Estuaries – how challenging are these constantly changing aquatic environments for associated fish species?

Alan K. Whitfield

Abstract Much has been written about the abundance of fishes in estuaries, and particularly the value of the littoral zone and associated macrophyte habitats as fish nursery areas. What has not been researched or discussed in the same amount of detail is that estuaries are demanding physico-chemical environments for fishes, yet each year millions of 0 + juveniles are recruited into these supposedly stressful nurseries. This review focuses on three primary variables; salinity, temperature and turbidity, and highlights the ability of estuary-associated fish species to withstand apparent extreme conditions associated with these physico-chemical drivers in order to benefit from the rich food resources and possible low predation rates present within most systems. However, there is increasing evidence that global change, including climate change, is resulting in these driving variables becoming more extreme, which will test even the most eurytopic estuarine species now and in the future.

Keywords Estuarine fishes · Eurytopic · Physico-chemical variables · Salinity · Temperature · Turbidity

A. K. Whitfield
South African Institute for Aquatic Biodiversity (SAIAB), Grahamstown, South Africa

A. K. Whitfield (✉)
Department of Ichthyology and Fisheries Science (DIFS), Rhodes University, Grahamstown, South Africa
e-mail: A.Whitfield@saiab.ac.za

Introduction

An estuary is a transition zone between the river catchment and adjacent coastal marine waters. In essence it is a zone where the flow of the river meets the flood of the tide and, as such, retains some characteristics of both fresh water and the sea. However, it also has unique properties that are not replicated either upstream or downstream of the estuary, which emphasizes its role as an ecosystem rather than a simple ecotone between two adjacent water bodies (Whitfield and Elliott 2011).

There are some processes that occur only in estuaries and are absent from either river or marine ecosystems. For example, in permanently open estuaries there are two opposing current systems that vary according to relative magnitudes of river inflow and tidal regime. These water currents often exert considerable influence upon water mixing, turbidity, sedimentation processes, nutrient exchange and other physical features within an estuary. In particular, the mixing of fresh- and sea-water produces a chemical environment, represented mainly by a continually changing salinity regime, that is unlike that found in either the adjacent marine or river system (Reid and Wood 1976).

Easy access to estuarine waters by fishes tends to be assumed because of the continuity of the aquatic medium between the river, estuary and sea. However, the salinity and other abiotic 'barriers' for many fish species entering an estuary from either the upstream or downstream ends are perhaps as great as the transition by ancestral tetrapods from water to land (Blaber 1991). This 'barrier effect' for many fish species is essentially a

function of the salinity differential between the upstream and downstream areas outside the estuary, but also includes other variables such as temperature and turbidity that can differ markedly between an estuary and the two adjacent aquatic ecosystems.

River flow and marine tides penetrate estuaries on a daily basis and therefore have a major influence on daily salinity, turbidity and water temperature regimes. The magnitude of these inputs to permanently open estuaries is also variable and depends on both catchment run-off (Kimmerer 2002) and whether the system is situated in a microtidal, mesotidal or macrotidal coastal region (Krumme 2009). In contrast, temporarily closed estuaries have little or no river flow or tidal interaction during the closed phase, and will therefore show much less short-term variability in salinity, turbidity or temperature regimes (Froneman 2002).

The estuarine ichthyofauna is well-adapted to cope with the environmental stresses within these environments, and the fishes are therefore regarded as resilient to this variability. Indeed, the ability of fishes and other estuarine organisms to absorb this stress without any apparent adverse effects has been termed 'Environmental Homeostasis' by Elliott and Quintino (2006). Thus, whilst most freshwater and marine organisms may find estuarine conditions extremely stressful, estuary-associated species are able to capitalize on these conditions to their benefit, the so-called 'Estuarine Quality Paradox' (Elliott and Quintino 2006). These benefits do, however, come at an extra physiological and energetic cost that is also highlighted this review.

There are a wide array of biotic and abiotic influences exerted on fish species utilizing estuarine environments. A diagrammatic representation of these influences in a southern African context is provided in Fig. 1, most of which are likely to apply to estuarine ichthyofaunas globally. These factors are not independent but interact directly and indirectly with the fishes that inhabit estuaries. For example, river floods directly influence estuarine water temperature, salinity, turbidity, tidal exchange, olfactory cues and dissolved oxygen concentrations, and indirectly affect mouth state and dimensions, aquatic habitat diversity, primary and secondary productivity, fish recruitment, food availability and competition between species (Whitfield 2019).

Although there are a wide array of physico-chemical variables that separate estuaries from the adjacent aquatic environments, this review focuses on three main variables: salinity, temperature and turbidity. It also highlights the benefits estuary-associated fishes are able to capitalize on by spending all or part of their life cycle within these challenging systems, viz. the diversity of nursery habits (e.g. Whitfield 2017), rich food resources (e.g. Wilson 2002), high potential growth rates (e.g. Sogard 1992), and low levels of piscivory (e.g. Whitfield 2020a).

The question is also posed in this review as to whether future global change, including climate change, will alter the nature and variability of physico-chemical conditions in estuaries to such an extent that some fish species will no longer be able to use these systems as they do at present. It is also accepted that the risks of climate change to fish in estuaries are not distributed equally and that they vary among estuaries and associated habitats, as well as across biogeographic regions (Gillanders et al. 2021). The question then arises – do we have a sufficient baseline understanding of the biology of many estuary-associated fish species, especially their environmental sensitivities and tolerances, such that we can tailor mitigation measures for estuarine fishes or habitats in the face growing global change pressures? Although some progress has been made towards assessing interactive stressors that impact on fishes (Toft et al. 2018), it is apparent that we still have a long way to go before we can adequately advise estuarine managers on ameliorating the impact of global changes on fishes in estuaries.

Salinity, temperature and turbidity regimes in estuaries

Salinity

Conditions in estuaries are more variable than those in either the freshwater or the coastal marine environment. This variation is primarily associated with the salinity of the water which increases horizontally from virtually zero in the river at the head of the estuary to coastal water salinities that are usually within the euhaline range at the mouth of an estuary. The salinity of the water may vary both vertically and horizontally, depending on estuarine morphometry, river flow, prevailing winds and tidal regime (Schroeder et al. 1990; Ralston et al. 2010). When river flooding occurs, saline waters in an estuary may even be flushed out to sea altogether, only returning weeks or months later (Nichols 1977).

In arid and semi-arid parts of the world, evaporation from the surface of temporarily closed estuaries, or those
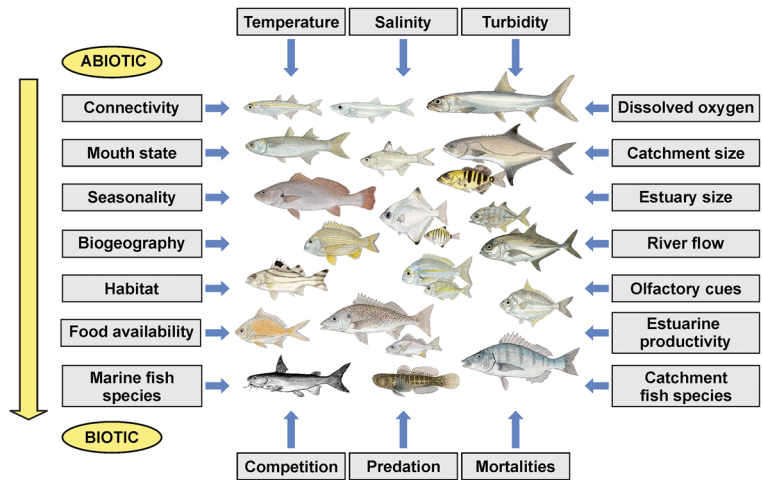
with a high surface to volume ratio, may considerably exceed local surface precipitation and runoff from land drainage. Such systems may be small (Largier et al. 1997) or large (Cyrus et al. 2010) and the hypersaline conditions may be seasonal or persist for years or even decades, depending on the region. With the advent of rapid climate change and global warming, it is likely that estuarine hypersalinity (> 40 psu) in semi-arid areas will become more widespread (Gillanders et al. 2011) and new extremes are therefore likely to be attained (Fig. 2).

Temperature

Water temperatures in estuaries usually differ considerably from the inflowing rivers and the adjacent ocean.

This is because rivers strongly reflect the influence of land-based and associated air temperatures whereas marine waters are strongly influenced by wind (e.g. upwelling events) and the temperature of major current systems associated with the coast. Consequently, in permanently open estuaries with a strong tidal prism, there is often a correlation between salinity and temperature (Garvine 1975).

Large tidal estuaries represent a mixture of temperatures from both freshwater and marine sources, as well as the considerable warming of shallow littoral waters in summer and cooling of these same waters in winter. Vertical and horizontal temperature gradients exist in some estuaries, often linked to the presence of a strong halocline which is, in turn, driven by riverine inputs

Fig. 2 A drone view of the Hamersley Inlet on the southern coast of Western Australia. This picture was taken in December 2020 when the average salinity in the estuary exceeded 300 psu and no fish were observed. Extensive crystallized salt layers are clearly visible in the mouth region and along the banks of the system (Photograph and other information provided by Dr James Tweedley, Murdoch University)

overlaying deeper more saline waters (Largier and Slinger 1991).

In high latitude estuaries, the surface waters often freeze during winter, creating an extreme environment for most fish species in these systems (e.g. Dionne 1984). Extreme environmental temperatures also develop in low latitude estuaries at the opposite end of the scale, especially in tropical and subtropical systems where global warming is having a major impact. Overall, water temperatures in 166 Australian estuaries, from all biogeographic regions, increased by an average of 2.16°C in the 12 years from 2007–2019 (Scanes et al. 2020).

Turbidity

Turbidity in estuaries is highly variable and can range widely, depending on catchment geology, river flow regime, tidal prism, sediments and suspensoids, estuarine morphometry, wind regime, estuarine hydrodynamics and phytoplankton production (e.g. Cloern 1987, de Jonge et al. 2014). Turbidity regimes in estuaries have been provisionally allocated into four major groupings; very turbid (> 80 Nephelometric Turbidity Units or NTU), predominantly turbid (51–80 NTU), semi-turbid (10–50 NTU) and clear (< 10 NTU) (Cyrus 1988a).

Turbidities in a single estuary can vary both spatially and temporally, linked closely to river inputs to the upper reaches and tidal influence in the lower reaches. In some estuaries, a turbidity maximum zone exists where water turbulence is high and suspension of sediments and particulate matter is maximal (Geyer 1993). Estuarine turbidities in large European and North American estuaries are strongly influenced by the length of the tidal intrusion, tidal range, and residence time of the water (Uncles et al. 2002). Indeed, turbidity gradients in many estuaries tend to be more prevalent and marked than either temperature or salinity gradients (Cyrus 1988a).

In some shallow estuarine lakes with muddy sediments, wind can be a major driver in generating very turbid (> 80 NTU) conditions through promoting wave action and associated water currents (Cyrus 1988b). Although very high turbidity (suspended particulate organic matter and/or suspended inorganic sediment) has been shown to depress phytoplankton production in some estuaries due to the shading effect (Cloern 1987), it is also noted that relatively high Chlorophyll *a* values can be recorded in very turbid waters where hydrodynamic processes circulate the individual plant cells into surface waters where photosynthesis is

possible (Grange and Allanson 1995; Irigoien and Castel 1997).

Impact of estuarine salinity, temperature and turbidity regimes on fishes

Where all three of these physico-chemical factors have been analysed in relation to estuary-associated fish species, turbidity and salinity were found to be primary drivers in terms of fish distribution and abundance. For example, in the Embley Estuary (Australia) there was a strong inverse relationship between turbidity and salinity but both variables were significant drivers in the catch per unit effort of 30 of the 45 sampled fish species (Cyrus and Blaber 1992). Temperature was not found to be a significant factor in the above study but this result is likely a reflection of the tropical nature of this system. Blaber and Blaber (1980) also dismissed temperature as an important variable in the subtropical Moreton Bay (Australia) study, but rated turbidity as an important driver for juvenile estuary-associated marine fishes and suggested that this variable may aid 0 + juveniles in locating estuarine nursery grounds.

In subtropical Lake St Lucia (South Africa) there is sometimes an absence of salinity gradients within the individual lake compartments. Such conditions prevailed during the 1980s when turbidity, temperature and food availability were found to be primary drivers in the juvenile distribution of 20 of the most common fish species within this system (Cyrus and Blaber 1987b). A principal component analysis indicated that the fish fauna could be divided into five major categories according to their occurrence in various turbidities. An example of a clear water species was *Gerres oyena* (Frabicius 1775) which occurred in water < 10 NTU, a clear to partially turbid water (< 50 TU) species was *Chelon dumerili* (Steindachner 1870), an intermediate turbid water (10–80 NTU) species was *Leiognathus equula* (Forsskål 1775), a turbid water (> 50 NTU) species was *Thrysaa vitrirostris* (Gilchrist and Thompson 1908) and a species indifferent to turbidity was *Acanthopagrus vagus* (Peters 1852).

In the 1990s Harrison and Whitfield (2006) studied fish assemblages in a wide range of South African subtropical, warm-temperate and cool-temperate estuaries, and determined that temperature and salinity were the main influences affecting the distribution and occurrence of estuary-associated fish species on the

subcontinent. Tropical estuary-associated fish species were largely confined to the warmer and more turbid subtropical systems of South Africa, whereas the fish assemblages in the temperate estuaries were dominated by endemic species that appeared to be more common in cooler, less turbid waters (Harrison and Whitfield 2006).

When the dynamics of freshwater and estuarine/ marine fish species in the littoral waters of the Mississippi Estuary (USA) were examined along a river-estuarine gradient, it was found that water temperature (positive relationship) and salinity (negative relationship) were the primary drivers for freshwater fish species occurrence in the estuary. In contrast, estuarine/marine species occurrence in the same estuary responded positively to both salinity and temperature. When freshwater fish abundance data was modelled, there was a significant negative relationship with salinity and turbidity, but when the same model was applied to estuarine/marine fishes, the abundance relationship was positive for both salinity and turbidity (Peterson and Ross 1991).

Mass mortalities of fishes in estuaries are often triggered by either low winter or high summer temperature, in combination with very low (< 3 psu) or high salinity (> 70 psu) water (Whitfield 1995; Whitfield et al. 2006). An example of a fish kill arising from an oligohaline/ low temperature combination was that recorded at Lake St Lucia (Blaber and Whitfield 1976), with a hyperhaline/high temperature fish mortality event documented in the same lake several decades later (Cyrus and Vivier 2006). An indication of how a combination of salinity and temperature, and sometimes dissolved oxygen and temperature, can interact to cause mass mortalities of estuary-associated species is illustrated in Fig. 3. Prolonged low salinities without access to more saline waters are also a factor, as indicated by a mass mortality of a number of marine species in the Bot Estuary (South Africa) following four years of isolation from the sea and salinities of approximately 3 psu throughout the system (Bennett 2010).

The dependence of some marine and many estuarine fish species on estuaries for all or part of their life cycle (Potter et al. 1990, Whitfield 2020b) suggests that these systems are vital for the survival of these taxa. Extreme physico-chemical conditions are tolerated within certain limits but it is probable that these limits will be increasingly tested in the decades and centuries of climate change that lie ahead (Roessig et al. 2004; Gillanders et al. 2011; Hoeksema et al. 2018). In this regard the lack of fish species redundancy in estuaries is also
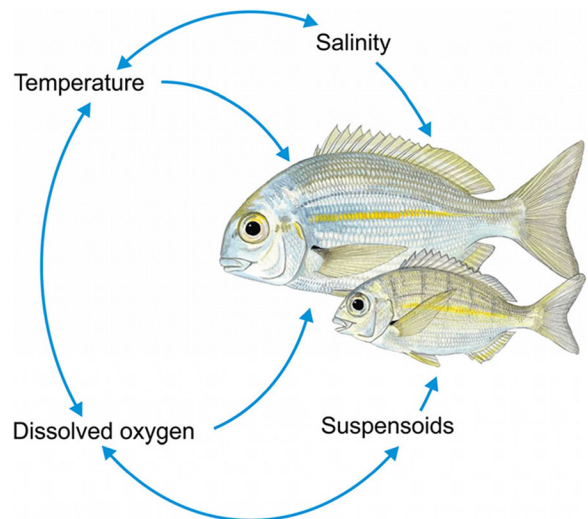

Fig. 3 Diagram showing the interactions between selected physico-chemical variables that can lead to mortalities of fishes in estuaries(modified from Whitfield 1995)

relevant (Whitfield and Harrison 2020), particularly if the species that are lost are dependent on these systems for their existence.

Salinity

Changing salinity requires major physiological adjustments by all fishes that inhabit estuaries. Indeed, it is perhaps the most important characteristic of any fish occupying an estuary that it is able to adjust the osmolality of its body fluids to an altered salinity regime. This salinity may be either above or below the isosmotic condition of the fish and will necessitate very different physiological responses, depending upon whether the fish is hypo- or hyper-osmotic relative to the external medium (Fig. 4).

Osmoregulory adaptations are facilitated by the teleost endocrine system which acts as the primary link between the change in environmental conditions and the physiological response of the fish. Although cortisol has been viewed as the main 'seawater'-adapting hormone and prolactin as the main 'freshwater'-adapting hormone, recent evidence suggests that growth hormone promotes acclimation to seawater and that cortisol interacts with both the growth hormone and prolactin in facilitating osmoregulatory adaptations to changing salinities (McCormick 2001). This view is supported by Sakamoto and McCormick (2006) who have proposed that control of salinity acclimation in fishes is facilitated
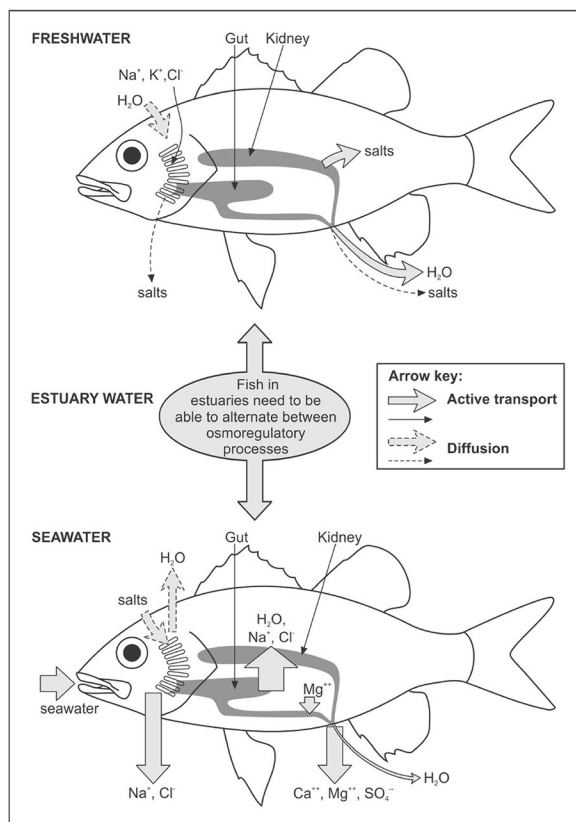
Fig. 4 Generalised models of a freshwater and marine teleost showing the pattern of salt and water movement during osmoregulation. The key to whether the transport is active, or due to diffusion, is shown on each fish and the sizes of the arrows provide an indication of quantity (modified from Smith 1982). Euryhaline fish species in estuaries require both osmoregulatory processes to fully exploit these environments.

by prolactin and growth hormone, primarily through the regulation of cell proliferation, differentiation and apoptosis, and that the actions of the above two hormones is strongly influenced by corticosteroids.

Numerous studies have reported an influence of environmental salinity on fish development and growth during early life stages (e.g. Holliday 1969). Fecundity, egg fertilization, embryonic development and larval growth for most fish species are strongly influenced by salinity (Nicholson et al. 2008, Martin et al. 2009). In addition, inappropriate salinities can lead to the complete failure of a breeding attempt by a particular species (Dando 1984). For some estuarine-associated species, the challenge for their eggs and larvae are high salinity (euhaline) conditions (e.g. Winger and Lasier 1994), whereas for other taxa the mortalities occur under low

salinity (oligohaline) conditions (e.g. Sylvester et al. 1975). Juvenile and adult fish of most estuary-associated species are usually strong osmoregulators (Whitfield et al. 1981), whilst the egg, embryo and larval stages of these same species are considerably more vulnerable to sub-optimal salinities (Giffard-Mena et al. 2020).

Monthly, seasonal and annual changes in river flow introduce a time scale of salinity variation that affects fishes in estuaries. Monthly changes in the longitudinal ichthyofaunal composition of the Great Fish Estuary (South Africa) was shown to be strongly influenced by increasing river flow, most notably a marked increase in the proportion of catadromous and freshwater species under high river flow conditions (Ter Morshuizen et al. 1996). Seasonal changes in estuarine salinity have been shown to be a primary driver of fish species richness, abundance and biomass in estuaries, especially those taxa that are dependent on these systems for their existence (Barletta et al. 2005). Annual and longer-term changes are reflected in the impact of an El Niño event on the estuarine fish assemblage in the Patos Lagoon (Brazil), driven by changes in salinity, temperature and water circulation within this system (Garcia et al. 2003).

Shallow estuarine lakes in arid and semi-arid regions of the world are particularly vulnerable to long-term cycles in hypersalinity (Tweedley et al. 2019). This often leads to the development of hyperhaline conditions which places additional stress on even euryhaline fishes living within these systems (Whitfield et al. 2006). In small, normally-closed hyperhaline estuaries in Western Australia, there is a progressive decline in fish species richness with increasing salinity (Tweedley et al. 2019). Only two estuarine resident species have been recorded in these estuaries above 110 psu, namely *Pseudogobius olorum* (Sauvage 1880) in a salinity of 114 psu and *Atherinosoma elongatum* (Klunzinger 1879) in a salinity of 147 psu, the latter being close to the record maximum salinity documented for *Atherinosoma microstoma* (Günther 1861) in the Coorong Estuary (Geddes 1987). Each species has its own salinity tolerance 'envelope', so different species are likely to experience mass mortalities at different stages in a rising salinity regime, e.g. *Acanthopagrus butcheri* (Munro 1949) in two normally closed Western Australian estuaries became stressed at a salinity of ~60 psu and underwent a massive mortality at salinities above 82 psu (Hoeksema et al. 2006).

Temperature

Laboratory experiments using estuarine fish species have shown clearly that water temperature has a major effect on the ichthyofauna in these systems. Oxidative stress responses in the muscles of several estuary-associated fish taxa from different families (Gobiidae, Moronidae, Mugilidae, Sparidae) showed that these species were highly sensitive to temperature increases as they approach their critical thermal maximum and that there is a relationship between thermal stress and oxidative stress responses (Madeira et al. 2013).

Different fish species have different thermal habitat preferences and this results in some separation between taxa along the thermal axis of an estuary. In a study by Attrill and Power (2004) in the Thames Estuary, temperature-abundance relationships for 16 fish species showed some degree of separation along the thermal niche axis. This provided some evidence for resource separation based on temperature preferences, thus reducing competition between the species feeding on similar types of prey. Also of relevance was the finding that only a few of the study fish species had a significant distribution overlap with that of their potential prey, thus indicating that optimal thermal habitat may be more important to certain fishes than food supply.

Some laboratory studies have shown little interaction between temperature and salinity tolerance 'envelopes' for estuary-associated species, e.g. results indicate that water temperature is the prime determinant for the distribution pattern of the southern African estuary-dependent sparid *Rhabdosargus holubi* (Steindachner 1881) (Blaber 1973). As a strong osmoregulator across a salinity range of 1–70 psu, *R. holubi* is capable of adjusting the internal osmotic concentration of its body fluids such that it can tolerate both oligohaline and hyperhaline salinities (Blaber 1974), with extremes in the above salinity range seldom being recorded in estuaries on the subcontinent.

Martin (1988) found a strong interaction between the salinity and temperature tolerances of three species of Anbassidae in subtropical South African estuaries. The distribution of the three species within estuaries reflect the differing physiological tolerances in the family, with *Ambassis ambassis* (Lacepéde 1802) restricted to the low salinity (< 10 psu) upper reaches of estuaries where water temperatures are lowest, *Ambassis natalensis* Gilchrist & Thomson 1908 in intermediate salinities and temperatures in the middle reaches, and *Ambassis*

dussumieri Cuvier 1828 in the lower reaches of these systems where salinities and temperatures are often the highest.

Fish species with high Critical Thermal Maximum (CTMax) temperatures, e.g. *Chelon ramada* (Risso 1827) with a CTMax of 38°C (Madeira et al. 2012), are usually found in intertidal areas that are shallow and prone to warming. Similarly, *Terapon jarbua* (Frabicius 1775) is frequently found in the littoral zone of tropical and subtropical estuaries and this species has a CTMax of 43.8°C, close to the biokinetic limits for vertebrate life (Eme et al. 2011). Although both the above fishes clearly have the capacity to tolerate further increases in current estuarine water temperatures associated with global warming, other estuarine species may already be near their thermal limits and therefore have limited acclimation capacity. Thus a number of estuary-associated fish species that occupy littoral habitats, particularly those early juveniles that occur in very shallow intertidal waters, are likely to be most vulnerable to global warming. Even deeper channel waters will not be immune to global warming and therefore be unable to offer thermal refugia to fishes on a scale that is currently available within these systems (Waltham and Sheaves 2017).

Global warming of estuaries does not have to be in the upper 30°C range to have a major impact on associated fish assemblages. In high latitude estuaries, a summer water temperature that exceeds 15°C can also have a significant influence on the cool-temperate fish species within such systems (Thorman 1986). Warm-temperate estuaries have fish species with higher temperature thresholds than those in cool-temperate regions. In a laboratory study of five estuary-associated fish species from the Tagus Estuary (Portugal), stress oxidative enzymes showed alterations with increasing temperatures above the control temperature of 24°C (Madeira et al. 2013). Clearly global warming is likely to increase the stress of many estuary-associated fish species but the degree to which this stress is translated into exclusion from estuarine habitats is largely unknown.

Turbidity

Laboratory studies have shown that suspended particles can have a major negative effect on the feeding efficiency of certain fish predators that rely on sight when foraging (Benfield and Minello 1996). The experiments indicated that scattering of light caused by these particles, and not light intensity per se, was responsible for

the lack of predator success. Reactive distances between fish predator and prey were governed primarily by turbidity, while light intensity had little influence except under low turbidity conditions. Fish larvae have a short visual field and therefore only detect individual zooplankton when close to the prey item. Hence, in turbid waters there are fewer particles between them and their prey than is the case with large predatory fishes (Utne-Palm 2002). In addition, turbid waters inhibit the detection of small fish by visual piscivores that do not use ancillary pressure, sound or chemosensory systems to detect prey, thus also being positive for these early life stages.

Most fish species in estuaries have the ability to adapt their foraging behavior according to prevailing turbidity conditions. However, the feeding rate of visual predators is negatively affected by increased turbidities but those fish species that are zoobenthic foragers, or use alternative foraging methods, are less affected (Hecht and van der Lingen 1992). Similar findings are expressed by Lowe et al. (2015) on the foraging success and health of *Chrysophrys auratus* (Forster 1801) in New Zealand estuaries. The juveniles of *C. auratus* changed their diet from zooplankton to zoobenthos as sediment induced turbidities increased, but there was a simultaneous increasing trend in gill deformation and parasite loads.

Detailed field and laboratory studies on the responses of juvenile marine fish species using South African estuaries as nurseries has shown that the majority of these taxa are attracted to turbid waters in these systems (Cyrus and Blaber 1987a, b, c). Similarly, Blaber and Blaber (1980) concluded that turbidity was the single most important variable influencing juvenile marine fishes entering estuaries in Moreton Bay (Australia). Indeed, Blaber (1981) has suggested that the evolution of many estuary-associated species in shallow northern Indo-Pacific areas was associated with reduced salinity turbid coastal waters, and that estuaries in south-eastern Africa and possibly elsewhere provide a replica of that type of natal environment.

Similar to water temperature, turbidity influences both fishes and invertebrates in estuaries. Changing turbidity alters trophic interactions by altering fish and invertebrate assemblages in estuaries, e.g. turbidity in certain Texas (USA) estuaries is increasing due to human disturbance and nutrient inputs, and this is impacting on both fish and crab species that have different turbidity preferences (Lunt and Smee 2014). Fish species such as *Sciaenops ocellatus* (Linnaeus 1766), *Pogonias cromis* (Linnaeus 1766) and *Archosargus probatocephalus* (Walbaum 1792) were most abundant in low turbidities (< 30 NTU), while crab populations were more abundant in high turbidities (> 30 NTU). Changing turbidities therefore result in altered estuarine fish and invertebrate assemblages and consequently changes in trophic interactions within such systems.

There is little interaction between turbidity and temperature but salinity does have an influence on turbidity levels, particularly that of river water entering an estuary. This is because dissolved and/or suspended organic and inorganic particulate matter is precipitated out of river water by elevated salinity (Sholkovitz 1976), thus reducing turbidity and changing the water characteristics for fish in an estuary.

Future trends

The ichthyofauna in estuaries, from a salinity tolerance perspective, can be grouped into five major guilds, the marine teleosts and elasmobranchs, estuarine and freshwater teleosts, and diadromous taxa (Whitfield et al. 1981). The marine and estuarine teleosts have been recorded in the full salinity range from oligohaline and hyperhaline waters, the diadromous species use freshwater, estuarine and marine environments during the completion of their life cycle, with marine elasmobranchs and freshwater taxa being the least euryhaline of the five guilds. Elasmobranchs tend to occur in euhaline and polyhaline waters, whereas freshwater fishes are normally restricted to oligohaline or slightly mesohaline areas of estuaries (Whitfield 2019). The euryhalinity, and therefore the ability of these different groups to tolerate further variability in estuarine salinity, is unlikely to change in the future.

Global change, including climate change, is gaining momentum and the impact on estuaries around the world is increasing (Gillanders et al. 2011). The question then arises, will the physico-chemical tolerance 'envelope' of many estuary-associated fish species be exceeded such that they are no longer able to occupy these systems on a continuous or even intermittent basis? Examples of two large estuaries that have suffered from such anthropogenic changes are Lake St Lucia (South Africa) and the Murray/Coorong Estuary (Australia). These systems have had major reductions in riverine inputs (Lawrie and Stretch 2011, Webster

2010), with extreme hypersalinity becoming a semi-permanent feature of both estuaries and having devastating consequences for the ichthyofauna (Whitfield et al. 2006, Cyrus et al. 2010, Hossain et al. 2016, Wedderburn et al. 2016). Indeed, there are strong indications that hypersalinity in certain other estuaries may also become a primary determinant as to whether such systems can continue to function as nursery areas for estuary-dependent marine species (Fig. 2; dos Santos Sales et al. 2018).

Turbidity in estuaries is also likely to continue to increase in the future, driven mainly by inappropriate agricultural methods, overgrazing by livestock, removal of natural vegetation, and general degradation of the associated catchments (Wolanski and Spagnol 2000). The increased sediment loads entering estuaries will not only lead to higher turbidities, they will also lead to a shallowing of the estuarine profile and therefore make these systems more vulnerable to global warming. Both the above trends are likely to have negative consequences for certain components of current estuarine fish assemblages.

Conclusions

Although the three primary physico-chemical drivers are dealt with mainly separately in this review, there are strong links between them that need to be emphasized. The interplay between salinity and temperature in particular is very important to most fish species in estuaries since osmoregulation is an energetically costly process and both salinity and temperature have a strong influence on the osmotic capabilities of each species in this regard. Similarly the elevated salinity levels in estuaries can cause the flocculation of dissolved organic and inorganic material in river water, thus improving turbidity levels for fishes in the estuary and thereby having a major influence on foraging success.

All three physico-chemical variables discussed in this review are responsible for creating an aquatic environment that is constantly changing from a spatial and temporal perspective (Fatema et al. 2014), with extreme conditions and the resetting of the estuarine ichthyofaunal composition often associated with poor marine and/or freshwater connectivity (Fig. 2; Sheaves and Johnston 2008). The above three driving variables, together with connectivity issues, have led to estuaries having a relatively low fish species diversity and

richness when compared to adjacent marine and freshwater environments (Blaber 1980; Whitfield 2015) but those species tolerating these conditions benefit from the rich food resources of estuaries.

This review provides strong support for Estuarine Paradigm 5 of Elliott and Whitfield (2011), namely "Estuaries are physico-chemically more variable than other aquatic systems but estuarine communities are less diverse taxonomically and the individuals are more physiologically adapted to environmental variability than equivalent organisms in other aquatic systems." However, the assumption that those fish species currently associated with estuaries are highly eurytopic and can therefore easily cope with further changes in salinity, temperature and turbidity brought about by global change, has yet to be fully tested.

The fact that some marine and many estuarine fish species have become completely dependent on estuaries for all or part of their life cycle bears testimony to the value of these systems for the survival of these taxa. Extreme physico-chemical conditions are tolerated within certain limits but it is probable that these limits will be increasingly tested in the climate change period that lies ahead. In this regard the lack of fish species redundancy in estuaries is also relevant, particularly if the species that are lost are dependent on these systems for their existence.

Declarations

Conflict of interest The author hereby declares that this review was written without any conflicts of interest.

Research involving animals This review used only published literature and did not include any research on living or preserved animals requiring ethical clearance.

References

Attrill MJ, Power M (2004) Partitioning of temperature resources amongst an estuarine fish assemblage. Est Coast Shelf Sci 61: 725–738

Barletta M, Barletta-Bergen A, Saint-Paul U, Hubold G (2005) The role of salinity in structuring in structuring the fish assemblages in tropical estuaries. J Fish Biol 66:45–72

Benfield MC, Minello TJ (1996) Relative effects of turbidity and light intensity on reactive distance and feeding of an estuarine fish. Environ Biol Fish 46:211–216

Bennett BA (2010) A mass mortality of fish associated with low salinity conditions in the Bot River estuary. Trans Roy Soc S Afr 45:437–447

Blaber SJM (1973) Temperature and salinity tolerance of juvenile *Rhabdosargus holubi* (Steindachner) (Teleostei: Sparidae). J Fish Biol 5:593598

Blaber SJM (1974) Osmoregulation in juvenile *Rhabdosargus holubi* (Steindachner) (Teleostei: Sparidae). J Fish Biol 6: 797800

Blaber SJM (1980) Fish of the Trinity Inlet system of north Queensland with notes on the ecology of fish faunas of tropical Indo-Pacific estuaries. Aust J Mar Freshw Res 31: 137–146

Blaber SJM (1981) The zoogeographical affinities of estuarine fishes in southeast Africa. S Afr J Sci 77:305307

Blaber SJM (1991) Deep sea, estuarine and freshwater fishes: life history strategies and ecological boundaries. S Afr J Aquat Sci 17:2–11

Blaber SJM, Blaber TG (1980) Factors influencing the distribution of juvenile estuarine and inshore fish. J Fish Biol 17:143–162

Blaber SJM, Whitfield AK (1976) Large scale mortality of fish at St Lucia. S Afr J Sci 72:218

Cloern JE (1987) Turbidity as a control on phytoplankton biomass and productivity in estuaries. Cont Shelf Res 7:1367–1381

Cyrus DP (1988a) Turbidity and other physical factors in Natal estuarine systems. Part 1: Selected estuaries. J Limnol Soc Sth Afr 14:6071

Cyrus DP (1988b) Turbidity and other physical factors in Natal estuarine systems. Part 2: Estuarine lakes. J Limnol Soc Sth Af 14:7281

Cyrus DP, Blaber SJM (1987a) The influence of turbidity on juvenile marine fish in the estuaries of Natal, South Africa. Cont Shelf Res 7:14111416

Cyrus DP, Blaber SJM (1987b) The influence of turbidity on juvenile marine fishes in estuaries. Part 1. Field studies at Lake St Lucia on the southeastern coast of Africa. J Exp Mar Biol Ecol 109:5370

Cyrus DP, Blaber SJM (1987c) The influence of turbidity on juvenile marine fishes in estuaries. Part 2. Laboratory studies, comparisons with field data and conclusions. J Exp Mar Biol Ecol 109:7191

Cyrus DP, Blaber SJM (1992) Turbidity and salinity in a tropical northern Australian estuary and their influence on fish distribution. Est Coast Shelf Sci 35:545–563

Cyrus DP, Vivier L (2006) Status of the estuarine fish fauna in the St Lucia estuarine system, South Africa, after 30 months of mouth closure. Afr J Aquat Sci 31:71–81

Cyrus DP, Vivier L, Jerling HL (2010) Effect of hypersaline and low lake conditions on ecological functioning of St Lucia estuarine system, South Africa: an overview 2002–2008. Est Coast Shelf Sci 86:535–542

Dando PR (1984) Reproduction in estuarine fish. In: Potts GW, Wootton RJ (eds) Fish Reproduction: Strategies and Tactics. Academic, London

de Jonge VN, Schuttelaars HM, van Beusekom JEE, Talke SA, de Swart HE (2014) The influence of channel deepening on estuary turbidity levels and dynamics, as evidenced by the Ems estuary. Est Coast Shelf Sci 139:46–59

Dionne J-C (1984) An estimate of ice-drifted sediments based on the mud content of the ice cover at Montmagny, middle St Lawrence Estuary. Mar Geol 57:149–166

dos Santos Sales N, Baeta ASBV, de Lima LG, Pessanha ALM (2018) Do the shallow-water habitats of a hypersaline tropical estuary act as nursery grounds for fishes? Mar Ecol 39: e12473

Elliott M, Quintino V (2006) The Estuarine Quality Paradox, Environmental Homeostasis and the difficulty of detecting anthropogenic stress in naturally stressed areas. Mar Poll Bull 54:640–645

Elliott M, Whitfield AK (2011) Challenging paradigms in estuarine ecology and management. Est Coast Shelf Sci 94:306–314

Eme J, Dabruzzi TF, Bennett WA (2011) Thermal responses of juvenile squaretail mullet (*Liza vaigiensis*) and juvenile crescent tarpon (*Terapon jarbua*) acclimated at near-lethal temperatures, and the implications for climate change. J Exp Mar Biol Ecol 399:35–38

Fatema K, Maznah WOW, Isa MM (2014) Spatial and temporal variation of physic-chemical parameters in the Merbok Estuary, Kedha, Malaysia. Trop Life Sci Res 25:1–19

Froneman PW (2002) Seasonal changes in selected physico-chemical and biological variables in the temporarily open/ closed Kasouga estuary, Eastern Cape, South Africa. Afr J Aquat Sci 27:117–123

Garcia AM, Vieira JP, Winemiller KO (2003) Effects of 1997–1998 El Niňo on the dynamics of the shallow-water fish assemblage of the Patos Lagoon estuary (Brazil). Est Coast Shelf Sci 57:489–500

Garvine RW (1975) The distribution of salinity and temperature in the Connecticut River estuary. J Geophys Res 80:1176–1183

Geddes MC (1987) Changes in salinity and the distribution of macrophytes, macrobenthos and fish in the Coorong lagoons, South Australia, following a period of River Murray flow. Trans R Soc S Aust 111:74–89

Geyer WR (1993) The importance of suppression of turbulence by stratification on the estuarine turbidity maximum. Estuaries 16:113–125

Giffard-Mena I, Hernández-Montiel AH, Pérez-Robles J, David-True C (2020) Effects of salinity on survival and plasma osmolality of *Totoaba macdonaldi* eggs, larvae and juveniles. J Exp Mar Biol Ecol 526. https://doi.org/10.1016/j.jembe.2020.151339

Gillanders BM, Elsdon TS, Halliday IA, Jenkins GP, Robins JB, Valesini FJ (2011) Potential effects of climate change on Australian estuaries and fish utilising estuaries: a review. Mar Freshwat Res 62:1115–1131

Gillanders BM, McMillan MN, Reis-Santos P, Baumgartner LJ, Brown LR, Conallin J, Feyrer V, Henriques S, James NC, Jaureguizar AJ, Pessanha ALM, Vasconcelos RP, Vu AV, Walther B, Wibowo A (2021) Chap. 7. Climate change and fishes in estuaries. In: Whitfield AK, Able KW, Blaber SJM, Elliott M (eds) Fish and Fisheries in Estuaries: A Global Perspective. Wiley, Chichester

Grange N, Allanson BR (1995) The influence of freshwater inflow on the nature, amount and distribution of seston in estuaries of the Eastern Cape, South Africa. Est Coast Shelf Sci 40: 403–420

Harrison TD, Whitfield AK (2006) Temperature and salinity as primary determinants influencing the biogeography of fishes in South African estuaries. Est Coast Shelf Sci 66:335–345

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

Hoeksema SM, Chuwen M, Potter IC (2006) Massive mortalities of black bream, *Acanthopagrus butcheri*(Sparidae) in two normally closed estuaries, following enormous increases in salinity. J Mar Biol Soc UK 86:893–897

Hoeksema SM, Chuwen M, Tweedley JR, Potter IC (2018) Factors influencing marked variations in the frequency and timing of bar breaching and salinity and oxygen regimes among normally-closed estuaries. Est Coast Shelf Sci 208: 205–218

Holliday FGT (1969) The effects of salinity on the eggs and larvae of teleosts. Fish Physiol 1:293–311

Hossain MA, Aktar S, Qin JG (2016) Salinity stress response in estuarine fishes from the Murray Estuary and Coorong, South Australia. Fish Physiol Biochem 42:1571–1580

Irigoien X, Castel J (1997) Light limitation and distribution of chlorophyll pigments in a highly turbid estuary: the Gironde (SW France). Est Coast Shelf Sci 44:507–517

Kimmerer WJ (2002) Physical, biological, and management responses to variable freshwater flow into San Francisco Estuary. Estuaries 25:1275–1290

Krumme U (2009) Chap. 8. Diel and tidal movements by fish and decapods linking tropical coastal systems. In: Nagelkerken I (ed) Ecological Connectivity among Tropical Coastal Ecosystems. Springer, Dordrecht, pp 271–325

Largier JL, Slinger JH (1991) Circulation in highly stratified southern African estuaries. Sth Afr J Aquat Sci 17:103–115

Largier JL, Hollibaugh JT, Smith SV (1997) Seasonally hypersaline estuaries in Mediterranean-climate regions. Est Coast Shelf Sci 45:789–797

Lawrie RA, Stretch DD (2011) Occurrence and persistence of water level/salinity states and the ecological impacts for St Lucia estuarine lake, South Africa. Est Coast Shelf Sci 95: 67–76

Lowe ML, Morrison MA, Taylor RB (2015) Harmful effects of sediment-induced turbidity on juvenile fish in estuaries. Mar Ecol Prog Ser 539:242–254

Lunt J, Smee DL (2014) Turbidity influences trophic interactions in estuaries. Limnol Oceanogr 59:2002–2012

Madeira D, Narciso L, Cabral HN, Vinagre C (2012) Thermal Influence and potential impacts of climate change on coastal and estuarine organisms. J Sea Res 70:32–41

Madeira D, Narciso L, Cabral HN, Vinagre C, Diniz MS (2013) Influence of temperature in thermal and oxidative stress responses in estuarine fish. Comp Biochem Physiol A 166: 237–243

Martin TJ (1988) Interaction of salinity and temperature as a mechanism for spatial separation of three coexisting species of Ambassidae (Cuvier)(Teleostei) in estuaries on the southeast coast of Africa. J Fish Biol 33(Suppl A):915

Martin SB, Hitch AT, Purcell KM, Klerks PL, Leberg PL (2009) Life history variation along a salinity gradient in coastal marshes. Aquat Biol 8:15–28

McCormick SD (2001) Endocrine control of osmoregulation in teleost fish. Amer Zool 41:781–794

Nichols MM (1977) Response and recovery of an estuary following a river flood. J Sediment Petrol 47:1171–1186

Nicholson G, Jenkins GP, Sherwood J, Longmore A (2008) Physical environmental conditions, spawning and early life-stages of an estuarine fish: climate change implications for recruitment in intermittently open estuaries. Mar Freshw Res 59:735–749

Peterson MS, Ross ST (1991) Dynamics of littoral fishes and decapods along a coastal river-estuarine gradient. Est Coast Shelf Sci 33:467–483

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 Fish 28:143178

Ralston DK, Rockwell Geyer W, Lerczak JA (2010) Structure, variability, and salt flux in a strongly forced salt wedge estuary. J Geophys Res 115. https://doi.org/10.1029/2009 JC005806

Reid GK, Wood RD (1976) Chap. 5. Estuaries. In: Ecology of Inland Waters and Estuaries. Van Nostrand, New York, pp 93–107

Roessig JM, Woodley CM, Cech JJ, Hansen LJ (2004) Effects of global climate change on marine and estuarine fishes and fisheries. Rev Fish Biol Fisher 14:251–275

Sakamoto T, McCormick SD (2006) Prolactin and growth hormone in fish osmoregulation. Gen Comp Endocrinol 147:24–30

Scanes E, Scanes PR, Ross PM (2020) Climate change rapidly warms and acidifies Australian estuaries. Nature Comm. https://doi.org/10.1038/s41467-020-15550-z

Schroeder WW, Dinnel SP, Wiseman WJ (1990) Salinity stratification in a river-dominated estuary. Estuaries 13:145–154

Sheaves M, Johnston R (2008) Influence of marine and freshwater connectivity on the dynamics of subtropical estuarine wetland fish metapopulations. Mar Ecol Prog Ser 357:224–243

Sholkovitz ER (1976) Flocculation of dissolved organic and inorganic matter during the mixing of river water and sea water. Geochem Cosmochim Acta 40:831–845

Smith LS (1982) Introduction to Fish Physiology. TFH Publications, Neptune, pp 1–352

Sogard SM (1992) Variability in growth rates of juvenile fishes in different estuarine habitats. Mar Ecol Prog Ser 85:35–53

Sylvester JR, Nash CE, Emberson CR (1975) Salinity and oxygen tolerances of eggs and larvae of Hawaiian striped mullet, *Mugil cephalus* L. J Fish Biol 7:621–629

Ter Morshuizen LD, Whitfield AK, Paterson AW (1996) Influence of freshwater flow regime on fish assemblages in the Great Fish River and estuary. Sth Afr J Aquat Sci 22:52–61

Thorman S (1986) Seasonal colonisation and effects of salinity and temperature on species richness and abundance of fish of some brackish and estuarine shallow waters in Sweden. Ecography 9:126–132

Toft JD, Munsch SH, Cordell JR, Siitari K, Hare VC, Holycross BM, DeBruyckere LA, Greene CM, Hughes BB (2018) Impact of multiple stressors on juvenile fish in estuaries of the northeast Pacific. Glob Change Biol 24:2008–2020

Tweedley JR, Dittmann SR, Whitfield AK, Withers K, Hoeksema SD, Potter IC (2019) Chap. 30 – Hypersalinity: global distribution, causes, and present and future effects on the biota of estuaries and lagoons. In: Wolanski E, Day J, Elliott M, Ramachandran R (eds) Coasts and Estuaries: The Future. Elsevier, Amsterdam, pp 523–546

Uncles RJ, Stephens JA, Smith RE (2002) The dependence of estuarine turbidity on tidal intrusion length, tidal range and residence time. Cont Shelf Res 22:1835–1856

Utne-Palm AC (2002) Visual feeding of fish in a turbid environment: physical and behavioural aspects. Mar Fresh Behav Physiol 35:111–128

Waltham NJ, Sheaves M (2017) Acute thermal tolerance of tropical estuarine fish occupying a man-made tidal lake, and increased exposure risk with climate change. Est Coast Shelf Sci 196:173–181

Webster IT (2010) The hydrodynamics and salinity regime of a coastal lagoon – the Coorong, Australia – seasonal to multi-decadal timescales. Est Coast Shelf Sci 90:264–274

Wedderburn SO, Bailey CP, Delean S, Paton DC (2016) Population and osmoregulatory responses of a euryhaline fish to extreme salinity fluctuations in coastal lagoons of the Coorong, Australia. Est Coast Shelf Sci 168:40–57

Whitfield AK (1995) Mass mortalities of fish in South African estuaries. S Afr J Aquat Sci 21:29–34

Whitfield AK (2015) Why are there so few freshwater fish species in most estuaries? J Fish Biol 86:1227–1250

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 Fisher 27:75–110

Whitfield AK (2019) Fishes of southern African estuaries: from species to systems. Smithiana Monogr 4:1–495

Whitfield AK (2020a) Littoral habitats as major nursery areas for fish species in estuaries: a reinforcement of the reduced predation paradigm. Mar Ecol Prog Ser 649:219–234

Whitfield AK (2020b) Fish species in estuaries – from partial association to complete dependency. J Fish Biol 97:1262–1264 ()

Whitfield AK, Elliott M (2011) Ecosystem and biotic classifications of estuaries and coasts. In: Wolanski E, McLusky DS (eds) Treatise on Estuarine and Coastal Science, vol 1. Academic, Waltham, pp 99–124

Whitfield AK, Harrison TD (2020) Fish species redundancy in estuaries: a major conservation concern in temperate estuaries under global change pressures. Aquat Conserv Mar Freshw Ecosyst. https://doi.org/10.1002/aqc.3482

Whitfield AK, Blaber SJM, Cyrus DP (1981) Salinity ranges of some southern African fish species occurring in estuaries. S Afr J Zool 16:151–155

Whitfield AK, Taylor RH, Fox C, Cyrus DP (2006) Fishes and salinities in the St Lucia system – A review. Rev Fish Biol Fisher 16:1–20

Wilson JG (2002) Productivity, fisheries and aquaculture in temperate estuaries. Est Coast Shelf Sci 55:953–967

Winger PV, Lasier PJ (1994) Effects of salinity on striped bass eggs and larvae from the Savannah River, Georgia. Trans Am Fish Soc 123:904–012

Wolanski E, Spagnol S (2000) Environmental degradation by mud in tropical estuaries. Reg Environ Change 1:152–162