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

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ABSTRACT

The South African coastline is just over 3000 km in length yet it covers three major biogeographic regions, namely subtropical, warm temperate and cool temperate. In this review we examine published information to assess the possible role of climate change in driving distributional changes of a wide variety of organisms around the subcontinent. In particular we focus on harmful algal blooms, seaweeds, eelgrass, mangroves, salt marsh plants, foraminiferans, stromatolites, corals, squid, zooplankton, zoobenthos, fish, birds, crocodiles and hippopotamus, but also refer to biota such as pathogens, coralline algae, jellyfish and otters. The role of pioneers or propagules as indicators of an incipient range expansion are discussed, with mangroves, zoobenthos, fishes and birds providing the best examples of actual and imminent distributional changes. The contraction of the warm temperate biogeographic region, arising from the intrusion of cool upwelled waters along the Western Cape shores, and increasingly warm Agulhas Current waters penetrating along the eastern parts of the subcontinent, are highlighted. The above features provide an ideal setting for the monitoring of biotic drivers and responses to global climate change over different spatial and temporal scales, and have direct relevance to similar studies being conducted elsewhere in the world. We conclude that, although this review focuses mainly on the impact of global climate change on South African coastal biodiversity, other anthropogenic drivers of change such as introduced alien invasive species may act synergistically with climate change, thereby compounding both short and long-term changes in the distribution and abundance of indigenous species.

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1. Introduction

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

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

Numerous studies, on a diverse array of biota, have documented the biogeographical provinces within the southern African coastal zone (e.g. Stephenson and Stephenson, 1972; Turpie et al., 2000; Harrison, 2002; Sink et al., 2011) and provided benchmarks with which to examine present and future distributional and functional changes in coastal systems. Southern African marine intertidal rocky shore invertebrates can be divided into three principal populations which have wide areas of overlap (Stevenson and Stevenson, 1972). The tropical group extends southwards from Mozambique and rapidly dissipates between Port St Johns and East London (Fig. 1). The so-called 'Cape' fauna is a warm-temperate group that is centred between False Bay and East London but has elements that penetrate north of Durban on the east coast and as far as Port Nolloth on the west coast (Fig. 1). The so-called 'Namaqua' fauna mainly inhabits the west coast from Cape Town into northern Namibia, with a few elements extending as far south as Cape Agulhas (Stevenson and Stevenson, 1972). These major faunal 'provinces' have had a significant influence on the proclamation of marine reserves in South Africa and it is anticipated that pioneers from each of the above faunal groups will change their coastal distributions in response to climate change, thereby necessitating a review of the adequacy of existing marine reserves on the subcontinent (Emanuel et al. 1992).

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

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

1.1. Some biotic range changes in global coastal ecosystems

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

In many cases, the colonisation of estuarine habitats by one group of species leads directly to the decline in another group of species from those same habitats, e.g. latitudinal mangrove expansion globally has led to the retreat of salt marshes from those