1 **Review Article**

2
3 **The role of pioneers as indicators of biogeographic range expansion caused by global change in**
4 **southern African coastal waters**

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24 **Abstract**

25 The South African coastline is just over 3000 km in length yet it covers three major biogeographic
26 regions, namely subtropical, warm temperate and cool temperate. In this review we examine
27 published information to assess the possible role of climate change in driving distributional changes
28 of a wide variety of organisms around the subcontinent. In particular we focus on harmful algal
29 blooms, seaweeds, eelgrass, mangroves, salt marsh plants, foraminiferans, stromatolites, corals, squid,
30 zooplankton, zoobenthos, fish, birds, crocodiles and hippopotamus, but also refer to biota such as
31 pathogens, coralline algae, jellyfish and otters. The role of pioneers or propagules as indicators of an
32 incipient range expansion are discussed, with mangroves, zoobenthos, fishes and birds providing the
33 best examples of actual and imminent distributional changes. The contraction of the warm temperate
34 biogeographic region, arising from the intrusion of cool upwelled waters along the Western Cape
35 shores, and increasingly warm Agulhas Current waters penetrating along the eastern parts of the
36 subcontinent, are highlighted. The above features provide an ideal setting for the monitoring of biotic
37 drivers and responses to global climate change over different spatial and temporal scales, and have

direct relevance to similar studies being conducted elsewhere in the world. We conclude that, although this review focuses mainly on the impact of global climate change on South African coastal biodiversity, other anthropogenic drivers of change such as introduced alien invasive species may act synergistically with climate change, thereby compounding both short and long-term changes in the distribution and abundance of indigenous species.

Keywords: marine; estuarine; propagules; biogeography; biotic responses; climate change

Introduction

South Africa has often been referred to colloquially as a “world in one country”, primarily due to its diversity of landforms, habitats, climate, races, religions and socio-economic conditions. This diversity is also reflected in marine ecosystems around the country, with coral reef habitats dominant in the subtropical neritic north-eastern waters and kelp beds in the cool-temperate southwest (Griffiths et al. 2010). Research in southern African coastal habitats has been conducted over many decades (e.g. Jackson 1991; Allanson and Baird 1999; Perissinotto et al. 2010) and we are now in a position to examine the possible impacts of global change on a variety of biota and ecosystems (e.g. Zietsman 2011; Mead et al. 2013; Moloney et al. 2013) in a way that is currently not possible from many other parts of the world.

From a terrestrial perspective South Africa is regarded as the third-most biologically rich country on Earth, despite the fact that it occupies a mere 0.8% of the land area on the planet (Gibbons, 1999). The South African coastline represents a mere 0.5% of the global total yet the marine taxonomic richness, especially in terms of endemic species, is unsurpassed by most other countries. Of the 22 free-living metazoan phyla occurring in South Africa’s marine environment, many have a high level of species richness, especially benthic taxa such as gastropod molluscs and decapod crustaceans. On average, the number of southern African endemics (4233) comprise approximately 33% of the total number of listed marine biota on the subcontinent, with 85% of the isopods and 71% of the cumaceans currently listed as endemic (Griffiths et al. 2010).

Numerous studies, on a diverse array of biota, have documented the biogeographical provinces within the southern African coastal zone (e.g. Stephenson and Stephenson 1972; Turpie et al. 2000; Harrison 2002; Sink et al. 2011) and provided benchmarks with which to examine present and future distributional and functional changes in coastal systems. Southern African marine intertidal rocky shore invertebrates can be divided into three principal populations which have wide areas of overlap (Stevenson and Stevenson 1972). The tropical group extends southwards from Mozambique and rapidly dissipates between Port St Johns and East London (Fig. 1). The so-called ‘Cape’ fauna is a

warm-temperate group that is centred between False Bay and East London but has elements that penetrate north of Durban on the east coast and as far as Port Nolloth on the west coast (Fig. 1). The so-called 'Namaqua' fauna mainly inhabits the west coast from Cape Town into northern Namibia, with a few elements extending as far south as Cape Agulhas (Stevenson and Stevenson 1972). These major faunal 'provinces' have had a significant influence on the proclamation of marine reserves in South Africa and it is anticipated that pioneers from each of the above faunal groups will change their coastal distributions in response to climate change, thereby necessitating a review of the adequacy of existing marine reserves on the subcontinent (Emanuel et al. 1992).

There are a large number of endemic coastal marine invertebrates in southern Africa, with many of them restricted to particular sections of biogeographic provinces. For example 73 species are restricted to ranges of less than 100 km in the Cape Point region and 28 species from the same region have a maximum range of 200 km (Scott et al. 2012). Climate change, which reduces the extent of the cool temperate and warm temperate biogeographic regions is therefore likely to impact negatively on these range restricted taxa. Coastal 'squeeze' may also be an issue and has been shown to be a threat to rocky shore fauna elsewhere in the world (Jackson and McIlvenny 2011). In contrast, sandy beach biota appear to be more resistant to climate change although some species are showing signs of distributional changes linked to this influence (Schoeman et al. 2015).

There is no coastal region of a similar size to southern Africa that can boast such biogeographical diversity which, at the same time, offers major opportunities to investigate numerous aspects of global change biology. The case studies and examples reviewed in this paper therefore have significance, not only for the African subcontinent, but for the world at large. In particular we focus on those organisms that are being influenced by climate change; however, invariably aspects of global change have a simultaneous impact and therefore also form part of this review.

Some biotic range changes in global coastal ecosystems

Warming of coastal and estuarine waters has resulted in many tropical and warm temperate neritic species extending their distributions towards higher latitudes. This trend applies to all biota, including both plant and animal taxa (Nielsen et al. 2013; Tsang et al. 2013; Saintilan et al. 2014). Indeed, it has been proposed that actual coastal habitats such as coral reefs may be able to move into higher-latitude coastal waters as a result of increasing seawater temperatures, thus increasing the chances of coral reef and associated biota survival despite global warming (Denis et al. 2013). Conversely temperate habitats such as kelp beds could be adversely affected and it has been estimated, for instance, that seawater warming off the Japanese coast could lead to the complete loss of *Ecklonia cava* from that region by the 2090s (Takao et al. 2015).

112
113 In many cases, the colonisation of estuarine habitats by one group of species leads directly to the
114 decline in another group of species from those same habitats, e.g. latitudinal mangrove expansion
115 globally has led to the retreat of salt marshes from those same systems that are experiencing global
116 warming (Saintilan et al. 2014). There is also evidence of shrinking distributions of certain temperate
117 species brought about by climate change on its own and, in some cases, by climate change and the
118 added impact of overfishing (Last et al. 2011). Poleward range shifts by known ‘ecosystem engineers’
119 such as tropical sea urchins can also have a devastating impact on the more temperate coastal
120 biodiversity by expanding the ‘barrens habitat’ in waters invaded by these sea urchins (Perkins et al.
121 2015).

122
123 Research has shown that coastal biota are affected by a range of physical aspects besides the response
124 to changes in seawater temperature brought about by climate change (Mead et al. 2013). In the case of
125 marine zoobenthos, these impacts include altered hydrodynamics, ocean acidification, and sea-level
126 rise that can lead to ‘coastal squeeze’ (Birchenough et al. 2015). Cooling of the southern Benguela
127 system off the west coast of southern Africa is placing a different type of ‘squeeze’ on warm
128 temperate coastal biota (Blamey et al. 2015) that are also being forced south-westwards by increasing
129 temperatures in the Agulhas system on the southern African east coast. Potentially these warm
130 temperate species could end up being confined to a relatively small section of the southern Cape if the
131 above two trends continue.

132
133 Short-lived species such as jellyfish and squid may respond rapidly to climate change. Jellyfish
134 populations seem to be increasing in many parts of the world (Richardson et al. 2009) including the
135 coastal waters off Namibia (Brierley et al. 2005; Lynam et al. 2006). This has been linked to a number
136 of global change drivers such as overfishing, eutrophication, habitat modification, introduced species
137 and climate change (Richardson et al. 2009). Warmer, more saline water associated with global
138 warming favour certain jellyfish taxa and, in a review of moderate-temperature species, 18 out of 24
139 increased when temperatures increased (Purcell et al. 2007).

140
141 Whilst the biota in estuaries are susceptible to changing marine conditions (Adam 2002), they are also
142 indirectly impacted by altered riverine run-off, changes in sedimentation rates and composition,
143 elevated nutrient concentrations and exceptional coastal storm events, all of which are showing signs
144 of attaining new extremes in a world undergoing global change (James et al. 2013). Changing
145 catchment run-off and nutrient imports/exports will affect not only estuarine ecosystem functioning
146 but also the ecology of nearshore coastal habitats (Lamberth et al. 2009).

The impacts of climate change on estuaries and coastal marine areas are not uniform in all regions on the same latitude. The orientation of a coast is particularly significant, since a north-south orientation offers options for temperate species to retreat towards higher latitudes as ocean warming increases the extent of tropical biogeographic zones. Wernberg et al. (2011) have highlighted the decline of the temperate giant kelp along the south-eastern Australian coast and also the poleward range extension of sea urchins and other important sub-tropical and warm temperate reef-associated organisms in this region.

Although there is considerable global evidence of climate change impacts on fish, plankton and intertidal zoobenthic organisms, there is much less evidence of sub-tidal benthic communities responding in a similar manner. A study by Hinz et al. (2011) showed that the predicted distributional changes in stenothermal ‘cold’ and ‘warm’ water sub-tidal benthic communities in the English Channel did not show any clear results that were consistent with climate changes over a 48 year sampling gap. However, some warm water species that were not recorded in the earlier 1958 survey were documented in 2006. Similarly, trawl data collected between 1925 and 2004 in the North Sea and Scottish west coast suggest that “waves of immigration” by fish species from the south (e.g. red mullet, pilchard and anchovy) are occurring in this region (Beare et al. 2004). Fish colonisation trends in the pelagic zone are overwhelming, with Montero-Serra et al. (2015) providing strong evidence for the ‘subtropicalization’ of pelagic fish assemblages in European shelf seas.

In other parts of the world, such as Western Australia, climate induced ‘tropicalisation’ of marine fish and invertebrate communities is an increasing trend which will lead to dominance by warmer-water species in previous temperate regions (Cheung et al. 2012). Ocean warming off the Tasmanian east coast has also resulted in range expansions of warmer-water fish and invertebrate species into this previously exclusive temperate zone. In particular, overgrazing of kelp beds by recently established populations of sea urchin have caused a major shift in the ecology of certain Tasmanian rocky reef systems (Johnson et al. 2011).

Where coastlines have an east-west orientation, such as those in southern Australia, any poleward movement of isotherms is likely to impact negatively on temperate species over very large areas (Wernberg et al. 2011). A similar situation may occur for coastal biota in southern Africa, with limited southward distributional opportunities for temperate species being offered once the southern coasts of these continents are significantly affected by global warming. Fortunately cool upwelling zones along some sections of both the southern African and Australian coasts can potentially offer some respite to temperate biota attempting to escape increasing water temperatures in previous parts of their distributional range. Cooling can also escalate at upwelling centres, providing opportunities of range expansion for cold water species. For example, the cooling of the False Bay area on the south

coast is effectively expanding the southern Benguela upwelling system eastwards, thereby facilitating a range extension for kelp species and the rock lobster *Jasus lalandii* (Lucas and Griffiths 2012; Bolton et al. 2012; Table 1).

Global change and biotic distributions in southern African waters

There are a number of examples of changes in biotic distribution of coastal taxa over the past few decades. In this section we have selected those species for which published information is available and which represent some of the major taxa that inhabit estuaries or the sea around the subcontinent.

Harmful Algal Blooms

Prymnesium parvum is an invasive algae that first appeared in South Africa's Zandvlei Estuary during the 1970s and was associated with a mass fish kill in the system (Begg 1976). This algae releases toxins that cause internal and gill haemorrhaging in most fish and some invertebrate species, and it thrives in low estuarine salinities (0-10), temperatures of 2-30°C and a pH >7 (Watson 2001; Lindehoff et al. 2011). Overall, *P. parvum* out-competes other algae by having wider physico-chemical tolerances and it can also chemically inhibit the growth of those species (Granéli, 2006). Consequently in southern African estuaries *P. parvum* has high invasive potential facilitated by eutrophication. Extreme global change events predicted for the future will increase the invasion potential of this species. In 2012 a *P. parvum* bloom in the Zandvlei Estuary intensified over a two week period, culminating in mass stress-induced spawning and mortality of most fish in that system.

Estuaries may also provide a refuge area for marine fish species attempting to escape coastal 'black tides'. An example of such an event is described by Lamberth et al. (2010) where fish catches within the Berg Estuary (Fig. 1) increased dramatically with the onset of the 'black tide' event in the adjacent marine environment. Future climate change that may impact on the accessibility of estuaries to coastal marine fish species during Harmful Algal Blooms (HABs) or low oxygen, hydrogen sulphide 'black tide' events, would severely affect the distribution and abundance of these taxa in southern African coastal waters.

Harmful algal blooms are more common and widespread in the southern African marine environment when compared to estuaries. It has already been suggested that changes in wind-driven upwelling in the southern Benguela due to climate change will influence the development of HABs which will, in turn, impact on the coastal biota in the region (Blamey et al. 2015). Indeed, the incidence of HABs in Western Cape coastal waters has shown a six-fold increase per decade between the 1960s until 2005 (Stephen and Hockey 2007), a trend that may well be linked to climate and global change along this coast. Evidence to support this trend is provided by a major dinoflagellate bloom recorded in southern

Benguela Current LME inshore waters during the austral spring of 2011 (van der Lingen et al. 2016). This bloom was dominated by the mixotrophic dinoflagellate *Gonyaulax polygramma*. Sardines *Sardinops sagax* associated with the bloom were in poor condition when compared to the same species further offshore.

Lingulodinium polyedrum (formerly *Gonyaulax polyedra*) is a widely distributed mixotrophic dinoflagellate species (Jeong et al. 2015) found in warm temperate and subtropical waters of coastal areas (Steidinger and Tangen 1997). Motile forms of *L. polyedrum* have been recorded in the northern Benguela region (Kruger 1980) and cysts of the species have been documented in sediment traps in the southern Benguela (Pitcher and Joyce 2009) but no bloom and no harmful effects have been attributed to this dinoflagellate in southern Africa prior to 2014. A few red tides (typically *Noctiluca miliaris*) but no HABs have been reported east of Cape Agulhas (Pitcher and Calder 2000). However, in January and February 2014, atypical climatic (reduced wind velocities) and oceanographic (strong stratification with >22°C surface water and <10°C upwelled bottom water) conditions resulted in the bloom of *L. polyedrum* (a non-indigenous species to the region) creating the most extensive (> 500 km from Mossel Bay to East London, Fig. 1) and persistent (>4 months) HAB ever recorded in southern Africa (Bornman et al. in preparation).

The turbulent nature of the southern African coast had previously restricted the spread and bloom of *L. polyedrum*, as the species is well adapted to lower energy, stratified and nutrient rich conditions (Eppley and Harrison 1975; Smayda 1997; Estrada and Berdalet 1998). Climate change (reduced wind velocities, more frequent but weaker upwelling and increased coastal water temperatures) and global change (eutrophication) created an ideal habitat for *L. polyedrum* to extend its range and flourish. The bloom impaired pelagic ecosystem functioning for more than a year, resulting in long term socio-economic consequences for the region. The accumulation of cysts in the sediment and the expansion of the subtropical zone will ensure the persistence of *L. polyedrum* along the eastern and southern coasts in the future.

Seaweeds

A major transition from the tropical Indian Ocean seaweed flora to a temperate macroalgal community occurs in the vicinity of St Lucia (Fig. 1), with further mixing of these two components occurring along the central and southern KwaZulu-Natal coast (Bolton et al. 2004). There is also a relative decrease in green algae from approximately 25% of the species present in more tropical northern waters to about 15% of species in more temperate southern waters.

A few southern African west coast seaweed species extend into southern Angolan waters but most temperate species south of 13°S come from the Benguela Marine Province of Namibia (Anderson et

al. 2012). Tropical West African seaweed flora is dominant in northern Angola, with this component likely to extend further southwards with the continuation of global warming. Thus changes in seawater temperature brought about by warming would be expected to have a significant impact on the ratios between tropical and temperate species at fixed points within the existing transition zones (Bolton et al. 2004), as well as changes in the relative distribution of tropical and temperate seaweed species along the south-eastern and south-western African coasts.

In contrast to the above patterns, recent distribution information on the kelp *Ecklonia maxima* by Mead et al. (2013) shows that coastal cooling is occurring along the southern and eastern parts of the Western Cape Province (Rouault et al. 2010).. For at least 50 years the eastern biogeographical limit of *E. maxima* was static just west of Cape Agulhas (Bolton et al. 2012; Fig. 1). However, post the mid-2000s there was a 70 km eastward shift and kelp beds are now found up to the De Hoop Nature Reserve in the southern Cape (Bolton et al. 2012). This increased distributional range may well be linked to the increased upwelling driven by wind changes that are influenced by global climate change (Fawcett et al. 2008).

Seagrasses

The eelgrass *Zostera capensis* is endemic to southern Africa and occurs in a number of permanently open estuaries around the coast. This submerged marine macrophyte is usually most abundant in the lower and sometimes middle reaches of estuaries but is known to extend its distribution into the upper reaches if suitable physico-chemical conditions are present (Adams and Talbot 1992), namely a reduction or loss of river flow into an estuary which results in the system becoming an ‘arm of the sea’. Such conditions may arise from global change (excessive freshwater abstraction from the river catchment) or climate change (reduced rainfall and frequency of river pulse events into the estuary). If climate change results in the closure of certain permanently open estuaries due to reduced catchment run-off, then eelgrass could well disappear from such systems. Eutrophication has also resulted in the reduced distribution of *Z. capensis* beds from certain southern African estuaries (e.g. Knysna), mainly through the proliferation of macroalgae (e.g. *Ulva* spp.), which then smother and replace the eelgrass (J.B. Adams, pers. obs.).

Seagrasses meadows around the world have been severely affected by human activities in the coastal zone, and southern Africa is no exception. A recent study by Pillay et al. (2010) has shown that there has been a 38% loss of eelgrass *Z. capensis* in Langebaan Lagoon between 1960 and 2007. This change in the extent of seagrass habitat has resulted in major shifts in the composition of invertebrate communities in the lagoon and the virtual loss of those species that were closely associated with the plants such as the limpets *Siphonaria compressa* and starfish *Parvulastra exigua* (Pillay et al. 2010).

Mangroves and salt marshes

Mangroves typically have a subtropical to tropical distribution and are thus excellent indicators of global warming, particularly in southern Africa where they occur at one of the most southerly distributions in the world. Although the white mangrove (*Avicennia marina*) is known as a pioneer, field studies from the Kei to the Mtamvuna estuaries (Fig. 1) showed that the black mangrove (*Bruguiera gymnorhiza*) was more widely distributed. It occurred in 13 of the 17 estuaries compared to *A. marina* that was found in 10 of the estuaries (Hoppe-Speer et al. 2015a), possibly because it can tolerate lower salinity, drier conditions and more basal inundation. Both species are therefore useful indicators of range expansion.

Species distribution modelling (Quisthoudt et al. 2013) showed that global warming would provide suitable sites for both *A. marina* and *B. gymnorhiza* colonization beyond their current latitudinal limits in southern Africa. A combination of increased temperature and rainfall would allow for the expansion of mangroves into new areas; 17 km towards the south by 2020 and 69 km by 2050. However, the estuaries along this part of the coastline are mostly temporarily open/closed systems, as opposed to permanently open, and this is expected to have the greatest impact on the range expansions of mangroves as well as competition with salt marsh plant communities that occupy the same intertidal region as mangroves. Nevertheless, possible increased rainfall patterns on the southern African east coast, coupled with sea level rise may result in an increase in the frequency and duration of mouth opening, with some estuaries becoming permanently open and thereby facilitating a corresponding increase in mangroves.

The historical range expansion of mangroves from the subtropical to the warm temperate region along the east coast has unfortunately been disturbed by transplant experiments. The southernmost natural population of *A. marina* was located in the Kobonqaba Estuary (Fig. 1) (Adams et al. 2004). However, this species was successfully artificially propagated to the Nahoon Estuary (Fig. 1) in the warm temperate region in 1969 (Steinke 1999), followed a few years later by the black and red mangrove. These trees have now formed a typical mangrove forest 0.6 km from the estuary mouth. A second site was artificially planted with *A. marina* at Tyolomnqa Estuary in the 1990s and these populations are producing propagules that are being moved around the coastline by currents.

With continued global warming, mangroves will naturally colonise permanently open estuaries to the south of these sites (Steinke and Ward 2003), a move that will inevitably result in competition with intertidal salt marsh habitats. If there is a contraction of salt marshes in the current warm temperate region due to global warming, there is little opportunity for these plants to expand southwards due to the shape of the subcontinent which has an east-west orientation in this biogeographic region. In

contrast, the expansion of *Spartina alterniflora* northwards in North America was possible and compensated for the loss of habitat in the south due to global change (Kirwan et al. 2009).

Evidence to support a natural south-westward expansion of mangroves into the current warm temperate region of southern Africa is the recent natural establishment of a single *Bruguiera gymnorrhiza* tree in a salt marsh in the Kariega Estuary (Fig. 2), more than 150 km south of the next known natural *B. gymnorrhiza* population. If this tree survives and grows, it will potentially shade out the salt marsh plants growing in its vicinity, leading to a change in ecology of the intertidal region around the plant. However establishment and survival are dynamic, as shown by studies at the Nahoon Estuary where regular freshwater flooding events deposit sediment that can smother small *A. marina* individuals. This increases the elevation of the intertidal area which allows salt marsh plants to dominate (Geldenhuys 2014).

Dense salt marsh mats can also prevent mangrove propagules from establishing. Hoppe-Speer et al. (2015b) mapped changes from historical aerial photographs and showed that the expansion of mangroves at the Nahoon Estuary was in open sandflat areas rather than at the expense of salt marsh habitats. Any perturbations to the characteristics of the intertidal zone could favour the mangroves over the salt marsh, or vice versa. Indeed, Guo et al. (2013) have shown that biotic interactions are a major factor in determining the expansion of the mangrove *Avicennia germinans* into salt marshes under climate change conditions.

Foraminiferans

The study by Langer et al. (2013) provides an excellent insight into actual and potential rates of shift in the distribution of foraminifera belonging to the genus *Amphistegina* in response to global warming. Foraminifera are ubiquitous components of shallow water ecosystems and their abundance in coastal waters, including estuaries, suggests that alterations in their ranges is also likely to trigger broader changes in ecosystem functioning.

Langer et al. (2013) have shown that *Amphistegina* spp. have recently progressed to the southwest along the KwaZulu-Natal coast towards 31°S (Fig. 1). Using a species distribution model, these authors calculated the amphisteginid range shift to be between 2.7 and 8 km year⁻¹, and that this genus will reach approximately 33.4° S by the year 2100 if present climate change trends persist. The above findings corroborate the fossil record which shows that large symbiont-bearing foraminifera adapt well to increasing water temperatures and are a group that benefits from global warming. However, any temperature related benefits may be negated by ocean acidification which poses a high risk of extinction for shallow tropical benthic foraminiferans later this century (Uthicke et al. 2013).

Stromatolites

An extensive network of extant stromatolite formations was recently discovered along the South African south-east coast (Smith et al. 2011; Perissinotto et al. 2014). Stromatolites are laminated microbialite structures generated through a process of biomineralization driven mainly by cyanobacteria, also known as blue-green algae. Regarded as the earliest forms of life on Earth and dating back 3.5 bya, microbialite structures are very common in the Precambrian fossil record, but virtually disappeared in the Phanerozoic as a result of the radiation of the metazoans which prevented their growth through grazing and bioturbation (Mata and Bottjer 2012). The carbonate supersaturation state of the primordial ocean, a primary requirement for the formation of microbialites, has also changed during this period and contributed further to their demise (Riding 2012). As a result, extant marine stromatolites are currently extremely scarce around the world, with substantial formations still found only in Australia (e.g. Shark Bay) and the Bahamas (e.g. Exuma Cays). In this context, the southern African coastal stromatolite formations, of the barrage pool or waterfall types, are very important as they extend over about 200 km of coastline, from the Storms River to Cape Recife and then further to the east around Cape Morgan and the Kei River mouth (Perissinotto et al. 2014).

As these important ecosystems have only just been described, there is virtually no information regarding the impact of climate change on their structure and functioning, or their original distribution around the southern African coast. Cyanobacteria generally operate best at high temperatures (Lee 1999; Paerl and Huisman 2009), so stromatolite growth could potentially increase in response to the warming of oceanic waters and a rise in air temperatures. Poleward range expansion may, however, not be possible unless the CaCO_3 supersaturation and nutrient requirements are satisfied (Perissinotto et al. 2014). These conditions are very specific in terms of stream input along the coast, so unless changes in rainfall patterns disrupt the seepage inflow, the position of these stromatolites would remain relatively unaffected. A complication could arise from sea level rise, which may force the repositioning of barrage pools further inland.

Historically stromatolites have acted in a contrarian manner during major extinction events (Mata and Bottjer 2012; Riding 2012) in that they have resurged when other taxa (e.g. metazoans) have disappeared. In the event of major extinctions, southern African stromatolites may benefit and become more extensive. However, the effects of an increasing human population, through changing nutrient inputs and the addition of other stressful factors, would be a far bigger driver of change to these systems (Perissinotto et al. 2014). For instance, the alien invasive estuarine tube-worm, *Ficopomatus enigmaticus* has been observed regularly in several stromatolite pools, where dense populations are established under favourable conditions and then disappear suddenly in response to cold spells driven by coastal upwelling, or freshwater dominance of the pools caused by increased groundwater seepage.

Corals

Subtropical reef-building corals in southern Africa live at the edge of their temperature range (Celliers and Schleyer 2008) and, as coastal waters become warmer, they are slowly expanding into new areas to the southwest (Lucas and Griffiths 2012). Events promoting rapid poleward range expansion of tropical reef corals have been described recently from temperate areas of Japan in response to rising sea temperatures (Yamano et al. 2011). This has led to the suggestion that temperate areas may serve as refugia for tropical corals, which are in decline because of rising sea temperatures (Hoegh-Guldberg 1999). In southern Africa, however, a major poleward expansion of coral reef range appears to be unlikely as coastal areas to the south of the current coral distribution are densely populated and characterized by river effluents with silt, sewage and agricultural nutrient inputs that are too high for coral reef formation, even if marine temperatures were to become suitable. In addition, most of the rivers south of Lake St Lucia carry naturally high sediment loads into the sea during the summer rainy season (Wright and Mason 1993) that are not conducive to coastal coral formation.

Coral bleaching, as a result of the expulsion of photosynthetic zooxantellae from polyps, has caused great concern regarding the future impact of ocean warming on the survival of reef-building corals. In southern Africa, unlike elsewhere, only minor bleaching effects were observed after the 1998 El Niño Southern Oscillation event. However, quantifiable bleaching occurred during an extended period of warming in 2000 (Schleyer et al. 2008), which also had a deleterious effect on coral recruitment success. High-latitude southern African coral reefs have also shown changes in community structure, with increases in hard coral cover and a reduction in soft corals resulting in a 5.5% decrease in overall coral cover (Schleyer et al. 2008). Susceptibility by both tropical and cool-water corals to potential ocean acidification may also limit any south-westward expansion of corals in southern African coastal waters.

Crustaceans

There are a number of mangrove-associated invertebrates that reach their southern-most distribution on the African continent in the Eastern Cape Province. Foremost of these are a number of fiddler crabs (Ocypodidae: Genus *Uca*) that are mainly tropical and subtropical in their distribution patterns. Two of these species, *Uca annulipes* and *U. urvillei*, are also found in the warm temperate Kariega Estuary (Fig. 1) salt marshes, with the latter fiddler crab being a dominant component of the macrobenthos within this system (Hodgson 1987). Until recently, the Kariega Estuary was regarded as the southernmost range of distribution for *Uca* in southern Africa. However, the recent discovery of *U. annulipes* in the Knysna Estuary constitutes a new southernmost limit for the genus (Peer et al. 2016). Also of significance is recent research (Fusi et al. 2015) on *U. urvillei*, which shows this air-breathing crab to be a thermal generalist, with specimens from the centre of their distribution (Kenya) having similar thermal tolerances to those from the southern edge of their distribution (South Africa).

Another crab that is usually associated with tropical and subtropical mangroves, but also occurs in the Kariëga Estuary salt marshes in low numbers is *Neosarmatium africanum*, a species that usually scavenges mangrove leaves and macro-detritus during low tide (Branch and Grindley 1979; Peer et al. 2014). The mollusc *Cerithidea decollata* is common in parts of the middle reaches of the Kariëga Estuary (Hodgson 1987) and would be one of the species that is likely to proliferate should mangrove habitat expand southwards into the area currently occupied by salt marshes within this system. Indeed the species has already been recorded in some warm temperate estuaries along the southern Cape coast, including the Knysna system where at high tide the snail climbs the rush *Juncus kraussii* (Hodgson and Dickens 2012) instead of mangrove trunks in the main part of its range.

The widespread and mainly tropical crab *Scylla serrata* is another species that extends into warm temperate estuaries of the Eastern Cape but is absent from cool temperate systems west of Cape Agulhas (Fig. 1). This species is known to stop all movements and cease feeding if the water temperature reaches 12°C (Hill 1980). Global warming may well increase the amount of suitable estuarine habitat available to *S. serrata* in southern Cape estuaries but the expansion of kelp beds to the east of Cape Agulhas suggests a cooling and not warming of coastal waters within this region. If *S. serrata* postlarvae can gain access to estuaries within the warm temperate/cool temperate transition zone during a period of coastal warming, then this species is able to survive within this environment and grow to adulthood.

The freshwater prawn *Macrobrachium petersi*, a subtropical species that makes extensive use of the estuarine environment during parts of its life cycle, was observed to occur in the Breede Estuary in 1995. Range extensions by this species southwest of Port Elizabeth were first recorded in 1984 in the Gamtoos Estuary (Coetzee 1986), with the Breede Estuary occurrence suggesting a significant westward expansion by this species. Similarly, the tropical paddler crab *Varuna litterata*, which migrates as larvae from the sea through estuarine waters to freshwater, has recently appeared in large numbers in certain cool temperate Western Cape estuaries (S.J. Lamberth, unpublished data).

In recent decades there have been major declines in the rock lobster *Jasus lalandii* on the Western Cape Province west coast to less than 3% of pristine populations, and this has been attributed to both over-exploitation and changes in productivity of the species in association with altered environmental conditions in recent decades (Melville-Smith and van Sittert 2005). There also appears to have been an increase in the main rock lobster populations towards the south-western parts of the Western Cape Province (Fig. 1) after 1989 and this has resulted in most of the commercial catches now being made in this area (Blamey et al. 2015).

This expansion by *J. lalandii* towards the southwest has also caused a regime shift in the ecosystem brought about by the predation of rock lobsters on the sea urchin *Parechinus angulosus*. Consequently the benthic community composition has changed dramatically with macroalgae and sessile invertebrates increasing by 2 600% and 453% respectively (Blamey et al. 2010). Predation by these shifting lobster populations have also resulted in high mortality of juvenile abalone that find refuge under the urchin spines (Tarr et al. 1996).

Another crustacean that has the potential to influence marine invertebrate communities in the Western Cape Province is the European shore crab *Carcinus maenas*, which is listed as among the World's 100 most invasive species. This crab occurs at sheltered localities between Saldanha Bay in the north (le Roux et al. 1990) and False Bay in the east (Fig. 1). It preys on a wide variety of intertidal organisms and can decimate bivalve and oyster populations as well as alter intertidal community structure (le Roux et al. 1990). Fortunately it is limited in its distribution to certain harbours and bays of the Western Cape coast and appears unable to flourish on wave-exposed shores in the region (Hampton and Griffiths 2007)

Mollusca

The mangrove snail *Cerithidea decollata* is common in parts of the middle reaches of the Kariega Estuary (Hodgson 1987) and would be one of the species that is likely to proliferate should mangrove habitat expand southwards into the area currently occupied by salt marshes within this system. Indeed the species has already been recorded in some warm temperate estuaries along the southern Cape coast, including the Knysna system where at high tide the snail climbs the rush *Juncus kraussii* (Hodgson and Dickens 2012) instead of mangrove trunks in the main part of its range.

Both Kilburn and Rippey (1982) and Branch et al. (2010) stated that the thick-shelled clam *Meretrix morphina* does not occur south of Maputo Bay, Mozambique. However, it has been recorded regularly and often in large numbers in the St Lucia Estuary since 2002 (Nel et al. 2012). It briefly disappeared at the peak of the drought within the region (2005-2011), when salinity levels increased to >100 (Mackay et al. 2010), but then reappeared as a new wet cycle occurred in the area and salinity returned to 'normal'. It has recently been recorded in densities as high as ≈ 200 individuals.m⁻² throughout the lake system (R. Perissinotto, pers. obs.), but is currently experiencing mass-mortality as desiccation and hypersalinity are again prevailing in response to the latest El Niño-driven drought in the region.

Further to the southwest, support for a cooling of waters in False Bay (Fig. 1) is provided by a reduction in the distribution and abundance of the warm-water intertidal brown mussel *Perna perna* in this bay. This species was common along the False Bay coast in the 1980s but was reduced to small

517 relict populations in the warmest part of False Bay by 2010 (Mead 2011). In addition, the main
518 population of this species in the Western Cape Province appears to have been pushed eastwards by
519 cooler waters to beyond Arniston on the Cape south coast (Blamey et al. 2015).

520
521 Recent evidence suggests that intertidal invertebrates on the southern African coast can undergo major
522 distributional changes associated with climate change. Muteveri et al. (2015) have shown that
523 phylogeographic patterns determined for the smooth plough shell *Bullia rhodostoma* indicate a major
524 westward range expansion along the coast following the Last Glacial Maximum 27 000-19 000 years
525 ago. The smooth plough shell appears to be very sensitive to changes in neritic marine temperatures
526 and the current climate change trends are therefore likely to have a significant impact on the
527 abundance and distribution of this sandy beach species around the southern African coast. Similarly,
528 work in the same region by Mmonwa et al. (2015) suggests that rocky shore patellid limpets also
529 showed spatial expansion during the Late Pleistocene or Early Holocene, when the present-day
530 coastline was formed.

531
532 Introduced marine molluscs are having profound effects on the distribution and abundance of
533 indigenous intertidal invertebrates along the southern African coast, and are impacting directly on the
534 colonisation patterns and abundance of species in these waters (Mead et al. 2011). Of particular
535 interest in this regard is the alien invasive snail *Tarebia granifera*, which is advancing at an alarming
536 rate into the estuaries of KwaZulu-Natal (Appleton et al. 2009; Picker and Griffiths 2011). The
537 species, originally from south eastern Asia, was introduced into southern Africa in the late 1990s
538 through the aquarium trade and has now occupied the upper and middle reaches of most estuaries to
539 the north of Durban, reaching as far south as the Mkomazi Estuary on the KwaZulu-Natal south coast
540 (Appleton et al. 2009). It is parthenogenetic and exhibits an extraordinary reproductive rate, attaining
541 maximum densities of 21 000 individuals per m² (Picker and Griffiths 2011). It also has the ability to
542 tolerate salinity levels of up to 30, despite having often been referred to as a freshwater dweller, and
543 this makes the species a serious threat to estuarine biodiversity (Miranda et al. 2010). Warming
544 trends in coastal waters will certainly lead to its expansion further south and other global change
545 factors may facilitate this species gaining a selective advantage over its native counterparts. In coastal
546 lakes of northern KwaZulu-Natal Province, *Tarebia granifera* is competing for food and space with
547 native snails and has already displaced *Assiminea* cf. *ovata* in Lake St Lucia and both *Melanoides*
548 *tuberculata* and *Bellamya capillata* in Lake Sibaya (Miranda and Perissinotto 2012).

549
550 Another alien mollusc species that has caused serious changes to local marine biodiversity is the
551 Mediterranean mussel, *Mytilus galloprovincialis*. This species was accidentally introduced from
552 Europe to the south-western Western Cape Province around 1979 and is now the predominant dweller
553 on the intertidal rocks of the South African west coast and part of the southeast coast, reaching Port

Elizabeth to the east (Robinson et al. 2005). However, it has also provided a favourable environment for a variety of small invertebrate rock dwellers, which have flourished within its beds (Picker and Griffiths 2011). According to Robinson et al. (2007) this species has provided a complex habitat, especially in the mid-intertidal zone, for a range of indigenous species that were previously absent or less abundant in this zone. Thus, in this case it appears that a ‘beneficial’ colonisation effect may be balancing the initial negative colonisation impact that resulted in the elimination of large limpet species, as invaded shores now exhibit increased biomass and species richness (Robinson et al. 2005). The African black oystercatcher, *Haematopus moquini*, which was regarded as endangered, has apparently benefited from this enhanced food availability provided by *M. galloprovincialis* beds (Picker and Griffiths 2011).

Zooplankton

An example of an estuarine planktonic species that could be a good indicator of global warming is *Acartiella natalensis*, a tropical calanoid copepod that occurs in large numbers in South African estuaries from Kosi in the north to Knysna in the south (Fig. 1) but was not recorded in cool-temperate estuaries to the west (Grindley 1981). Additionally, a contraction in the range of the temperate *Paracartia africana*, which has been recorded from Walvis Bay in Namibia to the Mbashe Estuary in the Eastern Cape Province (Grindley 1981), would also be indicative of global warming of estuarine and coastal waters. The Mbashe Estuary (Fig. 1) has been identified as being within the biogeographic transition zone between the subtropical estuaries in the northeast and warm temperate estuaries to the southwest (Harrison 2002). In contrast to the well documented information on the distribution patterns of some of the other coastal invertebrates, little work has been conducted on the biogeographic characteristics of estuarine zooplankton on the subcontinent and this topic therefore requires considerably more research effort.

A notable exception in this regard, is the work conducted by Wooldridge and Deyzel (2012) in the Mngazi Estuary (Fig. 1). This system is situated within the subtropical/warm temperate transition zone and is occupied by both tropical and temperate zooplankton species. Strong longitudinal temperature gradients occur, with the upper estuary reaches remaining consistently warmer than the lower reaches. Consequently it is not surprising that the two dominant tropical zooplankters (copepod *A. natalensis* and mysid *Mesopodopsis africana*) showed an increase in abundance towards the upper reaches, whereas their temperate congeners (*A. longipatella* and *M. wooldridgei*) were less abundant in an upstream direction (Wooldridge and Deyzel 2012).

In the marine environment, on the Western Cape west coast, there was a preponderance of large copepod species in St Helena Bay (Fig. 1) during the 1950s and 1960s, whereas smaller species dominated during the 1990s (Verheye 2000). This change was correlated to a two order magnitude

increase in copepod densities between 1950 and 1996 and an almost one order magnitude decline between 1998 and 2007 (Hutchings et al. 2009). Clearly the distributional and abundance profiles of coastal zooplankton species are showing major spatio-temporal changes over time, but the degree to which these are linked to climate change has yet to be proven shown.

Squid

Squid may be a good indicator of climate change as their physiology is able to respond rapidly to changes in the environment, with temperature being a key driver (Pecl and Jackson 2008). The squid *Loligo reynaudii*, known locally as chokka, occurs on the coastal shelf between the Orange Estuary and the Great Fish Estuary, mainly in waters <200 m depth. Spawning behaviour, embryonic development and survival of the species have been directly linked to temperature and upwelling frequency and intensity (Oosthuizen et al. 2002; Roberts 2005). As such, any changes in water temperature and upwelling, associated with short-term climatic change (such as ENSO events) and longer-term climate change will affect the abundance of squid. Turbidity near the seabed also affects the spawning behaviour of adult squid, with high turbidity causing them to avoid the shallower inshore spawning grounds and move into deeper waters, where they are unavailable to the inshore fishery (Roberts and Sauer 1994).

Severe winter storms along the southern African coast in 1992 resulted in high swells and beach erosion adjacent to the inshore squid spawning grounds, which may have accounted for the exceptionally poor catches in that year (Roberts and Sauer 1994; Roberts et al. 2012). Severe winter storms may be linked to El Niño conditions, which enhance severe westerly winds on the south coast, and to longer-term climate change. Extreme weather events are predicted to increase in frequency and intensity in the 21st century, which may have severe implications for the squid fishery. It should also be mentioned that sustained range expansion of Humboldt squid *Dosidicus gigas* in the North Pacific coincided with changes in climate-linked oceanographic conditions and a reduction in competing top predators, which are also important fishery species (Zeidberg and Robison 2007).

Estuarine fishes

Changes in the distribution and abundance of tropical and temperate ichthyofaunal species provides concrete evidence of global warming along the South African south-eastern coast. An early study in the Mngazana Estuary (Fig. 1) within the subtropical/warm temperate transition zone of the Eastern Cape Province revealed seasonal changes in the balance between tropical and temperate fish species within this estuary (Branch and Grindley 1979). A subsequent investigation in the same estuary indicated that the winter increase in temperate species was less apparent, and that tropical taxa were dominant throughout the year (Mbande et al. 2005).

628 Similarly, James et al. (2008a) documented an increase in tropical estuary-associated marine fish
629 species in the warm temperate East Kleinemonde Estuary (Fig. 1). These tropical pioneers were not
630 present within the estuary during all years in the past two decades but their colonisation is perhaps an
631 indication that conditions for large numbers to follow suit are developing. In addition, it should be
632 noted that the presence of increasing numbers of tropical species in the East Kleinemonde Estuary
633 was associated with a warming of the adjacent coastal waters (James et al. 2008a).

634
635 There are numerous once-off records of pioneer tropical species occupying other warm-temperate
636 estuaries along the South African coast, some for the summer season only and others persisting
637 throughout the year. In March 1994, a bigfin mudskipper *Periophthalmus sobrinus* was captured in a
638 salt marsh in the Kariega Estuary (Whitfield 1994a). This species is usually restricted to mangrove
639 habitats within permanently open subtropical and tropical southern African estuaries. Lamberth et al.
640 (2011) have also recorded the southward extension of a large number of tropical fish species into
641 Western Cape estuaries over the past 15 years, including the checked goby *Redigobius dewaali*,
642 lionfish *Pterois volitans*, triplefin *Lobotes surinamensis*, flutemouth *Fistularia petimba* and thornfish
643 *Terapon jarbua*. Overwintering of tropical estuarine-associated marine species in temperate South
644 African estuaries is possible, due to the similarity in water temperature ranges in estuaries throughout
645 the country.

646
647 There has also been a re-establishment of the summer-residency patterns of the tropical bull shark
648 *Carcharinus leucas* in certain Western Cape estuaries, four decades after being fished to near
649 extinction in the region (McCord and Lamberth 2009). The southward re-expansion of this species
650 into cooler waters coincided with a decade of extended drought and unavailability of the St Lucia
651 Estuary for pupping and nursery habitat on the subtropical coast of South Africa. The above alteration
652 in distributional range indicates the potential importance of climate change in affecting the
653 distribution of marine fish species that use both estuaries and the sea during their life cycles, i.e. in
654 some cases range expansion may be driven by loss of habitat or increasing physiological stress in the
655 'native' range, not by suitable conditions developing elsewhere.

656
657 Some, but not all, fish range expansions persist with the establishment of viable populations in the
658 new range (Lamberth et al. 2011). Subtropical spotted grunter *Pomadasys commersonnii* have
659 expanded southward into the warm temperate/cool temperate transition zone in the Western Cape
660 Province over the past five decades (Lamberth et al. 2013). Initially, occurrence of this species was
661 seasonal in summer with a return migration to warm temperate and subtropical waters during the
662 cooler months. Over the past two decades, *P. commersonnii* has become resident throughout the year
663 and now spawns within its new biogeographic range. It should be emphasized that the above changes

in distributional patterns and spawning behaviour of fishes in southern African coastal waters are linked to a broad range of climate change impacts and not to a single driver (Potts et al. 2015).

The Cunene Estuary on the northern border of Namibia is the northern limit of some temperate estuary-associated fish distributions (e.g. Cape silverside *Atherina breviceps* and white steenbras *Lithognathus lithognathus*) and southern most limit of some equatorial species (e.g. Senegal sleeper *Eleotris senegalensis* and West African freshwater goby *Awaous lateristriga*) (van Niekerk et al. 2008). This suggests that the Cunene may be the southernmost boundary of the overlap of Guinea and Benguela Current Large Marine Ecosystem (BCLME) fauna. Coastal warming raises the intriguing possibility of a southward shift of both the cool temperate and equatorial limits for estuary-associated species to the Orange Estuary on Namibia's southern border with South Africa.

Changes in river run-off associated with climate change also have a major impact on the distribution and abundance of marine fish juveniles that use estuaries as nursery areas. For example, Lamberth et al. (2008) predicted that an approximately 60% reduction in the mean annual run-off into the Breede Estuary would result in a 50% decline in the abundance of dusky kob *Argyrosomus japonicus* and spotted grunter *Pomadasys commersonnii*. River flow into South African estuaries plays a major role in attracting the postlarvae of estuary-associated marine fish species into these systems (James et al. 2008a) and any reduction in flow associated with climate change would be expected to have concomitant impacts on fish cohort strengths (Whitfield 1994b).

Estuaries, their fluvial plumes and warm-shallow bays on South Africa's cool temperate west coast are more critical as nurseries and refugia than those in the country's warm temperate and subtropical bioregions, where a wide range of estuaries are readily available to fishes (Harrison and Whitfield 2006; Lamberth et al. 2008). Cooling of the southern Benguela region will see this relative importance increase. These warm but limited estuarine habitats, associated fluvial plumes and shallow bays also serve to link coastal fish populations (e.g. *A. coronus* and *L. lithognathus*) in the northern and southern Benguela regions (Lamberth et al. 2008). Ostensibly, southward movement of these coastal fish populations commences during anomalous years when cold upwelling barriers break down or when there is a southward intrusion of warm water during Benguela El Niño years, where after these species retreat into warm-water estuarine refugia when upwelling resumes (van der Lingen et al. 2006, Lamberth et al. 2008). Future climate change predictions for South Africa are that flow from the summer rainfall catchments is set to increase, whereas that from the winter catchments is set to decrease (Hewitson and Crane 2006, Engelbrecht et al. 2009), with a corresponding decrease in river flow, fluvial plumes and available fish refugia in the major west coast estuaries, namely the Orange, Olifants and Berg.

A combination of altered freshwater flow, fishing, and anomalous events such as extended droughts have led to genetic bottlenecking and a collapse in the effective population size of *A. japonicus* throughout its South African range (Mirimin et al. 2015). *Argyrosomus japonicus* males are hybridising with sympatric silver kob *A. inodorus* females which have experienced similar population declines (Mirimin et al. 2014; 2016). It appears that the effective population sizes of both species has declined to such an extent that there are now impacts on mate choice, with the few remaining but relatively large *A. japonicus* males outcompeting the equally few but smaller *A. inodorus* males.

Marine fishes

In the western part of the subcontinent there is evidence of climate-driven distributional shifts in the closely related *Argyrosomus coronus* and *A. inodorus* that have placed the adults in contact with one another during spawning events (Potts et al. 2014a). This has led to hybridization as a direct result of the breaking down of isolating mechanisms that were previously in place. Global warming of coastal waters in the Angola-Benguela Frontal Zone has therefore altered the evolutionary history of these two fish species (Potts et al. 2014a). Further evidence of ocean warming causing changes in reproductive activities is provided by Potts et al. (2014b) for the blacktail *Diplodus sargus capensis*. These authors showed that over the past three decades the reproductive area for this sub-species in southern Angola has been shrinking by 7% per decade due to coastal warming and expanding by 6% per decade in northern Namibia, as waters in this region warmed.

Distributional changes in demersal fish populations in the BCLME on the southern African west coast have also been linked to climate change, especially global warming. However, whilst the change in distribution of several fish species in the above ecosystem over the period 1985-2010 is what was to be expected with increased warming, other species distribution patterns have responded in a contrarian manner (Yemane et al. 2014). Demersal fish biodiversity hotspots have also been identified within the BCLME and are generally associated with deeper, cooler bottom temperatures which have remained relatively consistent over a 20-30 year study period (Kirkman et al. 2013).

In the southern demersal fishing area of the BCLME (i.e. south of Cape Columbine, Fig. 1) there were temporal changes in the fish assemblage between the early 1990s and mid-2000s. These changes reflected a decline in slow-growing long lived species and an increase in fast-growing, early maturing species (Atkinson et al. 2011). The extent to which this change is due to selective demersal fishing activities, and how much is attributable to climate change, is unknown. As a general rule, however, it is to be expected that climate change will have more of an impact on littoral rather than deep water fish species around southern Africa's coast. However, if these climate changes extend to deep offshore waters it is possible that demersal fish in these previously stable environments could be

devastated by fluctuations that did not previously occur in such areas and to which these species are not well adapted.

Fishers in the South African sole trawl industry and elsewhere in the world have long used rainfall and associated terrestrial runoff as a predictor of catches in the following season (van Niekerk and Lamberth 2014). The west coast sole fishery collapsed in the mid-1970s (Crawford et al. 1987), which coincided with the period (1970 to 1980) when dam storage capacity on the Orange rose from 10% to 90% of present day levels (van Niekerk and Lamberth 2014). Demersal trawl survey data (DAFF 1984-2011) indicated a positive relationship between Orange River flow entering the sea and fish biomass estimates. Furthermore, impoundments and altered freshwater flow from the Orange catchment resulted in decreased sediment discharge into the sea and changes in composition from predominantly silt to cohesive clays. This probably influenced the burying ability and crypsis of juvenile sole, thus leaving them more exposed to predators on the sediment surface, which may have contributed to the abrupt stock collapse (Stoner and Ottmar 2003). In comparison, the stability in South Africa's east coast sole fishery may be partly attributed to there being relatively fewer impoundments and no substantial change in the nature and volume of terrigenous sediment reaching the sea in that region (van Niekerk and Lamberth 2014). The above trends suggest that the distribution and abundance of soles in coastal marine waters is likely to be strongly influenced by river flow alterations arising from climate and other global change factors.

In a long-term study (19 years) of the sub-tropical reef fish community in southern KwaZulu-Natal Province, based on recreational spearfish catches, Lloyd et al. (2012) found a general increase in the abundance of tropical species in catches, as well as a change in the proportion of tropical versus temperate species. The results from this study were consistent with a predicted poleward shift in the distributional ranges of marine fish with climate change in response to warming of the Agulhas Current. Average annual sea surface temperatures in the region were also found to have increased by 0.46°C between 1989 and 1996 and 2002 and 2007, with warming being most pronounced during summer (Lloyd et al. 2012).

Pelagic fish stocks associated with the southern Benguela region have also undergone major spatial shifts over recent decades. For example, the main spawner biomass of both the sardine *Sardinops sagax* and anchovy *Engraulis encrasicolus* moved from the west to the east of Cape Agulhas in the late 1990s (Roy et al. 2007). However, recent evidence suggests that the main spawner-biomass of sardine is shifting back to the west (van der Lingen et al. 2011) and that there are three discrete western, southern and eastern sub-populations or stocks of sardine (van der Lingen et al. 2016). Mixing between these stocks is highly variable but pulses of recruitment from one more productive stock to another may make a greater contribution to the receiving stock than above-average

recruitment (de Moor and Butterworth 2015). Consequently, the eastward shift and subsequent return of sardine biomass towards the west coast may be more a function of differential recruitment and mixing between stocks than climate driven. This does not, however, discount the indirect influence that climate change may have on spawner-biomass via altered environmental conditions and its influence on recruitment.

High biomasses of small-pelagic Engraulidae and Clupeidae in the coastal marine environment are often associated with river plumes (e.g. Tugores et al. 2010). Southern African small-pelagic fish are unlikely to be an exception, but few studies have addressed the links between catchment flows, fish behaviour, recruitment and production (Hutchings et al. 2010). South African populations of anchovy and sardine are monitored by means of hydro-acoustic spawner-biomass and recruitment surveys conducted annually since 1984 (DAFF 2012). In addition to the long-known association with upwelling cells, high densities of anchovy juveniles also appear to be associated with the river plumes of the larger catchments, specifically the Orange, Olifants and Berg on the west coast (van Niekerk and Lamberth 2014). The main driver is likely to be the refuge offered by these turbid plumes, productivity fronts being of lesser importance in this upwelling dominated region. Initial analysis of the relationships between river flow and pelagic fish biomass indicated a positive relationship between river-flow (by inference the fluvial plume) and the densities of the three small-pelagic species, but only the relationship between juvenile anchovy and flow was significant (van Niekerk and Lamberth 2014). What was also evident was that in years of anchovy being absent from much of the west coast there was measurable and persistent biomass of these fish in the fluvial plumes off the three larger catchments. Climate change and predicted changes in rainfall, terrestrial runoff and sediment discharge will result in spatial and temporal changes in the nature and extent of these plumes, thereby influencing the distribution and biomass of certain pelagic fish species.

Fish pathogens

Aphanomyces invadans is a pathogenic water mould that causes lesions and mass mortalities in wild and cultured fish populations, a disease known as Epizootic Ulcerative Syndrome (EUS). This pathogen was first reported in Africa from the Zambezi Basin in 2006, thereafter in the Palmiet River (Western Cape Province) in 2011 (Huchzermeyer and van der Waal 2012). The first estuarine occurrence of *A. invadans* in southern Africa was verified in the cool temperate Palmiet Estuary during the autumn of 2015 where it was responsible for a mass mortality of the barehead goby *Caffrogobius nudiiceps*. It was subsequently also suspected as being responsible for mass mortalities of the robust mullet *Valamugil robustus* and river bream *Acanthopagrus vagus* in the subtropical Mgobezeleni Estuary at Sodwana Bay over the same time period.

EUS zoospores infect fish via breaches in the epidermal barrier, whereafter the hyphae invade the skin, musculature and internal organs (Huchzermeyer and van der Waal 2012). Vectors include fishers, their fishing gear and aquaculture, in particular the ornamental fish trade. EUS outbreaks correspond to abrupt physico-chemical changes and infect fish that are compromised by environmental and behavioural stress. Consequently, future and existing habitat degradation, eutrophication and climate change may see this pathogen spread amongst fish assemblages in southern African estuaries that are being subjected to extreme levels of change.

Birds

Seabirds can also be used as indicators of environmental change, including localised warming or cooling. Long-term changes in sea surface temperature of the Agulhas and Benguela marine ecosystems around southern Africa (Smit et al. 2013) have resulted in south-eastward and eastward shifts in the distribution of pelagic prey fish species of the Cape gannet *Morus capensis*. Although the survival of adult birds were not correlated to any long-term trend, the recruitment of offspring into the adult population may well be affected by both climate change and human fishing activities (Disteller et al. 2012).

Altered breeding distribution by bank cormorants *Phalacrocorax neglectus* also appears to correspond to the south-eastward shift in abundance of rock lobsters (Crawford et al. 2008a). Therefore, if the rock lobsters are changing their centre of distribution in response to climate change, the changes in their natural predator distribution, in this case bank cormorants, is also a function of climate change.

Displacements of adult populations of sardine *Sardinops sagax* and anchovy *Engraulis encrasicolus* away from the northern parts of the Western Cape Province west coast, towards the south and east (Coetzee et al. 2008), resulted in increased numbers of swift tern *Thalasseus bergii* breeding in the latter regions and a decline in the north (Crawford 2009). Similarly, the proportions of mature African penguin *Spheniscus demersus* and Cape gannet *M. capensis* breeding in the south, east and north followed the same pattern (Crawford et al. 2008b), thus indicating that shifts in prey distribution almost invariably result in changes in predator distributions.

Mammals and reptiles

The ability to separate global warming effects from the human impact in coastal waters is sometimes very difficult to discern. Long-term biotic and abiotic monitoring data (1950-2010) from St Helena Bay on the South African west coast has revealed major variability and changes in primary productivity, zooplankton biomass and pelagic fish distributions, with only muted responses to long-term trends in oceanography and biogeochemistry (Hutchings et al. 2012). Indeed, the only distinctive trend that was identifiable by the above authors was the increase in abundance of marine mammals

associated with the earlier implementation of conservation measures to reverse past negative human impacts, a response that probably has little to do with global climate change.

In contrast, the diet of Cape clawless otters *Aonyx capensis* along the south-western Cape coast has been altered as a result of the eastward shift in the distribution of rock lobsters (Blamey et al. 2015). This latter shift is almost certainly linked to a cooling of south-western Cape littoral waters in the region and has nothing to do with fishing pressures on rock lobsters elsewhere.

The distribution of the hippopotamus *Hippopotamus amphibius* in estuarine systems around southern Africa was artificially reduced by intensive hunting of these animals, mainly during the 18th and 19th centuries (Taylor 2013). For much of the 20th century, their natural distribution in the South African coastal region, which had extended from the Western Province to northern KwaZulu-Natal (Fig. 1), was limited to Lake St Lucia, Lake Sibaya and the Kosi lakes system. In November 1928 a single female hippopotamus from Lake St Lucia set off southwards along the coast and reached the Keiskamma Estuary in the Eastern Cape Province in April 1931 where she was killed by a farmer. This pioneering journey of approximately 1600 km would not have re-established the distributional range of hippopotamus in South Africa since only a single individual was involved, but it did indicate the potential for this species to reclaim previous lost territory, provided humans did not interfere. More recently, the distribution of this species back into selected river and estuarine systems of the Eastern and Western Cape provinces has occurred due to reintroduction initiatives by conservation and coastal game farming operations. However, the genetic viability of these small isolated populations has been questioned (Taylor 2013).

The Nile crocodile *Crocodylus niloticus* was also decimated by hunting activities in all coastal systems during the 18th and 19th centuries, with Lake St Lucia containing the only viable coastal breeding population in the country for many decades (Combrink et al. 2013). The exact natural distribution of this species is largely unknown but skulls and teeth have been located between the Keiskamma and Keurbooms estuaries (Feely 2010). The last known living crocodiles in the Eastern Cape Province were killed in the Dwesa State Forest region in the late 19th and early 20th centuries but were reintroduced into the Dwesa Nature Reserve estuaries in 1980 (Feely 2010). The Dwesa reserve is situated within the subtropical/warm temperate transition zone and, despite the introduced crocodiles now being adults, there is no sign of any breeding activities. Global warming may, depending on magnitude and extent, enable this population to begin breeding in the future. In addition, increased river flooding associated with climate change along the east coast of southern Africa may facilitate the expansion of existing crocodile distribution patterns by washing individuals out to sea, followed by subsequent recruitment into adjacent estuaries.

Pioneer species as indicators of incipient ecosystem level changes

Pioneer species are hardy taxa that tend to be the first to colonize altered or damaged habitats, often starting an ecological succession that leads to a new steady-state ecosystem. In this review we have not limited our assessment to primary colonisers of disturbed habitats but have included species that occupy various levels within an ecosystem. In this manner, these pioneers are providing evidence of successful range shifts, with subsequent colonisation and transformation of existing habitats being a distinct possibility.

Co-incidental distributional movements of kelp beds, mussels and rock lobsters in a south-easterly direction from the Cape west coast suggests that these pioneers are indicative of a cooling taking place in the transitional zone between cool-temperate and warm-temperate waters of the Cape Agulhas region. Inevitably ecosystem changes will follow the occupation of new habitats in the south-east by these pioneers, especially when their numbers and biomass increase. Indeed, there are already indications that herbivores and coralline algae that were once abundant in the south-western Cape littoral zone, have now been replaced by rock lobsters, kelp beds and other sedentary species such as sponges and ascidians (Blamey and Branch 2012; Blamey et al. 2015).

Similarly, an eastward shift of the main sardine and anchovy biomass along the Cape coast resulted in a south-eastward shift in the distribution of piscivorous coastal bird species that are dependent on these pelagic fishes as their primary food source (Crawford et al. 2008b). Although these range shifts by both the fishes and birds may be linked to climate change, the detailed drivers of the recorded range extensions have yet to be fully unravelled (Crawford et al. 2008c). In addition, the links between climate change and the food resources of sardines and anchovies in south-western and south-eastern Cape waters is also in need of further research, particularly as three stocks of sardine have now been identified and the main spawner-biomass may be shifting back towards the west (van der Lingen et al. 2011; 2015; de Moor and Butterworth 2015).

Available evidence described in this review suggests that the south-westward expansion of the subtropical zone down the east coast of southern Africa is gaining momentum (Fig. 3), with strong evidence of pioneer mangrove, invertebrate and fish species now occupying Eastern Cape estuaries within the current warm-temperate biogeographic region (Table 1). This is epitomized by the situation in the permanently open Kariega Estuary where mangrove flora (e.g. *Bruguiera gymnorhiza*) and fauna (e.g. *Periopthalmus sobrinus*) are already showing an ability to establish isolated populations within the existing salt marsh habitats. Typical mangrove associated crab species (e.g. *Uca annulipes*) have also colonised this estuary in large numbers, a trend that is likely to be repeated in other permanently open Eastern and Western Cape estuaries. Further global warming will result in the

establishment of mangrove forests where salt marshes currently exist which will then be followed by an increase in dominance of invertebrate assemblages that are characteristic of such habitats.

The movement of tropical and subtropical fish species into the warm temperate biogeographic region has been documented very clearly and is likely to gain momentum as global warming continues. Some species are already common in the warm temperate/cool temperate transition zone where *Pomadasys commersonnii* and *Redigobius dewaali* have established robust breeding populations. Similarly, the tropical crustaceans *Macrobrachium petersi* and *Varuna litterata* have colonised the Cape south coast estuaries and rivers, with other tropical invertebrates likely to follow suite. In contrast to the expanding distribution by pioneer populations of tropical species into the warm temperate zone, endemics within this zone are being subject to a temperature ‘squeeze’ from both the east and the west (Fig. 3), with increased competition a likely outcome as tropical species become more abundant in the region.

Range expansions by marine and estuarine species around the southern African coast are likely to occur in a pulsed manner, especially during the early stages of colonisation following climate change. Part of the reason for this pattern is that most species are abundant towards the centre of their geographical range and then decline towards their range limits (Hidas et al. 2010). Hence the potential for colonisation at the edges of a species’ range is generally much less than at the centre, thus resulting in a pulsing of pioneers to new territories. In addition, for those plant and animal species relying on passive dispersal, the number of recruits finding distant settling areas is not as great as would be expected, e.g. *Mytilus galloprovincialis* larval dispersal along the Eastern Cape coast was <100 km, with the majority of successful recruits occurring <5 km from the parent population (McQuaid and Phillips 2000).

Although this review focuses on global climate change, other anthropogenic drivers of change may act synergistically with climate change causing changes in the distribution and abundance of species. One of the most obvious threats to fish species is overfishing. Fishing causes truncation of the age structure (through the removal of larger individuals) of exploited populations and loss of spatial heterogeneity (distribution may shrink), which makes exploited species more vulnerable to environmental variability and thus more sensitive to climate change effects. In an eight year study of coastal fish species in the warm-temperate Tsitsikamma Marine Reserve, which has been protected for more than 27 years, the fish assemblage was found to be relatively stable in terms of abundance, taxonomic distinctness, mean body size and species composition (James et al. 2012). Although abundance (CPUE) of most species was variable between years, a decrease in recruitment of the galjoen *Dichistius capensis* (an important shore-angling species) for several years did not result in a significant decrease in the abundance of this species within the MPA. Populations of exploited species

are likely to be more stable over time in MPAs than in fished areas because the accumulation of larger age/size classes in the protected area tends to smooth out fluctuations caused by recruitment variability (Babcock et al. 2010).

Conclusions

This review highlights the critical role of climate change in driving the distribution patterns of biotic groups within southern African coastal waters. Marine and estuarine organisms are not only sensitive to temperature changes associated with climate change, they are also strongly influenced by changing rainfall regimes that lead to differential river flow patterns when compared to the past. Pioneers or propagules, from either indigenous or invasive species, are often strong indicators of future colonisation processes in both estuaries and the coastal zone. In addition, anthropogenic drivers of global change often act together with climate change in causing both short and long-term changes in the distribution and abundance of species. This review represents the first time that a comprehensive synthesis has occurred across a wide range of biotic groups to substantiate current and possible future biogeographic trends at a subcontinental level. The broad patterns and processes recorded along the coast of southern Africa are likely to be reflected in similar biogeographic regions around the world, particularly in those areas that are being subjected to the same climate and global change pressures.

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Fig. 1. Map of South Africa showing selected localities mentioned in the text.

Fig. 2. A pioneering black mangrove *Bruguiera gymnorhiza* in the middle of a *Spartina* salt marsh habitat in the lower reaches of the Kariëga Estuary, Eastern Cape Province, South Africa (Photo: AK Whitfield, February 2015).

Fig. 3. Diagrammatic representation of the major distributional changes that are occurring in the three biogeographic zones along the southern African coastline. The MODIS satellite sea surface temperature image is a 10 day average from February 2009.

Table 1

Some examples from this review of the colonisation processes taking place for a variety of taxa in southern African coastal waters, including estuaries.

Taxon	Probable primary drivers	Recent distributional trends
Dinoflagellate (<i>Lingulodinium polyedrum</i>)	Climate change (upwelling and temperature) and global change (eutrophication and invasive species)	Expansion from the southern African west coast (non-blooming) to the south-eastern coast as a harmful algal bloom.
Seaweed (<i>Ecklonia maxima</i>)	Climate change.	Expansion from the southern African west coast into the southern Cape region.
Eelgrass (<i>Zostera capensis</i>)	Climate change (estuary mouth phase) and global change (e.g. eutrophication).	Contraction and partial recovery in most estuarine systems where it occurs.
Mangrove (<i>Bruguiera gymnorhiza</i>)	Climate change.	Expansion into warm temperate Eastern Cape Province estuaries.
Foraminiferans (<i>Amphistegina</i> spp.)	Climate change.	South-westward expansion in the subtropical region by 3-8 km per annum.
Squid (<i>Loligo reynaudii</i>)	Climate change.	Onshore/offshore movements and spawning linked to marine upwelling and resuspended terrigenous sediments.
Brachyuran (<i>Varuna litterata</i>)	Climate change, global change.	South-westward expansion as far as False Bay and associated estuaries.
Molluscan (<i>Cerithidea decollata</i>)	Climate change.	South-westward expansion as far as the Knysna Estuary.
Malacostracan (<i>Jasus lalandii</i>)	Climate change.	South-eastward expansion towards Cape Agulhas.
Fish (<i>Pomadasys commersonnii</i>)	Climate change, global change.	South-westward expansion into the southern Cape and False Bay estuaries.
Bird (<i>Morus capensis</i>)	Climate change.	Eastward expansion due to change in distribution of major prey fish species.
Crocodile (<i>Crocodylus niloticus</i>)	Global change (hunting) and climate change (improved breeding range).	Recent reintroductions south-westwards into its previous historic range.
Hippopotamus (<i>Hippopotamus amphibious</i>)	Global change (hunting), and prevention of coastal migration.	Recent reintroductions south-westwards into its previous historic range.