sometimes consume small fishes, this species comprised <1% of the littoral ichthyofauna during the study period (Whitfield 1977). No other species capable of piscivory were recorded in the littoral zone.

A major factor influencing the occupation of littoral nursery areas in estuaries is habitat availability linked to tidal inundation. The ability of fishes to occupy different intertidal habitats is strongly linked to water depth (Krumme & Saint-Paul 2003, Rountree & Able 2007, Gullström et al. 2008, Minello et al. 2012). Tidal amplitude is particularly important, and some emergent plant habitats (e.g. certain salt marshes) can only be accessed during spring high tides. A good example of changing nursery habitat use with changing tidal levels is provided by Saintilan et al. (2007), who found that fish use seagrass beds at low neap tides but then move into higher elevation mangrove and salt marsh habitats during spring tides.

Juvenile fish occupying shallow littoral waters may be particularly vulnerable to piscivorous fish predation if the slope from the intertidal to subtidal channel habitat is steep and aquatic macrophytes, used for refuge at the low tide level, are absent. Conversely, small fish need to access the safety of intertidal plant habitats from bare subtidal habitats as soon as possible with the rising tide. Rozas et al. (1988) documented that although small fish preferred to access marshes via intertidal rivulets, most of them used direct access across entire creek banks to rapidly colonize tidally submerged plant beds. Changing littoral habitat use by juvenile fishes according to tidal level and the type of aquatic plants present in the littoral has also been recorded in permanently open South African estuaries (Becker et al. 2012, Leslie et al. 2017).

The increased turbidity associated with estuarine waters has been proposed by a number of authors as contributing to a reduction in predation on juvenile fishes in estuaries (Hecht & van der Lingen 1992).

Although turbidity mainly interferes with visual piscivores, as opposed to those predatory fish using other mechanisms to detect prey (Lunt & Smee 2015), the presence of turbid waters in estuaries will enhance the littoral nursery habitat value in terms of reduced avian and piscivorous predation rates. This may explain why such a high proportion of juveniles belonging to a variety of marine fish species are attracted to, or are indifferent to, elevated turbidity levels in estuaries (Cyrus & Blaber 1987). An example of juvenile anadromous fishes using turbid estuarine waters to avoid predation is described by Gregory & Levings (1998), who showed that 0+ age group Pacific salmon *Oncorhynchus* spp. in the Fraser River system were less likely to encounter and be consumed by piscivorous fishes in turbid compared to clear water.

Shelter from high-energy wave action was one of the factors identified early on as contributing to the intensive use of the littoral zone in estuaries by juvenile fishes (Day 1959). In those areas of the world where limited wave action prevails along the coast, it would appear that the distinction between marine and estuarine nursery areas is less apparent. Evidence to support this view was provided by Potter et al. (1990), who determined that the juveniles of estuary-associated marine fish species in Western Australia also occur in wave-protected marine areas adjacent to these systems. This was not the case in the neritic zone along the warm-temperate South African coast, and the suggested cause for the absence of estuary-associated marine species in these waters was the comparative high-energy coastline on the subcontinent.

3.2. Macrophyte versus non-macrophyte habitats

This topic was reviewed by Whitfield (2017), and only the main points will be summarised here. Submerged and emergent macrophytes in estuaries are both important as fish nursery areas (Costa et al. 1994, Laegdsgaard & Johnson 1995, Jackson et al. 2001, Minello et al. 2003, Faunce & Serafy 2006), not only in terms of the shelter that they provide to small fish (Baltz et al. 1993) but also because of the substratum these plants provide for attachment and colonisation by both epiphytes and invertebrates, all of which are important food sources for the associated ichthyofauna (Carr & Adams 1973, Adams 1976, Boesch & Turner 1984, Edgar & Shaw 1995).

The abundance of detritus associated with littoral macrophyte habitats is of particular importance in

estuarine nursery habitats, since this food source is extensively consumed by the small invertebrates on which the juvenile fish prey (Whitfield 1988, 1989). The source of detritus in estuarine nursery areas varies according to locality (Paterson & Whitfield 1997), with the upper reaches being more influenced by riverine sources and the lower reaches by marine sources (Vinagre et al. 2008). Movement of this detrital organic matter directly and indirectly within the estuary is facilitated by both water current flows and the movement of fish (Howe & Simenstad 2015), thus increasing the detritus food web connectivity within estuaries and between these systems and the adjacent marine environment.

From a habitat connectivity perspective — a key component in the provision of viable fish nursery areas — it is important to emphasize that eelgrass and other seagrasses provide more extensive littoral and sublittoral habitats for fishes than other emergent macrophyte habitats (e.g. salt marshes and mangroves). Although submerged aquatic macrophytes occur in both intertidal and subtidal regions of estuaries, the development of these plants is often greatest in shallow subtidal areas where light penetration is sufficient, even at high tide, to promote growth in what is often a turbid environment (Moore et al. 1997). In addition, there is usually a cyclical abundance of submerged aquatic plants according to the seasons, with maximum growth rates and biomass occurring during spring and summer (Congdon & McComb 1979). This annual cycle associated with littoral plants often corresponds closely to the annual colonisation of littoral nursery areas by juvenile fishes (Wallace & van der Elst 1975).

A study by Halpin (2000) compared growth of, and predation rates on, *Fundulus heteroclitus* inside and outside of salt marsh habitat in Rhode Island (USA). He found that the salt marshes offered high growth rates and protection from predators, but when predation risk was uniform across the marsh, the fish selected those habitats that provided the best opportunity for growth. Small fish are strongly attracted to structured habitats such as mangroves for protection from predators, but as they grow, they begin to move out onto mudflat areas for foraging and are less vulnerable to predation by virtue of their size (Laegdsgaard & Johnson 2001).

An early review of seagrass habitat complexity and the impact thereof on fishes and large mobile invertebrates was undertaken by Heck & Orth (1980). In particular, vegetation density, plant morphology and the nature of the epifauna influenced the abundance and diversity of both predators and prey species in these habitats. A later review by Heck et al. (2003) synthesized fish studies on shallow seagrass meadows as nursery areas and noted that, although these habitats were linked to elevated juvenile fish abundance, other structured habitats had similar juvenile fish abundance. Their review concluded that, based on abundance data, Northern Hemisphere seagrass beds might be more important as fish nursery areas than similar littoral habitats in the Southern Hemisphere.

A comprehensive study on the relationship between vegetated and non-vegetated areas of Chesapeake Bay (USA) by Lubbers et al. (1990) showed that fish abundance, biomass and species richness were all higher in vegetated areas which extended from the littoral into the sublittoral zone. The epifauna selected by the fish for food were very abundant in the macrophyte beds, and the fish stomach contents were generally fuller in these habitats compared to fish from adjacent bare sediment areas. Higher numbers of large piscivorous fish were also captured in association with the plant beds, a finding that the authors attributed to the higher densities of small forage fish located within these habitats.

3.3. Food versus refugia from predators

The question as to whether small juvenile fishes are attracted to littoral nursery areas for foraging opportunities or protection from piscivorous fish (or both) is very difficult to answer. The circumstantial evidence that littoral aquatic macrophyte habitats are attractive to fish is almost beyond question; for example, studies by Sasekumar et al. (1992), Beck et al. (2001) and Ikejima et al. (2003) have all shown that creeks associated with mangrove forests or salt marshes have both a higher species richness and abundance of fishes than nearby mudflats or sandy beaches without fringing macrophytes.

One of the few studies to directly address the food versus refuge function in estuaries is that of Miltner et al. (1995), which was based on both field and laboratory studies involving juvenile spot *Leiostomus xanthurus* and the associated piscivores southern flounder *Paralichthys lethostigma*, hake *Urophycis* spp. and bluefish *Pomatomus saltatrix*. Field sampling showed that young-of-the-year (YOY) spot were most abundant in shallow creek margins where benthic invertebrate prey of *L. xanthurus* was also maximal. In addition, sampling the stomach contents of the piscivores from the area showed that large YOY spot were not preyed upon but small YOY fish

were consumed. Furthermore, laboratory experiments by these authors showed that food had a stronger effect on spot distribution than predator presence, thus reinforcing the findings from the field study.

Published studies have often assumed that submerged and emergent vegetation in estuaries provide both food and refuge from predation for small fish (e.g. Hindell et al. 2000). However, some studies, particularly those in salt marsh habitats, emphasized the refuge value and questioned the food resources available to fish in driving the use of these habitats (e.g. Boesch & Turner 1984). Furthermore, the level of protection provided by aquatic macrophytes is linked to the structural complexity of the particular habitat (Stoner 1983, Adams et al. 2004), so not all potential fish nursery habitats are equal in this regard.

Some studies have emphasized that reduced predation on early juvenile marine fish in littoral vegetated habitats may even be a function of the high densities and biomass of invertebrate prey available for large predatory fishes in these habitats (Hampel et al. 2005). In the same way that small fish attempt to escape large piscivorous fish in littoral nursery areas by moving towards the shore, some mobile invertebrates attempt to escape small predatory fish by moving into very shallow water (Clark et al. 2003).

Perhaps the most convincing evidence of the refuge function of littoral estuarine macrophyte habitats for fishes comes from experimental data. A laboratory study on the responses of small and large fish to the introduction of predatory fish showed that in the absence of a piscivorous species, all fish size classes occurred both within and outside the mangrove habitat. However, the behaviour of small individuals changed when a piscivore was introduced to the tank — the small fish then retreated to the shelter provided by the mangroves, whereas the larger individuals did not (Laegdsgaard & Johnson 2001).

Field evidence of refuge function is provided by the study of Rooker et al. (1998), who showed that mortality of newly settled red drum *Sciaenops ocellatus* postlarvae was significantly higher in non-vegetated compared to vegetated estuarine habitats. Further support of the protection offered to these juvenile fish by littoral macrophytes was demonstrated by Stunz et al. (2002), who determined that the highest densities of juvenile *S. ocellatus* were associated with seagrass (*Halodule wrightii*) meadows, and that when this particular habitat was absent, the red drum occupied the edge of salt marsh (*Spartina alterniflora*) habitats.

An innovative field experiment using artificial mangrove units (AMUs) was conducted by Nagelkerken & Faunce (2008). They showed that fish assemblages associated with AMUs collapsed when these structures were removed from a sheltered embayment site, thus emphasizing the protective nature of this structure to small fish. In the context of food versus protection provided to fish by littoral plant habitats, it is noteworthy that AMUs that were colonised by various species of fouling algae attracted a greater species richness and abundance of juvenile fish than clean AMUs (Laegdsgaard & Johnson 2001). From the above experiments we can conclude that littoral estuarine macrophyte habitats provide both food and shelter for juvenile fishes, 2 important criteria in the definition of a nursery area.

3.4. Habitat connectivity

In recent decades it has become increasingly apparent that many fish species that use estuaries as nursery areas move from one habitat type to another and that these can range from littoral macrophyte beds in estuaries for juvenile stages to coastal reefs occupied by adults (Gillanders 1997, Gillanders et al. 2003). There is now an abundance of evidence that coastal ichthyofauna can use habitat mosaics according to species and stage of ontogenetic development, all of which have major consequences for ecological connectivity (Sheaves 2009). The connectivity between estuarine nursery areas and adult marine locations can be almost adjacent, as evidenced by the *Pagrus auratus* (Sparidae) study of Gillanders (2002) in the Sydney (Australia) region, which showed that the spatial link between juvenile and adult populations was very close.

The location of aquatic macrophyte habitats, both within and between estuaries, is very important to the marine juvenile fishes that use these habitats (Bell et al. 1988). A study by Irlandi & Crawford (1997) showed that pinfish *Lagodon rhomboides* (Sparidae) were more than twice as abundant in intertidal marshes associated with adjacent subtidal seagrass beds than in those marshes associated with unvegetated subtidal bottoms. Perhaps the most significant finding of the above study was the fact that the *L. rhomboides* associated with both intertidal and submerged vegetation were 90% heavier than those individuals that were held in enclosures with intertidal vegetation and unvegetated subtidal bottoms.

Juveniles of certain fish species in estuaries also move from one estuarine nursery habitat to another

as they increase in size; for example, *Sphyraena barracuda* (Sphyraenidae) in the Kosi estuarine system move from shallow submerged macrophyte beds at a length of between 20 and 80 mm to inundated *Phragmites* beds between 80 and 300 mm, after which they move into open water areas (Blaber 1982). These habitat changes may be driven primarily by the changing dietary requirements of the juvenile fish, since a major influence in terms of nursery function is the fish food resources associated with these different habitats (Heck et al. 1995, França et al. 2009). Indeed, food quality and quantity in estuarine habitats has a major bearing on fish species richness and abundance within these nursery areas (Sogard & Able 1991, Able 1999). However, juveniles of many species also have the ability to modify their diet according to the available food resources within a particular nursery area (Sheaves et al. 2014), with this dietary plasticity providing options for nursery occupation.

3.5. Estuarine versus marine and riverine nursery areas

It is now widely accepted that most marine fish species have exclusively marine nurseries, a few have estuarine nurseries and some have a combination of both. Whitfield & Pattrick (2015) demonstrated very clearly that the juveniles of most coastal marine species in the Algoa Bay region (South Africa) have nursery areas that may be located in either estuaries or the sea. Only *Diplodus capensis* (Sparidae) and *Chelon richardsonii* (Mugilidae) appeared to be well represented in both marine and estuarine nursery habitats. However, as a generalisation, the top dominant juveniles occupying estuaries (*Rhabdosargus holubi*, *Chelon dumerili*), subtidal sandy beaches (*D. capensis*, *Lithognathus mormyrus*), subtidal estuary mouth regions (*Pomadasys olivaceus*, *Engraulis capensis*), intertidal rock pools (*Clinus superciliosus*, *Chirodactylus brachydactylus*) and subtidal rocky gulleys (*C. brachydactylu*s, *Sarpa salpa*) were derived from different marine fish assemblages (Whitfield & Pattrick 2015).

Although anadromous fish species such as certain salmonids use estuaries as nursery areas in their early juvenile stages, the bulk of the life cycle of these taxa is spent in the marine environment. For example, chum salmon *Oncorhynchus keta* are abundant in British Columbia (Canada) estuaries for 2 mo in early spring, coho salmon *O. kisutch* for 2 mo in late spring and Chinook salmon *O. tshawytscha* throughout the spring, summer and autumn (Healey 1982). Evidence from Oregon (USA) estuaries suggests that density-dependent mechanisms come into play to induce the movement of 0+ *O. tshawytscha* from estuaries to nearby surf zones, which can act as an alternative nursery habitat for these individuals (Marin Jarrin & Miller 2013).

Completely estuarine resident species are totally dependent on estuaries as their primary nursery area, and some of them are likely to lose eggs and larvae if they are washed out to sea (Strydom et al. 2002). From a piscivorous predator perspective, these small species are either pelagic (e.g. Clupeidae) or benthic (e.g. Gobiidae) and, because of the very small size as juveniles, may even escape fish and bird predation during this life stage. However, as adults these small species often constitute an important component of the diet of large piscivorous fishes (Whitfield & Blaber 1978a), but their *r*-evolutionary life-history strategy and abundance in estuaries allows for high levels of predation (Harrison & Whitfield 2012).

Although pelagic fish eggs and larvae do not appear to be consumed by large piscivorous fishes in estuaries, these early life stages are vulnerable to jellyfish-induced mortality, especially where blooms of these pelagic predatory cnidarians occur (Xian et al. 2005, Pereira et al. 2014). Fish eggs in particular are susceptible to capture and consumption by jellyfish (Marques et al. 2015), but juvenile fish do not appear vulnerable to this predation pressure in estuaries (Wintzer et al. 2011). Since jellyfish seldom occupy shallow marginal estuarine habitats during feeding because of the risk of stranding, it can be assumed that the impact of this source of predation on littoral nursery areas is minimal.

Predation on indigenous juvenile fishes in estuaries by alien fish species is poorly documented, but the available data suggest that non-native piscivores do prey on juvenile fish in the shallow waters of estuaries. Invasive striped bass *Morone saxatilis*, largemouth bass *Micropterus salmoides* and Sacramento pikeminnow *Ptychocheilius grandis* have all been recorded preying on native fishes in shallow estuarine habitats of the Sacramento-San Joaquin Delta (USA) (Nobriga & Frederick 2007). Similarly, *M. salmoides* have been shown to be a major predator of 0+ juvenile freshwater mullet *Pseudomyxus capensis* migrating from the Kowie Estuary (South Africa) into river catchment nursery areas (Weyl & Lewis 2006, Magoro et al. 2015).

The first proper assessment of estuarine association categories for juvenile marine fishes entering estuar-

ies was undertaken by Wallace et al. (1984a,b), with the latest species updates for these associations provided by Whitfield (2019). Perhaps the strongest indication of the critical importance of estuarine nursery areas to particular fish species was provided by a series of studies that documented larval and early juvenile recruitment into temporarily closed estuaries via marine overwash events (Cowley et al. 2001, Vivier & Cyrus 2001, Kemp & Froneman 2004, Tweddle & Froneman 2017). The individual fish participating in this type of estuary ingress risk everything in order to reach their favoured nursery ground. This is because most of the waves overwashing the sand berm at the estuary mouth disappear into the sand before reaching the actual estuary, resulting in the mortality of all fish present in that particular wave (Whitfield 2019).

4. PISCIVORY IN ESTUARIES

4.1. Fishes

A broad examination of the number of piscivorous fish species in coastal marine waters versus estuaries is best assessed by picking a specific section of coast that is well studied and includes a number of estuaries in the selected area. For the purposes of this review, piscivorous species are defined as those taxa whose diet consists mainly of fish.

Perhaps one of the most intensive series of studies on the presence of piscivorous fish species in estuaries and the adjacent marine environment is that conducted by CSIRO scientists in northern Queensland (Australia). Evidence from various estuaries and bays in the Gulf of Carpentaria suggests that predation is less inside large open estuaries (mostly turbid) than outside. For example, there are more piscivores in Albatross Bay, into which the Embley Estuary flows, than in the estuary (Blaber et al. 1989). This is particularly the case for certain piscivorous families such as Carcharinidae, Sphyrnidae, Scombridae, Carangidae and Sphyraenidae, which are seldom abundant in smaller estuaries of the region or the upper reaches of larger ones (Blaber et al. 1994). Specific examples of piscivorous species that are abundant in coastal bays of the region but do not enter the adjacent estuaries are also described, e.g. the feeding biology of *Caranx bucculentus* (Carangidae) in Albatross Bay but its absence from adjacent estuaries (Brewer et al. 1989). The above findings support the contention that estuaries, and littoral estuarine areas in particular, provide an element of protection for juvenile fishes.

Similar declines in piscivorous fish species richness between marine neritic and estuarine waters in South Africa have also been recorded. A section of the Eastern Cape Province coast was used by Whitfield & Pattrick (2015) to examine marine fish nursery use in that region. A total of 20 predominantly piscivorous marine fish species have been recorded in the neritic zone of this area, and 10 of these species have been recorded entering adjacent estuaries on a regular basis. Based on this analysis, which is a proportion likely to be reflected elsewhere on the subcontinent, estuaries are a safer place for the location of fish nursery areas, but other factors such as food and shelter would also need to be considered.

Many piscivorous fish species spend part of their juvenile life stage preying predominantly on invertebrates before switching to piscivory (Juanes et al. 2002). Even those species that prey on fish at a very young age do not necessarily prey on juvenile fish in shallow littoral waters; for example, YOY bluefish *Pomatomus saltatrix* prey mainly on small pelagic fish species rather than juveniles of other estuary-associated taxa (Juanes et al. 2001). In addition, those small piscivores that can access shallow estuarine littoral areas often prey on mysids, shrimps and other epibenthic invertebrates (Cabral & Ohmert 2001). Furthermore, small predatory species in littoral waters that occasionally consume fish (e.g. Gobiidae) also tend to have a diet dominated by invertebrates (Grossman et al. 1980, Contente et al. 2012, D'Aguillo et al. 2014), thus limiting their predatory impact on juvenile fish within this zone. If the small size of all the above species located in shallow waters is also taken into account, it is apparent that the amount of fish consumed in these nursery areas is limited.

Cannibalism in estuarine nursery areas has been suggested as a source of mortality for young fish (Henderson & Corps 1997). However, experimental evidence (Bell et al. 1999) indicates that even piscivorous fish species show a strong preference for their natural fish prey rather than cannibalism. Indeed, in the natural estuarine environment, age 0+ bluefish showed a distinct preference for age 0+ anadromous fish species as prey, and seldom consumed juveniles of their own species (Juanes et al. 1993). The lack of cannibalism of larval or early juveniles by larger individuals of the same species within shallow estuarine nursery areas is noteworthy (e.g. Mugilidae; Blaber 1977). However, the ingestion of conspecific fish eggs by some fish species has been recorded (Acha et al. 2002) and is especially prevalent among several pelagic filter-feeding taxa (Bailey & Houde

1989). In this regard, many zooplanktivorous clupeids and engraulids, upon which large piscivorous fishes in estuaries usually prey (Whitfield & Blaber 1978a), are often confined to pelagic or offshore estuarine waters (Blaber 1979) and tend to avoid shallow marginal habitats within these systems (Whitfield 1977).

When focusing on a particular estuarine system, in this case the largest estuarine lake in Africa, we are fortunate in having a detailed analysis of piscivory within this system (Whitfield 1977). The diet of all piscivorous fish species within the lake was assessed (Whitfield & Blaber 1978a), and the 2 dominant piscivores in terms of numbers and biomass were *Argyrosomus japonicus* and *Elops machnata*. Both these species preyed mainly on pelagic zooplanktivorous fish species and did not consume juvenile marine fish species that were abundant in shallow littoral waters surrounding the lake (Whitfield 1977).

4.2. Birds

Piscivorous birds have been almost completely ignored by scientists as a factor influencing predation pressures on fishes in estuaries. Detailed studies of the avifaunal component in relation to fishes in estuaries is globally limited, with the most detailed and comprehensive studies having been conducted in South Africa (Whitfield & Blaber 1978c, 1979a,b, Whitfield & Cyrus 1978, Berruti 1983, Jackson 1984, Froneman et al. 2011, Cowley et al. 2017, Hean et al. 2017).

Based upon a detailed bird predation study in the estuarine Lake St Lucia (Whitfield & Blaber 1978c, 1979a,b), the major piscivorous birds were divided into 3 major categories, namely wading (egrets and herons), swimming (cormorants and pelicans) and diving (kingfishers, terns and fish eagles). Littoral estuarine nursery areas were impacted mainly by egrets, herons and kingfishers. The fish species targeted by these birds were predominantly juveniles of the freshwater cichlid *Oreochromis mossambicus* and, to a lesser extent, juveniles of the marine families Mugilidae and Sparidae (Whitfield & Blaber 1978c, 1979a). The size of the fish consumed by the egrets and herons increased with increasing water depth and distance from the shore and was related to the tarsometatarsal length and bill sizes of these wading birds (Whitfield & Blaber 1979a). The fact that juvenile fish consumed by birds in the St Lucia littoral were also the most abundant species sampled by seine netting in the same area (Whitfield 1977) is

noteworthy and supports the contention by Dias et al. (2012) that birds can be good indicators of fish assemblages in estuaries.

There is evidence that piscivorous birds can exert considerable pressure on the survival of certain target species in shallow coastal waters. For example, conservative estimates of juvenile flatfish consumption by great cormorant *Phalacrocorax carbo* associated with the Dutch Wadden Sea coastline amounted to more than 12 million 0-group plaice *Pleuronectes platessa*, 9 million dab *Limanda limanda*, 5 million flounder *Platichthys flesus* and 0.3 million sole *Solea solea* (Leopold et al. 1998). Consequently, declines in the littoral abundance of juvenile flatfish in this region would be expected to have a major negative impact on piscivorous birds in the area (van der Veer et al. 2011).

The only published comparison between fish and bird predation on fishes in an estuary is that of Cowley et al. (2017) in the small East Kleinemonde Estuary. These authors calculated that piscivorous fish consumed approximately 700 kg of fish annually from this 17.5 ha temporarily closed estuary, whereas piscivorous birds consumed a maximum of 9800 kg in the same year. Clearly, bird predation in this system is considerably greater than fish predation and amounted to a maximum of 25 % of total fish production (Cowley & Whitfield 2002) over the same period (Cowley et al. 2017). This estimated consumption of fish by birds may actually have been lower because the assumption was made that the entire diet of the avifauna comprised fish, which is unlikely to be the case for all the assessed bird species. Nevertheless, it would appear that piscivorous birds are a major mortality factor for small fish in the East Kleinemonde and Riet estuaries (Froneman et al. 2011), a proportion of which will be juveniles from the littoral zone of these systems.

Average daily piscivorous bird biomass in the large St Lucia lake system, which accounts for approximately 50 % of the estuarine area in South Africa, was estimated at 8539 kg (Berruti 1983). Using the Nagy (2001) equation, which estimates food consumption based on the mass of each bird species, resulted in a mean daily consumption rate of 123 kg or 44 895 kg yr^{-1}. Using estuarine fish productivity estimates from Whitfield (2016), this consumption amounted to approximately 0.43 % of the estimated annual fish production in the lake (Cowley et al. 2017). Clearly, this mortality rate would not impact negatively on the fish nursery function of the St Lucia system.

A very important study relating to simultaneous fish and bird predation was that conducted by Crow-

der et al. (1997). They hypothesized that because juvenile spot *Leiostomus xanthurus* move into shallow water to escape predation by southern flounder *Paralichthys lethostigma*, these small fish would then be more vulnerable to avian predators along the margins of an estuary. However, the field experiments by Crowder et al. (1997) showed that overall predation by both piscivorous sources on this fish species was less than what would be expected and that this was due to the spot juveniles aggregating into tight shoals in response to the flounder pressures, thus limiting bird predator success.

One of the aspects that may assist in reducing fish mortalities arising from piscivorous birds foraging in estuaries is the structural habitat complexity in the littoral zone of many estuaries. The presence of dense stands of submerged macrophytes, mangroves or reed beds around the margins of estuaries can serve as a refuge from bird predation for small fishes. In contrast, open shorelines that are a favoured foraging area for wading birds such as egrets and herons do not provide small fish with structural protection from avian predation, although elevated turbidity levels on open shores may provide some protective function. Unfortunately, little or no research has been published to highlight the different shelter opportunities for juvenile fishes attempting to avoid piscivorous birds in littoral estuarine waters.

5. CONCLUSIONS AND FINAL COMMENTS

This review addressed only one aspect of the suite of drivers that determine the value of littoral estuarine nursery areas. Hopefully, the reader can now reach a more informed assessment of the true value of shallow sheltered estuarine waters to small juvenile fish from a predation perspective. In general, piscivory in the South African estuarine littoral (<1 m depth) appears to be considerably less than in deeper channel or offshore estuarine waters. However, this conclusion differs from the situation in the littoral of selected Australian estuaries, where the juveniles of piscivorous species, small adult piscivores and even large predatory fishes are present. Nevertheless, there is some evidence from both Australia (Gulf of Carpentaria) and South Africa (Algoa Bay region) that the number of piscivorous fish taxa in estuaries is considerably less than the species richness occurring in adjacent marine systems.

Bird predation is a factor that has been largely ignored in previous assessments of fish mortalities in relation to the nursery function of estuaries. Based on examples from South African systems in particular, this source of mortality can be significant in certain types and sizes of estuaries. However, where complex submerged or emergent plant habitats are present, these structures can potentially provide some form of protection for juvenile fish from both piscivorous fish and birds associated with these systems. Thus, when the predation component is viewed in its entirety, the fish nursery function paradigm for estuarine littoral areas is deemed to be valid.

LITERATURE CITED

Able KW (1999) Measures of juvenile fish habitat quality: examples from a national estuarine research reserve. Am Fish Soc Symp 22:134–147

Able KW (2005) A re-examination of fish estuarine dependence: evidence for connectivity between estuarine and ocean habitats. Estuar Coast Shelf Sci 64:5–17

Acha EM, Mianzan H, Lasta CA, Guerrero RA (1999) Estuarine spawning of the whitemouth croaker *Micropogonias furnieri* (Pisces: Sciaenidae), in the Río de la Plata, Argentina. Mar Freshw Res 50:57–65

Acha EM, Bremec C, Lasta C (2002) Cannibalism on planktonic eggs by a non-filter feeding fish, *Micropogonias furnieri* (Sciaenidae). Fish Res 56:321–326

Adams SM (1976) Feeding ecology of eelgrass fish communities. Trans Am Fish Soc 105:514–519

Adams AJ, Locascio JV, Robbins BD (2004) Microhabitat use by a post-settlement stage estuarine fish: evidence from relative abundance and predation among habitats. J Exp Mar Biol Ecol 299:17–33

Arai T, Chino N, Le DQ (2013) Migration and habitat use of the tropical eels *Anguilla marmorata* and *A. bicolor pacifica* in Vietnam. Aquat Ecol 47:57–65

Bailey KM, Houde ED (1989) Predation on eggs and larvae of marine fishes and the recruitment problem. Adv Mar Biol 25:1–83

Baker R, Sheaves M (2006) Visual surveys reveal high densities of large piscivores in shallow estuarine nurseries. Mar Ecol Prog Ser 323:75–82

Baker R, Sheaves M (2009) Refugees or ravenous predators: detecting predation on new recruits to tropical estuarine nurseries. Wetlands Ecol Manage 17:317–330

Baltz DM, Rakocinski C, Fleeger JW (1993) Microhabitat use by marsh-edge fishes in a Louisiana estuary. Environ Biol Fishes 36:109–126

Bamber RN, Henderson PA (1988) Pre-adaptive plasticity in atherinids and the estuarine seat of evolution. J Fish Biol 33(Suppl A):17–23

Barranguet C, Kromkamp J (2000) Estimating primary production rates from photosynthetic electron transport in estuarine microphytobenthos. Mar Ecol Prog Ser 204: 39–52

Beck MW, Heck KL Jr, Able KW, Childers DL and others (2001) The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates. Bioscience 51:633–641

Becker A, Cowley PD, Whitfield AK, Järnegren J, Næsje TF (2011) Diel fish movements in the littoral zone of a temporarily closed South African estuary. J Exp Mar Biol Ecol 406:63–70

Becker A, Coppinger C, Whitfield AK (2012) Influence of tides on assemblages and behaviour of fishes associated with shallow seagrass edges and bare sand. Mar Ecol Prog Ser 456:187–199

Becker A, Whitfield AK, Cowley PD, Cole VJ (2017) Does water depth influence size composition of estuary-associated fish? Distributions revealed using mobile acoustic-camera transects along the channel of a small shallow estuary. Mar Freshw Res 68:2163–2169

Beckley LE (1985) Tidal exchange of ichthyoplankton in the Swartkops estuary mouth, South Africa. S Afr J Zool 20: 15–20

Bell JD, Steffe AS, Westoby M (1988) Location of seagrass beds in estuaries: effects on associated fish and decapods. J Exp Mar Biol Ecol 122:127–146

Bell GW, Buckel JA, Stoner AW (1999) Effects of alternative prey on cannibalism in age-1 bluefish. J Fish Biol 55: 990–1000

Berruti A (1983) The biomass, energy consumption and breeding of waterbirds relative to hydrological conditions at Lake St Lucia. Ostrich 54:65–82

Blaber SJM (1977) The feeding ecology and relative abundance of mullet (Mugilidae) in Natal and Pondoland estuaries. Biol J Linn Soc 9:259–275

Blaber SJM (1979) The biology of filter feeding teleosts in Lake St Lucia, Zululand. J Fish Biol 15:37–59

Blaber SJM (1982) The ecology of Sphyraena barracuda (Osteichthyes: Perciformes) in the Kosi system with notes on other Natal estuaries. S Afr J Zool 17:171–176

Blaber SJM, Brewer DT, Salini JP (1989) Species composition and biomasses of fishes in different habitats of a tropical northern Australian estuary: their occurrence in the adjoining sea and estuarine dependence. Estuar Coast Shelf Sci 29:509–531

Blaber SJM, Brewer DT, Salini JP (1994) Comparisons of the fish communities of tropical estuarine and inshore habitats in the Gulf of Carpentaria, northern Australia. In: Dyer KR, Orth RJ (eds) Changes in fluxes in estuaries: implications from science to management. Olsen & Olsen, Fredensborg, p 363–372

Boesch DF, Turner RE (1984) Dependence of fishery species on salt marshes: the role of food and refuge. Estuaries 7: 460–468

Brewer DT, Blaber SJM, Salini JP (1989) The feeding biology of Caranx bucculentus Alleyne and Macleay (Teleostei: Carangidae) in Albatross Bay, Gulf of Carpentaria; with special reference to predation on penaeid prawns. Aust J Mar Freshwater Res 40:657–668

Cabral BHN, Ohmert B (2001) Diet of juvenile meagre, Argyrosomus regius, within the Tagus estuary. Cah Biol Mar 42:289–293

Carr WES, Adams CA (1973) Food habits of juvenile marine fishes occupying seagrass beds in the estuarine zone near Crystal River, Florida. Trans Am Fish Soc 102: 511–540

Clark KL, Ruiz GM, Hines AH (2003) Diel variation in predator abundance, predation risk and prey distribution in shallow-water estuarine habitats. J Exp Mar Biol Ecol 287:37–55

Congdon RA, McComb AJ (1979) Productivity of Ruppia: seasonal changes and dependence on light in an Australian estuary. Aquat Bot 6:121–132

Contente RF, Stefanoni MF, Spach HL (2012) Feeding ecology of the American freshwater goby Ctenogobius shufeldti (Gobidae, Perciformes) in a sub-tropical estuary. J Fish Biol 80:2357–2373

Cooper JAG (2001) Geomorphological variability among microtidal estuaries from the wave-dominated South African coast. Geomorphology 40:99–122

Costa MJ, Costa JL, de Almeida PR, Assis CA (1994) Do eelgrass beds and salt marsh borders act as preferential nurseries and spawning grounds for fish? An example of the Mira Estuary in Portugal. Ecol Eng 3:187–195

Cowley PD, Whitfield AK (2002) Biomass and production estimates of a fish community in a small South African estuary. J Fish Biol 61:74–89

Cowley PD, Whitfield AK, Bell KNI (2001) The surf zone ichthyoplankton adjacent to an intermittently open estuary, with evidence of recruitment during marine overwash events. Estuar Coast Shelf Sci 52:339–348

Cowley PD, Terörde AI, Whitfield AK (2017) Birds as major predators of fishes in the East Kleinemonde Estuary. Afr Zool 52:147–154

Crowder LB, Squires DD, Rice JA (1997) Nonadditive effects of terrestrial and aquatic predators on juvenile estuarine fish. Ecology 78:1796–1804

Cyrus DP, Blaber SJM (1987) The influence of turbidity on juvenile marine fish in the estuaries of Natal, South Africa. Cont Shelf Res 7:1411–1416

D'Aguillo MC, Harold AS, Darden TL (2014) Diet composition and feeding ecology of the naked goby Gobiosoma bosc (Gobiidae) from four western Atlantic estuaries. J Fish Biol 85:355–373

Daverat F, Limburg KE, Thibault I, Shiao JC and others (2006) Phenotypic plasticity of habitat use by three temperate eel species, Anguilla anguilla, A. japonica and A. rostrata. Mar Ecol Prog Ser 308:231–241

Day JH (1959) The biology of Langebaan Lagoon: a study of the effect of shelter from wave action. Trans R Soc S Afr 35:475–547

Dias E, Morais P, Leopold M, Campos J, Antunes C (2012) Natural born indicators: great cormorant Phalacrocorax carbo (Aves: Phalacrocoracidae) as monitors of river discharge influence on estuarine ichthyofauna. J Sea Res 73:101–108

Edgar GJ, Shaw C (1995) The production and trophic ecology of shallow-water fish assemblages in southern Australia. III. General relationships between sediments, seagrasses, invertebrates and fishes. J Exp Mar Biol Ecol 194:107–131

Faunce CH, Serafy JE (2006) Mangroves as fish habitat: 50 years of field studies. Mar Ecol Prog Ser 318:1–18

França S, Vinagre C, Pardal MA, Cabral HN (2009) Spatial and temporal patterns in the Tagrus estuary, Portugal: comparison between intertidal and subtidal habitat. Sci Mar 73:307–318

Froneman PW, Blake JD, Hulley P (2011) Aspects of population dynamics and feeding by piscivorous birds in the intermittently open Riet River estuary, Eastern Cape, South Africa. Afr J Aquat Sci 36:101–107

Gess RW, Whitfield AK (2020) Estuarine fish and tetrapod evolution: insights from a Late Devonian (Famennian) Gond-

wanan estuarine lake and a southern African Holocene equivalent. Biol Rev Camb Philos Soc 95:865−888

Gillanders BM (1997) Patterns of abundance and size structure in the blue groper, *Achoerodus viridus* (Pisces, Labridae): evidence of links between estuaries and coastal reefs. Environ Biol Fishes 49:153−173

Gillanders BM (2002) Connectivity between juvenile and adult fish populations: Do adults remain near their recruitment estuaries? Mar Ecol Prog Ser 240:215−223

Gillanders BM, Able KW, Brown JA, Eggleston DB, Sheridan PF (2003) Evidence of connectivity between juvenile and adult habitats for mobile marine fauna: an important component of nurseries. Mar Ecol Prog Ser 247:281−295

Gray CA, McElligott DJ, Chick RC (1996) Intra- and inter-estuary differences in assemblages of fishes associated with shallow seagrass and bare sand. Mar Freshw Res 47:723−735

Gregory RS, Levings CD (1998) Turbidity reduces predation on migrating juvenile Pacific salmon. Trans Am Fish Soc 127:275−285

Grossman GD, Coffin R, Moyle PB (1980) Feeding ecology of the bay goby (Pisces: Gobiidae). Effects of behavioral, ontogenetic, and temporal variation on diet. J Exp Mar Biol Ecol 44:47−59

Gullström M, Bodin M, Nilsson PG, Öhman MC (2008) Seagrass structural complexity and landscape configuration as determinants of tropical fish assemblage composition. Mar Ecol Prog Ser 363:241−255

Halpin PM (2000) Habitats use by an intertidal salt-marsh fish: trade-offs between predation and growth. Mar Ecol Prog Ser 198:203−214

Hampel H, Cattrijsse A, Elliott M (2005) Feeding habits of young predatory fishes in marsh creeks situated along the salinity gradient of the Schelde Estuary, Belgium and The Netherlands. Helgol Mar Res 59:151−162

Hannan JC, Williams RJ (1998) Recruitment of juvenile marine fishes to seagrass habitat in a temperate Australian estuary. Estuaries 21:29−51

Harrison TD, Cooper JAG (1991) Active migration of juvenile grey mullet (Teleostei: Mugilidae) into a small lagoonal system on the Natal coast. S Afr J Sci 87:395−396

Harrison TD, Whitfield AK (2012) Fish trophic structure in South African estuaries, with particular emphasis on estuarine typology and zoogeography. J Fish Biol 81: 2005−2029

Haywood MDE, Heales DS, Kenyon RA, Loneragan NR, Vance DJ (1998) Predation of juvenile tiger prawns in a tropical Australian estuary. Mar Ecol Prog Ser 162:201−214

Healey MC (1982) Juvenile Pacific salmon in estuaries: the life support system. In: Kennedy VS (ed) Estuarine comparisons. Academic Press, New York, NY, p 315−341

Hean JW, Craig AJFK, Richoux NB (2017) Seasonal population dynamics and energy consumption by waterbirds in a small temperate estuary. Ostrich 88:45−51

Hecht T, van der Lingen CD (1992) Turbidity-induced changes in feeding strategies of fish in estuaries. S Afr J Zool 27:95−107

Heck KL Jr, Orth RJ (1980) Seagrass habitats: the roles of habitat complexity, competition and predation in structuring associated fish and motile invertebrate assemblages. In: Kennedy VS (ed) Estuarine perspectives. Academic Press, New York, NY, p 449−464

Heck KL Jr, Thoman TA (1984) The nursery role of seagrass meadows in the upper and lower reaches of the Chesapeake Bay. Estuaries 7:70−92

Heck KL Jr, Able KW, Roman CT, Fahay MP (1995) Composition, abundance, biomass, and production of macro-fauna in a New England estuary: comparisons among eelgrass meadows and other nursery habitats. Estuaries 18:379−389

Heck KL Jr, Nadeau DA, Thomas R (1997) The nursery role of seagrass beds. Gulf Mex Sci 1997:50−54

Heck KL Jr, Hays G, Orth RJ (2003) Critical evaluation of the nursery role hypothesis for seagrass meadows. Mar Ecol Prog Ser 253:123−136

Henderson PA, Corps M (1997) The role of temperature and cannibalism in interannual recruitment variation of bass in British waters. J Fish Biol 50:280−295

Hindell JS, Jenkins GP, Keough MJ (2000) Variability in abundance of fishes associated with seagrass habitats in relation to diets of predatory fishes. Mar Biol 136: 725−737

Hoss DE, Thayer GW (1993) The importance of habitat to the early life history of estuarine dependent fishes. Am Fish Soc Symp 14:147−158

Howe ER, Simenstad CA (2015) Using stable isotopes to discern mechanisms of connectivity in estuarine detritus-based food webs. Mar Ecol Prog Ser 518:13−29

Humphries P, Potter IC, Loneragan NR (1992) The fish community in the shallows of a temperate Australian estuary: relationships with the aquatic macrophyte *Ruppia megacarpa* and environmental variables. Estuar Coast Shelf Sci 34:325−346

Ikejima K, Tongnunui P, Medej T, Taniuchi T (2003) Juvenile and small fishes in a mangrove estuary in Trang Province, Thailand: seasonal and habitat differences. Estuar Coast Shelf Sci 56:447−457

Irlandi EA, Crawford MK (1997) Habitat linkages: the effect of intertidal saltmarshes and adjacent subtidal habitats on abundance, movement, and growth of an estuarine fish. Oecologia 110:222−230

Jackson S (1984) Predation by pied kingfishers and white-breasted cormorants on fish in the Kosi estuary system. Ostrich 55:113−132

Jackson EL, Rowden AA, Attrill MJ, Bossey SJ, Jones MB (2001) The importance of seagrass beds as a habitat for fishery species. Oceanogr Mar Biol Annu Rev 39: 269−303

Juanes F, Marks RE, McKown KA, Conover DO (1993) Predation by age-0 bluefish on age-0 anadromous fishes in the Hudson River estuary. Trans Am Fish Soc 122: 348−356

Juanes F, Buckel JA, Scharf FS (2001) Predator behaviour and selectivity of a primary piscivore: comparison of fish and non-fish prey. Mar Ecol Prog Ser 217:157−165

Juanes F, Buckel JA, Scharf FS (2002) Feeding ecology of piscivorous fish species. In: Hart PJB, Reynolds JD (eds) Handbook of fish biology and fisheries, Vol 1: fish biology. Blackwell Science, Oxford, p 267−283

Kemp JOG, Froneman PW (2004) Recruitment of ichthyo-plankton and macrozooplankton during overtopping events into a temporarily open/closed southern African estuary. Estuar Coast Shelf Sci 61:529−537

Kjelson MA, Colby DR (1977) The evaluation and use of gear efficiencies in the estimation of fish abundance. In: Wiley M (ed) Estuarine processes, Vol 2: circulation, sediments, and transfer of material in the estuary. Academic Press, New York, NY, p 416−424

Krumme U, Saint-Paul U (2003) Observations of fish migration in a macrotidal mangrove channel in northern Brazil

using a 200-kHz split-beam sonar. Aquat Living Resour 16:175–184

Laegdsgaard P, Johnson CR (1995) Mangrove habitats as nurseries: unique assemblages of juvenile fish in sub-tropical mangroves in eastern Australia. Mar Ecol Prog Ser 126:67–81

Laegdsgaard P, Johnson C (2001) Why do juvenile fish utilise mangrove habitats? J Exp Mar Biol Ecol 257: 229–253

Leopold MF, van Damme CJG, van der Veer HW (1998) Diet of cormorants and the impact of cormorant predation on juvenile flatfish in the Dutch Wadden Sea. J Sea Res 40: 93–107

Leslie T, James NC, Potts WM, Rajkaran A (2017) The rela-tionship between habitat complexity and nursery provi-sion for an estuarine-dependent fish species in a perma-nently open South African estuary. Estuar Coast Shelf Sci 198:183–192

Lubbers L, Boynton WR, Kemp WM (1990) Variations in structure of estuarine fish communities in relation to abundance of submerged vascular plants. Mar Ecol Prog Ser 65:1–14

Lunt J, Smee DL (2015) Turbidity interferes with foraging success of visual but not chemosensory predators. PeerJ 3:e1212

Magoro ML, Whitfield AK, Carassou L (2015) Predation by introduced largemouth bass, *Micropterus salmoides* on indigenous marine fish in the lower Kowie River, South Africa. Afr J Aquat Sci 40:81–88

Manderson JP, Pessutti J, Hilbert JG, Juanes F (2004) Shal-low water predation risk for a juvenile flatfish (winter flounder; *Pseudopleuronectes americanus*, Walbaum) in a northwest Atlantic estuary. J Exp Mar Biol Ecol 304: 137–157

Marin Jarrin JR, Miller JA (2013) Sandy beach surf zones: an alternative nursery habitat for 0-age Chinook salmon. Estuar Coast Shelf Sci 135:220–230

Marques F, Chaino P, Costa JL, Domingos I, Angélico MM (2015) Abundance, seasonal patterns and diet of the non-native jellyfish *Blackfordia virginica* in a Portuguese estuary. Estuar Coast Shelf Sci 167:212–219

McDowall RM (1987) The occurrence and distribution of diadromy among fishes. Am Fish Soc Symp 1:1–13

McHugh JL (1967) Estuarine nekton. In: Lauff GH (ed) Estu-aries. American Association for the Advancement of Sci-ence, Washington, DC, p 581–620

McIvor CC, Odum WE (1988) Food, predation risk, and microhabitat selection in a marsh fish assemblage. Ecol-ogy 69:1341–1351

Melville-Smith R, Baird D, Wooldridge T (1981) The utiliza-tion of tidal currents by the larvae of an estuarine fish. S Afr J Zool 16:10–13

Miller JM, Reed JP, Pietrafesa LJ (1984) Patterns, mechanisms and approaches to the study of migrations of estuarine-dependent larvae and juveniles. In: McCleave JD, Arnold GP, Dodson JJ, Neill WH (eds) Mechanisms of migrations in fishes. Plenum Press, New York, NY, p 209–225

Miltner RJ, Ross SW, Posey MH (1995) Influence of food and predation on the depth distribution of juvenile spot (*Leiostomus xanthurus*) in tidal nurseries. Can J Fish Aquat Sci 52:971–982

Minello TJ, Able KW, Weinstein MP, Hays CG (2003) Salt marshes as nurseries for nekton: testing hypotheses on density, growth and survival through meta-analysis. Mar Ecol Prog Ser 246:39–59

Minello TJ, Rozas LP, Baker R (2012) Geographic variability in salt marsh flooding patterns may affect nursery value for fishery species. Estuar Coasts 35:501–514

Moore KA, Wetzel RL, Orth RJ (1997) Seasonal pulses of tur-bidity and their relations to eelgrass (*Zostera marina* L.) survival in an estuary. J Exp Mar Biol Ecol 215:115–134

Munsch SH, Cordell JR, Toft JD (2016) Fine-scale habitat use and behavior of a nearshore fish community: nursery functions, predator avoidance, and spatiotemporal habi-tat partitioning. Mar Ecol Prog Ser 557:1–15

Mwale M, Kaiser H, Heemstra PC (2014) Reproductive biol-ogy and distribution of *Syngnathus temmincki* and *S. watermeyeri* (Pisces: Syngnathidae) in southern Africa. Afr J Mar Sci 36:175–184

Nagelkerken I, Faunce CH (2008) What makes mangroves attractive to fish? Use of artificial units to test the influ-ence of water depth, cross-shelf location, and presence of root structure. Estuar Coast Shelf Sci 79:559–565

Nagy KA (2001) Food requirements of wild animals: predic-tive equations for free-living mammals, reptiles, and birds. Nutr Abstr Rev 71:21–31

Neira FJ, Beckley LE, Whitfield AK (1988) Larval develop-ment of the Cape silverside, *Atherina breviceps* Cuv. & Val., 1835 (Teleostei, Atherinidae) from southern Africa. S Afr J Zool 23:176–183

Nobriga ML, Frederick F (2007) Shallow-water piscivores–prey dynamics in California's Sacramento-San Joaquin Delta. San Francisco Estuar Watershed Sci 5:4

Nordlie FG (2003) Fish communities of estuarine salt marshes of eastern North America, and comparisons with temperate estuaries of other continents. Rev Fish Biol Fish 13:281–325

Paterson AW, Whitfield AK (1996) The fishes associated with an intertidal salt marsh creek in the Kariega Estuary, South Africa. Trans R Soc S Afr 51:195–218

Paterson AW, Whitfield AK (1997) A stable carbon isotope study of the food-web in a freshwater-deprived South African estuary, with particular emphasis on the ichthy-ofauna. Estuar Coast Shelf Sci 45:705–715

Paterson AW, Whitfield AK (2000) Do shallow-water habi-tats function as refugia for juvenile fishes? Estuar Coast Shelf Sci 51:359–364

Paterson AW, Whitfield AK (2003) The fishes associated with three intertidal salt marsh creeks in a temperate South African estuary. Wetlands Ecol Manage 11:305–315

Pereira R, Teodósio MA, Garrido S (2014) An experimental study of *Aurelia aurita* feeding behaviour: inference of the potential predation impact on a temperate estuarine nursery area. Estuar Coast Shelf Sci 146:102–110

Potter IC, Beckley LE, Whitfield AK, Lenanton RCJ (1990) Comparisons between the roles played by estuaries in the life cycles of fishes in temperate Western Australia and southern Africa. Environ Biol Fishes 28:143–178

Potter IC, Tweedley JR, Elliott M, Whitfield AK (2015) The ways in which fish use estuaries: a refinement and expansion of the guild approach. Fish Fish 16:230–239

Ré P (1996) Anchovy spawning in the Mira estuary (south-western Portugal). Sci Mar 60:141–153

Robichaud-LeBlanc KA, Courtenay SC, Locke A (1996) Spawning and early life history of a northern popula-tion of striped bass (*Morone saxatilis*) in the Miramitchi River estuary, Gulf of St Lawrence. Can J Zool 74: 1645–1655

Rooker JR, Holt SA, Holt GJ (1998) Vulnerability of newly settled red drum (*Sciaenops ocellatus*) to predatory fish:

Is early-life survival enhanced by seagrass meadows? Mar Biol 131:145–151

Rountree RA, Able KW (2007) Spatial and temporal habitat use patterns for salt marsh nekton: implications for ecological functions. Aquat Ecol 41:25–45

Rozas LP, Minello TJ (1998) Nekton use of salt marsh, seagrass, and non-vegetated habitats in a south Texas (USA) estuary. Bull Mar Sci 63:481–501

Rozas LP, McIvor CC, Odum WE (1988) Intertidal rivulets and creekbanks: corridors between tidal creeks and marshes. Mar Ecol Prog Ser 47:303–307

Saintilan N, Hossain K, Mazumder D (2007) Linkages between seagrass, mangrove and saltmarsh as fish habitat in the Botany Bay estuary, New South Wales. Wetlands Ecol Manage 15:277–286

Sasekumar A, Chong VC, Leh MU, D'Cruz R (1992) Mangroves as a habitat for fish and prawns. Hydrobiologia 247:195–207

Sheaves M (2001) Are there really few piscivorous fishes in shallow estuarine habitats? Mar Ecol Prog Ser 222: 279–290

Sheaves M (2009) Consequences of ecological connectivity: the coastal ecosystem mosaic. Mar Ecol Prog Ser 391: 107–115

Sheaves M, Sheaves J, Stegemann K, Molony B (2014) Resource partitioning and habitat-specific dietary plasticity of two estuarine sparid fishes increase food web complexity. Mar Freshw Res 65:114–123

Sheaves M, Baker R, Nagelkerken I, Connolly RM (2015) True value of estuarine and coastal nurseries for fish: incorporating complexity and dynamics. Estuar Coasts 38:401–404

Shenker JM, Dean JM (1979) The utilization of an intertidal salt marsh creek by larval and juvenile fishes: abundance, diversity and temporal variation. Estuaries 2: 154–163

Simionato CG, Berasategui A, Meccia VL, Acha M, Mianzan H (2008) Short time-scale wind forced variability in the Río de la Plata Estuary and its role in ichthyoplankton retention. Estuar Coast Shelf Sci 76:211–226

Sogard SM, Able KW (1991) A comparison of eelgrass, sea lettuce macroalgae, and marsh creeks as habitats for epibenthic fishes and decapods. Estuar Coast Shelf Sci 33:501–519

Stoner AW (1983) Distribution of fishes in seagrass meadows: role of macrophyte biomass and species composition. Fish Bull 81:837–846

Strydom NA, Whitfield AK, Paterson AW (2002) The influence of altered freshwater flow regimes on larval and juvenile *Gilchristella aestuaria* (Pisces: Clupeidae) abundance in the upper reaches of two South African estuaries. Mar Freshw Res 53:431–438

Strydom NA, Coetzer CJ, Pattrick P (2015) The complex early life history of a marine estuarine-opportunist fish species, *Solea turbynei* (Soleidae) from temperate South Africa. Sci Mar 79:169–178

Stunz GW, Minello TJ, Levin PS (2002) A comparison of early juvenile red drum densities among various habitat types in Galveston Bay, Texas. Estuaries 25:76–85

Teodósio MA, Paris CB, Wolanski E, Morais P (2016) Biophysical processes leading to the ingress of temperate fish larvae into estuarine nursery areas: a review. Estuar Coast Shelf Sci 183:187–202

Tweddle GP, Froneman PW (2017) Fish recruitment into a South African temporarily open/closed temperate estuary during three different hydrological mouth phases. Afr J Mar Sci 40:221–225

van der Veer H, Koot J, Aarts G, Dekker R, Diderich W, Freitas V, Witte JIJ (2011) Long-term trends in juvenile flatfish indicate a dramatic reduction in nursery function of the Balgzand intertidal, Dutch Wadden Sea. Mar Ecol Prog Ser 434:143–154

Veith WJ (1979) Reproduction in the live-bearing teleost *Clinus superciliosus.* S Afr J Zool 14:208–211

Vinagre C, Salgado J, Costa MJ, Cabral HN (2008) Nursery fidelity, food web interactions and primary sources of nutrition of the juveniles of *Solea solea* and *S. senegalensis* in the Tagus estuary (Portugal). Estuar Coast Mar Sci 76:255–264

Vivier L, Cyrus DP (2001) Juvenile fish recruitment through wave-overtopping into a closed subtropical estuary. Afr J Aquat Sci 26:109–113

Volk EC, Bottom DL, Jones KK, Simenstad CA (2010) Reconstructing juvenile Chinook salmon life history in the Salmon River Estuary, Oregon, using otolith microchemistry and microstructure. Trans Am Fish Soc 139: 535–549

Wallace JH, van der Elst RP (1975) The estuarine fishes of the east coast of South Africa. Part 4. Occurrence of juveniles in estuaries. Part 5. Ecology, estuarine dependence and status. Investigational Report of the Oceanographic Research Institute, Durban 42:1–63

Wallace JH, Kok HM, Beckley LE (1984a) Inshore small-mesh trawling survey of the Cape south coast. Part 2. Occurrence of estuarine-associated fishes. S Afr J Zool 19:165–169

Wallace JH, Kok HM, Beckley LE, Bennett B, Blaber SJM, Whitfield AK (1984b) South African estuaries and their importance to fishes. S Afr J Sci 80:203–207

Wasserman RJ, Whitfield AK, Welch RJ, Dalu T (2017) Are nest sites a limiting resource for speleophilic nesting fishes in sand dominated temporarily open/closed estuaries? Environ Biol Fishes 100:187–192

Weyl OLF, Lewis H (2006) First record of predation by the alien invasive freshwater fish *Micropterus salmoides* L. (Centrarchidae) on migrating estuarine fishes in South Africa. Afr Zool 41:294–296

Whitfield AK (1977) Predation on fish in Lake St Lucia, Zululand. MSc thesis, University of Natal, Pietermaritzburg

Whitfield AK (1988) The fish community of the Swartvlei estuary and the influence of food availability on resource utilization. Estuaries 11:160–170

Whitfield AK (1989) Ichthyoplankton interchange in the mouth region of a southern African estuary. Mar Ecol Prog Ser 54:25–33

Whitfield AK (1994) Abundance of larval and 0+ juvenile marine fishes in the lower reaches of three southern African estuaries with differing freshwater inputs. Mar Ecol Prog Ser 105:257–267

Whitfield AK (2016) Biomass and productivity of fishes in estuaries: a South African case study. J Fish Biol 89: 1917–1930

Whitfield AK (2017) The role of seagrass meadows, mangrove forests, salt marshes and reed beds as nursery areas and food sources for fishes in estuaries. Rev Fish Biol Fish 27:75–110

Whitfield AK (2019) Fishes of southern African estuaries: from species to systems. Smithiana Monograph No. 4. South African Institute for Aquatic Biodiversity, Grahamstown

Whitfield AK, Blaber SJM (1978a) Food and feeding ecology of piscivorous fishes at Lake St Lucia, Zululand. J Fish Biol 13:675–691

Whitfield AK, Blaber SJM (1978b) Scale-eating habits of the marine teleost *Terapon jarbua* (Forskål). J Fish Biol 12:61–70

Whitfield AK, Blaber SJM (1978c) Feeding ecology of piscivorous birds at Lake St Lucia. Part 1: diving birds. Ostrich 49:185–198

Whitfield AK, Blaber SJM (1979a) Feeding ecology of piscivorous birds at Lake St Lucia. Part 2: wading birds. Ostrich 50:1–9

Whitfield AK, Blaber SJM (1979b) Feeding ecology of piscivorous birds at Lake St Lucia. Part 3: swimming birds. Ostrich 50:10–20

Whitfield AK, Cyrus DP (1978) Feeding succession and zonation of aquatic birds at False Bay, Lake St Lucia. Ostrich 49:8–15

Whitfield AK, Pattrick P (2015) Habitat type and nursery function for coastal marine fish species, with emphasis on the Eastern Cape region, South Africa. Estuar Coast Shelf Sci 160:49–59

Wintzer AP, Meek MH, Moyle PB (2011) Trophic ecology of two non-native hydrozoan medusae in the upper San Francisco Estuary. Mar Freshw Res 62:952–961

Wolff WJ, de Wolf L (1977) Biomass and production of zoobenthos in the Grevelingen Estuary, the Netherlands. Estuar Coast Mar Sci 5:1–24

Xian W, Kang B, Liu R (2005) Jellyfish blooms in the Yangtze Estuary. Science 307:41