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Human-mediated drivers of change — impacts on coastal ecosystems and marine biota of South Africa

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Coastal ecosystems are highly vulnerable to human-mediated drivers of global change because they are located at the land-ocean interface and often host centres of urbanisation and development. The South African coastline comprises several distinct coastal ecoregions that support a wide range of coastal (inshore) ecosystems, including rocky, sandy and mixed shores, kelp beds, estuaries and seagrass communities. A growing body of evidence indicates that local air and sea temperatures, wind patterns, ocean current speed and upwelling regimes are all being affected by human-mediated climate change. In addition, anthropogenic activities, such as shipping (introducing coastal bioinvasives), exploitation of coastal marine resources, industry (releasing pollutants) and urban development, act synergistically with climate change to place pressure on coastal ecosystems and their biota. The aim of this review was primarily to synthesise and update research into causes of direct and indirect human-mediated global change and their effects on South African coastal systems. It incorporates both historic and the latest regional research on climate change and anthropogenic threats across the ecosystems listed above, much of which was supported by the South African Network for Coastal and Oceanic Research (SANCOR), specifically the SEACChange programme in recent years. It is evident that all these ecosystems are vulnerable to all the drivers considered, albeit to differing degrees, depending on their location on the coast. Whereas some bioinvasives have had a dramatic impact on rocky shore systems on the West Coast, their impact has been moderate on the South Coast and minimal on the East Coast; exploitation shows the reverse pattern. Furthermore, the impacts of human-mediated drivers on coastal ecosystems are synergistic. Of major interest is the fact that the West Coast and parts of the South Coast are exhibiting cooling trends in offshore sea surface temperatures, rather than warming. Correspondingly, a geographical spread of organisms associated with West and South-West Coast rocky shores and kelp beds has tended to be eastwards around Cape Point, rather than northwards along the West Coast as would have been expected with warming sea temperatures. Overall, significant progress has been made toward a better understanding of the combined pressures on each ecosystem and knowledge gaps have been identified, thus helping to direct future research themes.

Keywords: anthropogenic, bioinvasives, climate change, coastal development, exploitation, pollution

Introduction

Coastal ecosystems are the most easily accessible of all marine habitats and hence are subject to intense human-mediated pressures that drive change over a variety of spatial and temporal scales (Heip et al. 2011, Kennish and Elliot 2011, Sink et al. 2012). Within the South African region, directly induced pressures include the modification of biotic communities through the introduction of invasive species, pollution and exploitation of living marine resources (Griffiths et al. 2004, Sink et al. 2012). In

addition, transformation of the physical environment occurs through urban development, harbour construction or coastal mining (Griffiths et al. 2004, Sink et al. 2012). Change can be indirectly induced through anthropogenic activities that promote climate change effects, such as altered trends in air temperature, rainfall, wind, sea surface temperature (Mead and Robinson 2011, Rouault and Mead 2011) and sea-level rise (Whitfield and Elliot 2011). Thus, a better understanding of long-term natural regional change is a

prerequisite for elucidating the effects of human activities on these ecosystems.

The coastline of South Africa has an overall length of 3 113 km (Harris et al. 2011a) and is among the most variable of any nation on Earth, incorporating ecoregions that range from cool-temperate in the west to warm-temperate in the south to subtropical in the east (Bolton et al. 2004, Anderson et al. 2009, Griffiths et al. 2010). South Africa also supports a diverse marine biota of 12 914 described marine invertebrate species, some 33% of which are endemic to the region (Griffiths et al. 2010). Biodiversity differs markedly around the coastline, being universally low along the West Coast but rising progressively on the South and East coasts (Griffiths et al. 2010). Some taxa attain maximum diversity in the south and decline again to the east, whereas others continue to increase right up the East Coast (Awad et al. 2002, Bolton and Stegenga 2002, Bolton et al. 2004, Anderson et al. 2009). Still other very rare range-restricted endemics occur notably only in biogeographical transition regions (Awad et al. 2002, Anderson et al. 2009, Maneveldt and van der Merwe 2012).

A number of publications have addressed the impacts of human activities on the South African coastal zone. To date, the majority of these have addressed a single activity, most frequently direct exploitation or pollution of a particular resource, and most have confined their studies to specific sites or regions. Among the few studies that have taken a wider approach is the review by Siegfried (1994), which compared the history and patterns of human exploitation of rocky shores in Chile and South Africa. Griffiths and Branch (1997) and Anderson et al. (2003) provided similar historical overviews of the exploitation of marine invertebrates and seaweeds in South Africa. A subsequent publication by Griffiths et al. (2004) took a more inclusive approach, looking at all forms of human impact in the Benguela region on the west coast of the subcontinent.

In this review, we synthesise and update these earlier studies by incorporating both historic and the latest research, much of which has been funded under the auspices of the South African Network for Coastal and Oceanic Research (SANCOR), including its most recent programme, SEACChange. We examine what is known along the entire South African coastline, inclusive of sublittoral habitats close to shore. Thus, rocky and sandy shore systems, kelp bed communities, estuaries and seagrass beds are examined (see Whitfield and Elliott 2011 for an update on the classification of coastal ecosystems). Although present within South Africa, mangrove systems are not examined in this review. The major drivers explored for each system are human-mediated climate change, coastal bioinvasions, exploitation, pollution and coastal development. We examine these first before turning to an analysis of each ecosystem.

Important human-mediated drivers of global coastal change

Regional climate change

Building on previous research, SANCOR funded a SEACChange project to investigate change and variability in climate along the southern African coast, with a focus on rainfall, wind speed and sea surface temperature (SST) (Theron

and Rossouw 2008, Rouault et al. 2009a, 2009b, 2010, 2011, Dufois and Rouault 2012, Philippon et al. 2012). In addition, Rouault et al. (2010), Dufois and Rouault (2012) and Philippon et al. (2012) highlighted the impact of ENSO (El Niño-Southern Oscillation) on the climate of the West Coast, particularly in terms of air temperature, rainfall, wind and SST. These studies indicate that South African climate change will depend on the future of ENSO, in addition to anthropogenic-driven climate change.

Mean annual air temperature in South Africa increased by 0.13 °C per decade between 1960 and 2003 (Kruger and Shongwe 2004), potentially influencing intertidal ecosystems such as rocky shores and estuaries. In addition, rainfall has changed over recent decades. An increase in regionally averaged daily rainfall intensity and dry-spell duration has been found at the southern African scale by New et al. (2006). This finding was supported by Rouault and Richard (2003, 2005), who reported an increase in drought and wet periods at the seasonal scale. These trends were most significant along the south and lower east coasts of South Africa (Kruger 2006).

An important change in SST has been recorded in the Agulhas Current, which has warmed by as much as 1.5 °C since the 1980s (Figure 1) due to an intensification of the current that was caused by an increase in trade winds and westerly winds in the southern Indian Ocean, which, combined, have forced an overall increase in wind stress curl (Rouault et al. 2009a). Under the direct influence of the Agulhas Current, the East Coast exhibits a significant positive trend in annual SST throughout the year (Rouault et al. 2010). In contrast, a negative trend (a maximum of −0.5 °C per decade) occurs along the Cape west coast from January to August and, to a lesser extent, along the South Coast, and in the dynamic upwelling cell of the Port Alfred and Port Elizabeth region from May to August (Figure 1; Rouault et al. 2011). The cooling of the West Coast is caused by increased upwelling intensity and frequency, which, in turn, is driven by increased upwelling-favourable southerly winds (Rouault et al. 2010).

Among the consequences of the warming of the world's oceans is thermal expansion, which is a major contributor to sea-level rise (Miller and Douglas 2004). Although regionally variable, an increasing global sea-level trend of approximately $3.2 \pm 0.4 \text{ mm y}^{-1}$ has been recorded between 1993 and 2009 (Church and White 2011). This increase varies along the South African coast (Mather et al. 2009). Sea level (measured by tidal gauges) increased on average by 1.87 mm y^{-1} along the West Coast (from 1959 to 2006), 1.48 mm y^{-1} along the South Coast (from 1957 to 2006) and 2.74 mm y^{-1} along the East Coast (from 1967 to 2006, Mather et al. 2009). However, the barometric pressure has decreased along the West Coast (by 1.63 hPa per decade from 1987 to 2006), remained unchanged along the South Coast and increased on the East Coast by 0.30 hPa per decade from 1970 to 2007 (Mather et al. 2009). Correcting for sea-level rise through inclusion of the barometric pressure effect and vertical crust movements, eustatic sea-level trends appear to have increased from west to east, driven mainly by the influences and interactions of the Agulhas and Benguela currents (Mather et al. 2009) and the impact of the warming of the Agulhas Current (Rouault et al. 2009b).

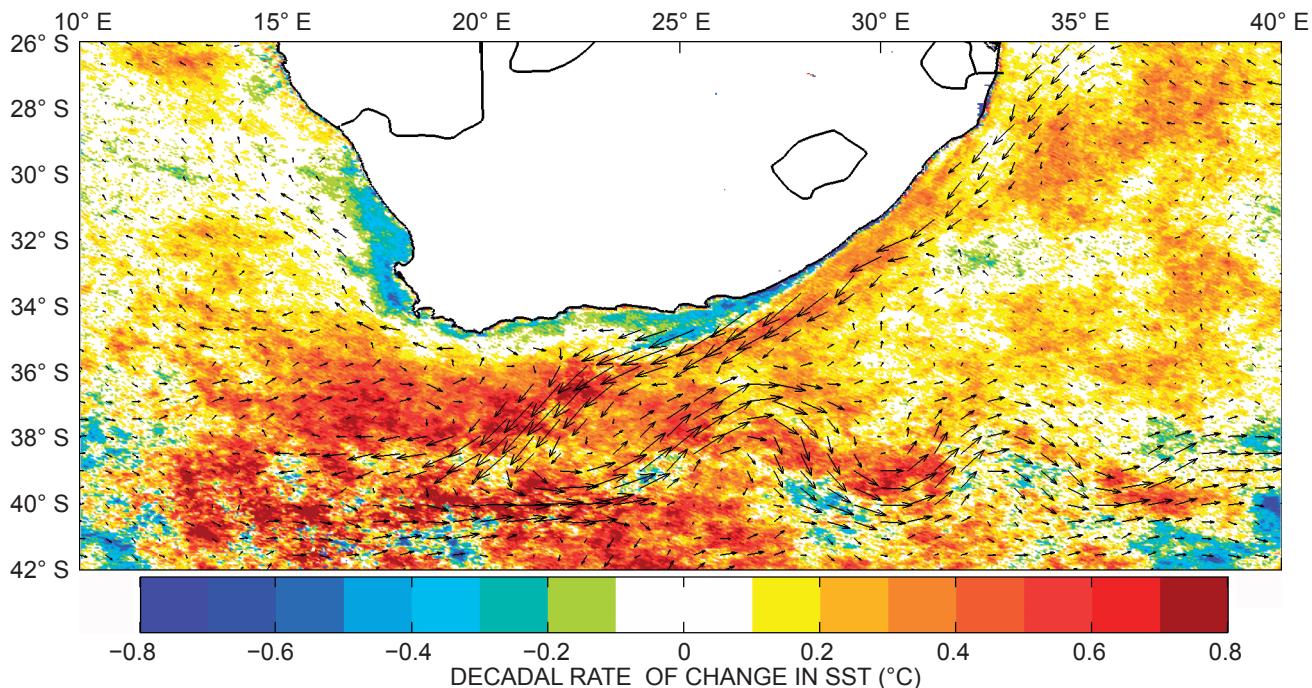


Figure 1: Linear trend of AVHRR sea surface temperature (SST) from 1985 to 2007. Mean 1993–2007 absolute geostrophic velocity vectors derived from combined altimeter are superimposed (after Rouault et al. 2011)

In terms of wave action, as part of the fourth assessment of the Intergovernmental Panel on Climate Change (IPCC), Trenberth et al. (2007), using ship data from 1950 to 2002, reported a significant increase in wave height of 5 cm decade⁻¹ around South Africa. In addition, a significant increasing trend (approximately 0.5 m over 14 years) in the peak wave height of individual storm events during winter has been shown for the period 1994–2008 in offshore waters near Cape Town (Guastella and Rossouw 2009).

Species introduced to coastal waters

Coastal organisms have been transported around the globe, intentionally or accidentally, since humans first began navigating the open ocean. Thus, there can be little doubt that species have been continuously introduced into South Africa since the earliest European explorers landed there. Despite the probable long history of bioinvasions in South Africa, the first paper to specifically list introduced coastal species (15 species only) only appeared in 1992 (Griffiths et al. 1992). The number of species listed has escalated rapidly in more recent years (Griffiths CL 2000, Robinson et al. 2005, Griffiths et al. 2009) to reach 86 confirmed and a further 39 suspected or ‘cryptogenic’ species (Mead et al. 2011a, 2011b). This number is still certainly a considerable underestimation as several additional introductions continue to be discovered annually (Mead et al. 2011a). Detection of introduced coastal species is complicated by several factors (Carlton 2009), particularly in light of the fact that the origins of species introduced centuries ago are difficult to determine. Also, few coastal sites in South Africa have been adequately surveyed for introduced species and many belong to taxonomically poorly known taxa, such as nematodes and benthic copepods (Mead et al. 2011a, 2011b).

Significantly, almost all marine invasions of South African coastal waters have been accidental, whereas in terrestrial and particularly freshwater habitats, many have been deliberately introduced, either as crop or ornamental species or as bio-control agents (Picker and Griffiths 2011). A wide range of marine taxa has been introduced, the most common groups being fouling organisms such as hydrozoans, tube-dwelling polychaetes, small crustaceans, molluscs, bryozoans and ascidians (Griffiths et al. 2011, Mead et al. 2011a, 2011b). There are few reports of introduced seaweeds, the first being the red alga *Schimmelmannia elegans*, that was recorded in the Two Oceans Aquarium in Cape Town by De Clerck et al. (2002). A few smaller algae such as *Antithamnionella spirographidis* and *A. ternifolia* that have also been introduced are generally widespread and well adapted to long-distance dispersal (De Clerck et al. 2002). For many seaweed groups, however, the lack of clear morphological/anatomical characters makes it necessary to use molecular techniques to determine their date of introduction, potential origins and relationships with local species. For example, the invasive strain of the green alga *Codium fragile* ssp. *tomentosoides* was shown, by sequencing of dried herbarium specimens, to have been present in South Africa since at least 1937 (Provan et al. 2008).

The mechanisms of transportation (vectors), and hence the types and numbers of species introduced, have varied enormously throughout history (Griffiths et al. 2009). Early wooden vessels were ideal habitats for wood-boring and external fouling organisms which were often stabilised by dry sand and rock ballast. These materials were dumped upon arrival in South Africa, along with driftline fauna and flora from the ports of origin (Mead et al. 2011b).

More-modern steel vessels, which tend to be larger, more numerous and travel more rapidly than the earlier vessels, transport different species and are mostly impenetrable to borers. Historically, hulls were painted with antifouling paint but with the banning of tributyltin (TBT)-based antifouling paints, this vector may increase in the future. Modern ships are stabilised with ballast water, which provides an additional vector for transporting a different suite of planktonic and nektonic species into South Africa (Griffiths et al. 2009, Mead et al. 2011b). The introduction of strict international ballast water laws for vessels entering and leaving South African waters may reduce the importance of this vector. Aquaculture provides an additional vector and several species are known to have been introduced along with imported oyster spat (Haupt et al. 2010). All known coastal introduced species to date have been catalogued by Mead et al. (2011a) and the characteristics of vector, biology and impacts of introduced species are detailed by Mead et al. (2011b).

Coastal development, exploitation and pollution

As with biodiversity, human utilisation patterns differ around the coast. Approximately 40% of South Africa's human population lives within 100 km of the coast, which has led to the necessary development of urban infrastructure at nodes along the coast and within estuaries. Although human population densities are very low on the arid West Coast, intermediate along the South Coast and attain their maxima on the East Coast (DEAT 2006), development is strongly biased to urban nodes that are associated with ports, particularly on the East Coast. In contrast, marine productivity and fisheries production decreases along the coast from west to east (Griffiths et al. 2004, DEAT 2006).

Interestingly, South Africa is considered to have relatively low levels of pollution, partly because industrialisation is low by world standards, but also because of stringent regulatory controls (Griffiths et al. 2004). However, the coast has about 67 pipelines that discharge daily $1.3 \times 10^6 \text{ m}^3$ of wastewater into the sea, under conditions controlled by the National Water Act 36 of 1998 (DEAT 2006). In addition, there are inputs of agricultural fertilisers into the sea through runoff and stormwater drains, with the latter pipelines transporting unacceptably high levels of the bacterium *Escherichia coli* into the coastal environment (DEAT 2006). Effluents associated with fish factories are particularly rich in organic nutrients, although their nutrient loads have been substantially reduced with the introduction of a 'dry offloading' system (Christie and Moldan 1977). Nevertheless, Monteiro et al. (1997) showed that nitrogen from fish factory effluents was a contributory cause of a bloom of the green alga *Ulva lactuca* in Saldanha Bay. Apparent intensification of the frequency of harmful algal blooms (HABs) that deplete oxygen from the water may be attributable to increasing pollution, particularly eutrophication (Pitcher and Calder 2000).

Changes in specific ecosystems

Rocky shores

In 2005, an International Conference on Environmental Future was tasked with forecasting changes in aquatic

systems, and the following question was asked: 'What are the current human impacts on rocky shores and what will the ecosystem be like by the year 2025?' (Branch et al. 2008a). Among the key factors listed as likely to change biological communities were invasive species, exploitation of living and non-living resources and pollution. Sink et al. (2012) concurred with these in the South African National Biodiversity Assessment. Rocky shore ecosystems are shaped by a balance of top-down and bottom-up controls (Menge and Branch 2001). However, both types of effect are likely to show dramatic change in the medium to long term. Underwood (2000) discusses in detail the need for correct experimental design in order to detect the effects of stressors on ecosystems, and this is the situation in which controls are virtually impossible so that our best approach will be to compare past and ongoing rates of change in ecosystems. Consequently, it will be difficult to discern change over periods shorter than a decade because of high background variability. Nevertheless, we have a clear understanding of the driving environmental factors that shape intertidal rocky shore communities across a variety of spatio-temporal scales (reviewed in Menge and Branch 2001) and can also make reasonable assumptions about how these driving factors are likely to change in the future. For example, given that community structure on rocky shores is powerfully affected by upwelling, wave exposure, and air and sea surface temperature, climate change effects are likely to have a strong impact on biodiversity and community composition. So far, there is little direct evidence of biological responses except for geographical range shifts (Mead 2010) and the clearest detectable change in the recent past has been the effects of invasive species, which are more obvious as they form a new element superimposed on normal variability.

An emerging body of evidence indicates that global climate change is altering air and sea temperatures, wind regimes, upwelling frequency (Rouault et al. 2009a, 2009b, 2010, 2011) and the intensity of wave action in South Africa (Trenberth et al. 2007, Guastella and Rossouw 2009). The consequences of upwelling shifts for rocky shores are therefore likely to be dramatic. Although it is unclear what the potential impacts of climate change on upwelling regimes will be (Walther et al. 2002, Harley et al. 2006), research indicates that upwelling intensity and frequency are increasing within the region. Upwelling has been described as setting the pace of rocky shore dynamics (Menge et al. 2003), having strong effects on the size structure of habitat-forming species, such as mussels (Cole and McQuaid 2010) and macroalgae (Mostert 2011), although these effects do not extend to the infauna, which unexpectedly responds more directly to biogeography than habitat structure (Cole and McQuaid 2011).

Globally, biogeography has been demonstrated to strongly reflect temperature. Within South Africa, Bolton and Anderson (1990, 1997), Emanuel et al. (1992), Bolton et al. (2004) and Sink and Branch (2005) describe the rocky shore biogeography of the South African coast based on benthic invertebrate and algal assemblages. These include a West Coast cool-temperate and South Coast warm-temperate ecoregion, as well as a subtropical ecoregion on the East Coast, grading via a transitional zone

in Maputaland into the tropical Indo-West Pacific. However, a recent spatio-temporal analysis covering the past 25 years has demonstrated homogenisation effects within rocky shore communities (Mead 2010). Intertidal communities located at the biogeographical breakpoints between the cool-temperate ecoregion on the West Coast and warm-temperate ecoregion on the South Coast have come to resemble each other over time (Mead 2010). This is in line with a localised regional cooling of sea temperature due to changes in the dynamic upwelling cell of the Port Alfred and Port Elizabeth region over a similar time-scale (Rouault et al. 2010). A comparable situation exists at the biogeographical breakpoint between the warm-temperate and subtropical ecoregions on the East Coast, in line with a localised regional warming of the sea temperature (Mead 2010). Thus, it is possible that with persistent and continued change in environmental temperatures, biogeographic transitional zones may shift over time, potentially reducing the extent of the warm-temperate province (Mead 2010).

Despite the above biogeographical shifts, there has been only one record of marked changes in the distribution of indigenous rocky shore species in the recent past. Over the past 25 years, the brown mussel *Perna perna* appears to have experienced a significant range recession, retreating eastwards from within False Bay (Mead 2010). This is paralleled by a reduced abundance along the South Coast as far as Arniston Bay, which has resulted in a patchy coastal distribution (Mead 2010). Again, this concurs with localised reducing temperatures over a similar time period, the result of changes in dynamic upwelling cells. A SANCOR SEACChange project, which involved monitoring South African mussel bed structure and recruitment over a 5-year period in the 1990s, showed a very strong geographic gradient of declining mussel recruitment from the West to the East coasts. However, there was little change in the size of mussel beds at most sites over that period (Reaugh-Flower et al. 2011).

Wave action has a profound influence on intertidal communities (Blamey and Branch 2008), which will respond to changes in nearshore hydrodynamics. The influence of wave action begins at the most fundamental level with its effect on species presence/absence and trophic structure (McQuaid and Branch 1984, 1985). Work on the indigenous mussel *P. perna* illustrates clearly the effects of wave action on recruitment and growth (McQuaid and Lindsay TL 2000, McQuaid et al. 2000, McQuaid and Lindsay JR 2005, McQuaid and Lindsay TL 2007), competitive interactions with the invasive mussel *Mytilus galloprovincialis* (Rius and McQuaid 2006, Zardi et al. 2006) and even endolith infestation (Kaehler 1999), with knock-on effects on condition and attachment strength (Zardi et al. 2009).

In other countries, wave action affects the efficiency of predators (Menge 1978). In South Africa, however, intertidal predation does not appear to be a major driver of community structure. A combination of benthic and pelagic predators exerts heavy pressure on juvenile mussels (Plass-Johnson et al. 2010). However, despite the activities of large animals such as the African black oystercatcher *Haematopus moquini* (Kohler et al. 2009, 2011) and the octopus *Octopus vulgaris* (Smale and Buchan 1981), there are few examples showing that adult populations are shaped by predation (e.g. Hockey

and Branch 1984, McQuaid 1985, Griffiths and Hockey 1987). Consequently, while wave regimes may well show long-term changes, this is unlikely to influence predation pressure strongly.

A critical development over the past 10 years has been the growth of research on the genetics of coastal species (reviewed in Teske et al. 2011). These studies have produced several important perspectives, of which one concerns cryptic speciation, which implies that biodiversity based on morphology alone will be underestimated. The second perspective is the relationship between phyogeography and biogeography, whereby some species that occur in adjacent biogeographic provinces form different evolutionary units within the different provinces (e.g. Zardi et al. 2007, von der Heyden et al. 2008). Not all species examined show this latter effect, and several that have low dispersal abilities show phylogeographic breaks that can only be explained by historical changes in environmental conditions, particularly changes in sea level and the strength of the Agulhas Current that has been associated with past glacial periods (Hutson 1980, Teske et al. 2006). Genetic structure appears to be maintained by several factors, including dispersal limitation, physical barriers to gene flow, and selection. *Perna perna* shows strong genetic structure, with two lineages that overlap on the South Coast. This structure seems to be maintained by a combination of dispersal limitation and regional adaptation, with differences between the two lineages in their tolerances of temperature, desiccation and sand inundation (Zardi et al. 2011). Three major phylogeographic transition zones have been identified:

1. on the South-East Coast between the cool-temperate West Coast and the warm-temperate South Coast biota (Cape Point to Cape Agulhas);
2. on the South Coast, between the warm-temperate and subtropical biota, a broader region (roughly central Transkei to Algoa Bay), with the exact position differing among species; and
3. on the East Coast, between the subtropical and tropical biota, a broad region between Mozambique and St Lucia.

There is another level of genetic structure evident in intraspecific comparisons among populations in different conditions. For example, populations of *P. perna* within different bays differ from one another in their haplotype composition, and they also collectively differ from open coast populations in having greater haplotype diversity. Bays act as source populations, with greater gene flow out of bays than into them (Nicastro et al. 2008), which highlights the importance of coastal topography and its interaction with nearshore hydrodynamics. This is another major driver of both recruitment and community structure (McQuaid and Phillips 2006, von der Meden et al. 2008, Pfaff et al. 2011), and is likely to change as thermohaline and wind-driven currents respond to climate change.

Although many of the known South African coastal introduced species remain restricted to sheltered harbours and estuaries, probably because conditions there most closely resemble their areas of origin, a few species have invaded the open coastline and specifically rocky shores (Mead et al. 2011a, 2011b). Few introduced species have shown significant ecological or economic impacts, although most remain unstudied. The most significant

macrospecies introduced to date are the Mediterranean mussel *Mytilus galloprovincialis*, the smaller South American mussel *Semimytilus algosus* and the Pacific barnacle *Balanus glandula*. *Mytilus galloprovincialis* now dominates most exposed rocky shores across the entire length of the West Coast in high abundance and along the South-East Coast as far as East London, although abundance there is highly site-specific (von der Meden et al. 2008). *Semimytilus algosus* was first reported on South Africa's west coast only in 2009, but already occupies a geographic range of c. 500 km, between Groenviersmond in the north and Melkbosstrand in the south (de Greef et al. 2013).

The two invasive mussels display strong spatial segregation within the intertidal zone of the West Coast, with *M. galloprovincialis* dominating in the mid-shore and *S. algosus* blanketing the lower shore. The former species has numerous ecological impacts, moving the centre of gravity of mussel beds much higher into the intertidal, greatly increasing overall intertidal biomass and providing habitat for many smaller invertebrates, enhancing recruitment of small limpets but displacing large limpets (Griffiths et al. 1992, Hockey and von Erkom Schurink 1992, Branch and Steffani 2004). This species also provides additional food resources for predatory species, such as the African black oystercatcher (Robinson et al. 2005, 2007a), and is their preferred prey when feeding their chicks (Kohler et al. 2009). As a result of its success on South African shores, *M. galloprovincialis* now forms the basis of a significant aquaculture industry (van Erkom Schurink and Griffiths 1990).

Mytilus galloprovincialis has shown strong effects on overall community structure on Marcus Island (Robinson et al. 2007a) on the West Coast and its effects elsewhere on that coast have been studied as part of general SANCOR funding initiatives and the SANCOR SEAChange programme (Robinson et al. 2007a, 2007b, 2008, Branch et al. 2008b, 2010). These effects were shown to be moderated by wave action as it reaches peak abundance in areas with strong (but not extreme) wave action (Steffani and Branch 2003a). There, it displaces the indigenous limpet *Scutellastra argenvillei* as it crowds it off the rock face, and the limpet is too large to secure a secondary substratum on shells of the mussel (Steffani and Branch 2003b, Branch and Steffani 2004). Conversely, *M. galloprovincialis* enhances densities of a smaller species of limpet, *Scutellastra granularis*, which experiences higher recruitment in beds of *M. galloprovincialis*, but achieves a smaller size and lower per capita reproductive output there (Griffiths et al. 1992, Hockey and van Erkom Schurink 1992, Branch and Steffani 2004).

Along the South Coast, *M. galloprovincialis* competes for space with *P. perna*. The two species show partial habitat segregation, with *M. galloprovincialis* occupying the upper mussel zone, *P. perna* the lower and both species the mid-mussel zone (Bownes and McQuaid 2006). This situation has been stable for multiple generations and is maintained by the complex interplay of pre- and post-settlement effects. These include initial settlement patterns, physiological tolerances and post-settlement mortality (Bownes and McQuaid 2006, 2009, 2010), as well as adult interactions (Rius and McQuaid 2006, 2009). Small-scale coexistence in the mid-mussel zone runs counter to ecological theory and is maintained because different tolerances to abiotic stress

allow these two species to facilitate each other, as well as compete (Erlandsson et al. 2011).

The European shore crab *Carcinus maenas* is a voracious predator currently confined largely to harbour areas on the Cape Peninsula (Le Roux et al. 1990, Robinson et al. 2005). Experimental studies indicate that it is incapable of surviving on the open wave-swept coastline (Hampton and Griffiths 2007), but it will almost inevitably spread to the important aquaculture centre of Saldanha Bay on the West Coast, where it is predicted to decimate the shellfish stocks (Griffiths et al. 2010). In addition, the Pacific barnacle, *Balanus glandula*, has become a dominant barnacle along much of the West Coast (Laird and Griffiths 2008), where it is expected to displace intertidal species, such as high-shore limpets, but also to provide additional habitat for other smaller species, thus altering community structure. In fact, the upper-shore is covered with *B. glandula*, which, when combined with the spread of the mussels *M. galloprovincialis* and *S. algosus*, results in the entire rocky intertidal along much of the West Coast becoming heavily transformed by introduced species (Figure 2). In comparison, the South Coast is moderately transformed and the East Coast appears largely unaffected (Mead et al. 2011a, 2011b).

Currently, there are few known algal bioinvasions on rocky shores. The red alga, *Schimmelmannia elegans*, however, has been recorded on an open rocky shore at the Cape of Good Hope, in a habitat similar to that of the species on Tristan da Cunha, its site of origin (Bolton et al. 2012). In addition, three separate cryptic introductions of the red alga *Asparagopsis* are present on South African coasts, including a lineage of *A. taxiformis*, collected in Knysna Lagoon in 2008, which is a major invader in the western Mediterranean (Bolton et al. 2012).

Although no major industrial exploitation of rocky shores takes place in South Africa, small-scale commercial extraction of algae and subsistence harvesting of intertidal invertebrates have important effects (Siegfried 1994). Removal of drift kelp from the shore has indirect effects, as this material subsidises rocky shore ecosystems. For example, larger pieces of drift are trapped by the limpet *Cymbula granatina*, and underpin the exceptional biomasses it achieves on the West Coast (Bustamante et al. 1995, Bustamante and Branch 1996). These indirect effects are, however, likely to be minimal, because the proportion of kelp input that is removed from rocky shores is not substantial compared to that removed from sandy beaches.

More direct are the effects of removing algae of the genus *Gelidium*, which are used to extract agar. Harvesting occurs mainly on the South Coast, in the Eastern Cape and originally (but no longer) on the Transkei coast. Approximately 100 t per annum are removed, with attention being focused on *G. pristoides*, which occurs only in the rocky intertidal zone, its upper limits being set by physical stress and its lower limits by competition with coralline algae (Carter and Anderson 1991). Harvesting *G. pristoides* inadvertently removes limpets and barnacles. However, concerns about the effects of harvesting on other species have been alleviated by studies showing that (1) no epiphytic species are unique to the alga, (2) 97.2% of the populations of species found on the alga occur elsewhere on the shore, (3) harvesting has no biologically meaningful



Figure 2: Rocks at Blouberg, Cape Town, pre- and post-coastal invasion by the mussel *Mytilus galloprovincialis* and barnacle *Balanus glandula* (after Reimers 2012)

effect on the densities of limpets and barnacles, and (4) the resource itself is being sustainably harvested, recovering to control levels within 3–5 months. Recovery and subsequent recruitment are severely retarded if plants are completely removed, but hand-plucking does not cause total removal (Carter and Anderson 1985, 1991, Anderson et al. 1991).

Subsistence exploitation of intertidal invertebrates has a history that extends back 160 000 years (Marean et al. 2007). Prehistoric harvesting was directed mainly at mussels — *Choromytilus meridionalis* on the West Coast and *P. perna* on the South and East coasts — but substantial amounts of limpets were also taken. There is good evidence that even in prehistoric times harvesting reduced the mean sizes of both mussels and limpets, particularly over a phase covering 2000–3000 BP, when settlements at sites on the West Coast were most intense (Jerardino et al. 2008).

Modern subsistence harvesting is concentrated along the South and East coasts, and intensification over time has led to substantial depletions of stocks and indirect effects on other components of rocky shore ecosystems (Lasiak 1991). Declines in the abundance of mussels, limpets and ‘redbait’ (the ascidian *Pyura stolonifera*) are clearly evident. The clearest case comes from a comparison of the abundance of the limpet *Cymbula oculus* inside and outside Dwesa, a marine protected area (MPA) on the South Coast: sizes, densities and biomass were ~40%, 75% and 60% respectively greater inside the MPA than outside it. As the species is protandric, the larger females are targeted, and reproductive output was a staggering 80-fold greater inside the MPA (Branch and Odendaal 2003). Some caution is required, however, as a wider-based comparison of multiple exploited and non-exploited limpet species across multiple reserves and non-reserve sites showed that the effects of reserves on growth and mortality are species-specific and difficult to generalise, even within categories of exploitation (Nakin et al. 2012). The removal of target species also alters species interactions, again with secondary effects (e.g. Erlandsson et al. 2011) and influences the supply of larvae of some, but not all species (Cole et al. 2011, Ludford et al. 2012). Removal of grazing limpets enhances algal growth and barnacle abundance, and reductions of

habitat-forming mussels and redbait affect a wide range of species, so that their depletion influences the rest of the community (Hockey and Bosman 1986, Dye 1995, Lasiak and Field 1995, Lasiak 1998, Maneveldt et al. 2009).

Depletion of mussels depends on the interplay of off-take rate and recruitment. Recruitment varies substantially from year to year, so in periods of low recruitment, the effects of harvesting become exaggerated (Dye et al. 1997). Kyle et al. (1997a) have argued that harvesting in Maputaland is sustainable because catch per unit effort remained constant over the period 1988–1994, but events have overtaken this view as stocks have declined radically in recent years, and there are signs of recruitment failure as recruitment success is positively linked to adult abundance. In addition, the heaviest human exploitation on rocky shores occurs on the South-East Coast where recruitment rates are lowest (McQuaid and Payne 1998, Reaugh-Flower et al. 2011).

Given that South Africa lies on a major shipping route and has an exposed coast subject to strong seas, the danger of oil spills is ever present, and spills can have dramatic effects on rocky shores. Since 1989, oil spills have occurred almost annually, although many have been minor. The most serious arose from the sinking of the *Katina-P* off Mozambique in 1992, discharging 67 000 t of oil (Moldan 1994). More stringent legislation introduced after 1999 has curtailed large-scale oil pollution (DEAT 2006), but the threat remains.

Strangely, there has been little documentation of the effects of oil spills on rocky shores in South Africa. Day et al. (1971) recorded the effects of the oil spill associated with the grounding of the *Wafra* near Cape Agulhas, and in 1977 oil spilled as a result of a collision between the *Venpet* and the *Venoil* was noted to have its most devastating effects in sheltered areas, such as estuaries and rocky coves (Moldan et al. 1979). In 1994, the sinking of the *Apollo Sea* off the West Coast released about 2 500 t of heavy fuel oil that deposited on both rocky and sandy shores (Glassom et al. 1997). Rock-pool fish were scarcely affected, with community composition and abundance of most species remaining unaltered. Rocky shore invertebrates and algae were affected to a minor extent, with mobile species that

occupy the upper section of the shore (notably the periwinkle *Afrolittorina knysnaensis* and the winkles *Oxystele impervia* and *O. variegata*) being most affected. The absence of any response from rock-pool fish and the majority of rocky shore invertebrates was probably because the spill occurred at a time of strong seas and high winds, which likely deposited most of the oil high on the shore. In addition, the oil spent some time weathering at sea before striking the coast, with most of the toxic volatile elements having been lost to the atmosphere (Glassom et al. 1997). Use of dispersant to remove the oil generally has far more adverse effects on rocky shore organisms than the oil itself (Southward and Southward 1978).

As a possible result of increased pollution, harmful algal blooms (HABs) that deplete oxygen, leading in some cases to the generation of hydrogen sulphide, have periodically caused mass mortalities of marine life along the West Coast (Matthews and Pitcher 1996). Rocky shores have not been immune to these events, with deaths of mussels, limpets, winkles, whelks and sea urchins approaching 100% in severely affected areas, and resulting in a proliferation of pioneer algae, such as *Ulva* and *Porphyra* (Branch et al. 2013). HAB-induced oxygen depletion led to the mass stranding of over 2 000 t of the rock lobster *Jasus lalandii* in the 1990s (Cockcroft 2001).

Heavy metal levels around the coast are monitored via the 'Mussel Watch Programme', which began in the Western Cape. The programme initially examined levels in the introduced mussel *M. galloprovincialis*, but expanded in 2004 to cover the Eastern Cape and KwaZulu-Natal, where *P. perna* is monitored. Thus far, levels have fallen within a range regarded as 'acceptable' and an encouraging recent decline in lead has taken place (Griffiths et al. 2004, DEAT 2006).

Chemicals that act as endocrine disrupters and affect sexual development have attracted much attention, with a particular focus on tributyltin (Branch et al. 2008a). No southern African studies have been done specifically on its effects on rocky shore species, but Marshall and Rajkumar (2003) showed that the gastropod *Nassarius kraussianus* experiences imposex that affects 29–100% of the populations occupying the Knysna Estuary, and the Durban and Richards Bay harbour areas.

Marine mining for diamonds on the northern West Coast has substantial but localised effects on rocky shores. In shallow waters, divers operate from the shore, using suction pumps to suck up diamond-bearing gravel that is screened on the shore and then returned to sea. Kelp is cut to improve access to the sea, and rocks are scoured by the artificial changes in the movement of sediments. In addition, both land-based and sea-based mining generate large quantities of waste sediment ('fine tailings') that are often deposited into the sea, where they accrete and smother and scour adjacent rocky shores, radically reducing grazers and promoting algal domination. The effects are severe, but fortunately local in their impact (Pulfrich et al. 2003a, 2003b).

Kelp bed communities

Large kelp beds extend along the southern African coast from northern Namibia to just west of Cape Agulhas (Bolton and Anderson 1997). In the south (Cape Agulhas to Cape Columbine), *Ecklonia maxima* dominates in shallower water

(to about 8 m) whereas *Laminaria pallida* forms a subcanopy that extends down to at least 20 m depth wherever there is a rock substratum. Northward of Cape Columbine, *L. pallida* progressively replaces *E. maxima* in shallow water, particularly at wave-exposed sites. The composition of Western Cape kelp beds was described by Field et al. (1980) and their results and extensive appendices are an invaluable baseline study, particularly in view of possible climate change effects. Considerable work in these kelp beds, including that on energy-flow, is summarised in the reviews by Field and Griffiths (1991) and Branch (2007). Recent research within kelp bed communities has been funded by the SANCOR SEACChange programme (e.g. Rothman et al. 2006, 2010, Anderson et al. 2007).

On the South African west coast, surface-reaching kelp beds have been mapped using aerial infrared photography (Anderson et al. 2007). Their biomass is estimated at about 590 000 t, but the extensive subsurface beds of *L. pallida* in the more southerly regions have not been quantified (Anderson et al. 2007). The West Coast rock lobster *Jasus lalandii* and two mussel species, *Choromytilus meridionalis* and *Aulacomya ater*, are characteristic of these kelp beds (Field et al. 1980, Branch and Griffiths 1988, van Erkom Schurink and Griffiths 1990) and dense red algae cover most of the substratum in the shallows (Anderson et al. 1997, Zeeman et al. 2013). In contrast, the South-West Coast, east of Cape Point, has been well-known for its abundance of herbivores, predominantly the Cape urchin *Parechinus angulosus*, but also the abalone *Haliotis midae*, two turban snails, *Turbo sarmaticus* and *T. cidaris*, and the winkles *Oxystele* spp. (Field et al. 1980). In the same region, foliose algae are largely replaced by extensive beds of encrusting corallines (Anderson et al. 1997).

Kelp beds dominated by *E. maxima* were recorded by Papenfuss (1942) to have occurred as far east as c. 10 km west of Cape Agulhas and this distribution has been relatively stable from 1937 until very recently. Further west, in a study comparing rocky shores in False Bay in 1986 and 2007, it was shown that there has been a significant increase in populations of *E. maxima*, which parallels the observed decrease in abundance and apparent range shift of the indigenous brown mussel *Perna perna* (Mead 2010, Griffiths and Mead 2011). In addition, a population of *E. maxima* was recorded for the first time about 60 km east of Cape Agulhas at De Hoop Nature Reserve in 2008, which is apparently a recent eastward shift of around 73 km in the distribution of this kelp bed-forming species (Bolton et al. 2012). Both in False Bay and around Cape Agulhas, Bolton et al. (2012) implicate recent (1982–2009) recorded decreases in average seawater temperatures (satellite temperature data: Rouault et al. 2010) as a likely cause of these distributional changes. While evidence for climate change is not conclusive, recent species shifts, increased low-oxygen events and harmful algal blooms, as well as reduced lobster growth rates, are indicative. The effects of these environmental changes are confounded by the overexploitation of linefish, lobsters and abalone, which may also result in a change in ecosystem structure, function and diversity (Blamey 2010, Blamey et al. 2010, 2013, Zeeman et al. 2013).

Several species inhabiting kelp bed ecosystems along the South African coast are targeted by both recreational and

commercial fisheries. Harvesting of linefish and rock lobster dates back to the late 1800s, whereas the development of a commercial fishery for kelp is fairly recent. Overexploitation of South Africa's linefish during the 20th century has severely depleted many of these stocks, including species that inhabit kelp beds. Commercial catches for a number of linefish species have declined by more than 75% (Attwood and Farquhar 1999, Griffiths MH 2000) and, in some areas, stocks have collapsed completely. Fish community structure has changed substantially since the early 1900s and large predatory fish are now virtually absent, particularly along the South-West Coast (Attwood and Farquhar 1999).

Since the early 1900s, commercial fishing for the West Coast rock-lobster *Jasus lalandii* expanded rapidly, reaching a peak in the 1950s when c. 17 000 t were landed. By the 1990s, landings had declined to approximately 10% of this value (Melville-Smith and van Sittert 2005). An eastward shift in the resource resulted in increased recreational fishing along the South-West Coast during the mid-1990s (Mayfield and Branch 2000) and an expansion of commercial fishing grounds in the early 2000s (Cockcroft et al. 2008). In 2011/2012 the total allowable catch (TAC) for the entire fishing region was set at only 2 425 t (DAFF 2012).

Jasus lalandii experienced severe declines on the West Coast since the late 1980s/early 1990s. This is most likely due to a combination of heavy fishing pressure, reduced growth rates and increased rock lobster walkouts (Cockcroft 2001) of which the latter two are linked to a change in environmental conditions during this period, e.g. increased low-oxygen water, *El Niño* events, and anomalous westerly winds (Pollock and Shannon 1987, Shannon et al. 1992, Pollock et al. 1997). During the same period, rock lobster abundance increased significantly along the South-West Coast (Cockcroft et al. 2008) and urchins, a preferred food-source of *J. lalandii* (Mayfield et al. 2000a, 2000b, 2001, Haley et al. 2011), had virtually disappeared by the mid-1990s (Tarr et al. 1996). Given that in this region juvenile abalone depend on urchins for protection and additional nourishment (Day and Branch 2002a, 2002b), the decline in sea urchin populations had serious consequences for the abalone stock, compounding their depletion by poaching. Some kelp beds once dominated by herbivores and encrusting corallines have become transformed into ecosystems dominated by lobsters and macroalgae (Figure 3; Mayfield and Branch 2000, Blamey et al. 2010, Blamey and Branch 2012).

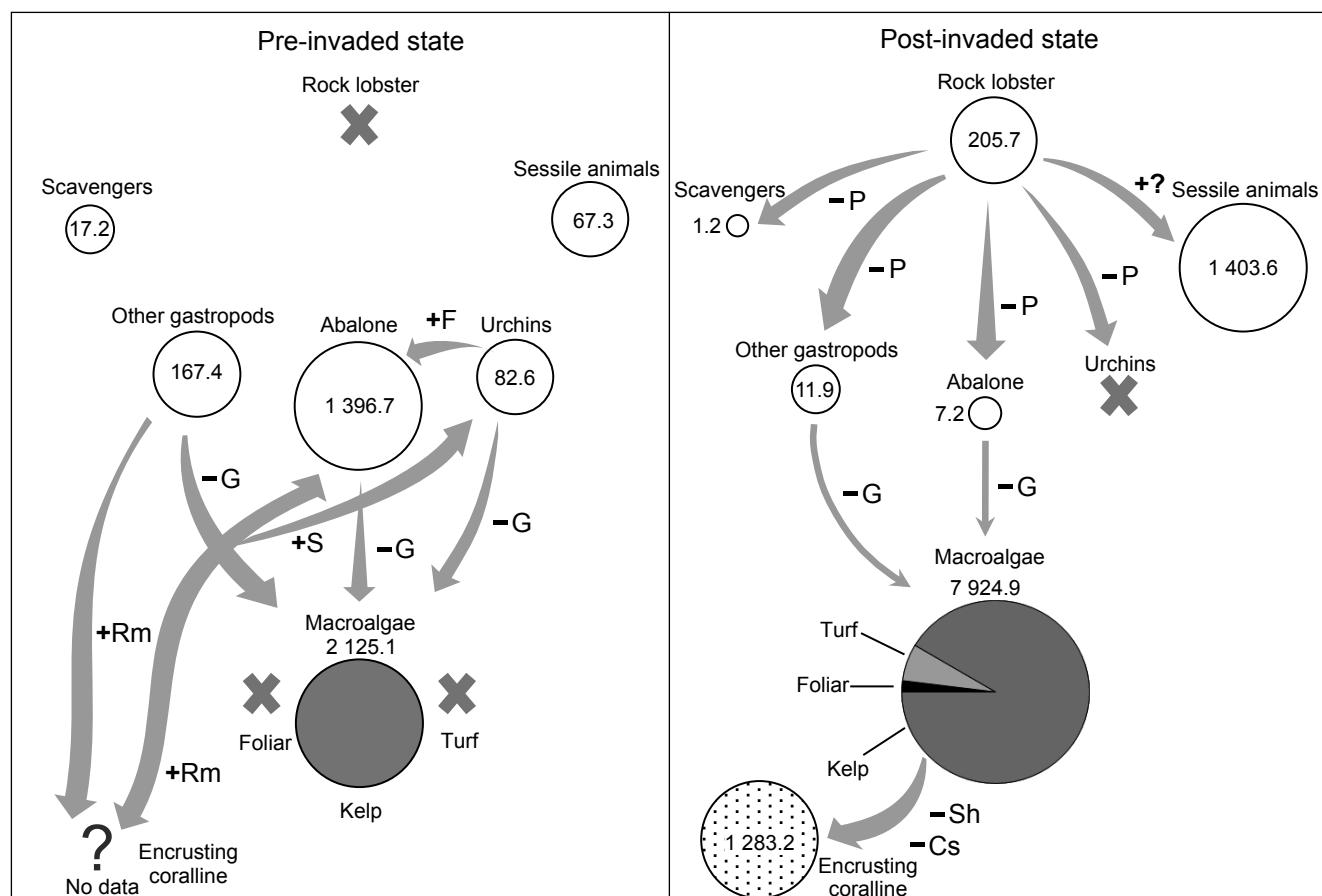


Figure 3: Interaction web of the South-West Coast kelp bed ecosystem (Betty's Bay) in a pre-invaded and post-invaded lobster state (derived from Blamey et al. 2010, 2012). Crosses indicate zero abundance recorded, block arrows imply strong effects and line arrows weaker effects. The likely positive (+) and negative (-) effects are represented as follows: P = predation, G = grazing, Cs = competition for space, Sh = shading, F = facilitation, Rm = removal of competitive algae, S = settlement on substratum. Mean wet biomasses (g m^{-2}) are indicated by numbers and the areas of the circles, which are proportional to biomass on a log scale

The abalone and the turban snail *Turbo sarmaticus* are two notable gastropods that are exploited in kelp beds. Whereas *T. sarmaticus* is harvested by subsistence and recreational fishers largely for food and bait respectively (Proudfoot et al. 2006), abalone formed one of South Africa's most lucrative commercial fisheries. The fishery dates back to 1949 (Tarr 1992). High exploitation levels in the 1950s and 1960s led to a steep decline in the resource, and fishing regulations were introduced in the late 1960s (Tarr 1992). Thereafter, abalone catches remained relatively stable for the next 20–30 years. However, by the late 1990s, illegal fishing and the 'lobster effect' in some areas (Tarr et al. 1996) were well established and commercial catches declined rapidly, resulting in the closure of the recreational fishery in 2003 and a temporary ban on commercial fishing in 2008 (Raemaekers et al. 2011).

Whereas beach-cast kelp has been collected since the early 1950s, the harvesting of growing kelp is more recent (Anderson et al. 1989, 2003). Since 1978, *Ecklonia* has been harvested for the extraction of a plant-growth stimulant and currently about 1 000 t wet weight of kelp is used annually for this purpose (Troell et al. 2006). The proliferation of onshore abalone farms in the past decade created a substantial demand for fresh kelp fronds as feed and, as a consequence, the harvesting of fresh-growing kelp has become increasingly important (Troell et al. 2006, Francis et al. 2008). Annual totals of 5 000–6 000 t wet weight of fronds are currently harvested, mainly where abalone farms are concentrated on the West and South-West coasts (Troell et al. 2006). In some areas, harvesting is approaching the maximum sustainable limits (Troell et al. 2006). Research shows that non-lethal kelp harvesting, by removal of kelp fronds, has little effect on kelp recruitment, subcanopy seaweeds and invertebrates (Anderson et al. 1997, Levitt et al. 2002, Rothman et al. 2006). However, despite the rapid recovery of *Ecklonia* biomass after harvesting (2–3 years), the red algal epiphytes that are usually abundant on older sporophytes, and that provide food and shelter for some fish and invertebrates, take about 4.5 years to recover their biomass (Anderson et al. 2006).

Along the northern west coast of South Africa, diamonds are mined in shallow water by divers. The mining process disturbs kelp communities by moving boulders, cutting kelp and sucking up gravel that is sorted ashore, which then may be deposited in the intertidal zone. Pulfrich et al. (2003a) showed that these activities reduce species diversity in southern Namibia, but that recovery is rapid. Mining had no negative effects on rock lobsters, their abundance and population structure being mainly affected by the environment (dissolved oxygen content) and habitat. Pulfrich et al. (2003b) found that sediments deposited by diamond-mining activities had no effect on rock lobsters, but they did have a localised negative impact on subtidal benthic communities and on wave-sheltered shores where wave action was insufficient to remove the sediments. However, these authors point out that the rock lobster results must be interpreted with caution because of large inter-site variations in the data.

Sandy shores

Research on sandy shores in South Africa was very productive in the 1970s to 1990s. The momentum this generated

initiated an interest in sandy beach ecology in international circles, with consequent growth in our global understanding of the ecosystem. Funding initially came from the National Research Foundation [NRF; previously the Foundation for Research Development (FRD)], but the field has essentially been underfunded since, until very recently. This past lack of funding was largely due to an emphasis on research on marine living resources and social sciences in South Africa, with only one beach-dedicated SANCOR SEAChange grant awarded to date (a current PhD at the Nelson Mandela Metropolitan University). Below, we refer to 'sandy shores' as the seasonal littoral active zone, which includes the surf zone, intertidal 'sandy beaches', and primary dunes, but excludes stable, climax dune communities.

There are two key consequences of global climate change that could cause changes in sandy shore communities, namely sea level rise and storm increase. The mean sea level in South Africa is rising (Mather et al. 2009) and trends suggest an increased frequency and intensity of extreme storms (Trenberth et al. 2007, Guastella and Rossouw 2009). Under natural conditions (untransformed habitat), sandy shores are resilient to these two phenomena, and respond to them with minimal effects (Harris et al. 2011b). However, when sea level rise and storms are superimposed on other anthropogenic modifications of the shoreline, the impacts are synergistically magnified. The most widespread form of coastal habitat transformation in South Africa is urban development (Harris 2012). Shorelines globally have been, and continue to be, inappropriately developed with buildings replacing primary dunes (Small and Nicholls 2003, Schlacher et al. 2008). Decoupling dunes from the littoral active zone severely reduces the resilience of sandy shores to natural disturbances (such as sea level rise and storms) that promote erosion. When urbanised coasts experience sea level rise, beaches get trapped in a coastal squeeze, leading to gradual inundation and loss of the entire habitat, as well as associated goods and services (Dugan et al. 2008, Fish et al. 2008). Similarly, urbanised shores tend to sustain greater impacts from storms (Figure 4) and subsequently recover much more slowly compared to pristine sandy shores (Lucrezi et al. 2010, Harris et al. 2011b).

There are no studies to date that explicitly test other effects of climate change on sandy shore communities. Harris et al. (2011c), however, concluded that climate change is generally not expected to cause dramatic shifts in sandy shore communities, relative to other pressures. Nevertheless, sandy shore communities could be affected by the observed regional changes in temperature, rainfall, wind and current patterns, as well as upwelling regimes, resulting in potential changes in the distribution of some biota, for example.

There are proportionately very few bioinvaders on sandy shores, compared to other coastal habitats (Mead et al. 2011a). Known introductions include the European shore hopper *Orchestia gammarella*, European rove beetle *Cafius xantholoma* and marram grass *Ammophila arenaria* (Mead et al. 2011b). Interestingly, these species have a patchy distribution along the South African coastline and are found high on the shore (along the driftline), or on primary dunes, where habitat stability is greatest (Mead et al. 2011a, 2011b). In the intertidal, however, sandy beach

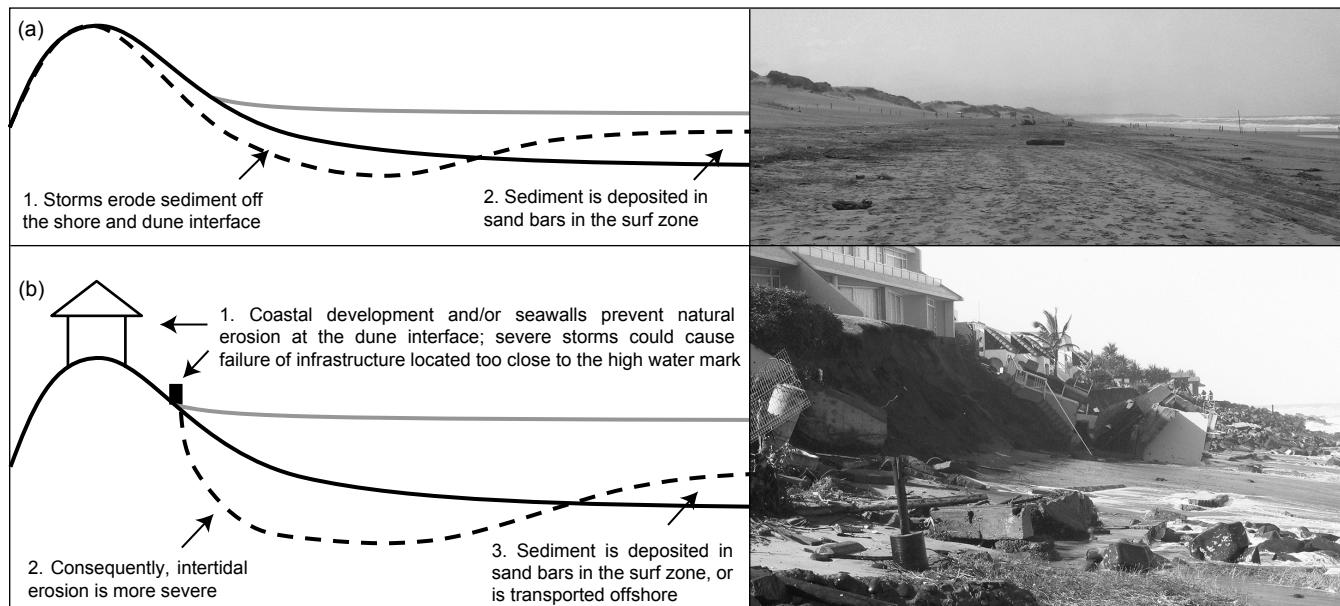


Figure 4: Comparison of storm impacts on (a) untransformed and (b) transformed sandy shores. Line drawings explain the mechanism of the impacts, with photographs serving as examples. Photographs were taken the day following a storm in March 2007 in KwaZulu-Natal, at beaches at (a) Mtunzini and (b) Ballito

ecosystems tend to be dominated by a high proportion of endemic species (Harris 2012), implying that survival by invasive species is doubtful. Although bioinvasive impacts on South African sandy shores remain unexplored, it can be predicted that successful bioinvaders will probably not have a significant impact on beach communities, because the biota is physically controlled, with few biological or competitive interactions among species, *sensu* the autecological hypothesis (Noy-Meir 1979, McLachlan et al. 1993). We suspect that bioinvaders are more likely to occur in surf-zone communities, but none have been reported from South Africa to date.

A variety of species are extracted from sandy shores for purposes ranging from food and bait to constituents for commercial products such as agar. Although removal of macrofauna for recreational and subsistence purposes is one of the most widespread activities on beaches in South Africa (Harris 2012), it is not a significant threat to sandy shore communities because the intensity of extraction is generally limited and sustainable (Kyle et al. 1997b, Clark et al. 2002). There are seven licensed, small-scale commercial fisheries operating in the Western Cape that harvest the white mussel *Donax serra*. However, this species is probably underutilised, because there is only a very small South African market for beach clams (Sims-Castley and Hosking 2003). Broadly speaking, surf zones are well protected from exploitation because of the improved regulation of launch sites, reduced access because of a ban on beach driving, and a fairly well-enforced MPA network.

Removing beach-cast kelp and seaweed from sandy shores, on the other hand, has the potential to alter local beach communities and ecosystem functioning significantly. Beach foodwebs are generally dependent on allochthonous input. Thus, removing wrack subsidies causes declines in

macrofaunal abundance, which ultimately reduces local shorebird abundance (Dugan et al. 2003). In addition, it severely retards nutrient remineralisation by microbes with knock-on implications for the interstitial and surf-zone communities (McLachlan and Brown 2006) and it reduces CO₂ efflux rates (Coupland et al. 2007). The social and economic gains from kelp-derived products (drift collection) and tourism (local beach grooming) thus need to be carefully traded off against the ecological losses.

The effect of pollution on sandy shore communities depends on the nature of the pollutant, and the nature of the affected beach (see McLachlan and Brown 2006). For example, sewage discharge may have a positive effect (Dauer and Conner 1980, Nanajkar and Ingole 2010), whereas solid waste (mostly plastics), oil and effluent discharges may be deleterious (Defeo et al. 2009). There has been relatively little recently published research on the effects of pollution on sandy shores in South Africa, the majority of the work being undertaken prior to 2000 (e.g. Oliff et al. 1967, Fricke et al. 1981, McLachlan and Harty 1981, 1982, Brown 1982, Ryan and Moloney 1990, Madzena and Lasiak 1997). Given that most of the South African coast is exposed to strong wave action that disperses pollutants fairly rapidly, the current, relatively low levels of pollution (by international standards) are unlikely to be a major driver of community change and are more likely to exert localised effects.

Beaches are easily accessible and thus highly utilised for a variety of activities, ranging from recreation to diamond mining. The resulting habitat transformation ranges from insignificant to severe, depending on the intensity and extent of the activities. The two greatest sources of habitat transformation for sandy shores in South Africa are urban development and diamond mining. Currently, 17% of the South African coast has development within 100 m of the

shoreline, which is largely associated with urban nodes around harbours and ports (Driver et al. 2012, Harris 2012, Sink et al. 2012). The impacts of coastal development on sandy beaches have been discussed above.

Diamond mining only takes place on the north-west coast of South Africa, but extends into Namibia. The impacts of the mining operations have been clearly demonstrated (e.g. McLachlan et al. 1993), with the magnitude depending largely on the type of mining. Recent evidence suggests that beaches can recover from these impacts in just a few years because the sandy shores in the region are well connected and exposed to strong wave energy (Nel and Pulfrich 2002). Thus, while these two pressures do affect our sandy shores, their current impacts are relatively limited in space (urban development and mining) and time (mining).

Other threats that have important consequences for beach ecosystems include the extraction of sediment from sandy shores (or from their external sources of sediment, e.g. estuaries) and groundwater from coastal aquifers. Starving beaches of their natural supply and stored reserve of sediment contributes to erosion, diminishing their resilience to other disturbances (e.g. La Cock and Burkinshaw 1996, Lucrezi et al. 2010, Harris et al. 2011b). Sand mining can also alter the mean grain size of beaches, and consequently change the resident communities (McLachlan 1996). Groundwater extraction could decrease the nutrient supply to surf zones and reduce diatom accumulations. As a result, surf-zone communities and associated ecosystem services, such as fish nursery functions along the South Coast, would be particularly vulnerable. It is also worth noting potential future pressures. Currently there is no generation of electricity in the surf zone, but ventures of this nature should be carefully researched before being implemented.

While there are a number of threats to sandy shores, there have also been a number of positive management interventions in South Africa. Construction of harbours, for example, generally requires breakwaters to shelter the harbour entrance. Such structures stop the longshore drift of sediment along the coast, causing erosion of beaches downstream. However, this has been successfully mitigated with the aid of sand-bypass schemes. Further, the beach driving ban (RSA 2001) has been the most successful beach-management intervention and has had far-reaching ecological benefits (Williams et al. 2004).

The recent promulgation of the Integrated Coastal Management Act (No. 24 of 2008; RSA 2009) places South Africa in an excellent position to proactively conserve and protect sandy shores, particularly by regulating future coastal development. Further, implementing integrated and well-designed ecosystem-based conservation and management strategies (see Harris 2012) will contribute to securing a sufficient proportion of intact beach ecosystems for this and future generations.

Estuaries

There are more than 250 estuaries along South Africa's coastline (van Niekerk and Turpie 2012), with each system dependent on river flow and tidal inputs. Changes to either the freshwater supply or the marine connectivity of these estuaries will have a major influence on the estuarine biota, primarily by altering the hydrodynamics, salinity and nutrient

regimes, as well as the predominant mouth state (Figure 5). Research on these topics in South Africa, inclusive of research funded by the SANCOR SEACChange programme, has shown that the trend of declining freshwater input and increasing closed mouth conditions is placing additional pressure on estuarine plants, invertebrates, fishes and birds, in an environment that is already naturally 'stressful' to many aquatic organisms (Elliott and Quintino 2007, Whitfield et al. 2008).

Global climate models suggest that changes in sea surface temperature will be associated with wetter conditions on the eastern margins of South Africa and drier conditions to the west (Hewitson et al. 2004). This will be accompanied by an overall shortening of the rainy season, an increase in high-intensity rainfall events, altered wave action and an elevated frequency of occurrence of hot extremes (New et al. 2006). Like other ecosystems, estuaries will be similarly affected by these changes, often in an unpredictable manner.

On the East Coast, the increase in sea surface temperature (SST), evident since the 1960s, has been associated with a southward range expansion of more tropical estuarine fish species (James et al. 2008a). Conversely, the more temperate species are no longer penetrating the transitional zone between the warm-temperate and subtropical bioregions in the numbers or diversity previously recorded (Mbande et al. 2005). Supporting these observations, Lloyd et al. (2012) showed that over a 19-year period during which the average SST increased by 0.46 °C on the South-East Coast, the relative abundance of temperate species decreased by 10–13%, whereas that of tropical species increased by 9%. According to James et al. (2011), it is important to be aware that each fish species responds differently to warming and that communities do not shift their distribution as a unit. Nevertheless, if the current warming trend continues to gain momentum, it is likely that the contribution of temperate fish species to the overall South African estuarine ichthyofaunal community will decline (Lloyd et al. 2012). This is because any reduction in habitat on the South-East Coast cannot be compensated for by increased equivalent habitat on the West Coast, where estuaries are scarce and upwelling within coastal waters may actually increase.

A more difficult change to predict is the effect of altered coastal wave conditions and sea level rise on estuarine functioning (Hughes et al. 1993). High seas in recent years have seen major overwash events entering temporarily closed estuaries in the Eastern Cape (James and Paterson 2011). These events not only bring large amounts of marine water and sand into these small systems, thus altering the salinity and sediment regime of the estuary, but also tend to flatten the sand bar at the mouth, which can lead to an earlier opening of the estuary (Begg 1978, Cooper 1990). Major overwash events may, however, represent important recruitment and emigration opportunities for the marine fish species associated with these systems (Bell et al. 2001), especially in those regions where river flow is reduced due to global change.

The susceptibility of estuarine systems to biological invasions is poorly understood, although indications are that estuaries under stress are more susceptible to invasive plant and animal species than less-disturbed systems. A good

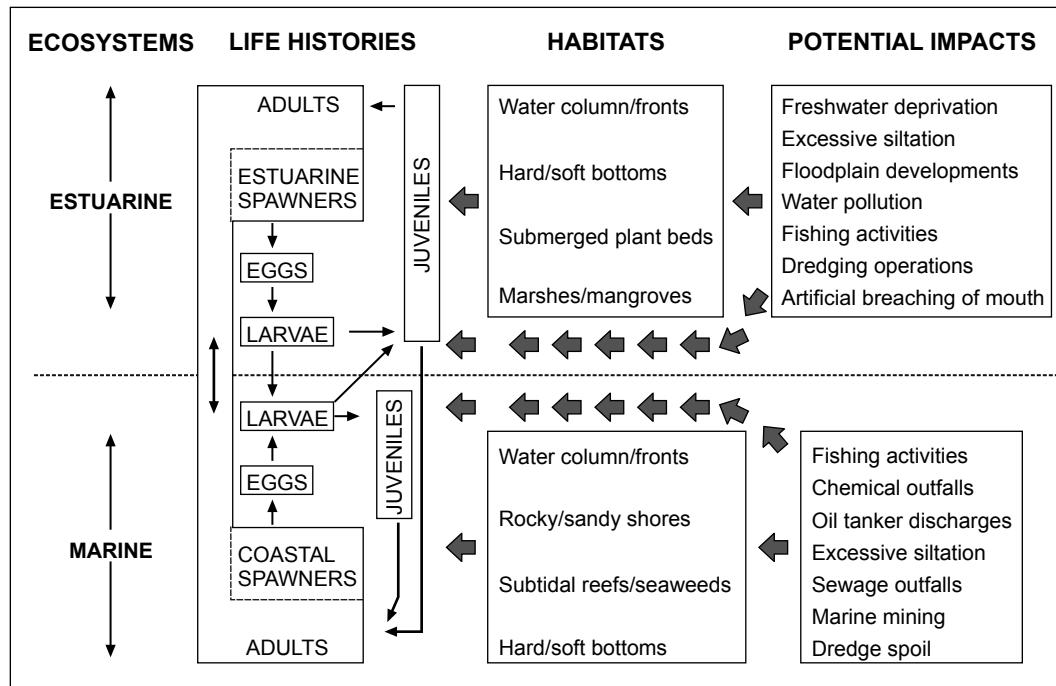


Figure 5: Diagram showing the sources of major anthropogenic impacts on estuaries and marine habitats, as well as the life cycles of fishes within the coastal zone (after Whitfield 1996)

example is the freshwater snail *Tarebia granifera* that has invaded many KwaZulu-Natal estuaries, especially those in a degraded state (Appleton et al. 2009). The apparent concentration of recorded estuarine invasions within degraded estuaries located on the East and North-East coasts (Mead et al. 2011a) is in contrast to the lower levels of documented invertebrate invasions in the less human-impacted estuaries along the South-East and southern coasts of South Africa.

To date, 15% of the known introduced species are within South African estuaries, the majority of which are invertebrate species (Mead et al. 2011a, 2011b). Interestingly, only one invasive fish is reported, the common carp *Cyprinus carpio*, which is really a freshwater species, but is included in the listing because its range extends into the upper reaches of some estuaries (Mead et al. 2011b, Picker and Griffiths 2011). It has been suggested that the marine cordgrass *Spartina maritima* may also be an introduced species in certain permanently open South African estuaries (Pierce 1982, Mead et al. 2011a), but the origin of this species in South African estuaries is still unknown (Yannic et al. 2004, Mead et al. 2011b). More recently, Adams et al. (2012) confirmed the presence and expansion of the invasive American cordgrass *Spartina alterniflora* in the temporarily open/closed Great Brak Estuary. In addition, two invasive algal species have been recorded within estuaries, namely *Antithamnionella spirographidis* in the Kowie Estuary, Port Alfred (Mead et al. 2011a, 2011b), and *Asparagopsis taxifolia* from Knysna Lagoon (Bolton et al. 2011). The possibility of large numbers of invasive microalgae and meiofauna, both poorly studied groups, being present but still undetected within South African estuaries, cannot be ruled out.

The overexploitation of renewable resources within estuaries (e.g. James et al. 2008b) can, through trophic cascading, have a profound impact on both estuarine and nearshore marine ecosystem functioning. Such exploitation and associated ecological disturbance can include both invertebrate (Hodgson et al. 2000) and fish species (Baird et al. 1996), and has reached crisis proportions for certain fish (Whitfield and Cowley 2010). Harvesting of mudprawns *Upogebia* spp. and sandprawns *Callichirus kraussi* for bait appears to be sustainable in both Knysna and Langebaan lagoons (Hodgson et al. 2000, Nel 2006), although attendant disturbance of sediments does have ripple effects on other components of the biota (Wynberg and Branch 1994, 1997). An innovative way of reducing overexploitation of fish and large invertebrates (e.g. swimming crabs and penaeid prawns) is the zonation of estuaries for different uses (van Niekerk and Turpie 2012). Apart from the designation of MPAs, the main direct means of reducing fishing pressures involves controls over fishing methods, effort, efficiency and seasonality (Whitfield and Cowley 2010). Current and future research within this field is making increasing use of acoustic telemetry to determine fish movements and migrations of major angling species (e.g. Childs et al. 2008), thus allowing MPAs to be planned with greater scientific certainty.

Estuaries act as the repository of contaminants generated by human activities. Unlike their Northern Hemisphere counterparts, the majority of estuaries along the South African coastline are not centres of industrial development and are not considered to be heavily polluted (Allanson and Winter 1999, Orr et al. 2008). Notable exceptions are systems in the vicinity of the industrialised large coastal

cities (e.g. Durban, East London, Port Elizabeth and Cape Town), which are subject to several point and non-point sources of contamination (organic and heavy metals). In these systems elevated concentrations of pollutants may be recorded (Watling et al. 1983).

Increased development of coastal resorts in the lower reaches of estuaries may represent a significant source of nutrient enrichment (Allanson et al. 2000). Unfortunately, for most South African estuaries, the degree of nutrient loading is unknown (van Niekerk and Turpie 2012). For the larger, permanently open systems, particularly in the vicinity of large coastal urbanised areas, nutrient loading can be substantial and contribute to the development of phytoplankton blooms and, in extreme cases, fish kills (Allanson and Winter 1999).

Altered freshwater inflow into estuaries in response to human demands, mainly through the building of impoundments, will be associated with changes in hydrodynamics, and salinity and nutrient regimes (Whitfield and Wooldridge 1994). In combination with the expected drier conditions on the West Coast as a result of global climate change, freshwater abstraction will increase closure of temporarily open/closed estuaries in the region. In contrast, predicted increases in rainfall on the eastern margin should prolong mouth opening and increase connectivity (James and Paterson 2011). Such changes are likely to impact on the recruitment opportunities for the invertebrate and fish biota, as well as ecosystem productivity.

Perhaps the best example of the potential influence of global change affecting estuaries in a South African context is the decline in freshwater inputs and connectivity of Lake St Lucia, one of the largest estuaries in Africa. This system was deprived of the considerable annual input from the Mfolozi River in the 1950s because of massive sediment loads entering the St Lucia Estuary following canalisation and cultivation of the Mfolozi Swamps. As a consequence of this impact, a new mouth was created for the Mfolozi River to the south of St Lucia, but unfortunately the associated freshwater was then lost to the lake system. The decline in freshwater inflow into the estuary can be linked with habitat loss, reduced recruitment opportunities for invertebrates and fishes (Cyrus et al. 2011) and changes in the productivity of the system (Perissinotto et al. 2010). These recent developments have seen a change in management approach and a plan is currently being devised to allow the Mfolozi River to re-link to the St Lucia system on a more permanent basis (Whitfield et al. 2013).

Seagrass communities

Seagrasses are aquatic, grass-like angiosperms that are confined to the marine and estuarine environment. Six submerged macrophytes dominate in South African estuaries: *Halophila ovalis*, *Stuckenia pectinata*, *Ruppia cirrhosa*, *R. maritima*, *Zannichellia palustris* and *Zostera capensis*. *Halophila ovalis* and *Z. capensis* are true seagrasses, whereas the other species grow in freshwater to saline conditions (Adams et al. 1992). *Zostera capensis* dominates in tidal permanently-open South African estuaries, whereas *R. cirrhosa* occurs in temporarily open estuaries, characterised by fluctuating salinities (Adams et al. 1992). The latter can,

however, also occur in the calm, brackish upper reaches of permanently-open estuaries (Adams et al. 1992).

The recently reclassified seagrass *Thalassodendron leptocaule* (Duarte et al. 2012) is an important component of rocky shore ecosystems in the extreme north-east of South Africa, and is a dominant species on inshore reefs in Mozambique (Browne 2012, Browne et al. 2013). In South Africa, it is restricted to the intertidal and shallow subtidal from Sodwana northwards, although a single small population has been present for at least 50 years at Maphelane, c. 100 km south of Sodwana (Ward 1962, Browne 2012, Browne et al. 2013). These are the southernmost populations in the Western Indian Ocean, and are likely to be affected by changes in seawater temperature regime or human activities.

In Langebaan Lagoon, roughly 38% of the seagrass (*Z. capensis*) area has been lost since 1960, with some sites showing up to 98% loss (Figure 6) (Pillay et al. 2010). Sites most affected experienced a reduction in invertebrate species richness by up to 50% and the localised extinction of seagrass-dwelling invertebrates (Pillay et al. 2010). Environmental and biotic homogenisation following seagrass loss was the main mechanism responsible for the loss of diversity. Crashes in seagrasses have also been linked to declines in seagrass-associated waders, such as terek sandpiper *Xenus cinereus*, as these birds feed almost exclusively on invertebrates in seagrasses (Pillay et al. 2010).

The localised extinction of the critically endangered eelgrass limpet *Siphonaria compressa* at sites most affected by seagrass loss in Langebaan Lagoon is a major conservation concern, as this false limpet is restricted to only two localities in South Africa, namely Langebaan Lagoon and Knysna Estuary. The future status of *S. compressa* is tightly linked with seagrass abundance. Angel et al. (2006) showed how *S. compressa* twice approached localised extinction during periods of major seagrass crashes.

As climate-driven reductions in freshwater inflow can increase the frequency of closed mouth conditions in temporarily open/closed estuaries, the seagrass *Z. capensis* may be lost, because it preferentially grows in the intertidal

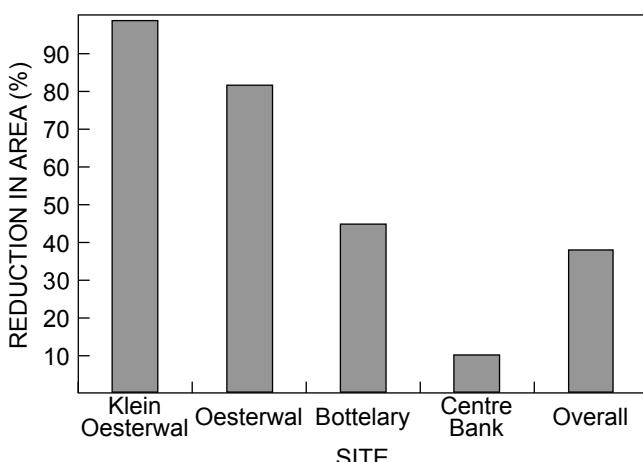


Figure 6: Change in seagrass area at four sites in Langebaan Lagoon between 1960 and 2007 (Pillay et al. 2010)

zone and requires tidal exchange to maintain healthy plant beds (Adams and Bate 1994). The mouth of St Lucia Estuary has remained closed since 2002 and *Z. capensis* has not been observed in this estuary since 2005. A decrease in freshwater input may also increase upstream salinity towards full seawater, which may lead to an expansion of *Z. capensis* into the upper reaches, as has occurred in the Kromme and Bushmans estuaries (Adams and Talbot 1992).

An increase in sea storms has been indicated as an effect of climate change within South Africa. A storm surge in September 2008 opened the mouth in the East Kleinemonde Estuary and an increase in salinity resulted in a displacement of submerged macrophytes by macroalgae (Sheppard et al. 2011, 2012). A loss of submerged macrophytes may have significant impacts on faunal composition and abundance (Sheppard et al. 2011, 2012) and also on the subsequent functioning of temporarily open/closed estuaries. This has serious ecological implications, given that 70% of South African estuaries are of this 'temporarily open' type (Riddin and Adams 2010).

Several studies have highlighted the potential for climate-driven changes in water temperature and pH to alter seagrass physiology and possibly their distribution and abundance (Duarte 2002). However, information on the temperature and pH tolerance of South African seagrasses is currently lacking and needs investigation.

To date, the only marine introduced species to have been recorded in association with seagrass communities is the cordgrass *Spartina maritima*, of unknown origin (but possibly linked to the arrival of European sailing vessels in South African coastal waters) and first collected in 1896 (Mead et al. 2011a, 2011b). However, surveys specifically targeted within seagrass beds may reveal a higher number of introduced seagrass species than presently reported.

Bait digging and associated trampling can, in some instances, negatively affect seagrasses. In Langebaan Lagoon, in areas where pumping of mudprawns and sandprawns is permitted, seagrasses have approached localised extinction, showing roughly 98% loss since 1960. Sediment turnover and trampling leads to physical burial and damage to plants (Pillay et al. 2010). However, despite intensive bait digging in the Swartkops and Knysna estuaries over many decades, *Z. capensis* has persisted in these systems and it appears that the extent of seagrass cover in these systems is determined primarily by river flooding. It is clear then that seagrasses may be prone to physical damage.

The distribution of *Z. capensis* beds in South African estuaries is strongly linked with flooding, sedimentation and circulation patterns (Adams et al. 1992), which in turn

are heavily influenced by human activities. Angel et al. (2006) reported two major seagrass crashes in Langebaan Lagoon in 1976 and 2003. The first coincided with blasting and dredging during harbour development in the adjacent Saldanha Bay, which may have enhanced sediment and nutrient loads, to the detriment of seagrasses. There are no obvious explanations for the second seagrass crash in Langebaan Lagoon. Dredging, mobile sediments and an increase in turbidity were responsible for reductions in cover of *Z. capensis* in the Mhlathuze Estuary (Cyrus et al. 2008).

Boating can reduce seagrass cover due to physical removal by propellers, or by increasing turbidity. Eutrophication, in conjunction with overfishing, can also reduce seagrass coverage. Eutrophication increases algal blooms and epiphytic growth on seagrasses, which reduce light availability and seagrass growth (Baden et al. 2010). Overfishing, especially removal of top predatory species, causes a trophic cascade, leading to the elimination of grazers that remove fouling epiphytes on seagrasses; in addition, both microalgae and macroalgae replace submerged macrophytes in disturbed estuaries where nutrient input is high (Baden et al. 2010).

Summary

It is clear from this review that the impacts of human-mediated drivers are consistently evident within each South African coastal ecosystem examined. The impacts span the entire South African coastline, albeit to differing degrees of intensity, depending on where the ecosystems are located geographically. It is difficult, at this point, to allocate a hierarchy of importance for specific drivers within each ecosystem, due to gaps in our knowledge (Table 1). This is important to note as facts and data are not available at this time to support wider statements of change. For example, exploitation is well understood within each ecosystem, probably due to the quality and quantity of historic data available and a historic focus on understanding its impacts. In contrast, the scale, and particularly the impacts, of introduced species — a relatively new area of research — are best understood within rocky shore communities, where impacts have been specifically tested through experimental manipulations.

In recent years, a clearer understanding of human-mediated climate change has emerged for the region, with impacts on communities and biota having been either predicted or observed across all coastal ecosystems. Moreover, it is anticipated that climate change will act synergistically with other anthropogenic drivers, increasing

Table 1: Indication of the state of knowledge related to each human-mediated driver and coastal ecosystem

Coastal ecosystem	Human-mediated driver of change					
	Climate change	Coastal invasives	Exploitation	Urban/rural development	Pollution	<i>State of knowledge</i>
Rocky shores	Moderate	Good	Good	Moderate	Good	Good
Kelp beds	Moderate	Poor	Good	Poor	Poor	
Sandy shores	Moderate	Moderate	Good	Good	Poor	
Estuaries	Moderate	Good	Good	Good	Good	
Seagrass	Poor	Moderate	Moderate	Moderate	Moderate	

the vulnerability of coastal ecosystems and their associated biota to human activities. Further research is essential to add to the growing body of knowledge on this topic, specifically to address the current gaps in knowledge that have been indicated within this review. Previous SANCOR-funded initiatives and the current SANCOR SEAChange programme have greatly facilitated research into global change effects along the South African coast and the latter initiative has positively contributed to progress within the field. Such research will continue to inform important future policy, law and management decisions within the region.

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