Vol. 57: 233–248, 2013
doi: 10.3354/cr01178

CLIMATE RESEARCH
Clim Res

REVIEW

Effects of climate change on South African estuaries and associated fish species

Nicola C. James[1,*], Lara van Niekerk[2,3], Alan K. Whitfield[1], Warren M. Potts[4], Albrecht Götz[3,5], Angus W. Paterson[1]

[1]South African Institute for Aquatic Biodiversity (SAIAB), Private Bag 1015, Grahamstown 6140, South Africa
[2]CSIR, Natural Resources and the Environment, PO Box 320, Stellenbosch 7599, South Africa
[3]Nelson Mandela Metropolitan University, PO Box 77000, Port Elizabeth 6031, South Africa
[4]Department of Ichthyology and Fisheries Science, Rhodes University, Grahamstown 6140, South Africa
[5]Elwandle Node, South African Environmental Observation Network (SAEON), Private Bag 1015, Grahamstown 6140, South Africa

ABSTRACT: Estuaries are dynamic and their physical and chemical characteristics can change over a scale of hours to years. Consequently, estuarine fish assemblages often exhibit large temporal variations in abundance and composition related to changes in a range of parameters such as river flow, estuarine mouth phase, habitat availability, temperature, salinity and turbidity, all of which are likely to be highly affected by climate change. Many organisms become more stressed towards their range boundaries and the distributions of these species can be expected to shift as environmental conditions change. Preliminary studies have highlighted the increased occurrence of tropical fish species in estuaries along the southeast coast of South Africa. Climate change is also predicted to alter precipitation patterns, which will affect the quality, rate, magnitude and timing of freshwater delivery to estuaries, and will potentially exacerbate existing human modifications of these flows. This is likely to result in changes to fish communities, as river flow has been found to have a major impact on the structure and functioning of fish communities in South African estuaries. The predicted increase in the frequency of extreme weather events, together with sea level rise, may result in a loss of estuarine habitat, which will ultimately affect estuarine fish communities and have implications for fisheries targeting estuary-associated species.

KEY WORDS: South Africa · Climate · Change · Estuaries · Impacts · Fishes

1. INTRODUCTION

Estuaries are the meeting place of freshwater from rivers and saltwater from the sea and, as such, are dynamic environments characterised by large fluctuations in environmental conditions (Elliott 2002). Changes in environmental conditions within an estuary may be fairly predictable, or they may be caused by short- and/or long-term unpredictable climatic fluctuations, all of which have large effects on the abundance and distribution of estuarine fish species (Flint 1985, Kupschus & Tremain 2001, Desmond et al. 2002). In most parts of the world, estuaries are shallow and strongly influenced by tidal action, freshwater inflow, wind, wave action, water and air temperature, and rainfall. Consequently, climate change is expected to modify the physical structure and biological functioning of estuaries (Kennedy 1990), and may have a range of implications for estuary-associated fishes. Such changes may also impact various life-history stages outside estuaries, depending on the timing and location of spawning and on when fish leave or enter estuaries (Able & Fahay 2010). In this review we will focus primarily on present and future climate change impacts on the fishes associated with South African estuaries, but will also emphasise the global nature of these influences by citing international studies on this topic.

---

*Email: n.james@saiab.ac.za

2. SOUTH AFRICAN ESTUARIES AND ESTUARY-ASSOCIATED FISH SPECIES

The South African coastline extends for 3650 km from the Orange River mouth in the west to Ponta do Ouro in the east (Fig. 1C). Approximately 250 functional estuaries (comprising a total area of 70 000 ha) intersect the coastline (Turpie et al. 2002), which spans a number of climatic zones and is subject to a range of oceanographic conditions. In terms of oceanography, South Africa uniquely lies at the juxtaposition of 2 major boundary currents, the Agulhas and Benguela (Hutchings et al. 2002, 2009). The oceanography of the west coast is dominated by the Benguela upwelling system, which extends from the vicinity of Cape Agulhas (34° 80′ S) to Cape Frio (18° 30′ S) in northern Namibia. It comprises a general equatorward flow of cool, nutrient-rich water (Olivar

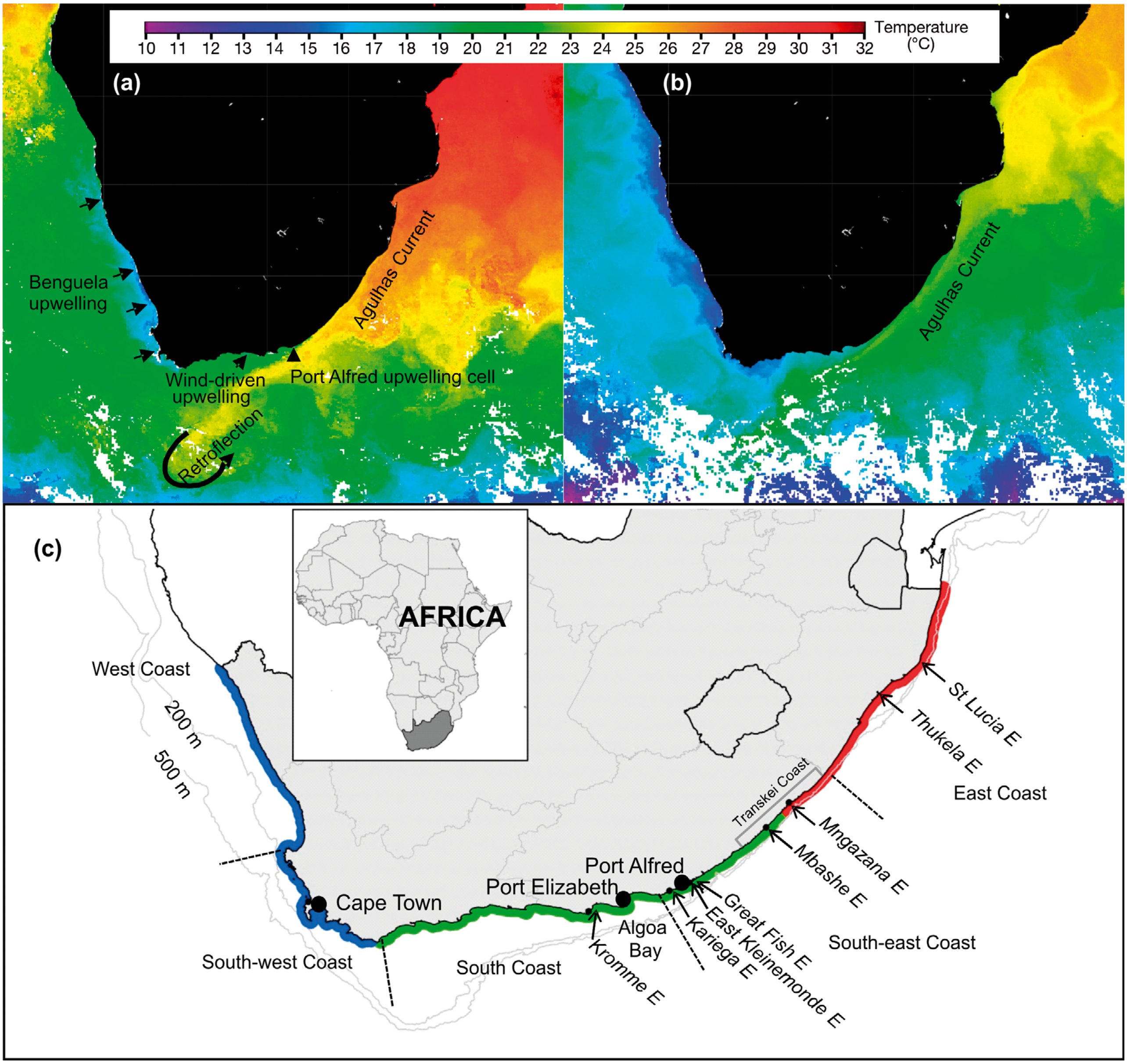

Fig. 1. (a) A MODIS satellite sea surface temperature image in February 2009 (10 d average) illustrating the warm (red) Agulhas Current flowing down the east coast of South Africa, and retroflection of the current at the southern tip of the continent, the location of the Port Alfred upwelling cell, wind-driven upwelling along the south coast and upwelling along the Benguela Current coastal region. (b) A MODIS satellite sea surface temperature image in July 2009 (10 d average) illustrating temperatures in winter. (c) Map of South Africa showing coastal biogeographic regions and estuaries (E) referred to in the text (blue: cool-temperate, green: warm-temperate, red: subtropical)

& Shelton 1993, Hutchings et al. 2002). Strong winds, blowing parallel to the shore, produce upwelling of deep (from 100 to 300 m) South Atlantic Central water along the entire Benguela Current coastal region (Olivar & Shelton 1993) (Fig. 1A).

The Agulhas Current flows strongly southward (poleward) along the South African east and south coast, bringing warm, nutrient-poor tropical water from the equatorial region of the western Indian Ocean (Fig. 1A,B). The current closely follows the continental slope before detaching as a free-flowing jet at the southern tip of the Agulhas Bank. There it retroflects and commonly sheds warm core rings into the South Atlantic (Roberts et al. 2010). Seasonal wind-driven upwelling occurs along the south coast, particularly at prominent headlands, during periods of strong and persistent easterly winds (Schumann et al. 1982, Beckley 1983). Where the current moves from a narrow shelf, past a wider shelf, a degree of upwelling is also experienced. This occurs at the northern corner of the Natal Bight along the east coast and where the Agulhas Current starts flowing along the Agulhas Bank (Lutjeharms 2006). The core of the latter upwelling cell is found at Port Alfred, although it can extend for up to 300 km, from Mbashe in the north to the eastern edge of Algoa Bay (Lutjeharms et al. 2000) (Fig. 1a).

Climatologically, South Africa can be divided into several zones (Tyson 1986). The east coast is a subtropical humid zone that has much higher rainfall (with a peak in summer) than the west coast, primarily due to heat and moisture being transferred from the ocean to the atmosphere in the former region (Cooper 2001, Hutchings et al. 2002, Taljaard et al. 2009). The southern portion of the west coast has a predictable winter rainfall regime (Mediterranean type climate) but the northern portion is a highly arid, cool-temperate zone, with erratic rainfall. The southern coast of South Africa is a warm-temperate zone, with varying rainfall regimes that include summer, winter or bimodal peaks in rainfall (Heydorn & Tinley 1980, Cooper 2001). This climatic variability results in variation in rainfall and river runoff patterns along the coastline.

Variations in coastal topography, fluvial and marine sediment supply have resulted in a variety of estuary types along South Africa's microtidal, wave-dominated coast (Cooper 2001). Estuaries range from permanently open tide-dominated systems to permanently open river-dominated systems, temporarily open/closed systems, estuarine lakes and estuarine bays (Whitfield 1992). The majority of estuaries along the coast of South Africa have small river catchments (<500 km^2) and are closed off from the sea for varying periods by a sand bar that forms at the mouth (Whitfield 1998, Taljaard et al. 2009).

Conditions in South African estuaries are markedly different from those in the adjacent marine inshore waters. These inshore waters are typically subjected to turbulent wave action (McLachlan et al. 1981), while the estuaries are calm, sheltered and shallow. As such they provide important nursery areas for many species of coastal marine fishes (Wallace 1975). Of the 155 fish species that have been recorded in South African estuaries, 103 species (66%) are either completely or partially dependent on estuaries (Whitfield 1994a), with the juveniles of marine-spawning species dominating the estuarine ichthyofauna (Harrison 2005).

Few species occur in all southern African estuaries and many species only occur within a single biogeographic zone. Harrison (2005) conducted an extensive survey of the biogeography and community structure of the ichthyofauna in estuaries along the South African coastline. He recorded a gradual decrease in taxonomic richness from east to west, and this was attributed to a decreasing number of tropical marine species, primarily associated with a decrease in the influence of the warm Agulhas Current in the same direction. Cool- and warm-temperate estuaries were found to be dominated by species that only occur in southern Africa and not by tropical species.

3. CLIMATE CHANGE AND POTENTIAL EFFECTS ON SOUTH AFRICAN ESTUARIES AND FISHES

Estuaries are subject to changes that are occurring in both the terrestrial and marine environments. A change in climate incorporates changes in temperature, wind patterns, evaporation rates, precipitation and CO$_2$ concentrations. Global warming could also result in altered ocean circulation patterns, sea level rise and increased storm frequency, all of which will have profound consequences for estuarine and coastal ecosystems (Roessig et al. 2004). However, we still do not understand the exact impact of these changes on ecosystems, especially in aquatic habitats that are less easily studied and monitored than their terrestrial counterparts (Able & Fahay 2010).

3.1. Temperature

Climate change effects on fishes are often interpreted relative to temperature change (Able & Fahay 2010). It is anticipated that estuaries and estuary-associated fishes will be affected by changes in both surface air and ocean temperatures, with anthropogenic greenhouse gases and aerosols having contributed to an increase in global air and ocean temperatures over the last 50 yr (Solomon et al. 2007). A time series analysis of ocean heat content showed that the global trend is one of warming, with an increase of 0.1°C estimated for the 0–700 m layer of the ocean for the period 1961 to 2003 (Solomon et al. 2007). However, significant decadal variation was observed in the time series, and there are large regions where oceans are cooling.

In the Benguela region, a gradual increase in sea surface temperature (SST) has been recorded, with the warmest years on record falling in the 1980s (Cury & Shannon 2004). Similarly, Rouault et al. (2009) found that since the 1980s the SST of the Agulhas Current has increased significantly by up to 0.7°C per decade (Fig. 2) (Rouault et al. 2009). The warming in the Agulhas Current is attributed to a strengthening of the current associated with an increase in wind stress curl in the South Indian Ocean (Rouault et al. 2009). In coastal areas, warming of up to 0.55°C per decade has been recorded along the Transkei and KwaZulu-Natal coastline (Rouault et al. 2010).

In line with the highly variable nature of the South African coastline, the trend is not uniform and there are several areas along the west, south and southeast coasts where nearshore SSTs are cooling seasonally as a result of an increase in upwelling-favourable winds or a combination of this and an intensification of the Agulhas Current. Along the west coast, a cooling trend is evident close inshore (Hutchings et al. 2009, Rouault et al. 2009), with this trend being pronounced in winter (Rouault et al. 2010). Cooling of up to 0.35°C per decade has been recorded for the south coast and up to 0.4°C per decade for the Port Elizabeth/Port Alfred upwelling region between May and August. No change in temperature was recorded during summer in these 3 regions (Rouault et al. 2010). Rouault et al. (2010) caution that the coarse resolution Reynolds SST that they used for this analysis does not define small-scale oceanic features such as the Port Alfred upwelling cell and this could mask smaller-scale coastal change.

Increasing air temperatures will also affect estuaries and may have a greater impact on temporarily

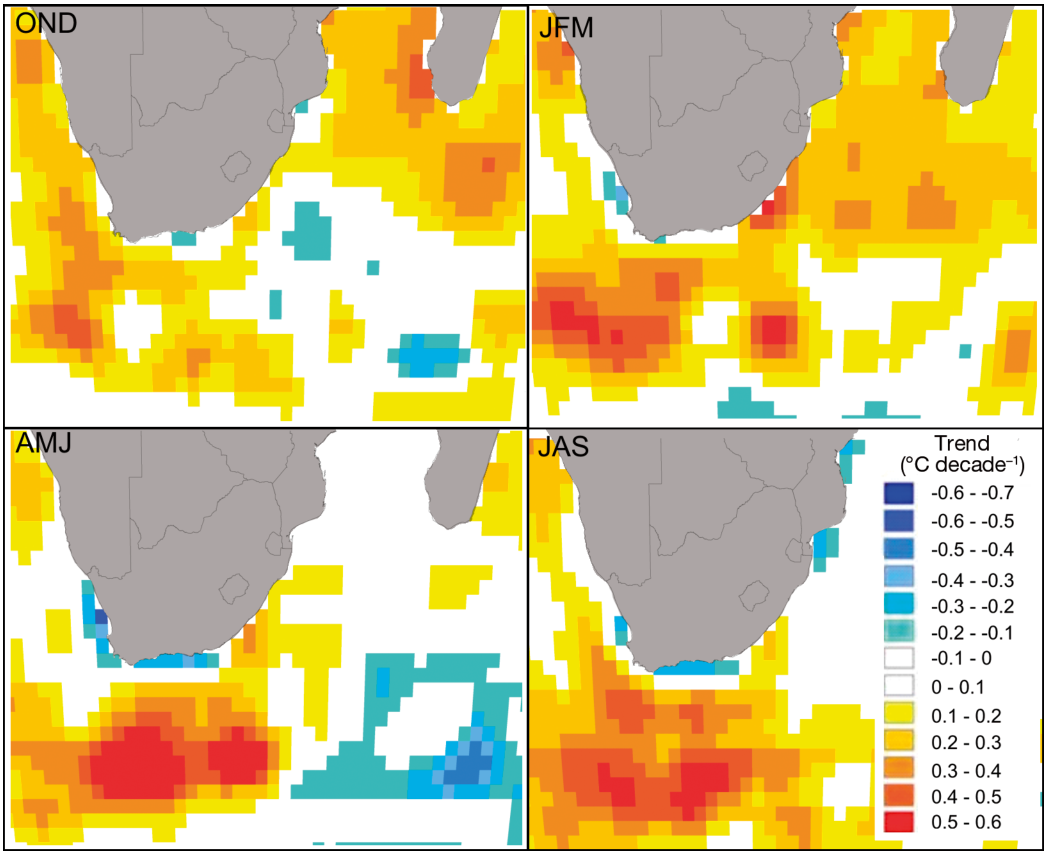

Fig. 2. Linear trend of Reynolds SST temperature from 1982 to 2010

open/closed than permanently open estuaries, as the former systems are cut off from the effect of sea temperatures for long periods and therefore respond to a greater degree to prevailing land, air and river water temperatures (James et al. 2008a). Kruger & Shongwe (2004) investigated a time series of South African surface air temperatures for temporal and spatial trends for the period 1960 to 2003, using a total of 26 climate stations. They identified warming trends in the annual average and annual average maximum and minimum air temperatures over the period. The warmest years were in the early 1980s, and seasonally this warming trend was highest in autumn and lowest in spring.

Temperature and salinity were found to be the primary determinants influencing the biogeography of fishes, particularly tropical species, in South African estuaries (Harrison & Whitfield 2006). According to Elliott (2002), climate change has the potential to affect major aspects of fish physiology, such as their salinity and temperature tolerances; this effect influences their ability to occupy estuarine habitats and ultimately the larger-scale distribution of species. Temperature-dependent processes vary over a species' latitudinal distribution, such that fish populations living at the edge of their species range may be more influenced by changes in temperatures than those living at the centre of their range (Martinho et al. 2012). Distributions of these edge populations can be expected to shift as environmental conditions change.

Changes in the distributional patterns of estuarine and coastal species, associated with warming temperatures, have been recorded both locally and globally. The fish assemblages in the East Kleinemonde Estuary, a warm-temperate temporarily open/closed system on the southeast coast of South Africa, have been studied since December 1995. A total of 38 species of fish were recorded in the East Kleinemonde Estuary between December 1995 and July 2006 (James et al. 2008a). Indicative of warming waters, 6 new tropical species were recorded in the surveys from 1999: *Valamugil cunnesius*, *Valamugil robustus*, *Liza alata* and *Liza macrolepis* (family Mugilidae), *Glossogobius giuris* (family Gobiidae) and *Terapon jarbua* (family Teraponidae). As a result of the increased occurrence of tropical species, the number of species recorded in the estuary between 1996 and 2006 has increased steadily (Fig. 3) (James et al. 2008a).

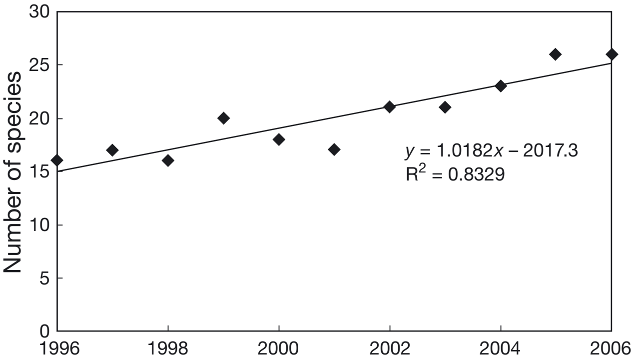

Fig. 3. The total number of fish species recorded in the East Kleinemonde Estuary between 1996 and 2006 (after James et al. 2008a)

There has been a significant increase in annual average maximum air temperatures recorded in summer at Port Alfred, 15 km south of the East Kleinemonde, between 1991 and 2011 (Fig. 4A). Increasing air temperatures may have resulted in increased estuarine water temperatures in summer. Interestingly, only 2 species (*Valamugil cunnesius* and *Liza macrolepis*) were recorded in winter samples. Annual average minimum air temperatures recorded in winter decreased significantly between 1991 and 2011 (Fig. 4B). Figueira et al. (2009) and Figueira & Booth

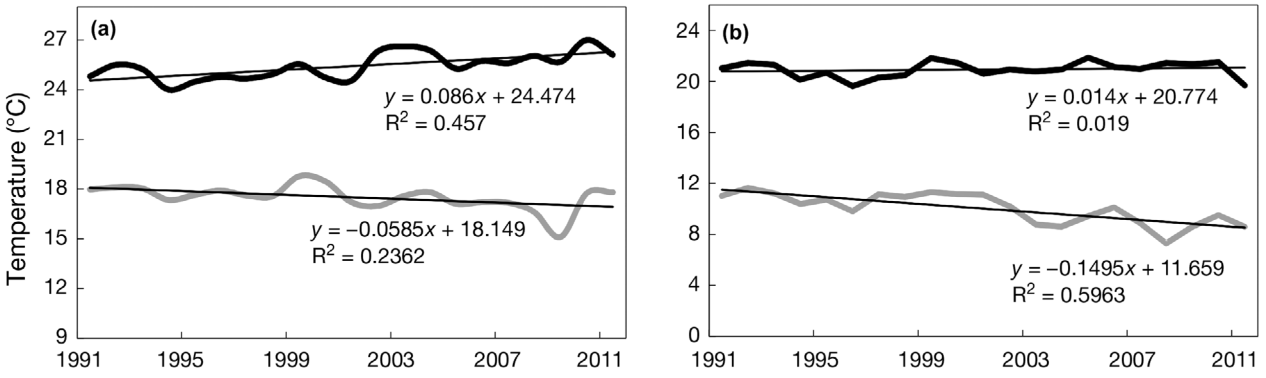

Fig. 4. Mean maximum (black line) and mean minimum (grey line) air temperatures recorded in (a) summer and (b) winter at Port Alfred between 1992 and 2011 (data provided by the South African Weather Service)

(2010) examined the performance of tropical fish species as they recruited into temperate environments along the southeast coast of Australia, and concluded that for the majority of tropical fish species overwinter survival is the ultimate bottleneck for population establishment, with the ability of some tropical species to survive at temperate latitudes determined by the frequency of survivable winters.

Although changes in the numbers of tropical fish species have been recorded in the East Kleinemonde Estuary, the numbers of temperate species have not declined, resulting in an increase in species richness. In time, there is the possibility of a decline in the number of temperate species in temperate systems. Hiddink & Ter Hofstede (2008) attributed increases in species richness in the North Sea to an increase in the occurrence of small warm-water species, such that the number of species lost is less than the number of species gained.

The effects of climate change on fish distributions have also been recorded further north in the permanently open Mngazana Estuary, which is situated in the transition zone between the subtropical and warm-temperate regions. In a study of the fish community undertaken in 1975 (Branch & Grindley 1979), the proportion of tropical species recorded was found to be lower during winter (43 %) than summer (88 %), while temperate species increased during winter (57 %). This was attributed to tropical species extending their ranges southwards during summer and temperate species extending their ranges northwards during winter (Branch & Grindley 1979). In a similar study conducted in the estuary 25 yr later, the proportion of tropical species recorded was identical in summer (71 %) and winter (71 %) (Mbande et al. 2005).

The increase in the proportion of tropical species recorded in the Mngazana Estuary during winter indicates that warming may have increased minimum winter water temperatures above the thermal limits of some of the tropical species. Higher winter water temperatures would favour tropical species during winter, while limiting the northwards penetration of certain temperate species (Mbande et al. 2005). Rouault et al. (2010) documented warming of coastal SSTs for all months of the year in the Transkei region. Similarly, Kruger & Shongwe (2004) found that annual average maximum and minimum air temperatures recorded at East London (south of the estuary) and Durban (north of the estuary) increased significantly for the period 1960 to 2003.

As climate change accelerates, it can be expected that there will be marked changes in the composition of estuarine fish communities, resulting in new mixes of predators, prey and competitors (Roessig et al. 2004, Clark 2006). However, it is very difficult to predict how communities will change in response to climate change, as each species responds differently to warming, and assemblages are unlikely to shift their distribution as a unit. In South Africa, predicting temperature-driven change is further complicated by the number of biogeographic zones found along a relatively short coastline, and the contrasting changes expected in each zone.

Studies conducted off the eastern United States have shown that the key prey species (such as Atlantic herring and Atlantic mackerel) of some non-shifting sedentary predators (such as Atlantic cod) were often the most temperature sensitive (Murawski 1993). Similarly, shifting species in the North Sea were found to have smaller body sizes, faster maturation and smaller sizes at maturity (Perry et al. 2005). These authors hypothesized that this was because fish species with faster turnover rates respond more rapidly to climate change, resulting in stronger distributional shifts. Although aquatic species generally face fewer constraints to their movement than terrestrial species, climate change may also pose a greater threat to species when their dispersal capabilities are limited or suitable habitat becomes unavailable (Perry et al. 2005, Sunday et al. 2012). Conversely, increasing water temperatures may have positive impacts (such as increased growth, maturity and feeding rates) on certain fish species, provided it occurs within their tolerance range (Murawski 1993). Faster growth may improve an individual's chance of survival through reduced susceptibility to predation during the shortened juvenile life stages (Drinkwater et al. 2010, Gillanders et al. 2011).

Seasonal cooling of nearshore SSTs, associated with intensified upwelling, further complicates predictions in temperate regions (Roessig et al. 2004) and may have severe consequences for coastal and estuarine species along the west and south coasts of South Africa. Sudden shifts in temperature can be lethal to fish, especially if shallow water prevents them from finding a thermal refuge (Roessig et al. 2004). In South Africa, estuaries can provide thermal refuge for coastal species; however, mass mortalities of coastal fish have been recorded along the south coast of South Africa when upwelling causes a sudden drop in water temperature (Hanekom et al. 1989). Sudden decreases in temperature will affect both temperate and tropical species and may prevent the range extensions of tropical species into temperate regions.

3.2. Rainfall and run-off

Climate change is predicted to alter precipitation patterns, which will affect the quality, rate, magnitude and timing of freshwater delivery to estuaries, and will potentially exacerbate human modifications of these flows (Alber 2002). The functioning of estuaries is strongly influenced by the magnitude and timing of freshwater runoff reaching them (Turpie et al. 2002, Taljaard et al. 2009). Downscaled regional climate models derived from global climate models indicate the likelihood of increased summer rainfall over the eastern part of South Africa and a slight decrease in wintertime frontal rainfall (during the latter half of winter) in the Western Cape (Hewitson & Crane 2006, Engelbrecht et al. 2009, 2011). The increased rainfall projected for the east coast would be in the form of more rain days and an increase in heavy/extreme precipitation events during summer (Hewitson & Crane 2006, Engelbrecht et al. 2009, 2011). If these scenarios are correct, the combination of generally wetter conditions and heavy precipitation events would result in more runoff being generated. The decrease in rainfall along the west coast and adjacent interior, with the possibility of a slight increase in inter-annual variability, would result in a decrease in flows and an increase in flow variability, as changes in precipitation are amplified in the hydrological cycle (Hewitson & Crane 2006, Engelbrecht et al. 2009, 2011, Lumsden et al. 2009).

Schulze et al. (2005) assessed the impacts of climate change (including rainfall) on South Africa's water resources and predicted that future climate may be characterized by 'hotspots' of hydrological change, one being the present winter rainfall region of the Western Cape. Reductions in the amount of freshwater entering the Western Cape estuaries would lead to an increase in the frequency and duration of estuary mouth closures and changes in the extent of seawater intrusion, nutrient levels, suspended particulate matter load, temperature, conductivity, dissolved oxygen and turbidity (Clark 2006). The degree to which seawater will enter an estuary is dependent on river inflow and the bathymetry of the system, i.e. seawater penetration into the narrow upper reaches is often constrained by river inflow, with relatively easy penetration into the wider middle reaches, and with the lower reaches generally dominated by tidal flows. Thus the middle reaches of an estuary are likely to show the most sensitivity to changes in flow (river and tidal) and it is this mesohaline region that is most important to larval and juvenile fishes as a nursery area (Strydom et al. 2003).

In large permanently open systems, flow reduction may initially result in a reduction in the extent of the river–estuary interface (REI) zone, i.e. that section of an estuary with an integrated vertical salinity of approximately 10. Major reductions in river flow can result in the complete elimination of this mixed zone so that, effectively, the system functionally becomes an arm of the sea, e.g. the Kromme Estuary (Bate & Adams 2000, Scharler & Baird 2000, Snow et al. 2000, Strydom & Whitfield 2000, Wooldridge & Callahan 2000). If there is no river inflow at all, a reverse salinity gradient may develop, where the salinity at the head of the estuary may exceed that of seawater due to higher rates of evaporation, e.g. the Kariega Estuary (Bate et al. 2002, Whitfield & Paterson 2003).

River flow has been found to have a major impact on the structure and functioning of fish communities within the permanently open Kariega and Great Fish Estuaries, particularly in the upper reaches or REI zone (Bate et al. 2002, Whitfield 2005). High conductivity in the REI zone of the Great Fish Estuary, a freshwater 'enriched' system, in which natural runoff is augmented by an inter-basin transfer of water from the Orange River (Grange et al. 2000), resulted in an abundance of marine and estuarine species in both the REI zone and the river above the ebb and flow (Ter Morshuizen et al. 1996). In contrast, the REI zone of the freshwater-deprived Kariega Estuary was much smaller, resulting in fewer individuals and species being caught in this part of the system (Whitfield & Paterson 2003). Similarly, Whitfield et al. (1994) recorded a higher biomass of fish in the Great Fish Estuary compared with the freshwater deprived Kowie Estuary, and this was attributed to greater nutrient and organic matter input in the Great Fish Estuary, which led to elevated levels of primary and secondary production.

In temporarily open/closed estuaries, mouth opening and closing is directly linked to freshwater input, with estuaries becoming isolated from the sea by the formation of a sand berm across the mouth during periods of low or no freshwater inflow. These systems stay closed until increased freshwater inflow causes their basins to fill up and their berms to breach (Whitfield et al. 2008). Reduced freshwater inflow leads to prolonged mouth closure and shorter open phases, which inhibits the immigration and emigration of fish between estuaries and the sea (Whitfield & Wooldridge 1994, Whitfield et al. 2008), thus resulting in a reduction in species richness and abundance. Changes in the marine fish community structure in the East Kleinemonde Estuary were found to be primarily driven by mouth state (James et al. 2008b), and consequently changes in the frequency of mouth closure may have a profound effect on the fish communities of this and other similar types of estuaries.

Flood events play an important role in the morphology of estuaries as they scour out sediment deposited during periods of low flow. This accumulated sediment is both catchment derived and that brought in from the sea by flood tides. Decreases in rainfall, especially in the Western Cape, would require the construction of additional dams to secure water supplies to support both urban and agricultural needs. Major dams may have the effect of capturing minor (annual) flood peaks entirely and attenuating major flood peaks. The degree to which this will occur depends on the ratio of dam volume to mean annual runoff, the level in the dam preceding the flood event, and the size of the flood event. Therefore, if floods are reduced in intensity and frequency, net sediment deposition and accumulation is likely to lead to a reduction in the water volume and surface area of estuaries. Numerous small farm dams, as well as barrages and weirs, collectively may also have a major impact on the variability and duration of river flow, and consequently the morphology and ecology of estuaries. Instead of being available as river flow to downstream estuaries, the water in these systems is stored and subjected to consumption and losses, including evaporation and seepage.

Although sedimentation is a natural process in estuaries, elevated rates of sediment delivery to estuaries from the terrestrial environment can significantly alter the structure and functioning of estuaries (through factors such as the smothering of benthic communities and elevated turbidity levels) (Thrush et al. 2004). Most terrestrial sediment enters estuaries during storm events as a result of runoff from the land, and river and stream channel erosion (Thrush et al. 2004). Soil erosion in catchments has been identified as a major threat to estuaries in South Africa, particularly those in KwaZulu-Natal and in the former Ciskei and Transkei regions of the Eastern Cape (Morant & Quinn 1999). The potential denuding of vegetation in arid catchments (i.e. increasing the erodibility of soils), coupled with an increase in the frequency of high intensity rain events due to climate change, would lead to a significant increase in the deposition of sediments in estuaries and would further compound the problem.

One of the most important ecological services provided by estuaries is their contribution to fisheries (Lamberth & Turpie 2003). Meynecke et al. (2006) identified clear links between estuarine fish catches and rainfall in Queensland, Australia. Estuarine fish catches in South Africa have been strongly linked to geographical location, size and estuary mouth state (Lamberth & Turpie 2003). Lamberth et al. (2008) predicted that with a 64 % reduction in mean annual runoff in the permanently open Breede Estuary, the abundance of 2 important fishery species, *Argyrosomus japonicus* (Sciaenidae) and *Pomadasys commersonnii* (Haemulidae), would decrease by 50 %. Freshwater runoff may also play an essential role in attracting larval and juvenile estuary-associated marine species into estuaries (Whitfield 1994b, James et al. 2008c).

A change in river flow also affects the nutrient load entering estuaries, with inflow being an important source of nutrients, both dissolved and particulate. Dissolved nutrients include nitrates, phosphates, silica and trace metals that are essential for primary production. Particulates such as organic detritus derived from riparian vegetation may also be an important source of carbon for the estuarine food web. Reduction in freshwater inflow (as a consequence of dam development or climate change in the Western Cape) will reduce the quantity of nutrients entering estuaries, with a resultant impoverishment of the biota. In particular, primary producers such as phytoplankton and benthic diatoms will be adversely affected, with a consequent 'knock-on' effect through the entire food web (Allanson & Baird 1999, Whitfield et al. 2008).

3.3. Climate variability

Resolving the effects of climate change on estuarine fishes is further complicated by the fact that there is strong inter-annual and inter-decadal climate variability in South Africa related to the El Niño Southern Oscillation (ENSO) in the eastern Pacific Basin (e.g. Reason & Rouault 2002, Rouault & Richard 2003, 2005, Rouault et al. 2010, Philippon et al. 2012), the Antarctic Annual Oscillation (Reason et al. 2002, Reason & Rouault 2005), Antarctic sea ice extent (Blamey & Reason 2007), SST in the neighbouring South Atlantic and South Indian Oceans (Reason et al. 2002, Reason & Jagadheesha 2005) and southward migrations of the Inter-Tropical Convergence Zone (Rautenbach & Smith 2001) .

The abundance of fish species worldwide is known to vary considerably as a result of inter-annual and decadal variability in the environment (e.g. Lehodey et al. 2006). Although estuary-associated species are adapted to the extremely variable nature of estuarine environments, many species are overexploited, which may reduce their adaptability to climatic variability and climate change. Hsieh et al. (2006) compared exploited and unexploited fish species living in the same environment and found that exploited fish populations showed higher temporal variability in their population size than unexploited populations. Fish populations may decline at the edge of their distribution under fishing pressure, reducing spatial heterogeneity, and the number of spawning individuals may decline as fishing tends to remove large individuals and thus truncate the age–size structure of exploited populations (Hsieh et al. 2008). This reduces the capacity of a species to counteract short-term unfavourable environmental conditions, ultimately resulting in a close correlation between environmental variability and population size and length frequencies (Hsieh et al. 2006).

The ENSO is thought to be the dominant type of natural variability responsible for changes in SST as well as wind and rainfall patterns in southern Africa (Rouault et al. 2010). Most severe droughts and major warm SST events have occurred during warm (El Niño) episodes and floods and major SST cooling events during cold (La Niña) episodes (Rouault & Richard 2003, 2005, Rouault et al. 2010). In the Northern Hemisphere, the ENSO has been found to affect estuarine fish communities through its effects on rainfall and SST (Garcia et al. 2001, 2004, Martinho et al. 2007). There are no studies linking the ENSO with the structure and functioning of estuarine fish communities in South Africa. However, extreme weather events (floods and droughts) have been found to adversely affect estuarine fish communities. Whitfield & Harrison (2003) recorded a decline in both fish species number and abundance in the Thukela Estuary during periods of high river discharge, which resulted in salinities of zero throughout the estuary on the ebb tide. A 40 % decline in the number of fish species in the St Lucia Estuarine System was attributed to prolonged mouth closure, high salinity and reduced water levels during a drought period between 2001 and 2005 (Cyrus & Vivier 2006).

There seems to be little consensus regarding future patterns of ENSO states in a changing climate. Rouault et al. (2010) analysed fluctuations in SST around the South African coast from 1982 to 2009 and found no trend towards more of an El Niño or La Niña state. However, with a steadily increasing baseline temperature and predicted increases in the frequency of extreme precipitation events, future ENSO episodes may trigger rapid range shifts and community change. According to Walther et al. (2002), species range shifts are often episodic rather than gradual, and in areas affected by ENSO, this rising sea temperature baseline, together with warm ENSO events, may trigger rapid latitudinal range shifts, with 'setbacks' occurring during cool ENSO events.

3.4. Sea level rise, wave energy and storm disturbance

Two significant predicted consequences of climate change are accelerated sea level rise and an increase in the frequency of high-intensity coastal storms and high water events. Several climate models project an accelerated rate of sea level rise over the coming decades (Solomon et al. 2007). An assessment of sea level rise in South Africa, using available tide gauge data for the last 50 yr, shows a 1.87 mm yr^{-1} rise on the west coast, a 1.48 mm yr^{-1} rise on the south coast and a 2.74 mm yr^{-1} rise on the east coast (Mather et al. 2009). Isostatic settling of the crust caused by the additional weight of water over areas with a wide continental shelf, such as the Agulhas Bank, will locally accentuate sea level rise, possibly by as much as 25 % (Reddering & Rust 1990). It is anticipated that the effects of sea level rise will be exacerbated by predicted increases in the frequency of severe storms and high tides impacting the coastal platform at a higher mean sea level (Bindschadler 2006). The South African coastline is intermittently affected by extreme swells associated with tropical cyclones and cut-off low pressure systems (Mather & Stretch 2012). Extreme weather events are predicted to increase in frequency and intensity in the 21st century and appear to be on the increase globally (Solomon et al. 2007, Engelbrecht et al. 2009, 2011).

An increase in the frequency of extreme weather events, together with sea level rise, may alter the hydrogeomorphology of estuaries and result in a loss of essential estuarine habitat (such as mangroves and salt marsh), which will ultimately affect estuarine fish communities and will have implications for fisheries targeting estuary-associated species (Elliott 2002, Clark 2006). Childs et al. (2008) found that during their estuarine-dependent phase, *Pomadasys commersonnii*, a species targeted by recreational anglers in both the estuarine and coastal environment, require specific habitat. Similarly, Mann & Pradervand (2007) found that for several estuary-associated fish species there was a close relationship between adult abundance in the marine environment and the availability of estuarine nursery areas.

Of all climate-induced changes, sea level rise is seen as the greatest threat to mangrove and salt marsh ecosystems in estuaries (Adam 2002, Gilman et al. 2008). If the rate of sedimentation within an estuary is able to keep up with the rate of sea level rise, South African estuaries will experience very little change (Reddering & Rust 1990). Estuarine wetlands will move inland, retaining a constant position relative to the shifting tidal regime (Gilman et al. 2008). In the Weser Estuary (Germany), a rise in sea level is predicted to result in an expansion of reeds and associated flora at the expense of managed pastures (Osterkamp et al. 2001). However, upward movement of estuarine wetlands may be constrained by hinterland topography and coastal developments such as artificial embankments, resulting in a net loss of estuarine wetlands (Adam 2002). Furthermore, if upward movement is constrained, estuary basins could potentially fill with marine sediments if these sediments are not eroded by river inflow. Depending on the degree of protection at the mouth, raised water levels may allow more wave energy into the estuaries, which will negatively affect mangrove ecosystems that do not survive when exposed to strong wave action (Mather & Stretch 2012). Wave energy may also increase with climate change. This can promote the formation of sandbars across tidal inlets (Reddering & Rust 1990). All of the above could result in a new equilibrium in erosion–deposition cycles and ultimately cause a reduction in estuarine water volume. This will be aggravated in areas that are predicted to receive less rainfall and particularly in estuaries with small catchments.

Hughes et al. (1993) suggest that, for the Diep Estuary in Cape Town, the sedimentation rate would not be able to keep up with sea level rise. They modeled the effects of a 1 m rise in sea level. The Diep Estuary comprises a temporarily open/closed estuary (Milnerton Lagoon) and a wetland system (Rietvlei). The model predicts that the wetland area will effectively become a large shallow body of seawater connected to the sea via a long narrow channel.

3.5. CO_2 and pH

From pre-industrial times to 2005, the atmospheric concentration of CO_2 has risen by 35% (Solomon et al. 2007). One of the primary impacts of elevated CO_2 levels is a concomitant decrease in ocean pH, which is expected to have profound implications for coastal ecosystems (Harley et al. 2006). It is estimated that the pH of surface seawater has reduced by 0.1 units over the last 200 yr (Royal Society 2005) and that the reduction will intensify, falling by 0.3–0.5 by 2100 as atmospheric CO_2 levels continue to increase (Caldeira & Wickett 2003). While the magnitude of this decrease may seem insignificant, pH is based on a log scale and therefore even this change can have significant physiological ramifications for aquatic animals.

Estuaries naturally have high and variable CO_2 and may also receive additional CO_2 via freshwater input (Miller et al. 2009, Gillanders et al. 2011). Estuary pH is closely related to changes in salinity, photosynthesis cycles associated with dissolved oxygen (Ringwood & Keppler 2002), and the pH of the marine environment, such that the pH gradients in estuaries can be strong. Eddy (2005) suggested that the lower reaches of permanently open estuaries often approximate seawater and, therefore, these areas may be more susceptible to the impacts of acidification. The pH in the upper reaches of estuaries is generally more acidic and more variable, being dependent on geology, climate and anthropogenic influences in the catchment (Eddy 2005).

One of the primary consequences of acidification is the reduced rate of calcification in numerous species, including calcareous microalgae, gastropods and corals (Orr et al. 2005, Doney et al. 2009), which will indirectly impact fishes through effects on prey (Gillanders et al. 2011) and habitat availability (e.g. oyster beds) (Miller et al. 2009). Acidification will also reduce the pH of the body fluids of aquatic animals (Fabry et al. 2008), which may influence a range of biophysical processes such as growth (Ringwood & Keppler 2002). Although fish may be more tolerant of increasing CO_2 than other organisms (Munday et al. 2008, Ishimatsu et al. 2004, Fabry et al. 2008), acidification may also influence the development of calcareous structures in fishes. Checkley et al. (2009) found that the otoliths of 7- to 8-day-old white seabass *Atractoscion nobilis* were larger when exposed to the CO_2 concentrations predicted for 2100, which may affect their sensory functioning. Browning et al. (2012) found that juvenile red drum *Sciaenops ocellatus* with abnormally large otoliths behaved differently from normal fish as a result of impaired sensory function. Red drum are adapted to hunting in turbid water; however, abnormal red drum did not respond to acoustic stimuli but responded to a greater extent to visual stimuli than normal fish, suggesting that they were compensating for impaired hearing. Recent research has shown that elevated CO_2 levels (1000 ppm CO_2) and reduced seawater pH (7.6–7.8) can affect the olfactory mechanism by which marine fish larvae locate suitable habitat (Munday et al. 2009) and detect predators (Dixson et al. 2010). Evidence suggests that estuary-associated marine fish trace land-based cues back to an estuary by following olfactory concentration gradients (Whitfield 1994b, James et al. 2008c). Disruption of this process would have significant consequences for estuary-associated marine species that are dependent on estuaries as nursery areas.

During the estuarine phase of their life cycle, estuary-associated fishes, owing to the high and variable CO_2 in estuaries, may be physiologically tolerant of acidification. Nevertheless, a decrease in the basal pH state may place them out of their tolerance range during times of extreme acidity and have deleterious effects. Acidification can also significantly affect the solubility of many substances. Changes in pH can result in the speciation of nutrients and metals (Huesemann et al. 2002) and this can significantly influence their biological availability and toxicity. Eddy (2005) reviewed the effects of ammonia on estuarine fishes and concluded that larval and juvenile fish in higher salinities were susceptible to ammonia toxicity during periods of elevated temperature and decreased pH. Thus acidification in heavily polluted estuaries may have significant consequences for the fish fauna.

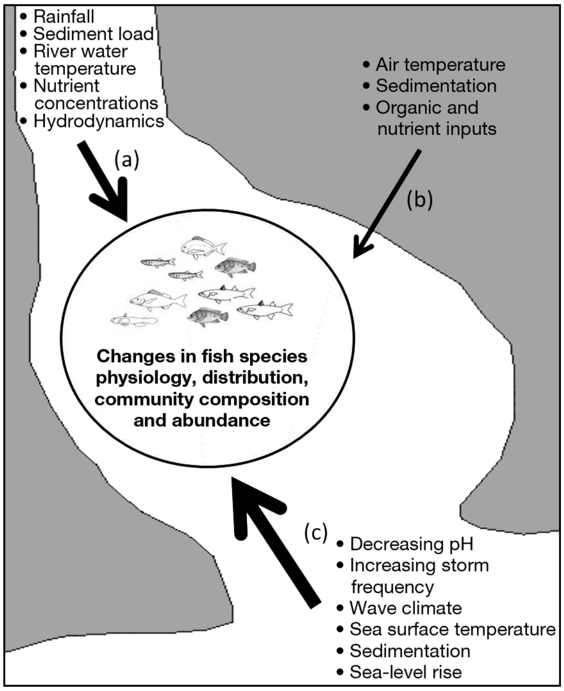

Fig. 5. Some major climate-change related variables in (a) freshwater, (b) terrestrial and (c) marine environments that are likely to directly or indirectly influence estuary-associated fish assemblages in the future, through changes in estuarine water temperature, turbidity, nutrient levels and general estuarine dynamics, affecting e.g. salinity and depth, and resulting in eutrophication and habitat loss

4. CONCLUSIONS

As estuaries are transition areas between rivers and the sea, and are influenced by changes in freshwater, terrestrial and marine conditions, climate change is likely to have a large impact on these ecosystems (refer to Fig. 5 and Table 1 for an overview).

The more immediate effects of climate change on South African estuaries and estuary-associated fishes will come from changes in rainfall, temperature and increased frequency of coastal storms. Local reduction in rainfall, such as along the west coast of South Africa, will result in a decrease in freshwater flow, and may cause estuaries to close more frequently, and for permanently open estuaries to become more constricted (and even close in the long-term). Estuarine-associated fish species are known to be sensitive to reductions in the volume of freshwater runoff and this may reduce the abundance of these species, which will also have fisheries implications. Reduction in freshwater flow will also reduce the quantity of nutrients entering estuaries, with a resultant impoverishment of the biota. Increases in extreme precipitation events projected for the east coast may result in increased freshwater flow and elevated delivery of sediment to estuaries as a result of runoff from land and river and stream channel erosion, which may significantly alter estuarine fish communities through the clogging of their gills and smothering of the benthos, and create indirect impacts through elevated turbidity (e.g. prey detection and predator avoidance).

Like most parts of the world, there has been a general upward trend in air temperatures throughout South Africa, which has a direct influence on river and estuarine water temperatures, especially small temporarily closed systems. Changes in the coastal SST around the globe and around South Africa, however, are expected to be more heterogeneous. For example, the mean SST increase of 0.25°C per decade in South Africa is not uniform, as there is evidence of cooling as a consequence of strengthened upwelling in certain areas (such as the western and southern Cape coasts). Increasing estuarine temperatures, together with future ENSO episodes, are predicted to result in shifts in species distributions, with tropical species moving south into estuaries dominated by more temperate taxa. However, coastal cooling in some areas may limit the ability of these species to shift their distribution poleward over long distances.

Table 1. Major climate change drivers and likely impact on estuaries and estuary-associated fish assemblages in the 3 biogeographic provinces

Driver	Physical response	Fish response	Zone
Wind regime shift	Increased frequency and intensity of upwelling	Fish kills Species range contractions	Cool- and warm-temperate
Increasing air temperatures	Increasing estuarine water temperatures	Physiological effects Species range changes Alterations in community composition	Cool- and warm-temperate, subtropical
Increasing SST	Increasing coastal and estuarine temperatures	Physiological effects Species range changes Alterations in community composition	Subtropical
Increasing rainfall and foods	Increasing runoff Changes in mouth state Increasing sediment delivery Increasing turbidity	Alterations in community composition	Subtropical
Decreasing rainfall	Decreasing runoff Changes in mouth state Increasing salinity Decreasing nutrients Increasing sediment deposition and decreasing estuarine surface area	Decreasing species diversity Decreasing fish stocks	Cool-temperate
Acidification	Decrease in coastal and estuarine pH Changes in solubility of nutrients and metals Decrease in prey abundance (calcifying organisms)	Physiological effects Alterations in community composition	Cool- and warm-temperate, subtropical
Sea level rise	Habitat loss Mouth closure	Decreasing species diversity Decreasing fish stocks	Cool- and warm-temperate, subtropical
Increasing wave energy	Habitat loss Mouth closure	Decreasing species diversity Decreasing fish stocks	Cool- and warm-temperate, subtropical
Increasing frequency and intensity of coastal storms	Habitat loss Mouth closure	Decreasing species diversity Decreasing fish stocks	Cool- and warm-temperate, subtropical

Furthermore, it is unlikely that the cooling, associated with strengthened, sporadic upwelling, will promote a movement of more temperate fish taxa beyond their existing range towards the equator. There is a very real threat that the range of certain temperate species may actually be restricted due to the increasing water temperatures in estuaries, particularly those occupying shallow closed systems, which will respond rapidly to elevated air temperatures.

Shifts in species distribution and changes in temperature-dependent processes such as growth, maturity and feeding will ultimately result in changes in community composition within estuaries, but this is very difficult to predict as different species will respond differently to warming. Species less able to respond to changes in climate may decrease in abundance, and this may ultimately result in localized extinctions. Many estuary-associated marine species are overexploited, and there is evidence that the stocks of some species have collapsed (Houde & Rutherford 1993, Whitfield & Cowley 2010). With the impacts of climate change likely to place additional stress on many exploited species, the sustainability of estuarine fisheries may be further compromised.

Increased frequency of high-intensity coastal storms and high water events may lead to more frequent mouth closures and related loss of nursery function. Conversely, large marine overwash events could trigger the premature opening of temporarily open/closed estuaries by introducing large volumes of seawater into the system and flattening the sandbars at their mouths.

A rise in sea level and decreases in the pH of coastal waters are likely to affect estuary-associated fishes in the long-term. A rise in sea level may have a range of implications for estuaries and estuary-associated fishes. The upstream shift of coastal wetlands in response to sea level rise may be limited by coastal development and hinterland topography. This may ultimately result in the loss of habitat, which will in turn affect the abundance of estuarine fish and the resilience of estuarine fisheries. Marine incursion into estuaries may alter the salinity and depth of estuarine habitats, which will then affect estuarine fishes. Sea level rise will also affect the mouth status of estuaries (open or closed), which will interact with reductions or increases in freshwater flow (from rainfall), but these effects have not as yet been fully explored.

Decreases in the pH of coastal waters associated with climate change may have physiological effects on the larvae of estuary-associated marine fishes before they recruit into estuaries, which may impair their sensory functioning. Within polluted estuaries, decreases in pH may result in the speciation of nutrients and metals, and this can significantly influence their biological availability and toxicity.

In order to address the uncertainty around the impacts of climate change on South African estuaries and estuary-associated fishes, existing long-term monitoring programmes need to continue in estuaries, particularly in estuaries situated at the boundary of species distributional ranges, and additional programmes need to be initiated. These programmes need to assess the biota as well as establish a network of temperature and salinity recorders in estuaries and the coastal environment around the country. Detailed habitat maps are also needed for all estuaries in order to quantify changes.

In summary, tropical fishes may move polewards in response to warming temperatures, resulting in an expansion of the subtropical zone. Estuaries in subtropical regions will also be impacted by probable increases in rainfall, a rise in sea level and increased frequency of high-intensity coastal storms. In contrast, temperate zones may contract, with estuaries and fishes being affected by probable upwelling-related extremes in temperature, reduced runoff and habitat loss, ultimately leading to a decrease in temperate fish species diversity and abundance.

Acknowledgements. This research was financially supported by the National Research Foundation (NRF) of South Africa. This paper arose from the IPCC country report process. The authors are grateful to the South African National Biodiversity Institute (SANBI) for the management of the country report process, and for the funding to complete the marine section. Finally, we are thankful to the anonymous referees for their valuable comments on an earlier draft.

LITERATURE CITED

Able KW, Fahay MP (2010) Ecology of estuarine fishes: temperate waters of the Western North Atlantic. The Johns Hopkins University Press, Baltimore, MD

Adam P (2002) Saltmarshes in a time of change. Environ Conserv 29:39–61

Alber M (2002) A conceptual model of estuarine freshwater inflow management. Estuaries 25:1246–1261

Allanson BR, Baird D (eds) (1999) Estuaries of South Africa. Cambridge University Press, Cambridge

Bate GC, Adams JB (2000) The effects of a single freshwater release into the Kromme Estuary. 5. Overview and interpretation for the future. Water SA 26:329–332

Bate GC, Whitfield AK, Adams JB, Huizinga P, Wooldridge TH (2002) The importance of the river-estuary interface (REI) zone in estuaries. Water SA 28:271–280

Beckley LE (1983) Sea-surface temperature variability around Cape Recife, South Africa. S Afr J Sci 79:436–438

Bindschadler R (2006) Hitting the ice sheets where it hurts. Science 311:1720–1721

Blamey R, Reason CJC (2007) Relationships between Antarctic sea-ice and South African winter rainfall. Clim Res 33:183–193

Branch GM, Grindley JR (1979) Ecology of southern African estuaries. XI. Mngazana: a mangrove estuary in the Transkei. S Afr J Zool 14:149–170

Browning ZS, Wilker AA, Moore EJ, Lancon TW, Clubb FJ (2012) The effect of otolith malformation on behaviour and cortisol levels in juvenile red drum fish (*Sciaenops ocellatus*). Comp Med 62:251–256

Caldeira K, Wickett ME (2003) Anthropogenic carbon and ocean pH. Nature 425:365

Checkley DM, Dickson AG, Motomitsu T, Radich JA, Eisenkolb N, Asch R (2009) Elevated CO_2 enhances otolith growth in young fish. Science 324:1683

Childs AR, Booth AJ, Cowley PD, Potts WM, Næsje TF, Thorstad EB, Økland F (2008) Home range of an estuarine-dependent fish species *Pomadasys commersonnii* in a South African estuary. Fish Manag Ecol 15:441–448

Clark BM (2006) Climate change: a looming challenge for fisheries management in southern Africa. Mar Policy 30: 84–95

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

Cury P, Shannon L (2004) Regime shifts in upwelling ecosystems: observed changes and possible mechanisms in the northern and southern Benguela. Prog Oceanogr 60: 223–243

Cyrus D, 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

Desmond JS, Deutschman DH, Zedler JB (2002) Spatial and temporal variation in estuarine fish and invertebrate assemblages: analysis of an 11-year data set. Estuaries 25:552–569

Dixson DL, Munday PL, Jones GP (2010) Ocean acidification disrupts the innate ability of fish to detect predator olfactory cues. Ecol Lett 13:68–75

Doney SC, Fabry VJ, Feely RA, Kleypas JA (2009) Ocean acidification: the other CO_2 problem. Annu Rev Mar Sci 1:169–192

Drinkwater KF, Beaugrand G, Kaeriyama M and others (2010) On the processes linking climate to ecosystem changes. J Mar Syst 79:374–388

Eddy FB (2005) Ammonia in estuaries and effects on fish. J Fish Biol 67:1495–1513

Elliott M (2002) An overview of the status, study and management of fishes in estuaries. In: Elliott M, Hemmingway KL (eds) Fishes in estuaries. Blackwell Science, Oxford, p 53–575

Engelbrecht FA, Mcgregor JL, Engelbrecht CJ (2009) Dynamics of the conformal-cubic atmospheric model projected climate-change signal over southern Africa. Int

J Climatol 29:1013–1033

Engelbrecht FA, Landman WA, Engelbrecht CJ and others (2011) Multi-scale climate modelling over southern Africa using a variable-resolution global model. Water SA 37: 647–658

Fabry VJ, Seibel BA, Feely RA, Orr JC (2008) Impacts of ocean acidification on marine fauna and ecosystem processes. ICES J Mar Sci 65:414–432

Figueira WF, Booth DJ (2010) Increasing ocean temperatures allow tropical fishes to survive overwinter in temperate waters. Glob Change Biol 16:506–516

Figueira WF, Biro P, Booth DJ, Valenzuela VC (2009) Performance of tropical fish recruiting to temperate habitats: role of ambient temperature and implications of climate change. Mar Ecol Prog Ser 384:231–239

Flint RW (1985) Long-term estuarine variability and associated biological response. Estuaries 8:158–169

Garcia AM, Vieira JP, Winemiller KO (2001) Dynamics of the shallow-water fish assemblage of the Patos Lagoon estuary (Brazil) during cold and warm ENSO episodes. J Fish Biol 59:1218–1238

Garcia AM, Vieira JP, Winemiller KO, Grimm AM (2004) Comparison of 1982–1983 and 1997–1998 El Niño effects on the shallow-water fish assemblage of the Patos Lagoon Estuary (Brazil). Estuaries 27:905–914

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 Freshw Res 62:1115–1131

Gilman EL, Ellison J, Duke NC, Field C (2008) Threats to mangroves from climate change and adaptation options: a review. Aquat Bot 89:237–250

Grange N, Whitfield AK, de Villiers CJ, Allanson BR (2000) The response of two South African east coast estuaries to altered river flow regimes. Aquat Conserv 10:155–177

Hanekom N, Hutchings L, Joubert PA, van der Byl PCN (1989) Sea temperature variations in the Tsitsikamma Coastal National Park, South Africa, with notes on the effect of cold conditions on some fish populations. S Afr J Mar Sci 8:145–153

Harley CD, Randall Hughes A, Hultgren KM and others (2006) The impacts of climate change in coastal marine systems. Ecol Lett 9:228–241

Harrison TD (2005) Ichthyofauna of South African estuaries in relation to the zoogeography of the region. Smithiana 6:1–27

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

Hewitson BC, Crane RG (2006) Consensus between GCM climate change projections with empirical downscaling: precipitation downscaling over South Africa. Int J Climatol 26:1315–1337

Heydorn AEF, Tinley KL (1980) Estuaries of the Cape. 1. Synopsis of the Cape coast – natural features, dynamics and utilization. CSIR Research Report 380. Council for Scientific and Industrial Research, Stellenbosch, p 1–97

Hiddink JG, Ter Hoftstede R (2008) Climate induced increases in species richness of marine fishes. Glob Change Biol 14:453–460

Houde ED, Rutherford ES (1993) Recent trends in estuarine fisheries: predictions of fish production and yield. Estuaries 16:161–176

Hsieh CH, Reiss CS, Hunter JR, Beddington JR, May RM, Sugihara G (2006) Fishing elevates variability in the abundance of exploited species. Nature 443:859–862

Hsieh CH, Reiss CS, Hewitt RP, Sugihara G (2008) Spatial analysis shows that fishing enhances the climatic sensitivity of marine fishes. Can J Fish Aquat Sci 65:947–961

Huesemann MH, Skillman AD, Crecelius EA (2002) The inhibition of marine nitrification by ocean disposal of carbon dioxide. Mar Pollut Bull 44:142–148

Hughes P, Brundrit GB, Swart DH, Bartels A (1993) The possible impacts of sea-level rise on the Diep River/Rietvlei system, Cape Town. S Afr J Sci 89:488–493

Hutchings L, Beckley LE, Griffiths MH, Roberts MJ, Sundby S, van der Lingen C (2002) Spawning on the edge: spawning grounds and nursery areas around the southern African coastline. Mar Freshw Res 53:307–318

Hutchings L, van der Lingen CD, Shannon LJ and others (2009) The Benguela Current: an ecosystem of four components. Prog Oceanogr 83:15–32

Ishimatsu A, Kikkawa T, Hayashi M, Lee KS, Kita J (2004) Effects of CO_2 on marine fish: larvae and adults. J Oceanogr 60:731–741

James NC, Whitfield AK, Cowley PD (2008a) Preliminary indications of climate-induced change in a warm-temperate South African estuarine fish community. J Fish Biol 72:1855–1863

James NC, Whitfield AK, Cowley PD (2008b) Long-term stability of the fish assemblages in a warm-temperate South African estuary. Estuar Coast Shelf Sci 76:723–738

James NC, Cowley PD, Whitfield AK, Kaiser H (2008c) Choice chamber experiments to test the attraction of postflexion *Rhabdosargus holubi* larvae to water of estuarine and riverine origin. Estuar Coast Shelf Sci 77: 143–149

Kennedy VS (1990) Anticipated effects of climate change on estuarine and coastal fisheries. Fisheries 15:16–24

Kruger AC, Shongwe S (2004) Temperature trends in South Africa: 1960–2003. Int J Climatol 24:1929–1945

Kupschus S, Tremain D (2001) Associations between fish assemblages and environmental factors in nearshore habitats of a subtropical estuary. J Fish Biol 58:1383–1403

Lamberth SJ, Turpie JK (2003) The role of estuaries in South African fisheries: economic importance and management implications. Afr J Mar Sci 25:131–157

Lamberth SJ, van Niekerk L, Hutchings K (2008) Comparison of, and the effects of altered freshwater inflow on, fish assemblages of two contrasting South African estuaries: the cool-temperate Olifants and the warm-temperate Breede. Afr J Mar Sci 30:311–336

Lehodey P, Alheit J, Barange M and others (2006) Climate variability, fish and fisheries. J Clim 19:5009–5030

Lumsden TG, Schulze RE, Hewitson BC (2009) Evaluation of potential changes in hydrologically relevant statistics of rainfall in southern Africa under conditions of climate change. Water SA 35:649–656

Lutjeharms JRE (2006) The coastal oceans of south-eastern Africa (15°W). In: Robinson AR, Brink KH (eds) The global ocean: the sea — ideas and observations on the progress in the study of the seas, Vol 14 (part B). Harvard University Press, Cambridge, p 783–834

Lutjeharms JRE, Cooper J, Roberts M (2000) Upwelling at the inshore edge of the Agulhas Current. Cont Shelf Res 20:737–761

Mann BQ, Pradervand P (2007) Declining catch per unit effort of an estuarine-dependent fish, *Rhabdosargus sarba* (Teleostei: Sparidae), in the marine environment following closure of the St Lucia Estuarine System, South Africa. Afr J Aquat Sci 32:133–138

Martinho F, Leitão R, Viegas I, Dolbeth M, Neto JM, Cabral HN, Pardal MA (2007) The influence of an extreme drought in the fish community of a southern Europe temperate estuary. Estuar Coast Shelf Sci 75:537–546

Martinho F, Cabral HN, Azeiteiro UL, Pardal MA (2012) Estuarine nurseries for marine fish: connecting recruitment variability with sustainable fisheries management. Manag Environ Qual 23:414–433

Mather AA, Stretch DD (2012) A perspective on sea level rise and coastal storm surge from southern and eastern Africa: a case study near Durban, South Africa. Water SA 4:237–259

Mather AA, Garland GG, Stretch DD (2009) Southern African sea levels: corrections, influences and trends. Afr J Mar Sci 31:145–156

Mbande S, Whitfield A, Cowley P (2005) The ichthyofaunal composition of the Mngazi and Mngazana estuaries: a comparative study. Smithiana 4:1–20

McLachlan A, Erasmus T, Dye AH and others (1981) Sand beach energetics: an ecosystem approach towards a high energy interface. Estuar Coast Shelf Sci 13:11–25

Meynecke JO, Lee SY, Duke NC, Warnken J (2006) Effect of rainfall as a component of climate change on estuarine fish production in Queensland, Australia. Estuar Coast Shelf Sci 69:491–504

Miller AW, Reynolds AC, Sobrino C, Riedel GF (2009) Shellfish face uncertain future in high CO_2 world: influence of acidification on oyster larvae calcification and growth in estuaries. PLoS ONE 4:e5661

Morant PD, Quinn NW (1999) Influence of man and management of South African estuaries. In: Allanson BR, Baird D (eds) Estuaries of South Africa. Cambridge University Press, Cambridge, p 289–320

Munday PL, Jones GP, Pratchett MS, Williams AJ (2008) Climate change and the future for coral reef fishes. Fish Fish 9:261–285

Munday PL, Dixson DL, Donelson JM, Jones GP, Pratchett MS, Devitsina GV, Døving KB (2009) Ocean acidification impairs olfactory discrimination and homing ability of a marine fish. Proc Natl Acad Sci USA 106:1848–1852

Murawski SA (1993) Climate change and marine fish distributions: forecasting from historical analogy. Trans Am Fish Soc 122:647–658

Olivar MP, Shelton PA (1993) Larval fish assemblages of the Benguela Current. Bull Mar Sci 53:450–474

Orr JC, Fabry VJ, Aumont O, Bopp L and others (2005) Anthropogenic ocean acidification over the twenty-first century and its impact on calcifying organisms. Nature 437:681–686

Osterkamp S, Kraft D, Schirmer M (2001) Climate change and the ecology of the Weser estuary region: assessing the impact of an abrupt change in climate. Clim Res 18: 97–104

Perry AL, Low PJ, Ellis JR, Reynolds JD (2005) Climate change and distribution shifts in marine fishes. Science 308:1912–1915

Philippon N, Rouault M, Richard Y, Faure A (2012) The influence of ENSO on winter rainfall in South Africa. Int J Climatol 32:2333–2347

Rautenbach CJ, Smith IN (2001) Teleconnections between global sea-surface temperatures and the interannual variability of observed and model simulated rainfall over southern Africa. J Hydrol 254:1–15

Reason CJC, Jagadheesha D (2005) Relationships between South Atlantic SST variability and atmospheric circulation over the South African region during austral winter. J Clim 18:3339–3355

Reason CJC, Rouault M (2002) ENSO-like decadal patterns and South African rainfall. Geophys Res Lett 29:16-1–16-4

Reason CJC, Rouault M (2005) Links between the Antarctic Oscillation and winter rainfall over western South Africa. Geophys Res Lett 32:L07705 doi:10.1029/2005GL022419

Reason CJC, Rouault M, Melice JL, Jagadeesha D (2002) Interannual winter rainfall variability in SW South Africa and large scale ocean atmosphere interactions. Meteorol Atmos Phys 80:19–29

Reddering JSV, Rust IC (1990) Historical changes and sedimentary characteristics of southern African estuaries. S Afr J Sci 86:425–428

Ringwood AH, Keppler CJ (2002) Water quality variation and clam growth: is pH really a non-issue in estuaries? Estuaries 25:901–907

Roberts MJ, van der Lingen CD, Whittle C, van den Berg M (2010) Shelf currents, lee-trapped and transient eddies on the inshore boundary of the Agulhas Current, South Africa: their relevance to the KwaZulu-Natal sardine run. Afr J Mar Sci 32:423–447

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

Rouault M, Richard Y (2003) Spatial extension and intensity of droughts since 1922 in South Africa. Water SA 29: 489–500

Rouault M, Richard Y (2005) Spatial extent and intensity of droughts in southern Africa. Geophys Res Lett 32:L15702 doi:10.1029/2005GL022436

Rouault M, Penven P, Pohl B (2009) Warming in the Agulhas Current system since the 1980s. Geophys Res Lett 36: 1–5, doi:10.1029/2009GL037987

Rouault M, Pohl B, Penven P (2010) Coastal oceanic climate change and variability from 1982 to 2009 around South Africa. Afr J Mar Sci 32:237–246

Royal Society (2005) Ocean acidification due to increasing atmospheric carbon dioxide. The Royal Society, London

Scharler UM, Baird D (2000) The effects of a single freshwater release into the Kromme Estuary. 1. General description of the study area and physico-chemical responses. Water SA 26:291–300

Schulze RE, Lumsden TG, Horan MJC, Warbuton M, Maharaj M (2005) An assessment of impacts of climate change on agrohydrological responses over southern Africa. In: Schulze RE (ed) Climate change and water resources in southern Africa: studies on scenarios, impacts, vulnerabilities and adaptation. WRC Report 1430/1/05. Water Research Commission, Pretoria

Schumann EH, Perrins LA, Hunter IT (1982) Upwelling along the south coast of the Cape Province, South Africa. S Afr J Sci 78:238–242

Snow GC, Bate GC, Adams JB (2000) The effects of a single freshwater release into the Kromme Estuary. 2. Microalgal response. Water SA 26:301–310

Solomon S, Qin D, Manning M, Alley RB and others (2007) Technical summary. In: Solomon S, Qin D, Manning M, Chen Z and others (eds) Climate change 2007: the physical science basis. Contribution of Working Group I to the fourth assessment report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, p 21–91

Strydom NA, Whitfield AK (2000) The effects of a single freshwater release into the Kromme Estuary. 4. Larval fish response. Water SA 26:319–328

Strydom NA, Whitfield AK, Wooldridge TH (2003) The role of estuarine type in characterizing early stage fish assemblages in warm temperate estuaries, South Africa. Afr Zool 38:29–43

Sunday JM, Bates AE, Dulvy NK (2012) Thermal tolerance and the global redistribution of animals. Nature Clim Change 2:686–690

Taljaard S, van Niekerk L, Joubert W (2009) Extension of a qualitative model on nutrient cycling and transformation to include microtidal estuaries on wave-dominated coasts: southern hemisphere perspective. Estuar Coast Shelf Sci 85:407–421

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

Thrush SF, Hewitt JE, Cummings VJ, Ellis JI, Hatton C, Lohrer A, Nørkko A (2004) Muddy waters: elevating sediment input to coastal and estuarine habitats. Front Ecol Environ 2:299–306

Turpie JK, Adams JB, Joubert A, Harrison TD and others (2002) Assessment of the conservation priority status of South African estuaries for use in management and water allocation. Water SA 28:191–206

Tyson PD (1986) Climatic change and variability in southern Africa. Oxford University Press, Oxford

Wallace JH (1975) The estuarine fishes of the east coast of South Africa. 1. Species composition and length distribution in the estuarine and marine environments. 2. Seasonal abundance and migrations. Investigational Report of the Oceanographic Research Institute 40. Oceanographic Research Institute, Durban, p 1–72

Walther GR, Post E, Convey P, Menzel A and others (2002) Ecological responses to recent climate change. Nature 416:389–395

Whitfield AK (1992) A characterization of southern African estuarine systems. South Afr J Aquat Sci 18:89–103

Whitfield AK (1994a) An estuary-association classification for the fishes of southern Africa. S Afr J Sci 90:411–417

Whitfield AK (1994b) 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 (1998) Biology and ecology of fishes in southern African estuaries. Icthyological Monograph of the J.L.B. Smith Institute of Ichthyology, No. 2. J.L.B. Smith Institute of Ichthyology, Grahamstown, p 1–223

Whitfield AK (2005) Fishes and freshwater in southern African estuaries — a review. Aquat Living Resour 18: 275–289

Whitfield AK, Cowley PD (2010) The status of fish conservation in South African estuaries. J Fish Biol 76:2067–2089

Whitfield AK, Harrison TD (2003) River flow and fish abundance in a South African estuary. J Fish Biol 62: 1467–1472

Whitfield AK, Paterson AW (2003) Distribution patterns of fishes in a freshwater deprived Eastern Cape estuary, with particular emphasis on the geographical headwater region. Water SA 29:61–67

Whitfield AK, Wooldridge TH (1994) Changes to freshwater supplies in southern African estuaries: some theoretical and practical considerations. In: Dyer KR, Orth RJ (eds) Changes in fluxes in estuaries. Implications from science to management. Olsen & Olsen, Fredensborg, p 41–50

Whitfield AK, Paterson AW, Bok AH, Kok HM (1994) A comparison of the ichthyofaunas in two permanently open Eastern Cape estuaries. S Afr J Zool 29:175–185

Whitfield AK, Adams JB, Bate GC and others (2008) A multidisciplinary study of a small, temporarily open/closed South African estuary, with particular emphasis on the influence of mouth state on the ecology of the system. Afr J Mar Sci 30:453–473

Wooldridge TH, Callahan R (2000) The effects of a single freshwater release into the Kromme Estuary. 3. Estuarine zooplankton response. Water SA 26:311–318

Editorial responsibility: Mauricio Lima,
Santiago, Chile

Submitted: January 17, 2013; Accepted: July 15, 2013
Proofs received from author(s): October 10, 2013