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REVIEWS

Review of the projected impacts of climate change on coastal fishes in southern Africa

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Abstract The coastal zone represents one of the most economically and ecologically important ecosystems on the planet, none more so than in southern Africa. This manuscript examines the potential impacts of climate change on the coastal fishes in southern Africa and provides some of the first information for the Southern Hemisphere, outside of Australasia. It begins by describing the coastal zone in terms of its physical characteristics, climate, fish biodiversity and fisheries. The region is divided into seven biogeographical zones based on previous descriptions and interpretations by the authors. A global review of the impacts of climate change on coastal zones is then applied to make qualitative predictions on the likely impacts of climate change on migratory, resident, estuarine-dependent and catadromous fishes in each of these biogeographical zones. In many respects the southern African region represents a microcosm of climate change variability and of coastal habitats. Based on the broad range of climate change impacts and life history styles of coastal fishes, the predicted impacts on fishes will be diverse. If anything, this review reveals our lack of fundamental knowledge in this field, in particular in southern Africa. Several research priorities, including the need for process-based fundamental research programs are highlighted.

Keywords Climate change impacts · Coastal fish · Ocean warming · Range shifts · South Africa

Introduction

The coastal zone, defined as the marine habitat between the low tide mark and the continental shelf (200 m depth), represents only 7.6 % of the world's ocean habitat (Yool and Fasham 2001). Despite its relatively small area, the coastal zone provides essential ecosystem services, such as habitat and food for both resident and migratory animals, as well as recreational and commercial opportunities for human populations, and thus is considered to be one of the most socio-economically and ecologically important ecosystems on the planet (Harley et al. 2006). Globally, Costanza et al. (1997) estimated the value of the goods and services provided by the marine coastal zone at over USD 14 trillion. Coastal areas generate biological production that supports over 90 % of the global fish catches (Pauly et al. 2002)

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and these support subsistence, small scale, artisanal, recreational and commercial fisheries that are not only significant in terms of local livelihoods (Béné 2003; Stobutzki et al. 2006; Glavovic and Boonzaier 2007), but also provide major benefits to local and national economies (McGrath et al. 1997; Costanza et al. 1999; Glavovic and Boonzaier 2007; Potts et al. 2009). Besides high levels of productivity, the diverse range of habitats found in coastal seas make these areas important biodiversity hotspots, and it is unsurprising that the majority of described marine taxa are found in this ocean zone (Ray 1991).

Besides its enormous biodiversity significance, the marine coastal zone provides both socially and economically valuable fish resources for large numbers of people in southern Africa. In Angola, the most recent surveys between 1995 and 2003 suggested that there were between 23,000 and 25,000 artisanal fishers (Duarte et al. 2005) utilizing the coastal zone. Although there is limited information on participation, the recreational, both foreign and local (Potts et al. 2009), and the subsistence fisheries appear to be growing rapidly. The Namibian coastal zone has a long history of recreational angling (both local and tourist), which is critical for the coastal economy (Barnes et al. 2002), a large commercial sector whose fishers operate from large vessels and commercial ski-boat anglers. South African coastal fisheries are multiuser, and include 24,700 commercial, 750,000 recreational and 29,000 subsistence line fishers as well as ~2000 small scale gillnet and seine net fishers (McGrath et al. 1997; Branch and Clark 2006). The coastal zone of Mozambique is host to multiuser fisheries, including a boat-based artisanal fishery with ~58,000 participants, a shore-based fishery with ~1500 participants and semi-industrial fisheries of which there are ~97 vessels (Alphonso 2004). In Tanzania, a recent marine fisheries framework study recorded 36,321 fishers in the artisanal fishery (FDD 2009). Besides the fishers, an estimated 181,600 people are thought to be involved in fisheries related activities (including processing and marketing), which support the majority of people living along the Tanzanian coastline.

With strong scientific agreement that the upper ocean (0–700 m depth) is changing rapidly as a result of anthropogenic global climate change (Rhein et al. 2013), adequate prediction of the likelihood and scale of these threats is key to the successful mitigation and adaptation required to conserve coastal marine fish species and to maintain sustainability of fisheries. Potential threats to the marine coastal zone are likely to include both physical and chemical stressors, which in turn can have direct and indirect effects on coastal fishes. Physical stressors include increase of sea temperature, sea level rise, intensification of upwelling, changes in current strength and changes in rainfall patterns and consequently the amount of freshwater input to the coastal zone. Chemical stressors include a rise in CO_2 and a concomitant decrease in the ocean pH (Harley et al. 2006).

The aims of this manuscript are to review the global understanding of climate related stressors on coastal fish communities and to identify the likely changes in the fish and fisheries in the southern African marine coastal zone. To do this, the manuscript is divided into five sections. The first will provide a description of the southern African coastal zone; the second will highlight how the environment is changing; the third will review the literature on the response of coastal fishes to climate change; the fourth will identify the trends and associated vulnerability by biogeographic zone, and the final section will outline the research priorities for understanding the impacts of climate change on coastal fishes, with particular emphasis on southern Africa.

The southern African coastal zone

For the purposes of this review, this coastal zone is defined as the region from the northern border of Angola on the West Coast to the northern Tanzanian border on the East Coast of southern Africa: a mainland coastline of ~8600 km (Fig. 1). The five countries along this coastline have contrasting physical and climatic coastal features.

The 1650 km Angolan coastline has a narrow (average 36 km) continental shelf (<200 m depth), except in the very north for the country around the Congo River mouth (Fig. 1). The majority of the coast is sandy (Anderson et al. 2012) with very few rocky outcrops and sandstone cliffs. There are 33 estuaries and one large embayment, Baia dos Tigres. The climate varies considerably with the Namib Desert (rainfall <20 mm) dominating the south, a subtropical climate with relatively low rainfall (<500 mm) in the central region and a tropical climate (>800 mm) in the north.

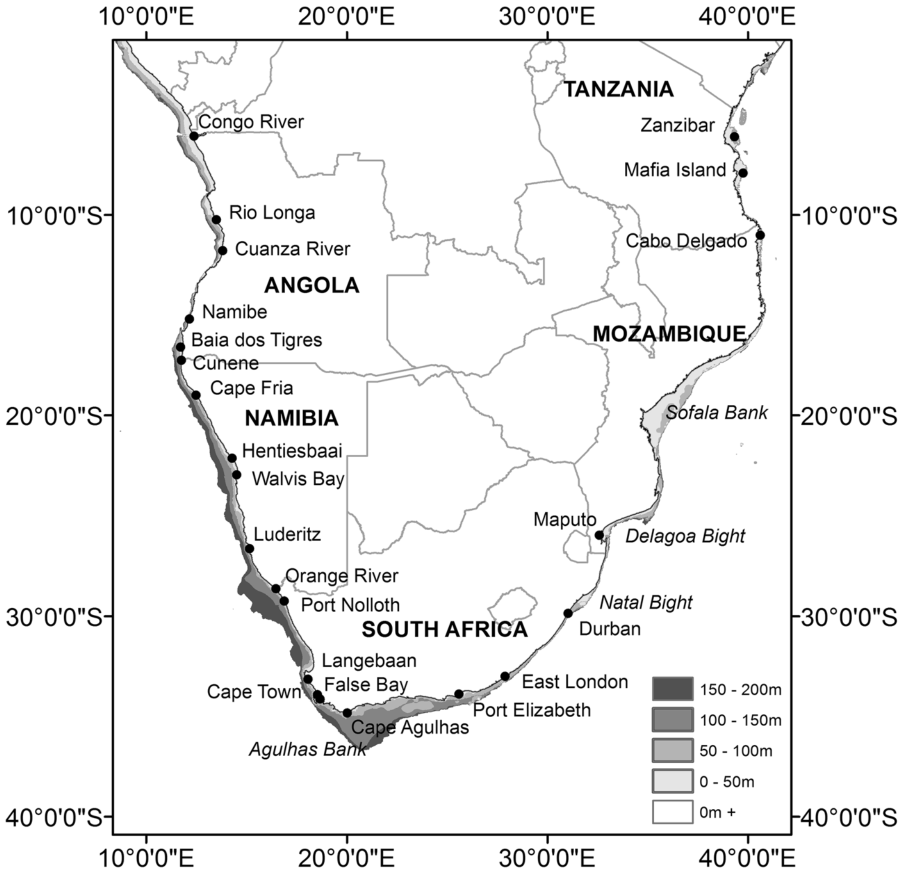


Fig. 1 Contour map of the continental shelf area of southern Africa

The Namibian coast, ~1570 km long, is relatively straight apart from the large bays at Lüderitz and Walvis Bay. The continental shelf is narrow (average ~30 km) but widens at the Orange River mouth (Fig. 1). Most of the coastline is sandy, with the only continuous rocky coast occurring in an 80 km stretch in the south. Rainfall is very low (<20 mm) and consequently the only permanent estuaries are the Cunene and the Orange, which border Angola and South Africa, respectively (Molloy and Reinikainen 2003).

The South African coastline extends for 3650 km and consists of ~27 % rocky shore, 42 % sandy beach and 31 % mixed shore (Bally et al. 1984). South Africa's continental shelf is wide along the west coast and broadens further into the Agulhas Bank, a triangular section between Cape Town and Port Elizabeth that extends about 250 km at its widest (Fig. 1). The shelf narrows considerably around East London and remains narrow, except for the Natal Bight, until the border with Mozambique (Fig. 1). The South African coastline has 250 estuaries (117, 123, and 10, on the east, south, and west coasts respectively; Whitfield 1995). Coastal rainfall varies with 800–1250 mm falling along the east coast but less than 300 mm along the west coast (Tinley 1985).

The Mozambique coastline, ~2700 km in length, is characterized by a wide diversity of habitats. The continental shelf is wide in the south at the Sofala Bank and at the central Delagoa Bight, but narrows on the north coast (average 20 km; Fig. 1). The parabolic dune coast in the south has patchy coral and rocky reefs colonized by corals (ASCLME/SWIOFP 2012). The northern part of the country supports true coral reefs, which occur as an almost continuous fringing reef. Mozambique has over 100 estuaries with well-developed mangrove forests. Coastal rainfall ranges from 800 to 1000 mm.

Tanzania has a coastline of ~ 800 km. The continental shelf is narrow (average 5 km) except in the vicinity of the relatively shallow Mafia and Zanzibar Channels, where the shelf reaches widths of 60 km

(Masalu 2008; Fig. 1). The intertidal zone consists mainly of sandy-muddy flats or rocky reef platforms, whereas the sublittoral zone comprises extensive seagrass beds and fringing coral reefs. There are at least 12 large estuaries along the Tanzanian coast. Coastal rainfall ranges from 1016 to 1930 mm (Tole and Marshall Crossland 2001).

Four major ocean currents, the Angola, Benguela, Agulhas and East African Coastal currents, dominate the region (Fig. 2). The Angola Current extends from approximately 2°00′N in northern Equatorial Guinea to 18°30′S in northern Namibia. The southward flowing current is thought to originate mainly from the southeast branch of the South Equatorial Countercurrent and the southward turning waters from the north branch of the Benguela Current (Dias 1983). Best described as a fast, but variably flowing (33–70 cm s^{-1}), warm water (>24 °C), coastal surface (<200 m) current (Dias 1983), its poleward flow is deflected westward as it meets the northward flowing Benguela current at what is known as the Angola Benguela Frontal Zone (ABFZ), a perennial frontal zone which migrates seasonally between 14 and 17°S (Ekau and Verheye 2005).

The southwest coast of southern Africa is dominated by the Benguela Current (Fig. 2). This current extends from the vicinity of Cape Agulhas (34°80′S) to Cape Frio (18°30′S) in northern Namibia. This eastern boundary current is unique as it is bounded on either side by warm currents, the Angolan Current in the north and the Agulhas Current in the south (Hutchings et al. 2002a, b). The Benguela Current comprises a general equatorward flow (average speed 17 cm s^{-1}; Shannon 1995) of cool, nutrient rich water (Olivar and Shelton 1993; Hutchings et al. 2002a, 2002b). The inshore component of the Benguela is strongly influenced by local winds which blow parallel to the shore and produce upwelling of deep (from 100 to 300 m) South Atlantic Central water along the entire Benguela Current coastal region (Olivar and Shelton 1993). This upwelling is concentrated in a number of distinct upwelling cells, the most dominant

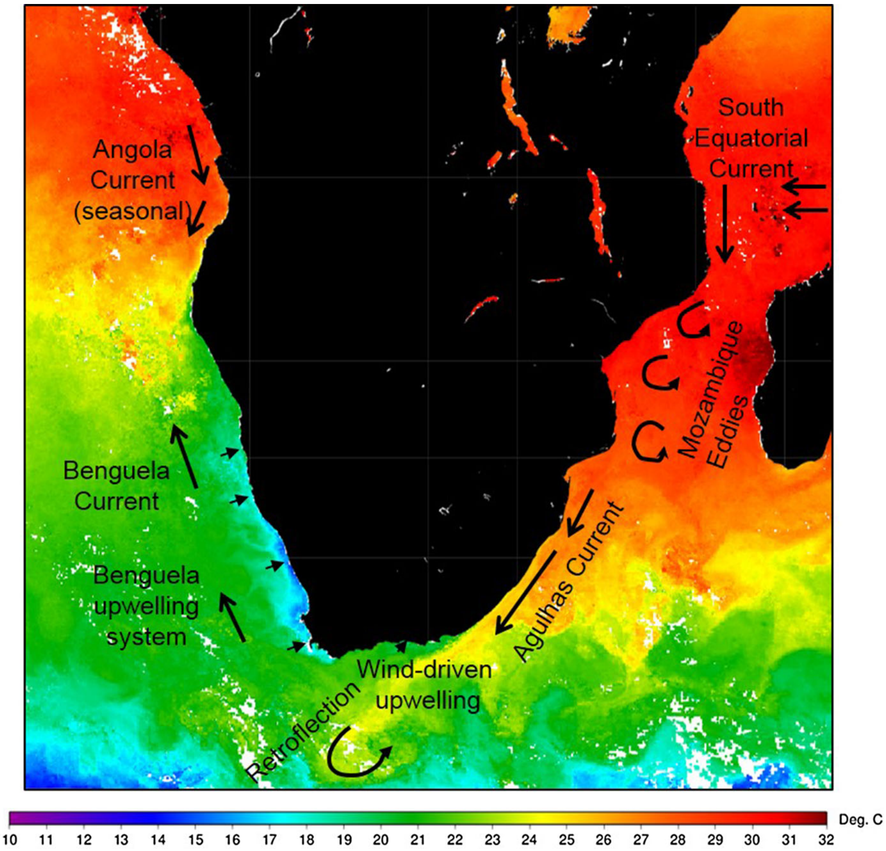


Fig. 2 A MODIS satellite sea surface temperature image in February 2009 (10 day average) illustrating the warm (*red*) Angola, Agulhas and South Equatorial and retroflection of the Agulhas Current at the southern tip of the continent, the location of upwelling cells (*blue*), wind-driven upwelling along the south coast (*green*) and upwelling along the Benguela Current coastal region

of which is the permanent Lüderitz upwelling cell which separates the Benguela into the northern and southern sub-systems.

The south and east coasts of South Africa are dominated by the Agulhas Current (Fig. 2): a western boundary current that carries warm water from the tropical Western Indian Ocean southwards into subtropical and temperate latitudes (Lutjeharms 2006). The current is fully constituted somewhere near 28°S between Maputo and Durban. The current continues south-west from its inception, increasing in volume and speed along the east coast before terminating in the Agulhas Current retroflection off the southernmost tip of Africa (Lutjeharms and van Ballegooyen 1988; Lutjeharms and Cooper 1996). 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) and where the current is deflected by a widening shelf (around the Natal Bight and along the Agulhas Bank; Lutjeharms 2006).

The South Equatorial Current (SEC) carries water from the Indonesian region across the Indian Ocean (Obura 2012; Fig. 2). The SEC passes the northern tip of Madagascar and splits into two branches when it reaches the African continent at Cape Delgado (11°S; Kai and Marsac 2010). The southern branch forms a net flow of variable eddies in the Mozambique Channel, which eventually join up with waters from the East Madagascar Current to form the Agulhas Current (Obura 2012). Eddies have a strong effect on biological production and inject nutrients into the euphotic zone (Ternon et al. 2014). The northern branch of the SEC forms the linear East African Coastal Current (EACC) that flows northwards along the coast of Tanzania and Kenya (Obura 2012). During the SE monsoon (June to September) the current continues north and leaves the continent at Somalia, while during the NE monsoon (November to March), winds slow the northerly water movement and eventually reverse the current forming the Somali Counter Current (McClanahan 1988). The coast of Tanzania is a major downwelling area, with low nutrient waters. Downwelling occurs throughout the year but is strongest during the SE monsoons when current speeds are greatest (McClanahan 1988).

While the coastal oceans are heavily influenced by the prevailing current systems, several other factors influence the environmental conditions in the coastal zone. These include meteorology, shoreline configuration and bathymetry (Kennish 2001). Although the area between southern Mozambique and southern Angola has been described as one of the smoothest and least convoluted in the world (Hutchings et al. 2002a, b), three large coastal embayments; Langebaan, Walvisbaai and Baia dos Tigres do offer shelter from wave action and increased temperature and salinity during the summer months (Shannon and Stander 1977). Other aspects, however, such as meteorological forcing, do significantly influence coastal ocean conditions. For example, strong winds that blow parallel to the coastline drive intense upwelling events and transport cool, nutrient rich water to the surface along the southwest and southern coasts of southern Africa. Besides the impacts of wind, regions with high rainfall, such as coastal Mozambique (Lutjeharms 2006) and northern Angola, may be heavily influenced by river runoff. In the Sofala Province of Mozambique, surface salinity may be as low as 20.0 ppt (Sætre and de Paula e Silva 1979, in Lutjeharms 2006) and the water highly turbid for up to 50 km offshore (Lutjeharms 2006).

The combination of the current systems and other local environmental factors has shaped the coastal latitudinal temperature gradient (CLTG) along the coasts of southern Africa. Baumann and Doherty (2013) in a global review of the coastal oceans, identified the east coast of southern Africa as having the weakest CLTG (−0.28 °C lat^{-1}), while the CLTG along the west coast of southern Africa was stronger (−0.42 °C lat^{-1}), in particular within the upwelling cells between 12° and 23° latitude (−0.98 °C lat^{-1}).

Biogeographic zonation of the southern African coastline

Current biogeographic zonation patterns based on coastal fish communities are either too broad (Briggs and Bowen 2012) or limited to South Africa (Turpie et al. 2000). As such, the most appropriate biogeographic zonation for the purpose of this review was one based on the estuarine fauna (Whitfield 2005). By this classification, Angola (warm-temperate, subtropical and tropical) and South Africa (cool-temperate, warm temperate and sub-tropical) host three biogeographic zones, Namibia (warm-temperate and cool-temperate) and Mozambique (sub-tropical and tropical) two, and Tanzania (tropical) one (Fig. 3).

Unfortunately, the lack of estuaries along the west coast of southern Africa does pose some limitations to Whitfield's (2005) biogeographic zonation for this review. Based on sea surface temperatures for northern Namibia and southern Angola, on biogeographic studies on seaweeds (Rull Lluch 2002; Anderson et al. 2012), and on our interpretation of the distribution of the fish fauna, a realignment of these zones seems appropriate. Here, the cool-temperate zone extends from False Bay in the Western Cape up to Hentiesbaai (22.1°S) and the warm-temperate zone extends from Hentiesbaai north to Namibe (15.2°S). The subtropical zone extends from Namibe as far as Rio Longa (10.1°S) and the tropical zone from that boundary northward (Fig. 3).

Southern Africa's coastal fish biodiversity

Southern Africa boasts a wealth of fish biodiversity, ranging from the highly diverse tropical faunas of Tanzania (>1000 species) and Mozambique (1510 species) to the low diversity of the cool-temperate coast fauna of Namibia (434 species).The response of fishes to climate change is largely dependent on their life history and behaviour. For the purposes of this review, we divided southern Africa's coastal fishes into a number of guilds: resident, migratory, estuarine-dependent and catadromous.

Resident species are 'site attached' for their juvenile and/or adult life cycle and are most often associated with reef or other structures. They either have a limited capacity for movement, such as the banded goby, *Caffrogobius caffer*, which is a rock pool species, or select a resident lifestyle (e.g. roman, *Chrysoblephus laticeps*). Migratory species on the other hand undertake large-scale (hundreds of km) and often seasonal migrations, primarily during the adult phase of their life cycle. Examples of these from southern Africa include the geelbeck (*Atractoscion aequidens*) and the Atlantic tarpon (*Megalops atlanticus*). The potential impacts of climate change on estuarine fishes were reviewed in James et al. (2013). Therefore, this review is restricted to the marine guild of estuarine species and includes 'stragglers', 'estuarine-opportunistic' and 'estuarine-dependent' species (see Potter et al. 2013), which are termed estuarine-

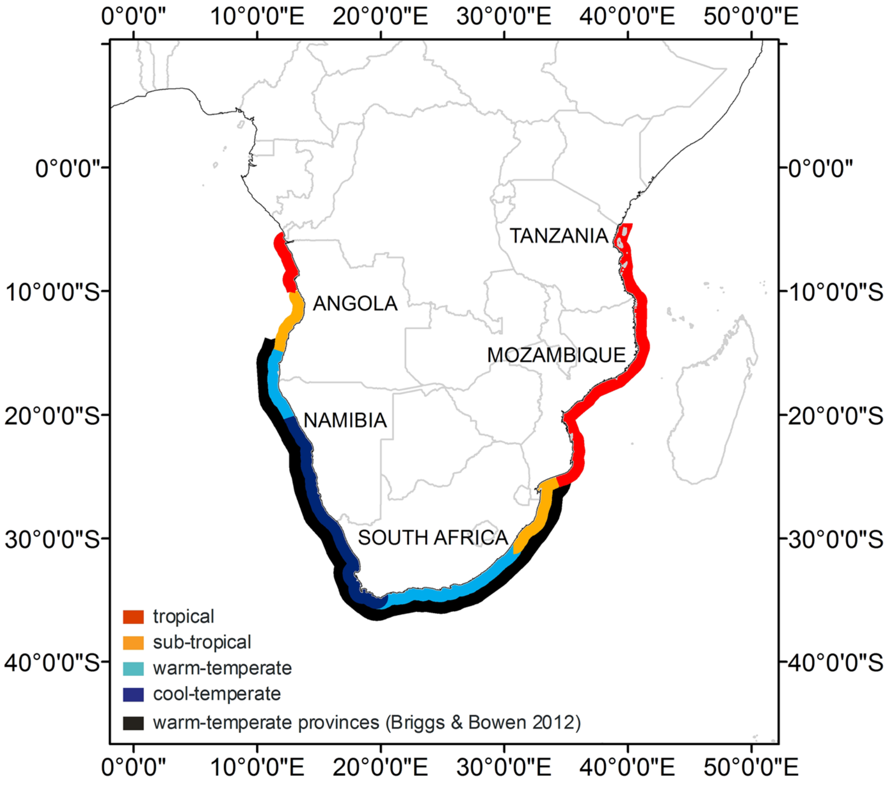


Fig. 3 Biogeographic zones of the coastal region of southern Africa as defined by Briggs and Bowen (2012) and Whitfield (2005), with modifications by these authors

dependent from here. Generally, southern African marine estuarine-dependent coastal species are important in the coastal fisheries. Examples of these species are the leerfish (*Lichia amia*) and spotted grunter (*Pomadasys commersonnii)* which are found along the South and East coast of South Africa. Catadromous species, which in southern Africa include the eels (Anguillidae), migrate from freshwater into the marine environment to spawn. After hatching, eels recruit back into the rivers as glass eels, where they remain until they reach sexual maturity. Catadromous species are only found from the south coast of South Africa eastward to Tanzania.

While the categorization of fishes into these guilds may assist in developing general predictions of the potential impacts of climate change, the authors acknowledge that they do not consider that the dispersal strategies of many coastal species change through their life history (for regional examples see Potts et al. 2010; Griffiths 1996; Watt-Pringle 2009).

The changing climate of the southern African coastal zone

Sea surface temperature

With a few exceptions, there is very little long-term in situ temperature data for the coastal waters of southern Africa with which to examine climate change impacts on temperature. The majority of historical sea surface temperature studies have therefore relied on satellite remote sensing. A recent study using three decades of high resolution coastal SST data (OI ¼ Degree Daily SST analysis) showed that 71.6 % of the world's coastline is warming significantly at a mean rate of 0.25 °C per decade (Lima and Wethey 2012). Warming rates are high (up to ±0.4 °C per decade) north of the Angola-Benguela front (Lima and Wethey 2012). Similarly, using AVHRR SST data, Potts et al. (2014) showed that this region is warming faster (0.8 °C per decade) than the global average. Rouault et al. (2009) using AVHRR SST showed that the subtropical eastern coast of South Africa is warming (max. 0.5 °C per decade). Lough (2012) used the HadISST dataset to examine changes in tropical SST. Warming was found to be more intense off tropical Mozambique and Tanzania, with the period between 1981 and 2011 being 0.2–0.4 °C warmer compared to 1950–1980 (Lough 2012). Some of the highest increases in the number of extreme hot days in the Western Indian Ocean were along the coast of southeast South Africa, southeast Mozambique and southeast Tanzania (Lima and Wethey 2012). Some localized areas, such as the Namibian and South African west and south coasts, are cooling seasonally (max. −0.5 °C per decade) (Rouault et al. 2010; Lima and Wethey 2012), with cooling in the cool-temperate regions being particularly apparent from January to May (Lima and Wethey 2012). Similarly, Lough (2012) found that waters off the Namibian cool-temperate coastline were significantly cooler in 1981–2011 compared to 1950–1980 (between −0.2 and −0.4 °C). Data presented by the IPCC (Watson et al. 1997) has suggested that the sea surface temperature (SST) in the southern African tropical oceans is projected to rise by less than the global average (i.e., only about 0.6–0.8 °C) by 2050. Besides direct temperature changes, changes in the thermal gradients along latitudinal gradients and hence changes in the location of biogeographical boundaries are also likely. Baumann and Doherty (2013) found that there was an overall strengthening of the already steep gradient along the west coast of southern Africa. In contrast, the temperature gradient along the South-African Indian Ocean had lost 7 % of its strength during the last 31 years (Baumann and Doherty 2013).

Wind and upwelling

Changes in wind strength and direction influence water circulation. The warming in the Agulhas Current since the 1980s is attributed to a strengthening of the current associated with an increase in trade winds and a poleward shift of the westerly wind in the South Indian Ocean (Rouault et al. 2009). Global climate models project that this will continue into the future (Rhein et al. 2013). Changes in wind strength and direction also influence the strength of upwelling. The seasonal cooling of SSTs in nearshore areas along the South African south, southeast and west coasts are attributed both to the intensification of the Agulhas Current, which could have increased dynamic upwelling, and an increase in upwelling favourable winds (Rouault et al. 2010). Bakun et al. (2010) suggest that as anthropogenic greenhouse gas concentrations increase, radiative cooling will be suppressed, which will enhance the heating rate over land relative to the ocean. This will result in an intensification of the low pressure cell over coastal landmasses in upwelling regions and an increase in upwelling favourable winds, resulting in an increase in intensity of upwelling.

Lutjeharms et al. (2001) in a review of climate change impacts on the Benguela upwelling system suggest that intensification of the South Atlantic Anticyclone may be associated with increased atmospheric subsidence, less cloud, increased insolation and higher air temperatures. As a result surface waters may warm, which may negate the increased upwelling. Furthermore, there is a limit to how cold the water in upwelling regions becomes. There is still, however, considerable uncertainty over what may happen in the Benguela upwelling system. The upwelling system is also characterized by the irregular occurrence of Benguela Niños. These occur with the sudden collapse of the Angola-Benguela Front and with an accompanying flow of warm water poleward along the coast. Benguela Niños cause marked increases in SSTs along the coast and can also result in the large-scale death of organisms in the coastal zone (Lutjeharms et al. 2001).

Elevated CO_2 and ocean acidification

With atmospheric CO_2 continuing to rise, its absorption could result in the reduction of the average pH of the ocean by 0.5 units by the year 2100 (Raven et al. 2005). This trend will not however be uniform across the sub-region. Acidification by 2100 is expected to be faster along the coastal waters of the west (−0.68 units), compared with the south (−0.60 units) and the east (−0.51 units) coasts of southern Africa (Hoegh-Guldberg and Bruno 2010). Although the magnitude of these changes may appear negligible, pH units are based on a log-scale and therefore even small changes can have profound impacts on marine fishes.

Sea level rise

Long-term in situ observations of sea level are scarce in southern Africa and the majority of predictions are reliant on models developed from satellite data. Rahmstorf et al. (2007) applied a range of models to predict an average global sea level rise of between 20 and 45 cm by the year 2050. However, variations are expected at regional, sub-regional and local scales. Hardman-Mountford et al. (2003) examined satellite data and estimated that the sea level was rising by ~0.6 mm $year^{-1}$ along the tropical West African coast. This rate was approximately halved along the warm-temperate west coast, while no trend was observed along the cool-temperate west coast. In contrast, Mather et al. (2009), through tidal records, estimated that sea level along the cool-temperate west coast was rising by 1.87 mm $year^{-1}$, compared with lower figures for the warm-temperate zone (1.48 mm y^{-1}) and higher figures for the sub-tropical east coast (2.74 mm $year^{-1}$). Mahongo (2009) examined tide gauge data for the Western Indian Ocean. Although mean sea levels (MSL) showed falling trends for northern Tanzania, the data sets examined are not long enough to make any conclusions about MSL change in the region. Han et al. (2010) employing a combination of satellite and in situ data suggested that sea level was falling. Overall, Joubert and Tyson (1996) concluded that although there will be sub-regional and local differences around the coast of Africa in average sea-level rise—depending on ocean currents, atmospheric pressure, and natural land movements—by 2050 a rise of 25 cm is a generally accepted figure.

Current speed and strength

There is limited information on expected changes to the speed and strengths of coastal currents around southern Africa. However, Lutjeharms and de Ruijter (1996) showed that the Agulhas Current will exhibit increased meso-scale meandering which will force the current on average further offshore from its contemporary mean position. In the present global climate regime the Agulhas Current is located within 15 km from the shore along the east coast of South Africa for ~77 % of the time. However, perturbations in the form of large-amplitude intermittent meanders (Natal Pulse) can force the current's core up to 300 km offshore. Lutjeharms and de Ruijter (1996) suggest that Natal Pulses will increase in frequency due to global warming and that the current will be located on average further from the shore. Any change in the average position and intensity of the Agulhas Current may impact on coastal zone currents. Backeberg et al. (2012) found that the eddies of the northern (22°–33°) Agulhas Current were increasing in velocity by more than 0.5 cm s^{-1} per decade. In contrast, the eddies in the southern Agulhas were more variable. They also found a general increase in the surface current speed between 8° and 30°S between 1993 and 2009.

Rainfall

Although climate models for the region (and globally) have shown a high amount of variability with regards to prediction, downscaled regional climate models, using two different downscaling techniques, project an increase in mean annual rainfall over the eastern portion of southern Africa, slightly drier conditions for the winter rainfall region in South Africa, no change over coastal Namibia and southern Angola and considerable declines (10–30 %) in mean annual rainfall in central and northern Angola (Hewitson and Crane 2006; Engelbrecht et al. 2009). The incidence of extreme rainfall is also projected to increase with anthropogenic climate change, and this may be more significant biologically. Engelbrecht et al. (2013) using a variable-resolution global model found that extreme rainfall events are projected to increase over large parts of southern Africa, particularly Mozambique.

Indicative of the difficulty in projecting rainfall trends are the observed rainfall patterns for coastal Tanzania. Regional climate projections (Solomon et al. 2007) indicate that there will be an increase in mean annual rainfall over East Africa (including Tanzania and Mozambique). Linear regressions of monthly rainfall for coastal Tanzania (1960–2009), however, showed a decreasing trend in rainfall at each station, with the last decade (2000–2009) being the driest in the last half century (Mahongo and Francis 2012).

A summary of the expected changes is presented in Table 1.

The response of coastal fishes to environmental change

Changes in temperature

Fish are thermoconformers and even small changes in water temperature can affect physiological processes including the fluidity of membranes and the function of organs (Hochachka and Somero 2002). Consequently, of all of the physical stressors, sea temperature is considered to be the most influential on coastal fishes. While an altered temperature regime will ultimately result in changes in the coastal fish assemblages, understanding the drivers of these changes is critical to predict how fishes with different life histories and movement characteristics will respond.

Pörtner and Knust (2007) first identified the oxygen limitation of thermal tolerance as a major driver of change in warming oceans. Since cooler water can hold more dissolved oxygen than warmer water, the concentration of dissolved oxygen in sea water is controlled by temperature. Although there is variation in oxygen limits between species and even within life history stages, fishes have generally evolved to respire optimally within a narrow range of temperatures (Pörtner and Peck 2010). As the temperature of coastal oceans change, it is likely that some species or certain life history stages, particularly those on the boundary of their distributions, will be exposed to the increased metabolic costs associated with respiration. Migratory species are likely to respond to this by moving to areas with favorable temperatures and thus alter their distributional range. These alterations would take place rapidly as migratory fishes track their preferred thermal range and may have significant and immediate effects on coastal fisheries.

Resident species, on the other hand, which are generally exposed to fluctuations in temperature at diel, tidal and seasonal time scales, are most often eurythermic in sub-tropical, warm-temperate and cool-temperate zones. Oxygen limitation is therefore unlikely to drive a rapid behavioural response as predicted for migratory species. For example, James et al. (2012), reporting on a medium-term (8 years) inshore resident fish monitoring dataset from the Tsitstikamma National Park, showed limited evidence of climate change impacts, with the overall species richness and abundance maintaining high levels of stability. This concurs with other medium and long-term monitoring studies (Holbrook et al. 1994; Malcolm et al. 2007) which have indicated that the composition of many resident coastal fish assemblages have remained stable, despite warming conditions. However, resident species that have evolved in stable thermal environments, such as those in the equatorial regions may only be adapted to a narrow range of temperatures in their local environment (Rummer et al. 2014). In these cases, even a 2–3 °C increase in temperature could result in population declines due to the effects of oxygen limitation

Table 1 Relative expected changes to the Southern African coastal ocean by 2050

	SST	Upwelling	Current strength	Rainfall	pH	Sea level
Tropical and sub-tropical west coast	🟥 ↑	🟩	🟩	🟥 ↓	🟥 ↓	🟨 ↑
Warm-temperate west coast	🟨 ↑	🟩	🟩	🟨 ↑	🟥 ↓	🟨 ↑
Cool-temperate west coast	🟥 ↓	🟥 ↑	🟩	🟥 ↓	🟥 ↓	🟨 ↑
Warm-temperate south coast	🟩 ↓	🟥 ↑	🟨 ↑	🟩	🟨 ↓	🟨 ↑
Sub-tropical and tropical east coast	🟥 ↑	🟩	🟥 ↑	🟨 ↑	🟨 ↓	🟥 ↑

Red = large change, yellow = small change, green = no change

(Rummer et al. 2014). While the rate of these changes is likely to be slower (years to decades) than the distributional shifts of migratory species, they will nevertheless have implications for coastal fisheries.

The response of estuarine-dependent species to oxygen limitation will be similar to that described above during their coastal life history phases. However, the obligate estuarine life stages will either be resilient to oxygen limitation if they are normally resident within an estuary (e.g. *Pomadasys commersonnii,* Childs et al. 2008) or may move rapidly to avoid unfavorable temperatures, if they normally follow a thermal window in the estuary (e.g. *Argyrosomus japonicus,* Næsje et al. 2012).

Catadromous species will be affected by the influence of oxygen limitation through all phases of their life history. Changes in water temperature will most likely have a profound impact, through oxygen limitation, on the survival of the early life stages as they have limited swimming capability in the open ocean. However, the sedentary life style and thus broad temperature tolerance of juvenile Anguillids during their freshwater phase suggests that oxygen limitation will influence them in a similar way to resident species in the coastal region. Oxygen limitation may however have a major influence on the spawning migration of adult Anguillids, and warming oceans may alter their migratory patterns as individuals seek optimal temperatures to maintain their significant respiratory requirements during the migration.

The second driver linked to changing water temperature is the reproductive output of fishes. Water temperature can influence fish reproduction including cueing (Bye 1990), egg production (e.g. Pauly and Pullin 1988) and larval survival and distribution. Since the perpetuation of a species is dependent on successful recruitment, fishes have evolved to reproduce during conditions that are favorable for egg and larval survival. These include optimal temperatures, peaks in food availability and reduced abundance of predators (Blaxter 1991). This is facilitated through the relationship between temperature and egg production, which is generally maximized within a narrow thermal range (Potts et al. 2013). It is therefore unsurprising that temperature is considered to be one of the most important environmental cues for fish reproduction (Pankhurst and Munday 2011).

Coastal fishes that rely on thermal cues to determine the timing of their spawning migrations will be influenced by changing ocean temperatures. For example, populations of flounder (*Platichthys flesus*) migrated to their spawning grounds between 1 and 2 months earlier during years that were up to 2 °C cooler (Sims et al. 2004). Changing temperatures may therefore influence the phenology of spawning migrations. As a result, it is likely that the species that use photoperiod as a proximate cue for reproduction, may arrive at spawning grounds with their gonads in an underdeveloped reproductive state. The gonadal development of many species is regulated by photoperiod (Bromage et al. 2001). However, Pankhurst and Porter (2003) found that photoperiod was a less important factor entraining the reproductive activity of tropical species. Therefore, poorly timed reproductive migrations are most likely to have an influence on the reproduction of sub-tropical, warm-temperate and cool-temperate species.

Changes in phenology can also have a major impact on reproductive success as the rate of egg and larval development will be negatively influenced by suboptimal conditions and most often, there will be a mismatch between larvae and their food supply or a convergence between larvae and their predators (Blaxter 1991). In addition, changes in the timing or location of spawning may also impact the day length experienced by the early life stages. For example, Shoji et al. (2011) found that growth of the early life stages of the black rockfish, *Sebastes chenithere* was significantly affected by photoperiod, with increased growth found during longer day lengths. This is not surprising as the larvae of coastal fishes that rely on visual cues for feeding generally grow better during periods with longer day length (Dowd and Houde 1980; Shoji et al. 2011).

Resident coastal fishes have generally evolved to reproduce in a thermal window that is suitable for optimal egg and larval survival. Changes in water temperature may therefore, through its impact on cueing, alter the reproductive scope, which is defined as the 'breadth' of opportunity for reproduction. In a review of the spawning temperatures of the *Diplodus sargus* complex, Potts et al. (2013) found that populations of this complex did not spawn when exposed to temperatures above 20 °C, regardless of the ambient temperature range. Based on these findings, they examined temperature trends in the northern Benguela ocean warming hotspot and estimated changes in reproductive scope since 1982. They found that if the warming trends were to continue, the reproduction of this species could cease in Angola by 2080. In contrast, the reproductive scope of this species was increasing rapidly in Namibia, suggesting that reproduction may become more successful in this region. While temperate species appear to be responding to rapid warming in warm-temperate areas, tropical species are possibly even more sensitive to warming. Pankhurst and Porter (2003) found that even relatively small changes in temperature can lead to endocrine changes in tropical species. They concluded that temperature is generally the most important factor entraining reproductive activity in tropical species and it is therefore likely that changes in the thermal regime in tropical regions will have a profound influence on reproductive activity.

Although much is still unknown, it is thought that many of southern Africa's estuarine-dependent and catadromous species (as defined earlier) undertake spawning migrations. Therefore, the impact of temperature change will primarily influence the phenology of these fishes, and the impacts of changing photoperiod on reproductive development may determine their reproductive success.

Regardless of the influence on reproduction, the growth and survival of the early life stages of all fishes is influenced by water temperature. Sund and Falk-Petersen (2005) found that the conversion of yolk after hatching may be less efficient at temperatures outside a fish's thermal preference. This may reduce the competitiveness of fishes at their first exogenous feeding (Cavalli et al. 1997). Elevated or reduced temperatures also change the metabolic rate of the early life history stages. Besides a negative impact on their ability to feed, it may also increase their susceptibility to predation. This can influence their tolerance to low oxygen habitats and their rate of development (Munro et al. 1990). The duration, dispersal potential and survival of larvae are likely to change, with cooler temperatures promoting increased larval duration, increased dispersal and poorer survival, while warmer temperatures promote the opposite trends (Hoegh-Guldberg and Bruno 2010). Figueira and Booth (2010) established a link between overwinter survival of tropical fishes transported to temperate latitudes and water temperature off the Australian coast. They found that southward distributional shifts by tropical species were limited by a specific minimum threshold temperature. If the sea temperature remained above that threshold temperature throughout winter, post larval settlement of several tropical species occurred south of their normal distribution.

Another driver of change is the impact of changing temperature on the life history of fishes. The growth of fishes, in particular, is considered to be closely linked to temperature and usually has a thermal maximum

(Munday et al. 2008; Neuheimer et al. 2011). This is however, not restricted to a particular life history stage as evidence of a relationship between environmental temperature and fish growth has been observed at the larval (Meekan et al. 2003; Jenkins and King 2006), juvenile (Thresher et al. 2007) and adult stages (Pauly 1979). Generally, warmer temperatures support faster growth while cooler temperatures have the opposite effect (Thresher et al. 2007). However, the growth of individuals that live in temperatures near to the upper thermal limit for the species are likely to decrease rapidly in response to warming (Neuheimer et al. 2011).

Although changing growth rates generally have an impact on life history characters (Roff 1992; Pauly 1980), changing water temperature is also expected to have an influence. Warmer water generally increases the rate of natural mortality (Pauly 1980), decreases the age-at-sexual maturity (Garrod 1986), increases the size-at-sexual maturity (Garrod 1986) and increases the age-specific fecundity of fishes (Fischer 2003). Although most fish species should be able to adapt certain life history traits to cope with temperature changes, these responses are only capable of counteracting a shift from the thermal optimum up to a species specific threshold, after which complex and detrimental changes are expected.

The influence of changing temperatures on the life history of coastal fishes is expected to impact resident species more, because migratory species are likely to track their preferred temperatures and maintain life history traits. Resident species that are subject to cooling will be impacted by reductions in their metabolic rate, which will in turn may reduce their growth, increase their age-at-maturity, decrease their size-at-maturity and decrease their age-specific fecundity. Warming trends should have the opposite effects. As the majority of southern African estuarine-dependent species have migratory life styles while in the coastal zone (Griffiths 1996), it is unlikely that changes in the life history characteristics will have a major influence during this stage. However, changes in the temperature of estuaries during their obligate phase can have significant life history consequences, similar to those expected for resident coastal species. Similarly, the life history of catadromous species will be primarily influenced during their sedentary juvenile freshwater phase. Here, warming temperatures will most likely increase growth rates and decrease the age-at-maturity in the temperate and sub-tropical parts of their distribution. However, the increasing temperature for populations in the equatorial part of their distributional range may exceed the optimal thermal range and result in rapid declines in their growth rate.

The fourth driver is the influence of changing water temperature on the activity patterns of fishes. Temperature can change the activity of fishes in two ways. Firstly, as poikilothermic animals, reduced temperatures will slow down metabolism, reducing activity and burst speed. Secondly, as temperatures warm, the reduction in dissolved oxygen (see discussion above) could reduce fish metabolism and reduce activity. The burst swimming speed of fishes is considered to be closely linked to water temperature and is an important strategy used by larval (Batty and Blaxter 1992; Hunt von Herbing 2002), juvenile and adult fishes to avoid predation and capture prey (Claireaux et al. 2006; Figueira et al. 2009). The burst speed of a species is maximized within the optimal thermal range of the fish. For example, elevated water temperature prompted an increase in the burst speed of a tropical damsel fish (*Abudefduf vaigiensis*), but had no effect on a sub-tropical damselfish (*Parma microlepis*) (Figueira et al. 2009). The activity patterns of migratory species are expected to be less influenced than resident species as they are more likely to remain in their thermal range. Resident species near their thermal range limits are, in particular, likely to suffer reductions in feeding success and increased predation. This also holds true for estuarine-dependent and catadromous species during their estuarine and freshwater phases, respectively.

Changing water temperature can also influence coastal fishes through its impact on fish habitat. In particular, elevated sea surface temperatures have coincided with several recent coral bleaching events in southern Africa (McClanahan et al. 2007). This will influence coral-reef fishes directly through the loss of food and shelter and indirectly by reducing the topographic complexity which moderates competition and predation (Pratchett et al. 2008).

Regardless of the drivers, the increase in sea temperatures predicted worldwide should cause a latitudinal shift in the distribution of migratory species towards the cooler waters of the poles. This shift has been predicted by many authors (Fields et al. 1993; Lubchenco et al. 1993; Harley et al. 2006; Clark 2006) and evidence has been found in many regions, including the North Atlantic (Stebbing et al. 2002), North Sea (Perry et al. 2005), Sea of Japan (Masuda 2008) and off the coast of Tasmania (Last et al. 2011). There is currently little evidence for latitudinal shifts in migratory coastal fish species in southern Africa. In some areas of southern Africa, this may because there is no clear climate signal due to complex oceanographic processes, in others it may due to a lack of quality observation and monitoring programs. However, there are two southern African examples of shifts in migratory species. The first, described by Coetzee et al. (2008) showed a shift in the sardine (*Sardinops sagax*) from the west to the south coast of South Africa. More recently, Potts et al. (2014) observed a southward shift in the distribution of the west coast dusky kob (*Argyrosomus coronus*) from southern Angolan into northern and central Namibian waters.

Increasing temperatures should also result in a latitudinal shift of resident species towards the poles. However, as the driving mechanisms (including changes in reproductive output and life history traits) are different, these ‘apparent’ shifts are most likely to be a reflection of a decline in population numbers in areas that become unfavourable for reproduction and growth and an increase in the population in areas that become favourable. These ‘distributional shifts’ will therefore most likely be slower than those for migratory fishes and may provide opportunities for mitigation.

Increased CO_2 and ocean acidification

Increases in CO_2 levels may lead to hypercapnia (elevated CO_2 partial pressure) and acidosis in the blood and tissues of fishes (Pörtner et al. 2004). The most likely consequence of this is a change in metabolic function, growth and reproduction (Pörtner et al. 2004). Ishimatsu and Kita (1999) found that short-term exposure of fish to elevated CO_2 can lead to changes in their acid–base status, respiration, blood circulation and nervous system function. However, the response of fish to elevated CO_2 changes through ontogeny. Generally, the egg and juvenile phases were more susceptible compared to the larval and adult stages (Ishimatsu et al. 2004).

In a review of the impacts of ocean acidification, Fabry et al. (2008) concluded that of all marine animals, fish appeared to be the most tolerant to ocean acidification. Ishimatsu et al. (2004) attributed this to a high capacity for internal ion and acid–base regulation, which is afforded through direct proton excretion and an intracellular respiratory protein that allows for high oxygen carrying capacity. Nevertheless, decreases in pH have been found to reduce the metabolic capacity and food intake of gilt-head bream (*Sparus aurata*; Michaelidis et al. 2007) and seabass (*Dicentrarchus labrax*; Cecchini et al. 2001).

Acidification may also affect the formation of calcareous structures in fishes. For example, Checkley et al. (2009) found that the otoliths of young (7–8 days) white sea bass (*Atractoscion nobilis*) were larger when they were exposed to CO_2 at levels predicted for 2100. Since Browning et al. (2012) found that the behaviour of another Sciaenid species, the red drum (*Sciaenops ocelatus*), with abnormally large otoliths was different from normal fish as a result of impaired sensory function, it is likely that this may have major behavioural implications for fishes. However, increased calcification has not been observed in all species. Munday et al. (2011) examined the influence of elevated CO_2 and reduced pH on the early life history development of the spiny damselfish (*Acanthochromis polycanthus*) and concluded that acidification would not have an influence on this species over the next 50–100 years. This suggests that not all species will react in the same way to ocean acidification and an understanding of the process driving the different responses by fish is critical for future prediction.

Besides its influence on the early life stages, a recent study (Miller et al. 2013) has found that the reproductive activity of coral reef fishes is influenced by ocean acidification. They found that breeding pairs of *Amphiprion melanopus* held at high levels of CO_2 produced more than double the number of clutches and two thirds more eggs per clutch over a nine-month period when compared with those held at present day CO_2 levels. However, although this study shows the short-term impacts, the long-term implications of increased levels of CO_2 on fish reproduction remain unknown. Elasmobranchs may also be influenced by ocean acidification. A review by Truchot (1987) indicated that the ventilation of dogfish (*Scyliorhinus canicula*) increased with a decrease in pH.

The behaviour of larval fishes may also be modified during dispersal as a reduction in pH has been shown to affect chemical cueing (Munday et al. 2009). This may decrease their ability to detect predators and increase their susceptibility to predation (Dixson et al. 2010). Estuarine-dependent and catadromous species, which rely on chemical cueing to identify suitable nursery habitats (Whitfield 1994; James et al. 2008b) may be particularly influenced by this change.

The impact of acidification on calcification may have a secondary effect on coastal fishes. Declines in coral cover can have a major influence on the diversity, abundance and resilience of coastal fish communities (e.g. Jones et al. 2004; Wilson et al. 2006). For example, Jones et al. (2004) found that 75 % of coral reef associated species declined following coral loss and almost half these declined to below 50 % of their original abundance. This resulted in a regime shift in the fish assemblage, from which it is difficult to recover. Generally, species that are specialized to inhabit corals, such as the Gobiidae and Carancanthidae, may be restricted to the remaining coral habitats, while those less reliant on coral habitats, such as the Lethrinidae and Lutjanidae, may become dominant in these altered habitats (Jones et al. 2004).

Sea level rise

The direct effect of sea level rise is a landward shift in distribution patterns of coastal organisms. This does not necessarily pose a problem to migratory or resident fish and invertebrates. However, sedentary organisms (such as slow growing corals) might not be able to keep pace with sea level rise, which would result in habitat alterations and influence the distribution of coastal fishes on subtropical and tropical shallow reefs (Harley et al. 2006).

Pethick (1993), using examples from the south-east coast of Britain, assessed the direct impacts of sea level rise on the physiological and biological processes of estuarine and coastal systems. He concluded that future changes in the intertidal profiles were likely and that this would result in increased wave energy and erosion in the upper tidal profile of coastal areas. Shallow intertidal areas would be lost in what is known as 'coastal squeeze', with a concomitant reduction in prey organisms in both the rocky and sandy intertidal zone. This is likely to have a negative impact on coastal fish species that utilize this zone for feeding or as nursery areas. Fish that utilize the intertidal zone are likely to move into areas that are less impacted by coastal squeeze and erosion.

Changes in estuarine profiles will directly influence coastal fish communities and fisheries through their impact on estuarine-dependent fish species (James et al. 2013). This may cause significant reductions in South African coastal fisheries as 83 % (in number and mass) of the recreational shore-angling and commercial gill- and seine-net catch consists of estuarine-dependent species (Lamberth and Turpie 2003). Changes in estuarine profiles will also have an indirect impact on coastal fishes and fisheries through an expected reduction in the organic nutrient load and food availability for fishes in the coastal environments adjacent to estuaries (Pethick 1993).

Changes in current speed

Changes in the strength of ocean currents can have a major impact on the dispersal of eggs, larvae and juveniles and influence the migrations of adult fishes (Lett et al. 2010). For example, the recruitment strength of the Australian salmon (*Arripis trutta*) has been directly related to Leeuwin Current flow, especially the southern Australian stock which is at the edge of its distribution (Lenanton et al. 1991, 2009). Hutchings et al. (2002a, b) described some of the spawning grounds and egg and larval transport mechanisms for coastal fishes in southern Africa. Many of South Africa's coastal migratory (e.g. *Atractoscion aequidens*), estuarine-dependent (e.g. *Argyrosomus japonicus*) and catadromous species (e.g. *Anguilla mossambica*) are thought to undertake up current spawning migrations from the south coast to the east coast of southern Africa (Heydorn et al. 1978; Joubert 1981; van der Elst 1981; Garratt 1988; Griffiths and Hecht 1995; Beckley and Connell 1996). However, with a strengthening Agulhas Current it is likely that the increased energy required for the migration may negatively impact reproductive output and recruitment. After spawning, changes in the strength of the currents may also affect the advection of eggs and larvae of coastal species, with consequences for larval survival due to suboptimal pelagic thermal regimes. These changes may alter the spatial pattern of juvenile recruitment along the coast, thereby influencing biogeographic patterns with unknown consequences for fishery productivity and biodiversity.

Changes in ocean current flow can also significantly influence the catchability of some fishery species. The catchability of fishes in the south coast fishery in Australia has been directly linked to the flow rate of the Leeuwin Current (Lenanton et al. 1991; Caputi et al. 1996). In South Africa, anecdotal information suggests that the current speed influences the catch rate of line fishes along the Transkei coastal region, with high current speeds, generally associated with poor catch rates.

Upwelling

The consequence of coastal upwelling is the arrival of cool nutrient rich waters in the inshore zone. Areas with large upwelling cells generally have a high phytoplankton biomass and productive fisheries. Strengthened upwelling may have positive effects on fisheries due to the increase in primary and secondary production. However, lower water temperatures may have a negative influence on the growth rates and hence productivity of some fishes (Munday et al. 2008).

Strengthened upwelling will have an influence on the thermal gradients around upwelling zones. Steeper thermal gradients will limit the dispersal potential of migratory species and limit the optimal thermal conditions for the growth and survival of resident fishes.

Strengthened upwelling may also have a profound influence on the movement patterns of coastal species. For example, several coastal and estuarine-dependent species use nearshore and estuarine habitats as a thermal refuge during the rapid cooling phase that is driven by upwelling (Hanekom et al. 1989; Childs et al. 2008). These species are often susceptible to exploitation during these times (Hanekom et al. 1989).

Besides having an impact on the feeding and growth of coastal species, permanent upwelling cells have also been recognized as barriers to the dispersal of many fish species (Floeter et al. 2005; Henriques et al. 2010, 2014). Strengthening upwelling cells, for example, along the south coast of South Africa, may reduce the dispersal potential of fishes across cold water barriers, possibly resulting in stock separation. However, if there is a weakening of the driving forces of these permanent upwelling cells, these phylogenetic barriers may break down (Harley et al. 2006) with significant consequences for fisheries productivity, species distribution and gene flow between regional fish populations. For example, on the west coast of southern Africa, the Lüderitz upwelling cell is known to be a barrier to the dispersal of coastal fish species (Henriques et al. 2010, 2014). However, with the increasing intensity of the southward displacement of the Angola-Benguela front and consequent warm-water intrusions associated with Benguela Niños (Shannon et al. 1986; Boyer et al. 2000), it is possible that this barrier will temporarily disappear. As a result, allopatric species such as the dusky (*Argyrosomus japonicus*) and west coast kob (*Argyrosomus coronus*) may again occupy the same environment, with potential evolutionary consequences for both species.

Effect of changing rainfall patterns

Freshwater input carries nutrients, sediment and detritus into the coastal zone and can have a direct and indirect influence on its fishes (Houde and Rutherford 1993; Gillanders and Kingsford 2002; Lamberth et al. 2009). Nutrients are assimilated by phytoplankton, which are consumed by zooplankton, which in turn provide an important food source for many larval, juvenile and adult fish (Morgan et al. 2005; Lamberth et al. 2009). The low visibility conditions created by suspended sediments in the coastal zone can provide refuge for fishes (Cyrus and Blaber 1992), but can also increase their catchability (Lamberth et al. 2009). Detrital input is normally subject to microbial colonization which renders it highly nutritious for detritivorous fish and invertebrates (Mann 1988; Whitfield 1998). Freshwater inputs also provide estuarine-dependent fishes with important cues used to locate and utilize estuarine environments (Whitfield 1994; James et al. 2008a).

Decreased and increased rainfall may result in alterations in the abundance of fishes in the coastal zone, particularly in those areas adjacent to large estuaries. For example, Lamberth et al. (2009) identified significant relationships between freshwater flow and the commercial and recreational catches of 14 fish species on the Thukela Banks. Under a scenario of a 44 % reduction in flow from the Thukela river, they forecast a 36 and 28 % decline in the catch of slinger (*Chrysoblephus puniceus*) and squaretail kob (*Argyrosomus thorpei*), respectively.

Predicted response of fishes by biogeographic region

Based on the review of the expected environmental changes ("Introduction" section) and the observed and predicted responses of fishes to environmental change globally ("The southern African coastal zone" section), the relative impacts of climate change and vulnerability of fish species in the southern African marine coastal zone could be predicted based on the life history and biogeographic region.

Tropical and sub-tropical west coast

Migratory species near the edge of their upper thermal range will most likely shift their distributions poleward in both of these zones (Fig. 4). However, the steepening of the temperature gradient along the south west coast will most likely restrict these fishes to a narrower distributional range; the exact location of these will be dictated by their thermal limits. The departure of migratory fish from the tropical zone will leave a vacant niche which is unlikely to be filled by new species (Fig. 4). However, fishes that are able to tolerate the warmer temperatures in the tropical regions may increase in abundance due to the reduction in competition. Tropical species that migrate southward into the sub-tropical zone will most likely replace the species that have migrated southward into the warm-temperate zone. However, the impact of these fish species and their interactions with the species from the sub-tropical coastal ecosystem is unknown. The reproduction of the fishes that have moved poleward may be influenced as adults either need to migrate further to reach their traditional spawning grounds or shift their spawning grounds poleward.

Resident species in the equatorial regions are generally hampered by their narrow thermal tolerance (Rummer et al. 2014), and the warming temperatures will most likely reduce the reproductive scope (Potts et al. 2013) of these fishes in the tropical and sub-tropical zones. However, their reproductive output may improve in the poleward parts of their distributional ranges. While the tropical species may reproduce successfully in the cooler water further south, it is unlikely that these species will be replaced by any other species, unless they are phenotypically plastic and can adapt to the warmer temperatures. The growth rate of the resident species may increase in the short-term. The warming ocean and increased rainfall predicted in this region should support faster growth as fishes increase their metabolism and consume the additional food provided by the nutrient input from the several large rivers situated in the coastal zone. However, since the thermal tolerance of tropical species is narrow, it is likely that these species will soon reach their thermal tolerance limits (particularly those in the equatorial part of this zone) and the trend in the growth rate will be downward for all but those in the poleward part of their distribution, where temperatures are expected to remain optimal for growth.

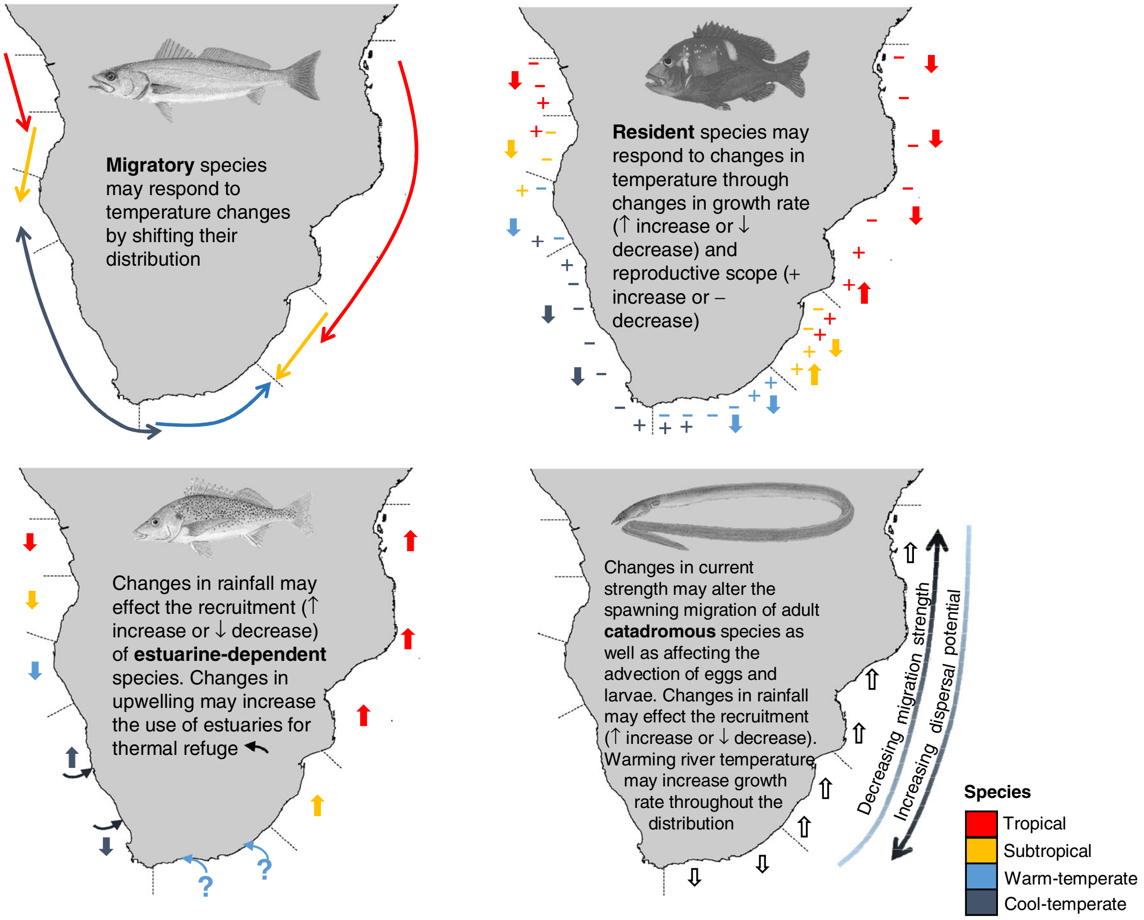
Ocean acidification may, through its impact on skeletal formation and the olfactory senses, reduce the survival of eggs and larvae of all coastal fishes in this region. In particular, the chemical cueing of the early life stages of estuarine-dependent species may be affected. In some areas this may be exacerbated by the declines in river flow.

The large estuaries such as the Congo and Cuanza provide essential nutrients to this coastal region. A decline in the mean annual rainfall of up to 30 % is likely to reduce the nutrient input, food availability and the growth and productivity of estuarine-dependent and coastal fishes in this region.

Although the rise in sea level is small when compared to the temperate regions in southern Africa, an approximately 22 cm rise in sea level by 2050 could have a profound impact on a number of coastal habitats. In particular, the large, mangrove estuaries in northern Angola will be negatively impacted, and this may in turn reduce the abundance of the fishes associated with mangrove habitats. These include many fishes that are important in coastal fisheries, such as the Guinea snapper (*Lutjanus endecacanthus*).

Warm-temperate west coast

Although a poleward distribution shift of migratory fishes has been observed in this region (Potts et al. 2014) (Fig. 4), this shift is not expected to be extensive due to the predicted intensification of the Benguela upwelling cells and cooling in the cool-temperate west coast zone (Rhein et al. 2013). This cold upwelling area already functions as a significant biogeographical barrier for warm-temperate fishes (Henriques et al. 2010, 2014) and its intensification along with the warming in the warm-temperate zone is expected to steepen the thermal gradient and "squeeze" the warm temperature sensitive migratory species into a small area along the biogeographical boundary zone. A shift of sub-tropical migratory fish into the warm-temperate zone from the north (Fig. 4) is also expected to have an



Migratory species may respond to temperature changes by shifting their distribution

Resident species may respond to changes in temperature through changes in growth rate (↑ increase or ↓ decrease) and reproductive scope (+ increase or – decrease)

Changes in rainfall may effect the recruitment (↑ increase or ↓ decrease) of **estuarine-dependent** species. Changes in upwelling may increase the use of estuaries for thermal refuge ↰

Changes in current strength may alter the spawning migration of adult **catadromous** species as well as affecting the advection of eggs and larvae. Changes in rainfall may effect the recruitment (↑ increase or ↓ decrease). Warming river temperature may increase growth rate throughout the distribution

Fig. 4 Predicted climate driven impacts for southern African coastal migratory, resident, estuary dependent and catadromous fishes

ecological impact and will most likely increase the competition for food in this region.

Some resident species may benefit from the warming water through an increase in growth in the short-term. Once the temperature rises above their thermal tolerance limits, however, their growth rates may fall rapidly. The reproductive scope of resident fishes may decline due to the warming in this region (Potts et al. 2013). While it is possible that these fishes may increase their reproductive scope further south, the cooling predicted in the cool-temperate zone suggests that this may only take place in a narrow area at the boundary of these biogeographical zones. Resident species whose eggs and larvae have higher thermal tolerance (sub-tropical species) may increase their reproductive scope in the northern part of this biogeographical zone and become more abundant in this region.

As along the sub-tropical west coast, ocean acidification may reduce the survival of eggs and larvae of the migratory and resident species in this region by impacting their skeletal formation and the olfactory senses. This will largely influence survival through its impact on their general fitness and their ability to escape from predators.

When compared with the other biogeographic zones, the sea level has not been rising at a rapid rate. However, the juvenile phases of some coastal fishes and the intertidal species may be negatively affected through the loss of intertidal habitat. Unfortunately, there is very little information on the number of species that use the intertidal habitat in this biogeographical zone.

Cool-temperate west coast

Migratory species (such as the snoek, *Thyrsites atun,* and yellowtail, *Seriola lalandi*) that are at their lower thermal limits may move either towards the equator or the poles into the warm-temperature zones situated on either side of this cool habitat (Fig. 4). However, as the northern Benguela region is warming rapidly, this distributional shift will most likely be poleward, particularly since the waters of the warm-temperate south coast zone are also thought to be cooling. It is unlikely that migratory species that move out of this region will be replaced by migratory species from the warm-temperate west coast or south coasts. However, those that are tolerant to cooler water may benefit from the reduced competition for food.

The phenology of migrations and reproduction may also be influenced, with delays in both of these expected due to the reduced water temperatures. Since photoperiod often drives the gonadal development in coastal fishes, it is possible that these fishes may begin migrating with fully ripe gonads and arrive at their spawning grounds after their gonads approach senescence. This will most likely result in reduced reproductive output in these fishes. The development of eggs and larvae will probably be retarded in the cooler water and this will have an influence on their dispersal, which will generally be further from the spawning grounds than during a normal thermal regime. However, growth of the larvae after feeding may be augmented by the additional food available due to the increased upwelling in the region. Larval survival may also be negatively influenced because of the increased likelihood of predation due to their reduced burst swimming speed in the cooler water.

Resident species (for example, the galjoen, *Dichistius capensis*) are unlikely to shift their distributions in the short-term. Although the reduction in temperature will most likely reduce their metabolism and growth rate, this may be mitigated by the augmented food supply due to the increase in nutrients brought about by upwelling. The timing of the reproductive activity of resident species may be influenced. Reduced temperatures may fall out of the reproductive scope of some species. Reproductive failure over several consecutive years may ultimately lead to local extinctions for some species. Changes in reproductive phenology may also have an impact on the reproductive output because of the mismatch between gonadal development and the timing of reproduction. The egg and larval development of species that do spawn in the cooler water temperatures are likely to be slower making these more susceptible to predation. A reduction in the burst swimming speed is also likely to reduce larval survival. Furthermore, the increased development time may result in changes in the dispersal patterns of the eggs and larvae because the juveniles take longer to settle out of the water column. This may alter the number of juveniles arriving at their nursery grounds and have negative implications for the population.

Ocean acidification is likely to have the same impact as in the other biogeographic regions along the west coast and may cause problems with skeletal formation and the olfactory senses, and reduce the survival of eggs and larvae of all coastal fishes in this region.

The eleven estuaries in the south of this biogeographic zone support a number of estuarine-dependent species. However, the reduced rainfall in this region will most likely influence the functioning and nutrient output of almost all of them. The negative impact of acidification on the chemical cueing of the early life stages of estuarine-dependent species may be exacerbated by the reduction in runoff that is expected for all but one estuary in the region. The Orange River Estuary is expected to receive additional freshwater due to the increased rainfall expected in its primary catchment. This additional freshwater should transport more suspended sediment and increase the turbidity and nutrient input in the region of the estuary mouth. This estuary will most likely provide an important habitat for estuarine-dependent species in the future and its nutrient output will further increase the food availability to coastal fishes in this region.

Estuarine-dependent species and other coastal species in this region may become more reliant on the thermal refuge provided by the estuaries and shallow coastal embayments in this region, particularly during periods of intense upwelling. These shallow areas will be heavily influenced by the terrestrial temperatures which are predicted to be rising in the area and may therefore provide suitable shelter from upwelling driven cold water events. However, it is likely that these fishes will be more susceptible to fishing during these periods.

Sea level rise in this area is expected to influence coastal species through the loss of some shallow intertidal areas (coastal squeeze). The intertidal fish community along the cool-temperate west coast is dominated by intertidal species belonging to the families Clinidae and Gobiesocidae (Prochazka and Griffiths 1992) and the populations of species belonging to these families may be negatively influenced by a reduction in intertidal habitat. Sea level rise is also expected to change the estuarine profiles in this region (see James et al. 2013), which will have an influence on coastal species (such as *Liza richardsonni*, *Mugil cephalus* and *Pomatomus saltatrix*), that utilize these environments.

Warm-temperate south coast

Migratory species near the lower end of their thermal range may respond by moving out of the region into the sub-tropical zone along the east coast (Fig. 4). However, since this region is thought to be warming, they will most likely be squeezed into the narrow region between the two biogeographic zones. These species may be replaced by migratory species near the lower ends of their thermal tolerance in the cool-temperate west coast region (Fig. 4). The phenology of the spawning migrations undertaken by many of the warm-temperate fishes in this zone (Hutchings et al. 2009) is expected to be influenced by the reduction in water temperature. Delayed migrations are the most likely outcome and this could, as in the cool-temperate west coast zone, reduce the reproductive output because fish could arrive at the spawning grounds after gonadal senescence has begun. Unlike the cool temperate west coast zone, the eggs and larvae of warm-temperate fishes that spawn along the sub-tropical east coast are likely to develop faster due to the warmer water predicted in this region. Although this will most likely reduce the dispersal distance of these species, the increased velocity predicted for the Agulhas Current may mitigate this to some degree. Once the larvae have been transported into the warm-temperate south coast zone, the additional food available from the increased upwelling may increase their growth rate. However, this may be mediated by the cooler water temperatures.

Based on the similar changes along the cool-temperate west coast, the response of resident species should be the same, with reductions in metabolism and growth rate expected in this zone. The abundance of species that rely on warmer water for their reproduction may be reduced over time. In contrast, species that spawn in cooler water may become more abundant. Changes in reproductive phenology may also have an impact on the reproductive output because of the mismatch between gonadal development and the timing of reproduction. The egg and larval development of species that do spawn in the cooler water temperatures are likely to be slower, making these more susceptible to predation. A reduction in the burst swimming speed is also likely to reduce larval survival. The increased development time may also result in changes in the dispersal patterns of the eggs and larvae because the juveniles will settle out of the water column later than in areas with warm temperatures. This may reduce the number of juveniles settling in their nursery grounds and have negative implications for the population.

Ocean acidification may, through its impact on skeletal formation and the olfactory senses, reduce the survival of eggs and larvae of all coastal fishes in this region. In particular, the chemical cueing of the early life stages of estuarine-dependent species as they recruit into estuaries may be affected and this may be exacerbated by the reduced rainfall and freshwater input in this zone.

The rapidly rising sea level in this zone is expected to influence coastal species through the loss of some shallow intertidal areas (coastal squeeze). Along the warm-temperate south coast, these habitats have been identified to be important nursery areas for many resident (Watt-Pringle et al. 2013) and migratory (Strydom 2008; Pattrick and Strydom 2014; Rishworth et al. 2014) species, and a reduction in suitable habitat will most likely result in a reduction in the recruitment of these species. The rise in sea level predicted in this region may also negatively influence estuarine-dependent species in this region by altering and even reducing their feeding habitat in estuaries.

Estuarine-dependent and other coastal species may become more reliant on estuaries as warm water refuges during intense upwelling. However, this may make them more susceptible to exploitation during these periods. The decrease in rainfall in the region may reduce the number of permanently open estuaries available to these fishes for thermal refuge, and mortalities following rapid upwelling events could become more common. The migration patterns of many estuarine-dependent species that are thought to spawn in the sub-tropical east coast zone may also be influenced as described in the migratory fishes section.

Catadromous species will be influenced during all phases of their life history. Juveniles will benefit from the warmer riverine temperatures in the region and most likely exhibit faster growth. However, the decreased rainfall and runoff may limit the productivity and food availability in these rivers. Once mature, the metabolism and swimming speed of the adults will be negatively influenced by the reduction in sea temperature during their initial migration until they reach the sub-tropical zone. The phenology of the migration may also be altered and influence the timing of the arrival of the adults from this zone when compared to those of other biogeographic zones. Eggs and larvae are expected to develop rapidly in the warming tropical east coast biogeographic zone, suggesting that their dispersal distance will be reduced. However, the increased strength of the Agulhas Current will most likely mitigate this to some degree. The decrease in rainfall along the warm-temperate south coast may however reduce the freshwater cues for the recruitment of the glass eels into the estuaries. In addition, an increase in the duration of the closure of the mouths of estuaries as a result of the reduced rainfall may also reduce their recruitment success.

Tropical and sub-tropical east coast

Migratory species that are near the upper part of their thermal range may respond to the warming by shifting poleward (Fig. 4). It is likely that the species departing poleward from the sub-tropical region will be replaced by some tropical migratory species, which may shift poleward to avoid warming temperatures in the tropical ocean (Fig. 4). This exodus of migratory species from the tropics will probably not be mitigated by the arrival of temperature tolerant species as it would in the sub-tropical zone and thus the most likely outcome is a vacant ecological niche. It is possible that the species that can tolerate the warmer temperatures in this zone will have additional opportunities and may become more abundant in this region. However, this would be dependent on the thermal sensitivity of all of their life history stages. Based on the broadening thermal gradient that is predicted in this region, it is likely that the distributional ranges of many species will expand. As many of the migratory species are top predators, this may have significant ecosystem consequences for this and the sub-tropical region. Temperature sensitive fishes in the sub-tropical zone may not be able to shift their distribution poleward into the warm-temperate zone as this region is cooling. It is likely that the steepening of the thermal gradient around the biogeographical boundary will restrict successful reproduction of some species to a narrow area. The poleward distributional shifts of migratory species in the tropical and sub-tropical zone may have an influence on the success on their reproduction. Since photoperiod is normally an environmental cue for gonadal development for all but the tropical species, it is likely that the adults of sub-tropical species will arrive at the spawning grounds with under- or over-developed gonads. The influence of changing photoperiod on the gonadal development of tropical species is unknown.

Sub-tropical and tropical resident species may be able to tolerate the warming temperatures until the environment warms to their critical thermal limits. Growth rates are likely to increase in the short-term due to an increase metabolism of the fishes in this region. This will most likely be supported by the increased rainfall, which should provide additional nutrients via the several large rivers situated in the coastal zone. However, once temperatures exceed the thermal tolerance limits, their growth will most likely slow rapidly (Neuheimer et al. 2011). It is likely that the recruitment of resident species in the sub-tropical and tropical zones may be impacted by alterations in the reproductive scope of thermally sensitive species (see Potts et al. 2013). This will probably lead to reductions and expansions in reproductive output of resident fishes in their northern and southern distributions, respectively. Some tropical species with a broad thermal reproductive range may begin to dominate the tropical environment. However, tropical species with a narrower thermal tolerance may increase their reproductive scope in the sub-tropical zone. The increasing reproductive success in the southern distribution of the tropical species may promote broader distributions of these species and the composition of resident species in the sub-tropical zone will most likely shift slowly to one characterized by a mixture of sub-tropical and tropical species. Sub-tropical species may not be able to increase their reproductive scope in the warm temperate zone along the south coast as this region is cooling. Thus thermally sensitive sub-tropical species may only become reproductively successful in a narrow section in the south of this biogeographic zone.

The eggs and larvae of fishes that spawn in the subtropical and tropical zones are likely to develop faster due to the warmer water predicted in this region. This will be supported by the food available as a result of the increase in the rainfall and nutrients in this these zones. Although rapid growth will most likely reduce the dispersal distance of these species, the increased velocity predicted for the Agulhas Current may mitigate this to some degree. Larval development may also be faster, but this will likely occur to a tipping point after which growth and survival will decline rapidly.

The coral reef associated resident fauna is extremely diverse in this region and the influence of climate change on the coral habitats is one of the environmental factors most likely to influence resident fishes in this zone. Although sea level rise, ocean acidification and temperature rise are expected to be lower here than in most other biogeographic zones in southern Africa, the sedentary corals are unlikely to adapt to these changes. Hughes et al. (2003) suggested that coral reef habitats will change, rather than disappear entirely as certain species have higher resilience to climate change. These changes are likely to be reflected in the fish fauna, with major reductions in species that are specialized to inhabit coral habitats, while other, more generalist species will become more dominant (Jones et al. 2004).

Although acidification is predicted to be slower in this region than around the rest of southern Africa, it is still expected to impact the skeletal formation and olfactory senses of all coastal fishes. This will most likely reduce the survival of eggs and larvae. The chemical cueing of the early life stages of estuarine-dependent and catadromous species may be negatively affected, but this will be mitigated by the increase in rainfall and freshwater input in this region.

There are several estuarine-dependent species that form a critical component of the catch composition of coastal fisheries in this region. For example, the St Lucia Estuary is the largest estuary in South Africa and with the increased rainfall, has the potential to support the juveniles of a significant proportion of many estuarine-dependent species. Similarly, the estimated fish catch in the Rufiji Delta in Tanzania is ~10,000 t per year (RUBADA 1981). These fishes are expected to benefit from the increased rainfall in this region. Besides the increased nutrients and food availability, there are numerous temporary open/closed estuaries in the sub-tropical zone and the additional rainfall may increase the periodicity and duration of the open phases and allow these fishes additional opportunities for recruitment.

The rapidly rising sea level in this region is expected to have a considerable influence on resident coastal species through the loss of some shallow intertidal areas (coastal squeeze). For example, Beckley (2000) found that the sub-tropical intertidal areas supported significant fish biodiversity (18 families and 50 species) and served an important nursery function for fishery species such as those belonging to the family Serranidae and Sparidae. Mangrove habitats in the sub-tropical and tropical zones will be negatively impacted and this may, in turn, reduce the abundance of the fishes associated with mangrove habitats. Little et al. (1988) found 83 species of fishes in an East African mangrove creek. As 90 % of the individuals captured were juveniles, it is clear that these habitats provide a critical nursery habitat for coastal fishes.

Changing climate will influence catadromous species during all phases of their life history, as described for the warm-temperate south coast zone. The warming terrestrial environment will probably result in warming freshwater environments, which will in turn most likely increase the metabolism and growth of these fishes in this environment and possibly result in earlier maturation. The adult migration, which is thought to be north-eastward against the prevailing Agulhas Current, will be impacted as the current strengthens. This may result in a shift in the location of the spawning ground or in reduced egg production due to the increased energy expenditure during the migration. The warming conditions may result in a shorter egg and larval phase. However, they are expected to be transported more rapidly as the Agulhas Current increases in speed. The reduced pH may have an impact on the chemical cueing of the leptocephalus larvae of eels, and this in turn may impact recruitment; however, this will be mitigated to some extent in this region by the increase in rainfall and increased chemical cues at the estuary mouths.

Future of climate change research and prediction in southern Africa

These broad predictions of trends are based on our knowledge of predicted climate change, a global review (primarily including research from the

Northern Hemisphere and Australasia) of the available literature, and some patterns that have been observed in the region. This poor level of knowledge would be similar for the majority of the coastal areas in the Southern Hemisphere, with the exception of Australasia and, while these predictions represent our best estimates of likely changes, they provide no quantifiable data or confidence limits. In many ways, this illustrates a lack of fundamental knowledge on the effects of climate change on coastal fishes. There are several key research areas that need to be addressed as a matter of priority.

There are several research groups that are developing climate models in southern Africa; however, these are primarily focused on predicting change in the terrestrial and offshore environments. Unfortunately, this is the case for many parts of the Southern Hemisphere and, while some long-term coastal monitoring programs have been initiated in South Africa, we cannot overemphasize the need for the development of accurate predictive coastal oceanographic models for understanding the impacts of climate change on coastal fishes. Ultimately, a systematic program that aims to sample the interacting physical, chemical and biological components (Hollowed et al. 2013) of our coastal waters are essential to improve our understanding of the climatic drivers of the observed trends. The development of regional and international observation networks will be advantageous, while modelling of mesoscale structures such as upwelling cells and fronts will be necessary to improve our understanding of change at a spatially relevant scale.

Besides the urgent need for models for the prediction of coastal oceanography, there is a clear need to understand the consequences of a range of changing environmental variables on fishes. Research such as those by Coetzee et al. (2008) and Potts et al. (2014) have shown that monitoring programs are critical for examining changes in fish distributions. However, at present, the authors are only aware of a few other long-term monitoring projects (all in South Africa) on coastal fishes for the entire region (James et al. 2012; Mann and Tyldesley 2013; Bennett and Attwood 1991). Besides the establishment of long-term monitoring programs, research that aims to understand climate change consequences should initially focus on understanding the impacts of single environmental drivers on marine fishes at all levels of biological organization; including cellular-, organismal-, population- and ecosystem- perspectives (Rijnsdorp et al. 2009). This can be approached at two levels. The first is pattern-type research, which represents the primary body of knowledge on this subject in this region up to now. This approach relies on either long-term data (e.g., James et al. 2012) or shorter-term data in climate change hotspots (e.g. Potts et al. 2013, 2014) to examine patterns of change and project that information forward (usually assuming a linear trend in climate drivers). While there are several long-term datasets of this nature in South Africa and one in Angola, the authors are unaware of others in the rest of southern Africa. Based on satellite sea surface temperature data, Potts et al. (2014) recognized at least one global coastal hotspot (southern Angola) in a warm-temperate biogeographic zone, where shorter-term data could provide an 'early warning system' for the expected impacts of climate change on coastal fishes. Another recognised hotspot is Agulhas Bank region (South Africa) and the observed changes in these 'marine hotspots' should also be used to frame working hypotheses to guide future research needs (Hobday and Pecl 2014).

While monitoring the patterns can develop our knowledge by indicating the direction of change, this approach has been criticized because the bounds of the predictions based on this research are undefined. This is largely because the processes driving these patterns of changes are not understood. Process-type research on the other hand, aims to identify the mechanisms driving the observed patterns. For example, Pörtner and Knust (2007) used physiological research on eelpout (*Zoarces viviparus*) and concluded that the mismatch between the demand for oxygen and the capacity of the oxygen supply is the first mechanism that would drive a distributional shift or local extinction of a species. Pörtner and Peck (2010) then used physiological research to determine the tolerable thermal habitats for a range of species through their life history. This combination of process driven and applied physiological research will be key to make predictions of the impacts of climate change on coastal fishes.

Although the prediction of the response to changes in a single driver is critical, the interactive impacts of multiple drivers must be explored. For example, the combined effects of rising temperature and falling pH on larval growth and survival may be quite different than when these factors are examined in isolation.

Information on the response of coastal fishers to multiple drivers can be employed to develop physiological-based models that incorporate information from dynamically downscaled oceanographic data for prediction of change (Hollowed et al. 2013).

Crucial to the success of these research foci will be the availability of research funding. Surprisingly, there are few agencies funding climate change science in southern Africa. The majority of the climate change funding programmes (e.g. South African Regional Climate Change Programme, Africa Climate Change Fund) have been channelled directly towards the development of adaptation and mitigation strategies. We believe that a more holistic approach that addresses both the development of adaptation and mitigation strategies as well as the uncertainty surrounding the expected changes is necessary. Without more investment into the science of understanding the impacts of climate change on coastal fishes, fishing communities will be subjected to a range of inappropriate interventions that are based on guesses about future scenarios.

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