THE EFFECTS OF CLIMATE CHANGE ON MARINE BIODIVERSITY IN SOUTH AFRICA

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INTRODUCTION

B.M. Clark

Climate change is as old as the atmosphere itself and has occurred for many millions of years. Prior to the industrial revolution, the principal causes of climate change included factors such as plate tectonics, orogenic activity, changes in solar output and the position of the earth relative to the sun. Changes in global climate between now and the middle of the 21^{st} century, however, are likely to be dominated by the influence of the greenhouse effect caused by increasing concentrations of carbon dioxide (CO_2), methane (CH_4), nitrous oxide (N_2O), ozone (O_3) and halocarbons (CFCs etc.) (Wigley 1992). Rising concentrations of these gases, caused by human activities such as the burning of fossil fuels, various industrial processes and changing land use are enhancing the natural greenhouse effect, resulting in additional warming of the earth’s surface.

Various climate models and scenarios have been developed to simulate past climate and predict future trends. The most successful and widely favored of the methods use results from large-scale atmospheric models, known as General Circulation Models (GCMs). Several climate change scenarios have been developed for southern Africa, based mainly on the results generated by GCMs (see for example Tyson 1990, Tyson 1993, Schulze & Kunz 1993, Shackleton *et al*. 1996). Studies have focussed mainly on terrestrial systems and there is some preliminary consensus regarding the likely effects of climate change on terrestrial biodiversity (Siegfried *et al*. 1990, Fields *et al*. 1993). Marine ecosystems have not been considered to the same extent, with the result that there is a general lack of knowledge regarding the likely impacts of climate change on marine and coastal environments (Field *et al*. 1993, Beardall *et al*. 1998). Siegfried *et al*. (1990) examined some scenarios for global-warming induced change in the open-ocean environment off the west coast of south Africa and Shackleton *et al*. (1996) summarised current knowledge regarding the impacts of global climate change on marine and coastal environments in South Africa. Few studies have, however, examined the effects of climate change on the various components of the marine environment in any detail.

The aim of this report was to study the likely effects of climate change on aspects such as biodiversity and ecosystem functioning in a few key marine environments. Rather than provide another general overview of possible changes in the marine environment in South Africa as a whole, it endeavours to provide as detailed an assessment as possible of the likely implications for climate change in several of the component parts. Three systems were chosen for study and they included the open ocean environment off the South African west coast, rocky intertidal environments, and estuaries. These studies are obviously constrained by the quantity and quality of information available on likely changes in key environmental or climatic variables and by the current knowledge regarding species' and community responses to changing environments. In many instances it was only possible to develop "what if" scenarios or speculate broadly on possible changes in or in response to a changing climate. These three reports stand very much on their own and very little attempt has been made to draw them together. Rather than reiterating the detail from each of the reports, the Conclusions and Recommendations section at the end attempts rather to provide overarching comments on the likely effects of climate change on the marine environment as a whole and actions that need to be taken in order to mitigate some of these effects.

A summary of the data available on the distributions of selected marine species and protected areas has been included in an Appendix. The databases described can be used in further research concerning the effects of climate change at the species, rather than ecosystem level. Such a study was beyond the scope of the present report.

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POSSIBLE EFFECTS OF CLIMATE CHANGE ON PELAGIC FISH RECRUITMENT IN THE SOUTHERN AFRICAN BENGUELA SYSTEM

S. Young and A.J. Richardson

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2. INTRODUCTION

2.1 GLOBAL CLIMATE CHANGE

Climates have changed radically in the geological past, and it is certain that they will change again in the future (Bernal 1991). Global CO_2 concentrations have been increasing at a rate of ~1.3 parts per million by volume per year for the last 35 years, with a doubling of atmospheric CO_2 over the past one hundred years. The Intergovernmental Panel on Climate Change (IPCC) have calculated that if carbon dioxide emissions are maintained at 1994 levels, then concentrations will reach double pre-industrial values (280ppmv) by the end of the 21st century (IPCC Report 1996a). An increase in CO_2 produces an enhanced greenhouse effect in the atmosphere, which decreases the amount of outgoing long wave radiation. This alters the radiative balance, impacting factors in the climate system (IPCC Report 1996a). The increase in CO_2 emissions is thought to be directly responsible for the 0.3 to 0.6°C increase in global atmospheric temperatures over the last century (Fig. 1). Results now show that for mid latitudes, air temperatures can be expected to rise 1.2°C by 2020, 2.1°C by 2050 and 3.2°C by 2080 (IPCC 1996a).

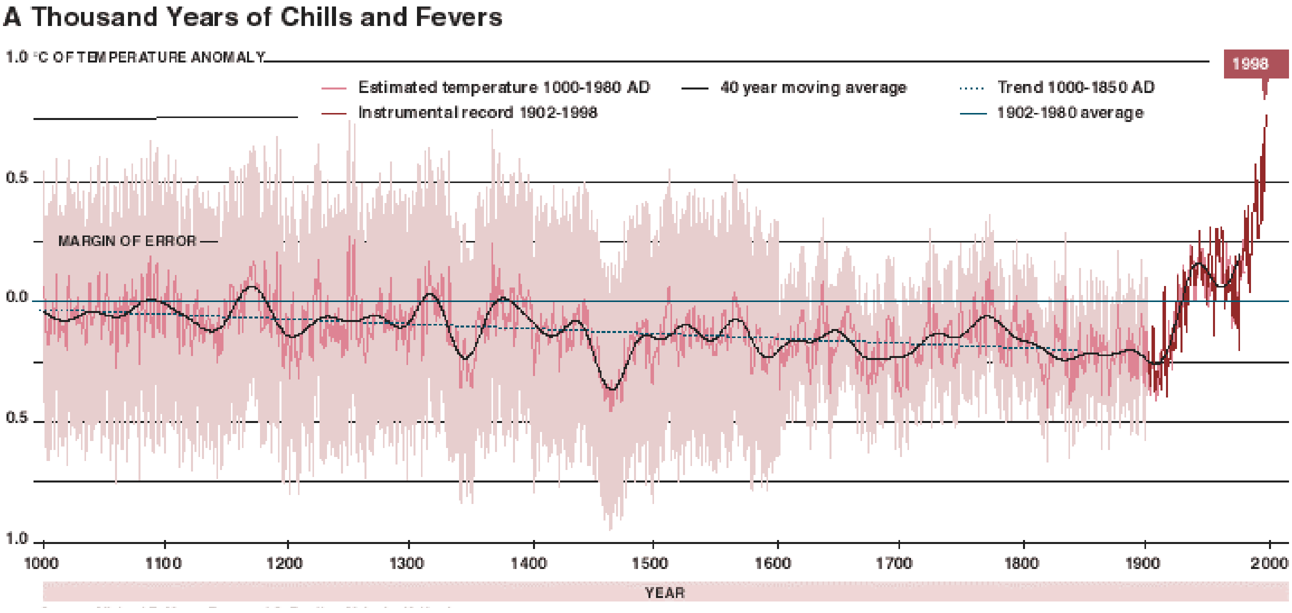

Fig. 1: The global increase in temperature over the past century with the most notable increase in the recent decade (source: Michael E. Mann, Raymond S Bradley and Malcolm K. Hughes).

Studies by the UK Meterological Office (Hadley Centre) have indicated that sea surface temperature increases along with air temperature, although not as rapidly or to the same degree, owing to the greater thermal inertia of the ocean compared with the atmosphere. Thus, an increase in air temperatures in the future will result in higher sea surface temperatures. This rise in sea temperature is likely to be the most prominent effect of climate change on the ocean (IPCC 1996b).

The principle force behind the changes in sea surface temperatures is likely to be changes in the circulation patterns of the oceans (IPCC Reports 1996a, b). Currents driven by geographic and seasonal patterns of heat at the earth's surface and in the lower atmosphere, distribute heat from the tropics to colder regions via a global heat 'conveyor belt'. However, global warming of the atmosphere may alter these patterns. It is not likely that the ocean-atmosphere system will respond linearly to increasing greenhouse gases, but will possibly undergo sharp, worldwide reorganisation, switching from one stable state to another. A major shift in the ocean-atmosphere system could markedly alter temperature regimes in places like southern Africa, whose climate depends on heat carried by ocean currents (Hockey and Buxton 1989).

2.2 EFFECTS OF CLIMATE CHANGE ON MARINE SPECIES

The effects of climate change may have both positive and negative impacts on even the same species. Marine resources could either benefit or collapse in response to climate change, depending on which environmental signal is most important and on the biological responses to environmental change (Siegfried *et al.* 1990). However the capacity of each species to adapt genetically to change will depend on existing genetic variation and the speed of genetic change (Peters and Lovejoy 1992). It is not likely for widespread extinctions to occur, although changes in community distributions and composition are probable.

With changes in sea surface temperatures, climate change has the potential to significantly affect the ecology and biodiversity of aquatic systems. An increase in temperature, no matter how subtle, can influence growth and metabolic processes of a species and thus biological production (Peters and Lovejoy 1992). This is because the body temperature of most marine organisms varies with the external environment and thus temperature influences behavioural and physiological responses. Furthermore, organisms that rely on heat from their environment are typically active near their upper rather than lower thermal limit, and although this provides greater scope for activity and maximises power output, it also increases their vulnerability to a rise in temperature (Fields 1993).

2.3 SMALL PELAGIC FISH AND CLIMATE CHANGE

Clupeoids such as sardines, sardinellas and anchovy are small, schooling pelagic fish inhabiting the upper layers of the ocean in coastal upwelling regions (Shannon *et al.* 1996). The main upwelling areas of the world are on the eastern boundaries of the oceans, where there are strong equatorward winds. This causes offshore transport of the surface layers as a result of Ekman drift (Mann and Lazier 1991). Thus, cool water containing phosphates and nitrates then upwells into the euphotic layer, replacing the water that has moved offshore. This nutrient-rich upwelled water promotes growth of phytoplankton, which supports large standing stocks of zooplankton. In turn, this supports large stocks of planktivorous pelagic fish (Waldron *et al*. 1997a).

In upwelling regions, high primary productivity supports large commercial fisheries (Crawford *et al.* 1987). An average of 18.2 million tonnes of clupeiods were caught annually worldwide in the 1980s, amounting to 20% of the world's marine fish catch (Armstrong and Thomas 1989). In the southern Benguela upwelling system, between 2-3 million tonnes are caught per year (Crawford *et al*. 1987, Hutchings 1994). Anchovy and sardines are presently the mainstay of the South African purse-seine industry, and in 1994 were worth approximately US$78 million in fishmeal, canned and baked fish, and oil. It is also responsible for the employment of roughly 6 000 people (Hutchings and Boyd 1992).

Clupeoids are also important ecologically, being a source of food for larger fish, seabirds and marine mammals. It is often noted that the collapse of small pelagic fish populations is accompanied by sharp declines in the marine bird and mammal populations that depend on them for their source of food (Crawford 1987).

Small pelagic fish are likely to be susceptible to climate change. This is because pelagic fish undergo large natural fluctuations in spatial range and stock size as a result of environmental variability (BENEFIT 1997, Lluch-Belda *et al.* 1992). There are several reasons for the susceptibility of pelagic fish to environmental fluctuations. Firstly, they are an r-selected species (Lalli and Parsons 1993). R-selected species are characterised by being small in size, serial spawners, early sexual maturity and high fecundity (Lalli and Parsons 1993). Secondly, pelagic fish feed on short, plankton-based food chains that are highly affected by changes in upwelling. Lastly, their recruitment is controlled by larval survival, which is highly dependent upon the ocean climate and could be directly influenced by increasing ocean temperature (Bernal 1991). For instance, small changes in water temperature could influence the survival rates of larvae and hence recruitment to the fishery. Also, larval retention areas depend on the existence of precise circulation patterns that may be altered by climate change (Bakun 1996). Furthermore, warming of the surface layer will increase stratification and if other factors remain equal, this change may enhance the formation of high food concentration layers, and extend their area of occurrence. These layers are a key limited food resource for fish larvae survival, since average concentrations of particles in the ocean do not provide enough food for maintaining a positive daily energy budget for larvae (Bakun 1990). Winds also influence larval survival and are discussed in the next section. All of these characteristics of pelagic fish make them highly sensitive to environmental perturbations, making them ideal subjects for the study of marine impacts of climate change.

2.4 FISH RECRUITMENT AND THE OPTIMAL ENVIRONMENTAL WINDOW

Cury and Roy (1989) have analysed the relationship between annual pelagic fish recruitment indices and wind intensity in various upwelling areas. They found that this relationship was in the shape of a dome (Fig. 2), with maximum recruitment at intermediate wind speeds. This optimal environmental window is thought to be a consequence of the effect of wind on larval survival and hence on recruitment. The primary causes of larval mortality are predation and starvation (Blaxter and Hunter 1982) and these are influenced by wind.

On the left side of the curve there are two factors limiting pelagic recruitment. Firstly, low wind speeds result in weak upwelling and little nutrient enrichment. Thus, there is higher larval mortality because of the lack of food (Cushing 1969). Secondly, the low wind speeds cause little mixing and turbulence in the water column. This reduces the encounter rate between larvae and food particles (MacKenzie *et al.* 1994).

On the right side of the graph, strong wind speed limits recruitment (Cury and Roy 1989). Strong winds result in excessive offshore transport, causing pelagic eggs and larvae to be lost from their preferred food-rich coastal habitat (Bakun and Parrish 1980, Sinclair 1988). Strong winds also enhance turbulent mixing in the surface layer (Kullenberg 1971, Serra et al. 1998) that disperses larval prey organisms that aggregate in patches or layers (Lasker 1978, Theriault and Platt 1981). This makes it difficult for larvae to obtain sufficient food.

Wind mixing can also affect primary production (Huntsman and Barber 1977) by mixing phytoplankton below a critical depth at which photosynthesis is no longer greater than wind respiration (Steele 1974). Moreover, the ability of larvae to capture prey is inhibited at high speeds (MacKenzie *et al*. 1994).

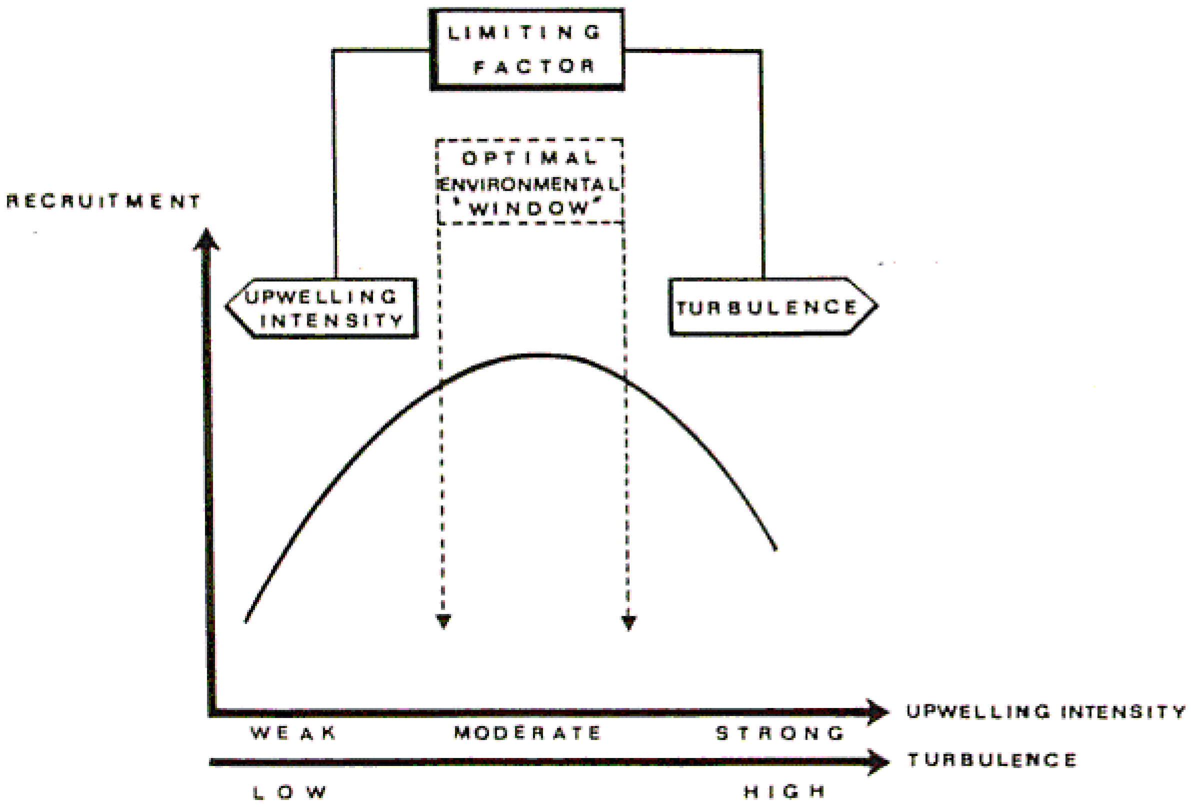

Fig. 2: The relationship between recruitment and both turbulence and upwelling intensity (Cury and Roy 1989).

The peak of the curve is termed the optimal environmental window and is the optimal area for larval survival, where the wind intensity is neither too weak (left side of the diagram) nor too strong (right side of the diagram). At this wind speed, there is both moderate upwelling and turbulence, conditions for optimal larval survival and hence recruitment. For different upwelling systems, there is a common and optimum wind speed of about 5-6 m.s^{-1} (Cury and Roy 1989).

In an upwelling area, pelagic fish attempt to maximise reproductive success by optimising the physical constraints. For instance, in a weak upwelling area pelagic fish are inclined to reproduce in the most productive time-space areas. In moderate upwelling areas, fish reproduce in areas that are a compromise between the limiting factors of productivity and turbulence. Under strong upwelling conditions, areas of high offshore Ekman transport and turbulence are avoided by spawning fish (Cury and Roy 1989). Changes in wind intensity may either benefit or negatively impact recruitment. Moreover, changes in wind may alter the optimal habitats for spawning and recruitment so that pelagic fish may adopt new reproductive strategies in time or space.

2.5 THE BENGUELA SYSTEM

The Benguela system, situated along the West Coast of southern Africa, is one of the four dominant eastern boundary current regions in the world. The Benguela system is part of the South Atlantic gyre, extending from approximately the tropical water regime of southern Angola, as far south as the area of interaction with the Agulhas Current, with the offshore boundary being fairly open ended (Shannon 1985).

Similar to the other eastern boundary current regions of California, Peru and North West Africa, the oceanography of the west coast of southern Africa (south of approximately 15 ºS) is dominated by coastal upwelling (Shannon 1985). Wind-induced upwelling occurs at many areas of the west coast, one of the major areas being Lüderitz in Namibia. Here, a semi-permanent tongue of cool water acts as a barrier, separating the Benguela into two regions - the northern and southern Benguela. It is the latter which forms the focus of discussion in this report. In this region there are wind-driven upwelling centres off the Cape Peninsula, Cape Columbine and Hondeklip Bay (Nelson and Hutchings 1983).

There are three major influences on the prevailing winds over the Benguela region, namely the South Atlantic High Pressure System, the pressure field over the adjacent subcontinent and the eastward moving midlatitude cyclones produced by perturbations in the subtropical jet stream (Nelson and Hutchings 1983). In the southern Benguela these three factors result in the seasonal pattern of upwelling, which reaches its maximum in spring and summer (Waldron *et al.* 1997b). The South Atlantic High, which is maintained throughout the year, undergoes a seasonal shift in position from approximately 26 ºS, 10 ºE in winter to 30 ºS, 5 ºE in summer. There is a strong change in pressure over the African subcontinent, from a well-developed low during summer to a weak high during winter, as the continental heat low and Inter-tropical Convergence Zone move northwards. As a result, the pressure gradient along the west coast is seasonally variable. Along the coast, the orography of the continental escarpment and the arid conditions of the coastal plain, acting as a thermal barrier, guide the anti-cyclonic flow of the South Atlantic High (Nelson and Hutchings 1983, BENEFIT 1997). Consequently, the winds along the west coast of southern Africa are mainly southerly and favour upwelling.

There are marked differences between the seasonal wind regimes of the southern and northern parts of the Benguela system. In winter, when the pressure systems shift northwards, the seasonal effect is more pronounced in the south where the frequency of westerly winds (non-upwelling favourable) increases. It is in this southern region of the Benguela, that wind-induced upwelling is highly seasonal and reaches a maximum during spring and summer. The upwelling season lasts from September to March. However, this large seasonal variation in the macroscale windfield is only experienced in the south. North of 31 ºS upwelling is perennial, but there is a spring-summer maximum and an autumn minimum as far north as 25 ºS and a late winter-spring maximum north of this latitude (Shannon 1985).

In the southern Benguela, there is an important modulation of upwelling at a period of about one week. This is caused by the wind relaxation or reversals associated with the movement of midlatitude cyclones south of the continent during the upwelling season. Between 35 ºS and 45 ºS in the belt of westerly winds, low pressure cells form ahead of planetary waves in the subtropical jet stream. These cells advect eastward with associated cyclonic rotation of air, causing the wind field as far north as the Olifants River to be modulated with an intensity that increases southwards to Cape Point. Usually, but not always, the effect in the summer months is weak, displaying itself as a periodic weakening of the South Atlantic High and a slackening of south-easterly winds along the coast. In winter, with the northward movement of the pressure systems, the effect is stronger, with midlatitude cyclones bringing gale-force north-westerly to south-westerly winds lasting several hours in cycles of three to six days (Nelson and Hutchings 1983).

Accompanying the advance of cyclonic systems, coastal low pressure cells form near Lüderitz, and travel round the subcontinent as trapped waves. This is particularly apparent in the summer months under conditions of weak modulation of the South Atlantic High pressure cell. As the coastal low travels along the coast, the cyclonic rotation of air around the low pressure locally suppresses upwelling and the relaxation of the wind at the centre causes appropriate conditions for the generation of inertial motions and possibly shelf waves (Nelson and Hutchings 1983).

The most significant source of interannual variability in weather and climate around the world is the El Niño Southern Oscillation, (ENSO) (IPCC 1996b). Although ENSO is a natural part of the Earth’s climate, a major question is whether the intensity of ENSO events may change as a result of global warming. In the past, ENSO has been correlated with winds on the west coast of southern Africa. The ENSO high phase in 1994 coincided with strengthened SE winds after three years of below-average winds during its low phase. It also coincided with the worst anchovy recruitment in ten years, thereby proposing that the increase in SE winds resulted in an increase in upwelling intensity and a decrease in recruitment (Boyd *et al*. 1998). This negative relationship between anchovy recruitment and the spring/summer wind anomaly at Cape Point is illustrated by Boyd *et al*. 1998 (Fig. 3).

The majority of spawning by the Cape anchovy, *Engraulis capensis*, takes place from October to January in the area extending east of Cape Point down to Cape Agulhas (Shelton 1981). Anchovy are pelagic spawners, therefore their eggs and larvae are transported by currents. Strong south-easterly winds yield poor conditions for spawning and a greater risk of fish eggs and larvae being transported offshore into the deep ocean (Boyd et al. 1998). From the spawning grounds in the south, some eggs and larvae are transported northwards and westwards to the recruitment area further north (Shelton and Hutchings 1982). From the recruitment area young migrate inshore to nursery areas along the coast where they continue to grow before migrating southwards back to the spawning areas (Crawford *et al*. 1987). During the southward migration anchovy (about 6 months in age) recruit to the purse-seine fishery (Shelton 1981).

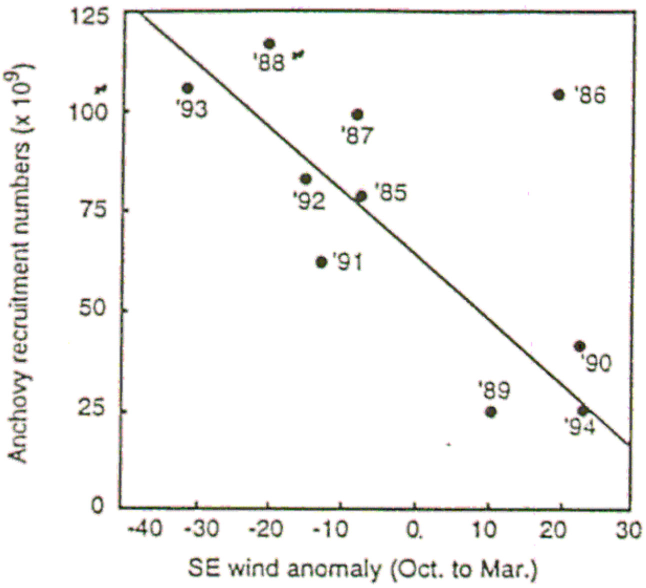

Fig. 3: The correlation between anchovy recruitment and the spring/summer SE wind anomaly at Cape Point (Boyd et al. 1998).

2. METHODS

Numerical climate models have been developed to simulate past climate change, and to project future trends. They are able to model the earth-atmosphere system by taking into account the primary components of the climate system (i.e. the atmosphere, ocean, cryosphere and land surface) and to simulate many of the large-scale features of the observed climate. These climate models can be used to explore the effects of changes in factors such as greenhouse gases, small aerosol particles from anthropogenic and volcanic sources, and solar output. In addition to these external factors, climate varies from year to year and decade to decade of its own accord, and this internal variation is also captured in the models.

The analysis is restricted to the spring and summer months in which anchovy spawn, i.e. from September to February (Parrish *et al.* 1983, Shin *et al.* 1998). The months are separated into early summer months (i.e. September, October, November) and late summer months (i.e. December, January, February). The analyses have been performed over a window extending from 20 °S to 44 °S and from 10 °W to 40 °E, thus including southern Africa, as well as portions of the surrounding oceans. The model used to simulate the sensitivity of the climate to gradual increases in CO_2 is a coupled ocean-atmosphere general circulation model (GCM). A transient climate change simulation from the National Centre for Atmospheric Research's (NCAR) fully coupled ocean atmospheric Climate System Model (CSM) is used for the climate change scenario. The transient simulation uses a 1% per year increase in atmospheric CO_2, and sulphate forcing is not included. Ten years of data for each of the periods corresponding to present-day CO_2 and doubled-CO_2 concentrations have been analysed respectively.

Broad scale pressure maps are used to identify overall features in the pressure system. Once the main features are identified, specific focus is given to some stations in the area. Specific data is obtained from two grid points in the southern Benguela, namely -34.883 °S, 16.875 °E and -34.883 °S, 19.688 °E. These are the grid points closest to those used in available literature (Fig. 3) on the southern Benguela upwelling region (Boyd *et al.* 1998). The grid points are used to compare the u-component (west-east direction) and the v-component (north-south direction) of the wind data and illustrate both present and future (double CO_2 conditions) wind data.

3. RESULTS AND DISCUSSION

Figure 4 shows model output for sea-level pressure (SLP) at the present day, and the change in sea level pressure from the present day to the future under doubled CO_2 (i.e. 2 x CO_2 minus 1 x CO_2). It is representative of the early summer months (i.e. September – November). Under the future climate regime, the South Atlantic High Pressure System is weaker at the beginning of summer (Fig 4b), but becomes slightly stronger later in the year (Fig. 4f). The continental trough over the interior of southern Africa is also weaker at the beginning of summer, which has implications for the west coast pressure gradient.

Figure 5 shows the model output for sea-level pressure (SLP) at the present day and the future scenario (under doubled CO_2 conditions) and is representative of the late summer months (i.e. December – February). Figure 5d suggests that the South Atlantic High Pressure System will extend further south in the future climate scenario in the late summer months, as well as moving further east and ridging south of the continent. There is also an intensification of the pressure cell. The largest changes are found in January (Fig. 5d). In this month the anomaly map displays a general SW – NE pressure gradient extending across the analysis window. The anomaly geostrophic vector would thus be directed from the SE. This suggests that in the future state over the west coast of South Africa there would be a greater SE component to the general flow.

Figure 6 shows the present day and future wind anomalies in the early summer months (i.e. September-November). In September, due to the weaker pressure gradient, the west coast wind speeds are 0.5 $m.s^{-1}$ to 1 $m.s^{-1}$ lower in the future scenario (Fig. 6b). However, by October (Fig. 6d) there is a definite increase in average wind speed along the west coast. This increase may be up to 0.5 $m.s^{-1}$ higher than the average wind speed of 8-9 $m.s^{-1}$.

In the late summer months of (Fig. 7), January wind speeds in the southern west coast are significantly faster and more easterly in direction. This may be due to the South Atlantic High Pressure System shifting south and ridging further east under the future climate scenario. By contrast, further north, future climate scenarios show a greater westerly component. February (see Fig. 7f) shows a similar but slightly weaker anomaly to January.

Figure 8 shows the u-component (west-east direction) and v-component (north-south direction), of the wind data in the southern Benguela system at the grid points -34.883 °S, 16.875 °E and -34.883 °S, 19.688 °E from September to February. The data represent wind data for the 1 x CO_2 simulation (illustrated in blue) and the future simulation (illustrated in red). Results show that the frequency of easterly winds (Fig. 8a) less than 10 $m.s^{-1}$ in the southern Benguela system are expected to increase from September to February and that they will be of a higher wind speed than at present. The most notable increases in frequency are wind speeds in the categories of 0-2.5 ; 2.5-5 and 5-7.5 $m.s^{-1}$ in an easterly direction. Wind speeds in the range of 2.5-5 $m.s^{-1}$ show the largest increase in frequency from approximately 13% in present day to 26% in the future. With the increase in easterly winds is an expected decrease in westerly winds in the southern Benguela system.

Figure 8b shows that that there is an expected increase in strong southerly winds under double CO_2 conditions in the future. The graph shows increases in wind speeds exceeding 7.5 $m.s^{-1}$ in a southerly direction. There is a 20% increase in the frequency of 7.5-10 $m.s^{-1}$ southerly winds and a 16% increase in southerly winds with the velocity of 10-12.5 $m.s^{-1}$. Figure 8b shows that there is a decrease in southerly winds of a smaller velocity (less than 7.5 $m.s^{-1}$) and a decrease in northerly winds in the future.

As mentioned previously, the optimal wind speed for anchovy recruitment is 5-6 $m.s^{-1}$ (Cury and Roy 1989). However, the results show that the present day average wind speed in the southern Benguela is 8-9 $m.s^{-1}$ and that expected increases in the future are in the order of 0.5 $m.s^{-1}$. Present day wind speeds fall to the right of the Optimal Environmental Window (Fig. 2). Hence, an increase in wind speeds in the future will result in a position more to the right on the graph (Fig. 2). An increase in wind speed has a number of implications regarding anchovy recruitment in the southern Benguela system. Firstly, stronger winds are likely to result in excessive offshore transport, which could cause anchovy eggs and larvae to be lost from their preferred habitat (Bakun and Parrish 1980). Secondly, an increase in wind velocity could result in greater turbulent mixing in the surface layer, thus dispersing larval prey organisms, decreasing the likelihood of larvae being able to obtain sufficient food (Lasker 1978). Thirdly, high wind speeds could inhibit larvae to capture prey due to a reduction in the encounter rate between larvae and food particles (MacKenzie *et al*. 1994). Hence, an increase in wind speed in the future is likely to result in reduced anchovy recruitment during the spawning period.

The effects of a change in wind intensity may not have the same effect on all pelagic fish. As sardines are larger than anchovy they are able to migrate greater distances to more suitable reproductive areas when conditions are unsuitable. By contrast, anchovy are less likely to migrate and more likely to adapt to the changes in the environment, remaining in the same area (Bakun, 1996).

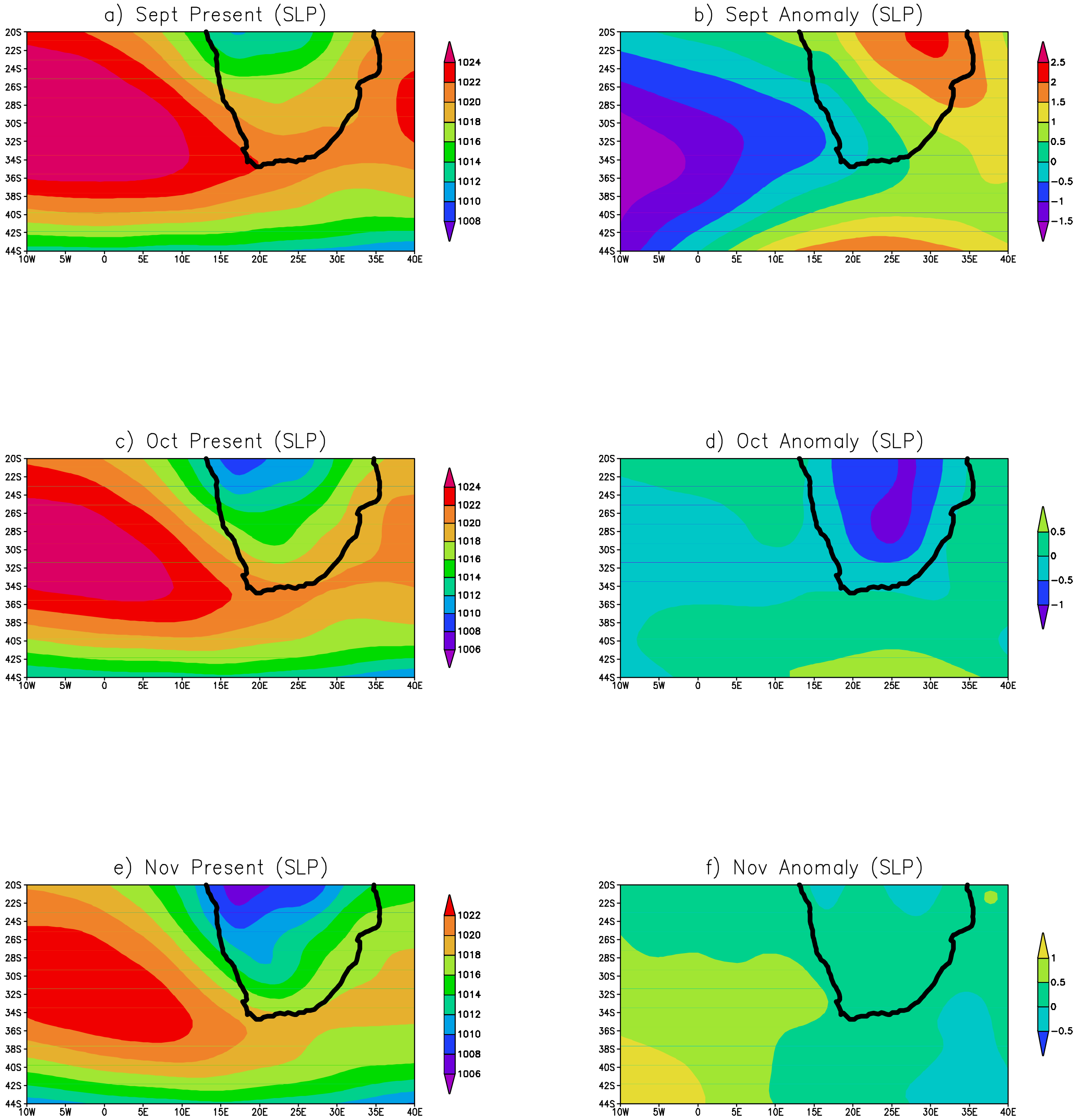

Fig. 4. Mean sea level pressure (hPa) for the 1 x CO_2 simulation (*a*,*c* and *e*) and the future anomaly (i.e. 2 x CO_2 minus 1 x CO_2) (*b*,*d* and *f*) for the early summer months.

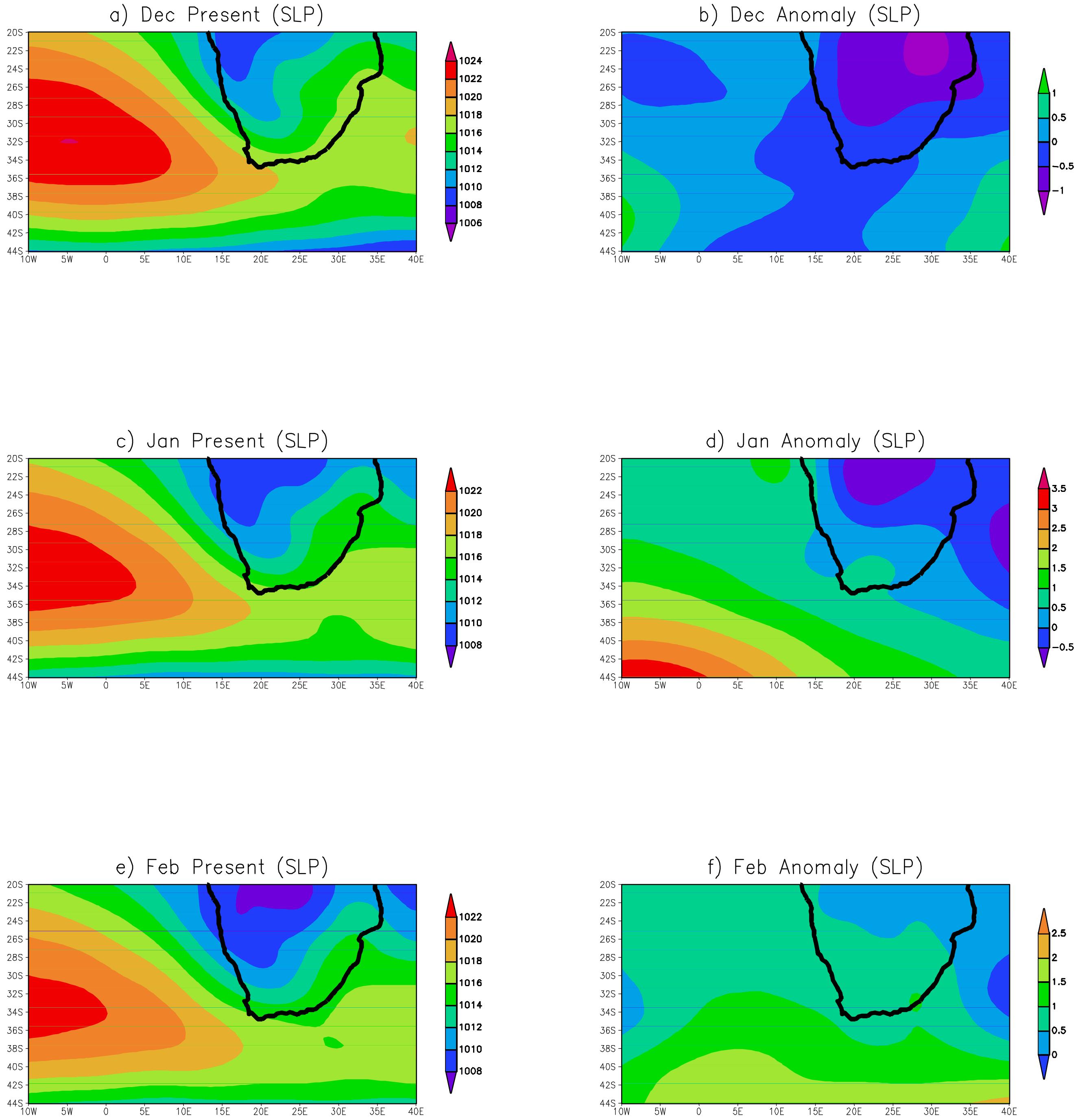

Fig. 5. Mean sea level pressure (hPa) for the 1 x CO_2 simulation (*a*,*c* and *e*) and the future anomaly (i.e. 2 x CO_2 minus 1 x CO_2) (*b*,*d* and *f*) for the late summer months).

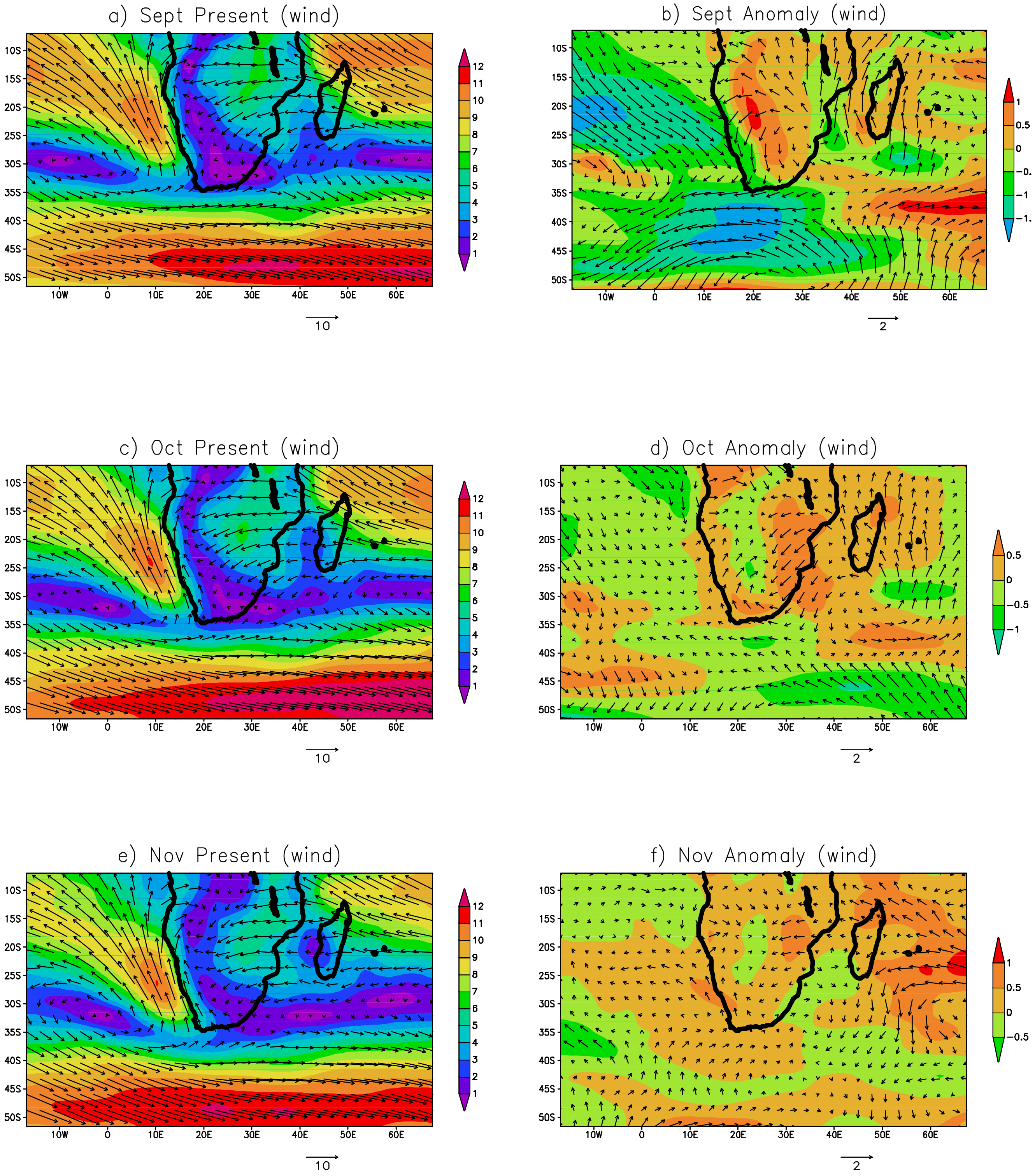

Fig. 6. Wind vectors for the 1 x CO_2 simulation (*a*,*c* and *e*) and change in magnitude and direction of the wind (*b*,*d* and *f*), i.e. 2 x CO_2 minus 1 x CO_2 for the early summer months.

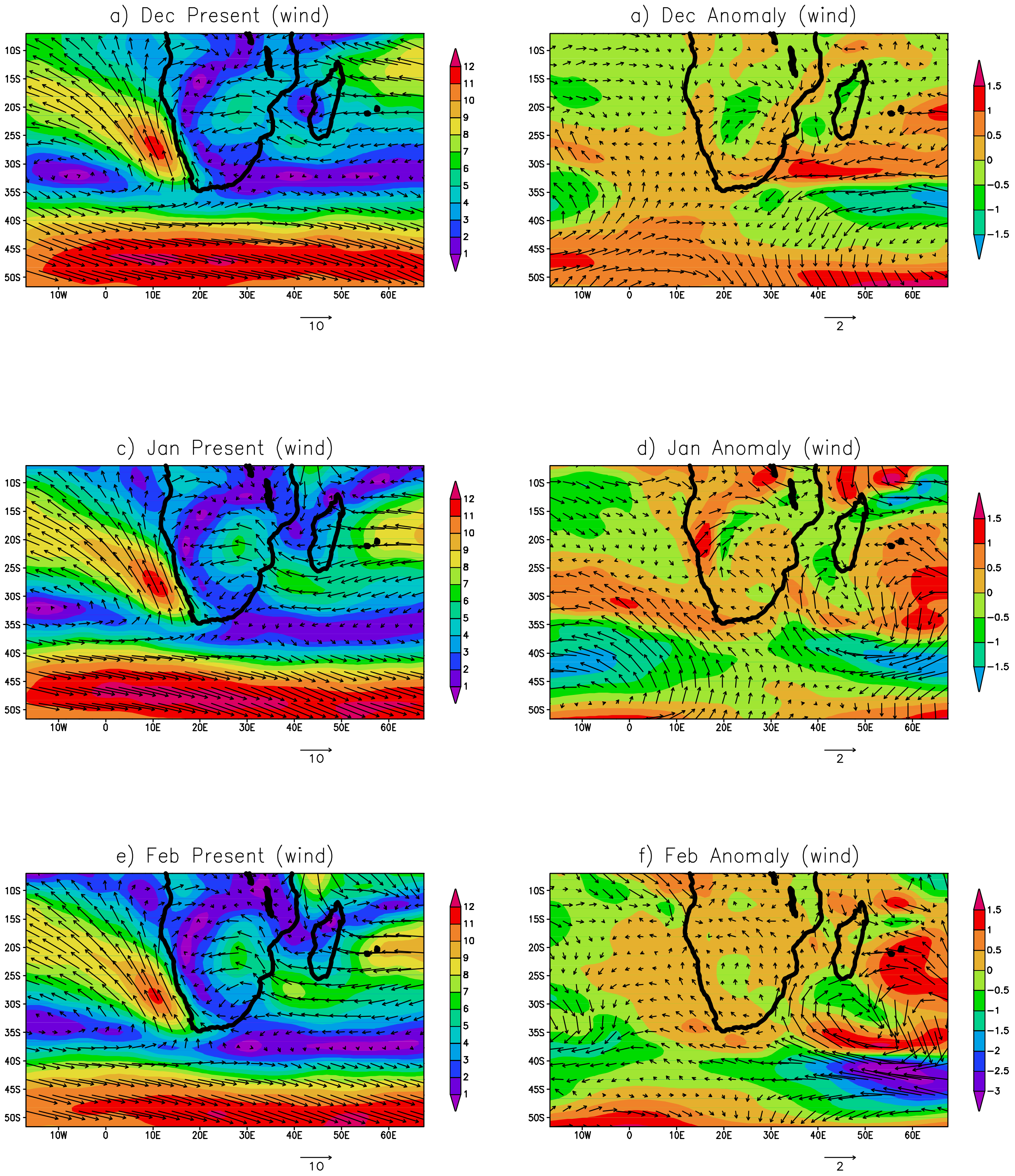

Fig. 7. Wind vectors for the 1 x CO_2 simulation (*a*,*c* and *e*) and change in magnitude and direction of the wind (*b*,*d* and *f*), i.e. 2 x CO_2 minus 1 x CO_2 for the late summer months.

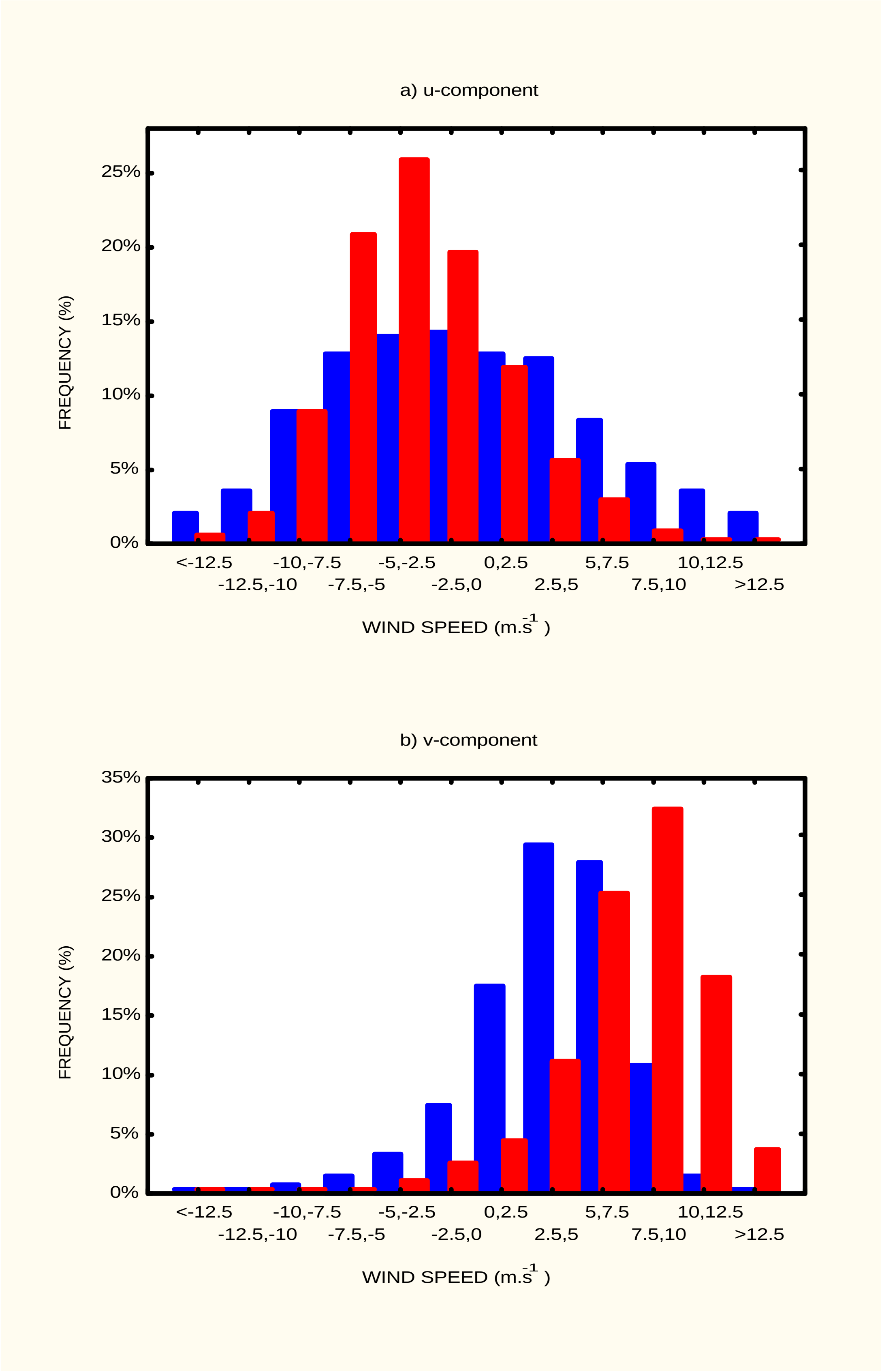

Fig. 8. Wind data (u-component and v-component) in the southern Benguela system for the 1 x CO_2 simulation (blue) and the future simulation (red) from September to February.

5. CONCLUSIONS

A transient climate change simulation from the National Centre for Atmospheric Research's fully coupled ocean-atmosphere Climate System Model has been examined for the early summer months (September, October, November) and late summer months (December, January, February) over southern Africa and the adjacent oceans. The analysis was restricted to the spawning months of anchovy. Present day simulations have been compared to future scenarios (doubled CO_2 conditions) focussing on sea-level pressure and wind data. Broad scale pressure maps examined the changes in the pressure field. Two grid points were selected in the southern Benguela System. The grid points were used to compare the u component (east-west direction) and the v component (north-south direction) of present and future (double CO_2 conditions) wind data. The Optimal Environmental Window Hypothesis is used to explain the relationship between anchovy recruitment and wind intensity.

In general, the future simulation scenario shows an intensification of the South Atlantic High Pressure Cell, especially in the late summer months, ridging further south and east than in the present day. During these months the anomaly gradient extends generally from the south-west to the north-east implying anomalous geostrophic flow from a south-easterly direction. A specific area in the southern Benguela system was selected, which included data from two grid points. The model output from this area suggested an increase in southerly winds exceeding 7.5 $m.s^{-1}$ in strength at present. The most notable increases in easterly winds in the future were those which are presently less than 7.5 $m.s^{-1}$. Present day average wind speed is expected to increase 0.5 $m.s^{-1}$. Thus, there is an overall expected increase in southerly and easterly winds in the southern Benguela in the future. This will result in an increase in upwelling.

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POSSIBLE EFFECTS OF CLIMATE CHANGE ON THE BIODIVERSITY OF SOUTHERN AFRICAN ROCKY SHORES

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1. INTRODUCTION

The greenhouse effect is a natural phenomenon that makes life on earth possible. Incoming solar radiation is trapped by certain gases in the atmosphere and acts to warm the earth's surface. Changes in greenhouse gas concentrations have varied naturally in the geological past due to natural causes, but since pre-industrial times (about 1750), greenhouse gases are thought to have increased due to human activities such as the burning of fossil fuels, intensive agriculture and industrial processes. The result is the 'Enhanced Greenhouse Effect', which will probably ultimately cause a rise in atmospheric and ocean temperatures, which in turn will alter the associated circulation and weather patterns. This global climate change and the related environmental changes are likely to have vast impacts on terrestrial and marine ecosystems (IPCC 1996). Intense studies of the possible effects of global warming on terrestrial ecosystems have led to a preliminary consensus on the likely influence of climate change on temperature and precipitation and on terrestrial biodiversity (Fields *et al.* 1993, Siegfried *et al.* 1990). Marine ecosystems have not been considered to the same extent, and thus there is little predictive ability regarding the effects of climate change on marine biota (Fields *et al.* 1993 and references therein). Rocky shores are one of the most striking ecosystems along the coastline and effects of climate change on rocky shore communities may be numerous. This may be no less true for South African rocky shores and the aim of this report is to address these issues.

South Africa has a coastline of about 3 000 km, comprising 1 300 km of rocky shore, 1 700 km of sandy beaches and a total of 343 estuaries (Shackleton *et al.* 1996). Its coastal zone contains the highest proportion of species diversity, considering the entire range of South African marine ecosystems (Huntley 1989). Rocky shores range from exposed rocky headlands with vertical rock faces and cliffs, to wide wave-cut rock platforms, and also include aggregations of different sized boulders in sheltered bays. These shores can extend for kilometres along the coast, while in other areas, they consist of rocky outcrops, separated by sandy beaches, estuaries or river mouths. Rocky shores support a wide range of marine organisms and are subject to varying degrees of subsistence or commercial exploitation. They are also intensively used for recreational purposes. The following report is divided into two sections. The first section describes the ecological functioning and present state of South African rocky shores, while the second section discusses the possible implications of a global warming for this ecosystem.

2. THE ECOSYSTEM FUNCTIONING OF ROCKY SHORES

The intertidal rocky shore is a very stressful habitat. Animals and plants must be adapted to live in the marine environment during high tide and to being exposed to air during low tide. They are additionally influenced by a number of other physical and biological factors, and the difference in the strength and interaction of these factors over time and space results in a considerable diversity of rocky shore community structures. This section provides a short introduction to the functioning of rocky shores and the distribution patterns exhibited on South African intertidal shores. It also gives some information about the oceanography around the southern African coast and its influence on rocky shores. Its central aim is to clarify the importance of certain climate-dependent environmental conditions and oceanographic processes in shaping intertidal assemblages.

3.1. OCEANOGRAPHY AROUND THE SOUTH AFRICAN COAST

The oceanography of the west coast of South Africa is governed by the coastal Benguela upwelling system. Strong southeasterly winds, mainly in the summer, cause coastal upwelling of cold (8°-10°C), nutrient-rich water from deep waters. Upwelling originates close to the coast and results in a well-developed thermal front, which separates warm water further offshore from cold water near the shore (Shannon 1985). In the southern Benguela system, upwelling is intermittent, since the southeasterly winds occur mainly during summer in this region (Andrews & Hutchings 1980). North of Saldanha Bay, winds are more moderate and consistent, and upwelling is less seasonal. However, the major upwelling region is centred around Lüderitz in Namibia. On average, there are occurrences once every ten years of ‘Benguela Niño’ events, named after the more intense counterpart in the Pacific, the El Niño (Taunton-Clark & Shannon 1998). They are characterised by the intrusion of large volumes of warm saline tropical/equatorial waters into the northern Benguela and a reduction in upwelling of nutrient rich water and are evidently caused by a sudden relaxation in zonal wind stress in the equatorial western Atlantic (Shannon *et al.* 1986). They are accompanied by altered distributions in sea-surface temperatures, salinities and changes in local winds (Shannon *et al.* 1990b, Taunton-Clark 1990). These events have been reported to have substantial impacts on biota, e.g. declines in anchovies and sardines and changes in primary production (Boyd *et al.* 1985, Shannon *et al.* 1984). Another phenomenon of the west coast are ‘red tides’. ‘Red tides’ are harmful blooms of algae, characterised by the proliferation and occasional dominance of a particular species of toxic or otherwise harmful alga, which typically belong to the group of the dinoflagellates. In many instances the proliferation of the alga colours the water red. These toxic blooms can cause mass mortalities of fish, shellfish, marine mammals, seabirds and other animals, and human illness and death may result from contaminated seafood (Horstman 1981, Horstman *et al.* 1991). The formation of ‘red tides’ is closely related to the prevailing winds of the Benguela. Their occurrence is highest towards the end of the upwelling season, when thermal stratification of the water column increases (Pitcher *et al.* 1993, Pitcher *et al.* 1995). Higher incidence of ‘red tides’ is also noted in years during reduced upwelling and is attributed to the north-west retreat of the South Atlantic anticyclone and increased westerlies - weather patterns, which coincide with and follow the Pacific ‘El Niño’ events (Pitcher *et al.* 1995).

The east and south coast of South Africa are, on the other hand, influenced by the Agulhas Current, which brings warm water from the tropics to the east coast. The current flows southwards, closely following the continental shelf with a sporadically occurring inshore counter-current (Schumann 1982) and is finally retroflected over the wide Agulhas Bank. The retroflection area is characterised by a highly variable degree of advection, structure and shedding of warm Agulhas rings. Due to the ring shedding there is always a flow of Agulhas water into the South Atlantic, which plays an important role in the transport of heat in the ocean’s climate conveyor belt (Heydorn 1978, Gordon 1986). However, occasional ‘Agulhas intrusions’, leakages of very large volumes of pure Agulhas water into the South Atlantic, such as occurred in 1986, are observed (Shannon *et al.* 1990a). Parts of the south coast are occasionally subjected to local wind-generated upwelling of cool bottom water (Field & Griffiths 1991). The Agulhas Current plays a central role in the short- and long-term variability of the circulation systems of the oceans surrounding southern Africa. Due to the narrow continental shelf and a steep shelf slope, the trajectory of the Agulhas exhibits great stability. The only substantial perturbation takes place with the passage of the irregularly occurring Natal Pulse, a meander that moves with the current (Lutjeharms & Connell 1989). The Natal Pulse forces the core of the Agulhas Current so far offshore that it can cause upstream retroflection of Agulhas water just south of Port Elizabeth, long before it reaches its normal point of retroflection (Lutjeharms & de Ruijter 1996).

During the summer upwelling season surface temperatures on the west coast frequently fluctuate between 8° and 18°C over a very short time (Field & Griffiths 1991), although the summer mean of 14°C differs little from the winter mean of 15°C. By contrast, mean monthly sea surface temperatures range from 22°C in the winter to 27°C in the summer on the east coast and 15°C to 22°C on the south coast, respectively. The whole of the coast is subjected to a simple semi-diurnal mesotidal regime, with spring tides ranging from 2 to 2,5 m and neap-tides around 1 m (Field & Griffiths 1991).

3.2. BIOGEOGRAPHY OF THE SOUTH AFRICAN COAST

Substantial geographic differences in the species composition of the rocky intertidal communities around the South African coast warrant the division of the coast into three marine biogeographic provinces: the West, South and East Coast Provinces (Fig. 1.) (Brown & Jarman 1978, Bustamante & Branch 1996a). This demarcation was found to apply to both the faunal (Emanuel *et al.* 1992) and the floral (Bolton & Anderson 1997) components of the communities.

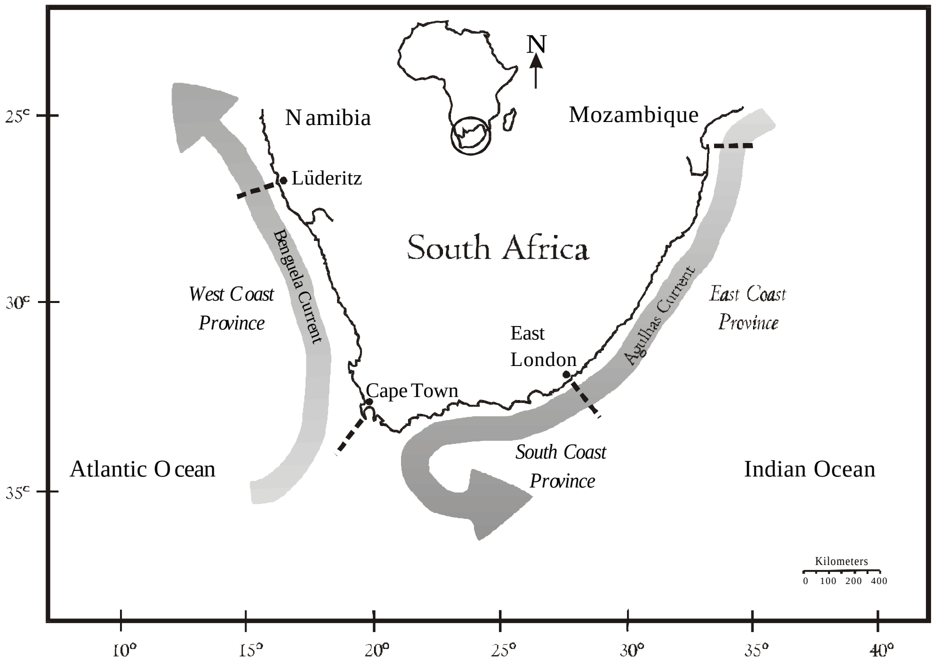

Fig. 1. Map of the southern African shoreline south of 25°. The boundaries of the South African biogeographic provinces are indicated by dashed lines.

The cool temperate West Coast Province (also known as the Namaqua or Benguela Province) extends from Lüderitz to Cape Point, the warm temperate South (Agulhas) Coast Province stretches from Cape Point to East London and the subtropical East (Natal) Coast Province extends between East London and southern Mozambique (Emanuel *et al.* 1992) (Fig. 1.). Bolton & Anderson (1997), in their overview of the marine vegetation of southern

Africa, doubt the existence of a subtropical East Coast Province and refer to the east coast rather as an ‘Eastern Overlap’ between the South Coast Province and the much larger subtropical Indo-West Pacific Marine Province. They also define another overlap region, the ‘Western Overlap’, which separates the West from the South Coast Province.

3.3. COMMUNITY STRUCTURE AND TROPHIC LEVELS

Community structure on rocky shores is composed of the distribution, abundance and diversity of its component species and their trophic interactions and depends on many physical and biotic factors or processes (Menge & Sutherland 1987). These structures can exhibit great variability and can differ over scales ranging from 10 to 100 meters to 100s of kilometres.

3.3.1. Biogeographic scale

Viewed on the scale of the biogeographic regions, the west coast supports a greater average biomass of all groups than the two other provinces, but with fewer species than the south and east coast communities (Bustamante & Branch 1996a, Bolton & Anderson 1997). The high biomass per unit area can probably be related to the ample nutrient supply and high productivity of the Benguela upwelling system (Brown 1992, Bosman *et al.* 1987, Pitcher *et al.* 1992, Brown & Cochrane 1991). However, a reason for the poorer species diversity on the west coast could be the relatively young age of the Benguela system (2-3 million years: Shannon 1985), which might have been insufficient to allow the evolution of adapted species (Bolton & Anderson 1997). On the other hand, the south and east coast fauna and flora derive many species from the rich Indo-Pacific radiation (Kohn 1990, Vermeij 1992).

Nutrient status is an important factor influencing the production rate of marine assemblages. There is a strong gradient of nutrient concentrations around the South African coast, with high values along the west coast, resulting from upwelling, followed by progressively decreasing concentrations towards the south and east coasts (Bustamante *et al.* 1995a). Intertidal microalgal production has been found to correlate positively with nutrient availability, and shows the same gradient (Bustamante *et al.* 1995a). Different seasonal patterns exist for the *in-situ* production between the provinces, with summer-spring peaks in the West Coast, autumn-winter peaks in the South Coast and a lack of seasonality in the East Coast Province. This is consistent with inshore phytoplankton seasonal patterns reported by Brown (1992). It is well known that high nutrient concentrations enhance primary productivity (de Boer 1982) and since intertidal epilithic algae and nearshore phytoplankton show matching gradients, it is likely that both are similarly influenced by nutrient levels and therefore concepts applied to phytoplankton dynamics are probably equally applicable to intertidal productivity (Bustamante *et al.* 1995a). The macroalgal standing stocks reported by Bustamante *et al.* (1995a) do not conform with this gradient, with both the west and the east coast having higher values than the south coast. But macroalgal standing stocks per-unit-area represent the fraction of algae that survive after physical and biological disturbances and may not therefore be an adequate measure of *in-situ* productivity due to nutrient availability. Moreover, there is a strong gradient of large, foliose macroalgae in the cooler, nutrient rich waters of the west coast to smaller, particularly turf-forming algae towards the warmer waters to the east (Bustamante *et al.* 1995a, Bolton & Anderson 1997) and a large proportion of the macroalgal biomass in the East Coast Province is attributable to turf algae. One important characteristic of the turf life-form, next to resistance to desiccation, sand inundation and fish grazing, is its ability to recycle nutrients in nutrient-poor tropical waters (Hay 1981, Adey & Goertemiller 1987). Temperature seems to be the more important factor for the distribution of macroalgal seaweeds. A study by Bolton & Anderson (1990) in South Africa documented that the seaweed community gradient closely follows the temperature gradient around the coastline, providing important evidence that patterns of intertidal seaweed vegetation on a biogeographic scale can be correlated with sea-water temperature conditions (Bolton & Anderson 1997). Work done elsewhere conforms to these findings (Breeman 1988).

The average level of biomass of intertidal primary consumers (grazers and filter-feeders) declines from west to east in parallel with the decline in intertidal microalgal productivity and nutrient levels. The traditional notion of trophic functioning of biological communities is that the abundance of primary consumers in a food web is positively correlated with *in-situ* productivity (Menge & Olson 1990). Thus, enhancement of the basal level in a food web should be reflected in an increase in the abundance of the next trophic level, which in turn might be controlled by secondary consumers, the predators. On the South African rocky shores, herbivore biomass appears to be directly influenced by *in-situ* production and suggests a strong bottom-up controlling effect (Bustamante *et al.* 1995a). However, filter-feeders depend on phytoplankton and suspended organic matter, transported from the subtidal to the shore by waves. They are thus much more likely to be affected by local wave action and nearshore phytoplankton concentration (Menge *et al.* 1997a, Menge *et al.* 1999), than by large-scale intertidal productivity gradients around the coast. Moreover, at the west coast of South Africa, subsidy in the form of particulate kelp from the subtidal seems to be a more important food source than phytoplankton. Bustamante & Branch (1996b) demonstrated that the production of the west coast subtidal kelp forests is of great importance as food supply for intertidal primary consumers and showed that filter-feeders and two specialised grazers, the limpets *Patella granatina* and *P. argenvillei*, use kelp-derived detritus as their main source of organic carbon and nitrogen.

3.3.2. Local scale

Factors such as different current systems, oceanographic conditions and varying sea temperatures account for distribution patterns on a broad geographical scale (Bustamante & Branch 1996a). However, a suite of biotic and abiotic factors has been postulated to explain the structure of communities on a local scale. Competition, predation and grazing are important biological factors that contribute to the structure of intertidal assemblages and interact with physical conditions such as desiccation, wave force and nearshore current systems to produce specific community patterns (Menge & Sutherland 1987, Menge & Olson 1990, Menge *et al.* 1997a, Connolly & Roughgarden 1999). These patterns of vertical and horizontal distributions have been found to be similar in equivalent habitats, regardless of the biogeographic regions. This indicates that the underlying processes must operate in similar ways in different biogeographic regions (Bustamante *et al.* 1997).

3.3.2.1 Vertical zonation patterns

Intertidal organisms experience varying degrees of physical stress. The up-shore gradient of desiccation is the main physical force that structures vertical zonation on rocky shores (Broekhuysen 1940, Stephenson 1943, Stephenson & Stephenson 1972, Underwood 1981, Underwood & Jernakoff 1984, Menge & Sutherland 1987, Menge & Farrell 1989). Low on the shore, the period of exposure to air during low tide is short. With height up the shore the periods of exposure increase and the conditions becoming harsher and harsher because the danger of desiccation rises. Together with physical factors, competition, predation and grazing also play important roles in further regulating the upper and lower limits of intertidal organisms. Grazers, for example, are thought to set the upper limits of macroalgal colonisation by consuming their spores and sporelings (Underwood 1980, Underwood & Jernakoff 1981, Underwood 1984, Branch 1985a), while predation can influence the distribution and abundance of filter-feeders (Paine 1966, 1974, Menge & Farrell 1989, Petraitis 1990, Navarette & Menge 1996, Menge *et al.* 1999). Interspecific competition for food and/or space may exclude certain species from particular zones on the shore, while intraspecific competition can control the abundance of a species, resulting in some cases in a vertical gradient of distribution of juvenile and adult conspecifics (Branch 1984a, 1985b). The combination of physical factors and biological interactions results in the zonation of different species into vertical bands on the shore.

In South Africa, four distinct zones can be recognised on rocky shores. The highest band up the shore is the Littorina zone, almost exclusively inhabited by littorinid snails. Below it follows the Upper Balanoid zone, where barnacles are usually abundant, especially at the east and south coasts. Next is the Lower Balanoid zone with a mix of barnacles, macroalgae and mussels, and on the east coast additional zoanthids. At the bottom of the shore seaweeds and red bait may dominate the Infratidal zone. These zones vary for each biogeographic region with different species inhabiting the zones (Branch & Branch 1981). Certain additional zones can be identified within each region such as the Cochlear zone at the south coast, found between the Infratidal zone and the Lower Balanoid zone. The Cochlear zone is inhabited by dense populations of the limpet *Patella cochlear* that displaces almost all other species from this band. A similar zone also occurs on the west coast, where *P. cochlear* is joined by a second limpet, *Patella argenvillei*. The zone is thus called the Cochlear/Argenvillei zone (Branch & Branch 1981). The west coast zonation used to be similar to the zonation of the south coast, the only striking difference being the addition of vast subtidal kelp beds. However, the relatively recent arrival of an invasive alien, the Mediterranean mussel *Mytilus galloprovincialis*, has changed the appearance of the west coast dramatically (Griffiths *et al.* 1992). The mussel was probably first introduced anthropogenically some 30 years ago and now reaches very high densities on west coast intertidal shores (Grant *et al.* 1984, Grant & Cherry 1985). It is a highly competitive species, superior to the indigenous mussels in withstanding desiccation, with higher reproductive output and faster growth (Hockey & Van Erkom Schurink 1992, Van Erkom Schurink & Griffiths 1991, 1992, 1993). The mussel is now dominant in almost all zones within the west coast intertidal rocky shores, and competes strongly with the limpet *P. argenvillei* (Steffani, unpublish. data).

3.3.2.2. Horizontal zonation patterns

Whereas shore height and desiccation are the main driving forces behind vertical zonation, the role of wave force in particular has been shown to be one of the most important physical factors influencing the horizontal zonation of intertidal communities due to physical stress and moderation of biotic interactions (Menge & Sutherland 1987, Menge & Olson 1990, McQuaid & Branch 1984, 1985, McQuaid *et al.* 1985, Emanuel *et al* 1992, Bustamante & Branch 1996a). Biomass increases strongly with wave action, with filter-feeders being the dominant group on exposed shores along the west and the south-east coasts of South Africa (McQuaid & Branch 1985, Bustamante & Branch 1996a, Bustamante *et al.* 1997). Owing to greater concentrations of food particles and higher water turnover rates, wave exposed environments favour growth and survival of filter-feeders (Bustamante & Branch 1996a).

Grazing herbivores are the only trophic group that shows higher biomass on sheltered than on exposed shores, particularly in the West Coast Province. However, exposed shores are dominated by only a few species, whereas on sheltered shores, a greater number of species contribute to the bulk of the biomass. Wave force has its greatest influence on the low to mid shore, whereas the interaction of rock temperature and shore elevation, which control desiccation processes, were found to play a more important role for high shore assemblages (Bustamante *et al.* 1997). Wave action not only influences biomass directly by providing food and nutrients (bottom-up effect) to intertidal organisms, but also indirectly by affecting the strength of biological interactions such as grazing and predation (top-down effects). Increasing wave action is likely to reduce the controlling effects of grazers and predators by decreasing the available feeding time (Brown & Quinn 1988, Menge & Olson 1990, Etter 1996). This in turn enhances the biomass of intertidal autotrophs and filter-feeders at wave exposed sites.

Another important factor associated with strong wave action is disturbance. Clearance of areas of different sizes by physical disturbance results in patchiness - a common feature of wave exposed rocky shores. Following clearance, a rapid succession of organisms ensues, usually starting with ephemeral algae, followed by longer-living more persistent species (Paine & Levine 1981, Sousa 1985, Bolton & Anderson 1997). This form of disturbance is proposed as a mechanism that prevents the exposed rocky intertidal system from culminating in a monoculture of the key dominant competitor species, e.g. mussels, and preserves a mixed community instead (Paine 1966, Dayton 1971). But this role is only important if the settlement rate is sufficiently high, because interference competition for vacant rock space only occurs at high densities (Roughgarden *et al.* 1987). The keystone species concept is another mechanism thought to prevent dominant species from taking over the rocky shore habitat (Paine 1969). A keystone predator species is defined as a species whose impact on the prey community structure is disproportionately large relative to its biomass and thus inhibits the colonising of the entire shore by the dominant space occupier (Navarette & Menge 1996). However, this role also seems to depend on high recruitment rates of the prey, because weaker predator-prey interaction was found with lower prey recruitment (Menge *et al.* 1994).

3.3.3. Larval supply and phytoplankton concentration

Most of the animals that spend their adult lives on rocky shores have a planktonic larval phase. In recent years, more and more attention has been given to the role played by variation in recruitment on the structure of marine populations with pelagic larvae. Intertidal systems exhibit considerable regional variability in percentage cover and in the strength of biological interactions such as competition and predation, which may be largely due to the effect of varying larval transport (Underwood & Denley 1984). Differences in larval supply can directly influence the distribution and abundance of marine organisms by dictating recruitment patterns (e.g. Gaines & Roughgarden 1985, Roughgarden *et al.* 1988, Menge *et al.* 1999). The transport of larvae to the shore depends, at geographic spatial scales, on oceanographic conditions such as offshore currents and upwelling and on an intermediate scale on surface waves, nearshore currents, internal waves and tidal bores (Shanks 1983, Bertness *et al.* 1996, Piñeda 1991). Larval supply may also differ on a local scale due to coastal heterogeneity, differences in microhabitat and varying wave forces (Archambault & Bourget 1996). These transport mechanisms strongly influence the rate of settlement and oceanographic processes can therefore exert an important control on benthic population and community dynamics, which can match the effect of local processes, such as predation and competition (Roughgarden *et al.* 1987, Connolly & Roughgarden 1999). Recently, studies have suggested that observed variability in benthic intertidal community structures at sites with similar physical stress are related to differences in the nearshore oceanography. For example, differences in percentage cover of filter-feeders on the west coast of North America were explained in terms of contrasts in oceanographic conditions, with nearshore circulation promoting higher settlement and therefore higher percentage cover at Oregon, and offshore currents inhibiting recruitment with resulting lower percentage cover along the coast of California (Connolly & Roughgarden 1998). Wind directions themselves are also found to dictate settlement patterns (Bertness *et al.* 1996). Mussels, which are an important group of the intertidal benthic community and are widely recognised as key species structuring rocky shore communities (Suchanek 1985), showed striking variability in recruitment rates around the South African coast. A comparison of South Africa’s east and west coast rocky shores revealed higher recruitment densities on the west coast, and that significant spatial variations in recruitment can occur over scales of 100-1000 km as well as on smaller scales of 1-25 km (Harris *et al.* 1998). This suggests that the influence of dispersal processes through nearshore oceanographic conditions on recruitment patterns acts not only on large scales but also on a relatively small scale. These processes in concert with biological factors such as i.e. high adult mussel stock, which enhances mussel settlement and survival by providing a protected habitat (Nielson & Franz 1995, McGrath *et al.* 1998), can affect the distribution and biomass of adults among shores close by. Nearshore phytoplankton concentrations might in the same way be affected by variation in currents on scales of 10-100 and 100-1000 km. Menge *et al.* (1997b) found a high variability in the coastal mesoscale patterns of phytoplankton concentration along the Oregon coast, which they attributed to inshore oceanographic conditions, specifically to alongshore and offshore currents. They further suggested that the observed differences of filter-feeder cover, growth and recruit survival among similar wave exposed sites only few kilometres apart may be due to these variations in phytoplankton concentration.

3.3.4. Food webs

The trophic structure of intertidal biota can best be described by dividing species into functional groups such as autotrophs, grazing herbivores, filter-feeders and predators (Hairston, Smith & Slobodkin 1960, Paine 1980). These functional groups appear in different trophic levels in the food web and are connected through energy transfer and linkages between levels. The strength of the linkages is influenced by factors such as wave exposure, larval supply and nearshore oceanographic processes. The general models of food webs are based on few trophic levels with autotrophs and filter-feeders in the basal level, herbivore in the intermediate and predators in the top level (Hairston, Smith & Slobodkin 1960, Paine 1980, Menge & Sutherland 1987). The community structure can be affected both by the effect of higher trophic levels on those below (top-down effect) and by the effects of lower trophic levels on those above (bottom-up effects).

A simple model of energy transfer in the intertidal food web on South African shores (Bustamante 1994) emphasises the division of this transfer into two different compartments according to the main food source: the herbivore and filter-feeder pathway (Fig.2.). While the intertidal herbivores are directly supplied by *in-situ* intertidal primary production, filter-feeders are using energy ‘imported’ from the adjacent pelagic and subtidal ecosystems (Bustamante 1994, Menge *et al.* 1997a). Two specialised limpets at the west coast of South Africa are also dependent on imported material from the subtidal, at least the adult populations, and thus belong to the same compartment as the filter-feeder (Bustamante & Branch 1996b).

Menge & Sutherland’s (1987) model incorporates biotic and abiotic interactions and suggests that the relative importance of environmental stress factors (e.g. wave force and desiccation), competition and predation (the latter of which includes grazing) varies predictably with trophic position, magnitude of recruitment, and environmental conditions. Roughly, the model predicts that with higher environmental stress, physical factors are strong regulators, while at low stress levels, predation is more important with the exception of the top level, where predation is always unimportant. Competition increases with increasing recruitment density. In extremely harsh environments, mobile consumers are excluded or ineffective and the simple food web that results consists of sessile organisms that are assumed to be more resistant to stress (Menge 1978). Increased nutrient or larval supplies are examples of bottom-up factors while controlling agents such as predator pressure are top-down factors. Both bottom-up and top-down factors are thought to be tightly linked and to act on intertidal assemblages simultaneously. The variation in the controlling strength of each factor is determined by differences in environmental conditions (Menge 1992).

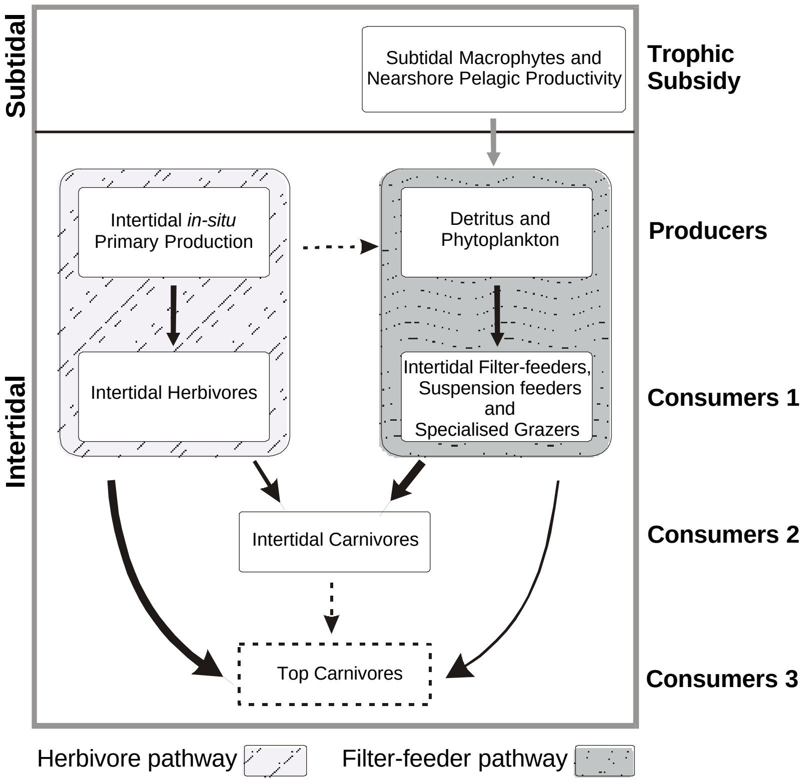

Fig. 2. Diagram of the main pathways of energy-matter transfer in a hypothetical rocky intertidal food web. Arrow thickness and pattern indicate the relative importance of the transfer between the different trophic compartments (Diagram modified after Bustamante 1994). (Note that in this model the filter-feeders are on the same level as the herbivores due to the division into two compartments)

3.3.5. Tidepools

Tidepools are conspicuous components of rocky intertidal shores. The tidepool community structure can vary greatly from that found on the surrounding emergent rock. The organisms in the tidepools are constantly submerged and although the physical environment is regulated by the tidal cycles, fluctuations in physical factors are less severe in pools than on open rock. The upper limits of the distribution of organisms are extended in tidepools and some species either favour or avoid them. Vertical zonation is thus less pronounced. Algae are usually the dominant space occupiers and competition between algal species is of great importance in regulating the community structure in pools. Herbivory has been shown to influence algal distribution and abundance, but little is known about the effect of predation.

Tidepool-specific characteristics such as depth, volume, orientation, shading and flushing rate make individual pools unique and results in large spatial variability in community structure (Huggett & Griffiths 1986, Metaxas & Scheibling 1993).

4. POSSIBLE EFFECTS OF CLIMATE CHANGE ON ROCKY SHORE COMMUNITIES

The first section of this report describes the strong connection of rocky shore community structure and environmental conditions. It serves as a base for this second part in which the possible changes of these environmental conditions under a global warming and the implications for rocky shore communities will be discussed.

A variety of models have been used to understand the atmospheric processes responsible for climate change, the most effective ones being the General Circulation Models (GCMs) which describe the full three-dimensional character of climate. In recent years, concern about climatic change and its possible consequences have led to a considerable development of GCMs, and fully coupled ocean-atmosphere models are now being used to predict changes in future climate. In 1988, the World Meteorological Organisation (WMO) and the United Nations Environment Programme (UNEP) jointly established the Intergovernmental Panel on Climate Change (IPCC) to assess the science and impacts of climate change, as well as potential response options. IPCC has since then published extensive authoritative reports comprising the current state of knowledge on the issue of climate change (e.g. IPCC 1990, 1992, 1996).

Several possible scenarios of a climatic change in southern Africa exist in the literature (Tyson 1990, Tyson 1993, Schulze & Kunz 1993, Shackleton *et al.* 1996). They are based mainly on evidence from current GCMs and although there is some confidence in the predictive power of these models on a global scale, confidence in their regional simulations of climate change remains low (Tyson 1993, Shackleton *et al.* 1996, IPCC 1996). It is therefore inadvisable to use these scenarios as predictions, given the uncertainties involved (Schulze & Kunz 1993). There is however hope that the accuracy of GCMs will improve in time, as modifications of these models incorporate more realistic land cover representations, ocean-atmosphere interactions and improved simulation of the hydrological cycle (Schulze & Kunz 1993, Shackleton *et al.* 1996). Due to all these limitations in regional climate models, the aim of the present study is not to produce predictions, but rather to develop ‘what-if’ scenarios for various possible environmental changes and their impacts on rocky shores.

To assess the possible impacts of climate change on rocky shores, it is necessary to determine which environmental changes induced by global warming are likely to affect rocky intertidal assemblages. Several come to mind, the most obvious being sea level rise and changes in sea-surface temperature. A rise in air temperature could also have an impact affecting the communities higher on the shore. Others are possible upwelling changes, nearshore current modification and alteration in sand transportation due to a shift in wind stress. Higher levels of radiation may also be important, as is the likelihood of an alteration in the frequency of storm events. All these possible environmental changes are likely to have an influence on South African rocky intertidal communities, although impacts might differ between different biogeographic regions. Moreover, the additive effects of many of these changes, even if individual alterations are minor, may increase the effects on marine assemblages. Alternatively, they might counteract each other. Unfortunately, very little is known about possible effects of the combinations of different environmental changes and therefore, in this study, each factor will be discussed separately.

4.1. SEA LEVEL

Analyses of world-wide tide-gauge records and long-term vertical land movement data suggest that the sea level has risen by 10-25 cm over the last 100 years and that this rise is largely due to the concurrent increase in global temperature. Climate-related factors contributing to this rise include thermal expansion of the oceans and melting of ice caps and sheets and glaciers (IPCC 1996). Hence, one of the main consequences of the greenhouse effect and the associated climate change will be an acceleration of the world-wide rise in sea level. South African and global historical sea level trends are in good agreement and it is therefore reasonable to accept that the globally predicted rates of sea level rise are also applicable to South Africa (Brundrit 1995). Under the “Business-as-Usual” scenario the sea level is estimated to rise by 20 cm by the year 2050, with a range of uncertainty of 7-39 cm. By the year 2100, the sea level will be 49 cm higher than today, within the range of uncertainty of 20-86 cm (IPCC 1996).

The topography of the coast plays an important role in determining the outcome of a sea level rise for rocky shores. At relatively strong sloping shores the vertical zones will be displaced upwards with probably no visible changes to the communities in the different zones. In contrast, at particularly narrow shores, zones could be displaced completely off the available rocky substratum. The level of the greatest erosive effects would move higher up the shore (Shackleton *et al.* 1996). Flat reefs and wave-cut platforms could be permanently submerged and would be lost to intertidal assemblages. Along the coast of Zululand at the subtropical east coast, beaches are relatively flat and only few rocky outcrops exist (Jackson 1976). Beachrocks, formed by cementation during Holocene sea level highs (Ramsay 1995), are the main features here, stretching for miles at low water. A sea level rise may totally submerge these flat beachrock formations. However, contemporary beachrock is forming at present at elevations of 0.1-0.2 m above mean low water neap tidal level (Ramsay 1995) and it may thus be possible, that new beachrock formation, perhaps additionally accelerated by increasing sea surface temperature, is able to keep up with the rise in sea level.

4.2. AIR AND SEA SURFACE TEMPERATURE

All species have limited ranges of tolerance towards specific environmental conditions and each species tends to be most abundant at its particular range optimum (Whittaker 1975). Since most marine organisms are thermoconformers, which means that they cannot maintain body temperatures different to their surrounding environment, temperature is one of the most important factors determining the distribution of marine species on a biogeographical scale (e.g. Bolton & Anderson 1990, Emanuel *et al.* 1992, Bustamante & Branch 1996a). It not only governs the species distribution, but also controls the rates of metabolism and development, and induces many important behavioural and physiological responses, such as migration and reproduction (Ray *et al.* 1992). Most marine organisms have some acclimatisation capacity, an adjustment of thermal tolerance depending on the season. Such acclimatisation can either be behavioural or physiological (Ray *et al.* 1992, Little & Kitching 1996).

The intertidal community is influenced by both the temperature of the sea at high tide and the temperature of the air at low tide. The geographical distribution of intertidal organisms is mainly controlled by sea temperatures (Bolton & Anderson 1990, Southward *et al.* 1995, Bustamante & Branch 1996a), but air temperature has some effect on the vertical zonation of rocky shore organisms. Desiccation is one of the physical factors thought to contribute strongly to the setting of upper limits for intertidal species (Little & Kitching 1996). Desiccation results from exposure to air during low tide and its impact depends on the prevailing temperature of the air. Many mechanisms have been developed that reduce heat and desiccation stress. Limpets cling firmly to the rocky substrate, mussels shut their shells tightly, some algae are able to withstand a considerable loss of water and other species take refuge in crevices and under boulders (Branch & Branch 1981, Branch 1981).

One of the main effects of an increase in greenhouse gases will be a change in the global mean surface air temperature (IPCC 1996). High-resolution GCMs predict a temperature increase of 2°- 3°C for southern Africa, for an effective doubling of atmospheric CO_2 concentration. For the year 2030, the models forecast a 1,5°- 2,0°C rise in air temperature (Schulze & Kunz 1993). It is further predicted that warming in the winter months will be greater than the annual warming, while the increase in warming in the summer will be less. Elevation of surface air temperature could cause an increase in heat stress and desiccation and their resulting effects, particularly in the upper intertidal (Gunnill 1980). Species at the upper ends of their tolerance ranges may be reduced to shaded areas, or to zones lower down on the shore, and heat-induced mortality may increase. The possible outcome could be a reduction in the abundance of certain organisms and a change in species composition, towards more heat-resistant organisms. But since heat and desiccation stress is at its highest in summer, and a rise in air temperature is predicted to be more pronounced in winter, the predicted temperature increase for the near future may not be enough to have any measurable impact. Moreover, intertidal species can often tolerate a much greater temperature range than they experience in their natural habitat (Wolcott 1973). The west coast of South Africa experiences a strong temperature difference between the land and the sea and is therefore characterised by heavy fog banks. These fog banks are thought to enhance the intertidal biomass of fleshy seaweeds, because they reduce insolation, and hence the desiccation effect of emersion (Stephenson & Stephenson 1972). On the west coast, an increase in air temperature may increase fog banks, which in turn may protect the biota from the negative effects of higher temperatures.

An increase in sea surface temperature is likely to lag behind the rise of air temperature by about 20 years (Shannon *et al.* 1990b, IPCC 1996). Long term-series of sea surface temperature (SST) have already shown an increasing trend in SST over the last decades at the west and south coasts of South Africa (Taunton-Clark & Shannon 1998, Schumann *et al.* 1995) and a further global warming will very likely support this trend. An increase of SST will probably be not evenly distributed around the coast. Intensification of the Benguela upwelling for example will rather reduce the SST than enhance it (Siegfried *et al.* 1990). But the long-term scenario might very well be a substantial increase in SST in the coastal waters off southern Africa (Mikolajewicz *et al.* 1990).

The effect of sea temperature on marine intertidal organisms can be either direct or indirect or through a combination of both. The direct influence of temperature could cause changes in the survival, reproductive success and behaviour of species, and may alter dispersal patterns. Larval and juvenile stages often tend to be less tolerant than adults and it thus would appear that recruitment may be more important than adult mortality in constraining the limits of species with a planktonic larval phase (Underwood & Fairweather 1989). The enhancement of the competitive advantage of one of two competing species over the other one would be for example an indirect effect. Predator-prey interactions may also be influenced if either one of them is currently at the lower or upper end of their temperature tolerance range and is thus sensitive to a change in temperature (Southward *et al.* 1995). The intensity of predation can also be affected by sea surface temperature. For example, the foraging activity of the keystone predator on the Oregon coast, the sea star *Pisaster ochraceus*, was reduced drastically during drops in water temperature associated with upwelling events (Sanford 1999). An increase in the magnitude or frequency of upwelling events on the west coast of South Africa will be accompanied by a decrease in sea temperature and therefore predation rates may be strongly reduced. This would favour competitive dominant species, which could cause further changes in the rocky intertidal community structure.

Few studies of probable climate-related rocky shore community changes are presented in the literature. Southward *et al.* (1995) have observed extensive changes in the rocky intertidal benthic communities in southwest Britain and the western English Channel over the last 70 years. They identified a broad correlation between these changes and small climatic changes of the order of 0.5°C in sea surface temperature. Warm-water species increased in abundance and extended their range during warming, while cold-water species declined or retreated. Future latitudinal shifts of 200-400 miles in distribution of plankton, fish and benthos, with extensive restructuring of their respective communities, are predicted. Similar observations are described for a Californian rocky intertidal community by Barry *et al.* (1995). The annual mean SST at the Californian site increased by 0.75°C over the past 60 years and this change was accompanied by an increase of southern (warm-water) and a decrease of northern (cold-water) invertebrate species, while cosmopolitan species showed no trend. In South Africa, only one set of long-term monitoring data exists for three sites on the east coast but unfortunately no additional environmental data are recorded for this area (Dye 1998b). However, several observations of range extensions and population changes were recorded during the unusual warm surface water temperatures measured in the southern Benguela and along the south coast of South Africa in 1982/83 (Branch 1984b), probably connected to the strong 1982/83 El Niño event in the Pacific (Schumann *et al.* 1995). The limpet *Patella longicosta* and the winkle *Oxystele variegata* extended there usual range by about 150 km and 480 km respectively. The warm-water limpet *Patella oculus* showed marked increases in recruitment on the west coast at the end of its normal distribution, while the cold-water limpet *Patella granatina* experienced a recruitment failure during the summer

1982/83 (Branch 1984b). Palaeontological and archaeological work can be of great importance in predicting future distribution patterns by comparison of current intertidal assemblages to findings of the geological past under different climate conditions. Several studies focused on a possible correlation between population changes and SST changes (Cohen *et al.* 1992, Jerardino 1997) but presently not enough information exist to distinguish between different plausible explanations for a change in community structure.

The cited studies indicate that a rise in sea surface temperature could affect the biogeographic pattern along the South African coast by shifting warm-water species from the east coast further west and tropical species from the northern west coast further south. Cold-water species may become more restricted in their ranges. The species that showed increasing or decreasing abundances along the South African coast during the unusual warm summer of 1982/83 were all at the limits of their ranges while populations of species in their optimum range displayed no changes. This suggests that changes in communities are most likely to occur through animals at the extreme limits of their ranges. A change in SST will not only influences directly the distribution pattern of species but may also alter the existing strength of biological interactions. Changes in competition, grazing or predation patterns can therefore also affect the animals, which are in their optimal range and would otherwise not be influenced by a temperature change. It is also predicted that even a small rise in SST will have significant effects on the life histories and growth, and hence distribution, of some macroalgae (Beardall *et al.* 1998). A disappearance of the kelps between False Bay and the Agulhas region, their eastern limit, is thought to be possible (Shackleton *et al.* 1996). Similar scenarios exist for the North Atlantic where a northward shift in the southern boundaries of some arctic to cold-temperate *Laminaria* seaweeds is predicted (Breeman 1990). Since these seaweeds are the major canopy forming species in kelp forests, their decrease could be followed by significant changes in community structure. A decrease in the production of kelp forests would also affect intertidal filter-feeder communities due to reduction of food availability. Another possibility is the southward penetration of the east coast mussel species *Perna perna*. *P. perna* has a strong reproductive output and may be superior to the west coast mussel species *Choromytilus meridionalis* and *Aulacomya ater*, and could also be a strong competitor with the currently dominating alien mussel *Mytilus galloprovincialis* (Shackleton *et al.* 1996).

4.3. UPWELLING SYSTEM

There are two contradicting scenarios in the international literature regarding the general response of coastal upwelling to global warming. Bakun (1990) has proposed a mechanism whereby global warming could induce an acceleration of coastal upwelling. Higher concentrations of greenhouse gas in the atmosphere could inhibit nightime cooling and enhance daytime heating of the land, leading to intensification of the continental thermal lows adjacent to upwelling regions. This would increase the onshore-offshore pressure gradient and intensify alongshore winds, thereby accelerating the upwelling process. Bakun (1990) provided some evidence to suggest that certain major upwelling systems (e.g. California, Marocco, Peru and Iberian Peninsula system) have been growing in intensity. Other scenarios suggest, however, a weakening of coastal upwelling processes, because of a slackening of trade-wind intensities on a global scale as a result of the diminished equator-to-pole temperature gradient under warmer conditions (Hsieh & Boer 1992). The reverse effect is known to have happened during glacial periods, when trade winds were stronger and upwelling greatly increased (Berger *et al.* 1978, Romine 1982, Oberhansli 1991). Sea surface temperatures in the southern Benguela decreased significantly during periods of Holocene cooling and would therefore fit this pattern (Cohen *et al.* 1992, Cohen 1993). For South Africa, it is considered possible that the atmospheric circulation over the South Atlantic Ocean, known as the South Atlantic High Pressure Cell (SAH), may alter its location and/or configuration and increase its ridging south of the continent, and that this may enhance the land/ocean temperature gradient and thus the strength of longshore winds (Shackleton *et al.* 1996, Shannon *et al.* 1990b). This would possibly result in an increase in upwelling in the central Benguela system, in a reduced upwelling in the northern and the southern Benguela, and in the displacement of the southern boundary of the Benguela eastwards along the south coast with a resultant increase in coastal upwelling there. But an increase in the longshore winds could well be only an initial effect (Shackleton *et al.* 1996). Thus, it may be that Bakun's scenario (1990) is an intermediate phase, while the long-term effect could be reduced upwelling (Siegfried *et al.* 1990, Shackleton *et al.* 1996).

If the hypothesis of an increase in coastal upwelling due to higher wind stress is adopted, at least as a first response to global warming, more nutrients should be available in these areas, probably also for longer periods of time. Higher nutrient concentration should then result in an increase in primary production, including both phytoplankton and intertidal *in-situ* production. Enhanced input into the basal level of the food web in the form of intertidal microalgal biomass would increase the abundance of primary consumers such as grazing herbivores (bottom-up effect). But a large proportion of the west coast grazer biomass uses kelp-derived detritus as its main food source (Bustamante & Branch 1996b) and would probably not be affected by an increase in intertidal algal production. Increasing nearshore phytoplankton concentrations could also enlarge the filter-feeder biomass of the west coast, since average biomass of filter-feeders has been shown to be positively correlated to nearshore phytoplankton concentration (Bustamante *et al.* 1995a). But in all three biogeographic provinces, filter-feeders are able to achieve similar maximal biomass values, suggesting that the limiting factor for a maximum biomass at the west coast is probably space availability due to biotic interactions and the effects of wave action rather than productivity (Bustamante *et al.* 1995a). Nevertheless, the enhancement of non kelp-dependent grazers could result in an augmentation of secondary consumers, may strengthen the control of grazers over algae and could also intensify biotic interactions such as competition for space. A different scenario was found for the upwelling system off the Californian coast, where a decline in zooplankton was linked to an observed warming trend in the surface water layers (Roemmich 1992, Roemmich & McGowan 1995). It was proposed that, owing to the heated sea surface, the stratification of the water column intensifies and results in less lifting of the thermocline by wind-driven upwelling. The shallower source of upwelled waters results in fewer nutrients being brought up for new primary production. Hence, the effect of heating could offset or even reverse the effect of an increase in wind stress on upwelling (Roemmich & McGowan 1995). This scenario would have the reverse effects. Lower concentrations of nutrients would be available, which would result in a decrease in the *in-situ* intertidal primary production and phytoplankton production. Although lower concentrations of nutrients would have a negative effect on more generalised grazers, which rely mainly on intertidal *in-situ* production, lower phytoplankton concentrations would probably have very little effect on filter-feeders and on the two common grazers *Patella granatina* and *P. argenvillei*, since they depend on food supply from the kelp beds. It appears that either an increase or a decrease in nutrient and phytoplankton availability would mainly influence the *in-situ* production and those herbivores that are dependent on it, whereas filter-feeders and specialised grazers may be less affected. But this would only be the case if a decrease in nutrient concentrations is not too drastic, and reduces the production of the subtidal kelp forest to such an extent that it is unable to support the high biomass of the west coast's grazers and filter-feeders.

Another consequence of rising wind stress and enhanced upwelling could be stronger offshore advection and turbulence. This may result in phytoplankton being displaced out of the photosynthetic active shallow layers into deeper waters and/or reduced onshore transport (Brown & Cochrane 1991). Another important consequence of stronger offshore advection could be a possible reduction in the supply of larvae to the rocky intertidal. Roughgarden *et* *al.* (1988) found a negative relationship between an index of upwelling intensity and the recruitment of barnacle larvae, based on the fact that during upwelling events larvae are transported to far away from the coast to return to the coast.

'Red tide' events in the Benguela are closely related to wind stress and upwelling, and occur mainly when water column stratification increases and during years of reduced upwelling (Pitcher *et al.* 1993, 1995). A global warming induced increase in upwelling may therefore reduce 'red tide' events, but the possible intensification of thermal stratification due to a rise in air and sea surface temperature (Roemmich & McGowan 1995) could on the other hand result in an increase of such events. Globally, there is belief that the scale and complexity of the phenomenon of 'red tide' is already expanding (Pitcher 1998). 'Red tide' impacts on ecosystems are not only direct ones such as poisonous shellfish and dead fish, but include also effects on trophic structure. It is now known that all trophic compartments of the marine food web are vulnerable to harmful blooms and it has been suggested that through time chronic, sublethal impacts may be of greater significance for ecosystems by altering food webs or causing trophic dysfunction (Pitcher 1998).

4.4. NEARSHORE CURRENT SYSTEM

If a change in the global climate brings with it an alteration in wind stress, then this will not only influence the future strength of upwelling but will also have an impact on the nearshore current systems around the southern African coast. Wind has been identified as a key determinant of ocean variability on all spatial scales (Harris 1978). The effect of wind stress on the sea surface is a transfer of momentum such that the surface picks up 2-3% of the winds velocity. Due to the earth's rotation, the induced wind drift in the southern hemisphere is directed somewhat left of the wind direction. Winds with the coast on their left may thus produce a piling up of water at the coast, while those with the coast on their right may produce a divergence or upwelling. Both effects result in altering the slope of the seas surface normal to the coast, which induces currents in sympathy with the wind throughout the whole of the water column (Harris 1978). The two major current systems affecting the South African coast, the Benguela Current and the Agulhas Current, are directly influenced by wind and are thus highly sensitive to even small changes in large-scale wind fields (Harris 1978, Heydorn 1978, Shannon *et al.* 1990b, Lutjeharms & de Ruijter 1996). Well-known wind-stress related phenomena include the 'Benguela Niño' and the 'Agulhas intrusion'.

A change in the equator-pole temperature gradient due to global warming can lead to a poleward shift in oceanic and atmospheric systems. This could well result in an increased frequency in the occurrence and intensity of ‘Benguela Niños’ (Siegfried *et al.* 1990). One effect associated with ‘Benguela Niño’ events are changes in local winds. These changes can in turn result in modifications of nearshore oceanographic conditions.

Lutjeharms & de Ruijter (1996) speculated that an increase as well as a decrease in the wind stress curl over the Indian Ocean would result in an increase in the frequency of the occurrence of a Natal Pulse. The Natal Pulse forces the core of the Agulhas Current further offshore and thus causes an earlier retroflection of Agulhas water (Lutjeharms & de Ruijter 1996). This implies that less water will be available for an exchange with the South Atlantic (inter-basin exchange) and less heat flux into it (Lutjeharms & Van Ballegooyen 1988), which would slow down the global upper-water conveyor belt. Other components of variability caused by the Natal Pulse are dramatic changes in the inshore current system (Lutjeharms & Connell 1989) (Fig. 3.).

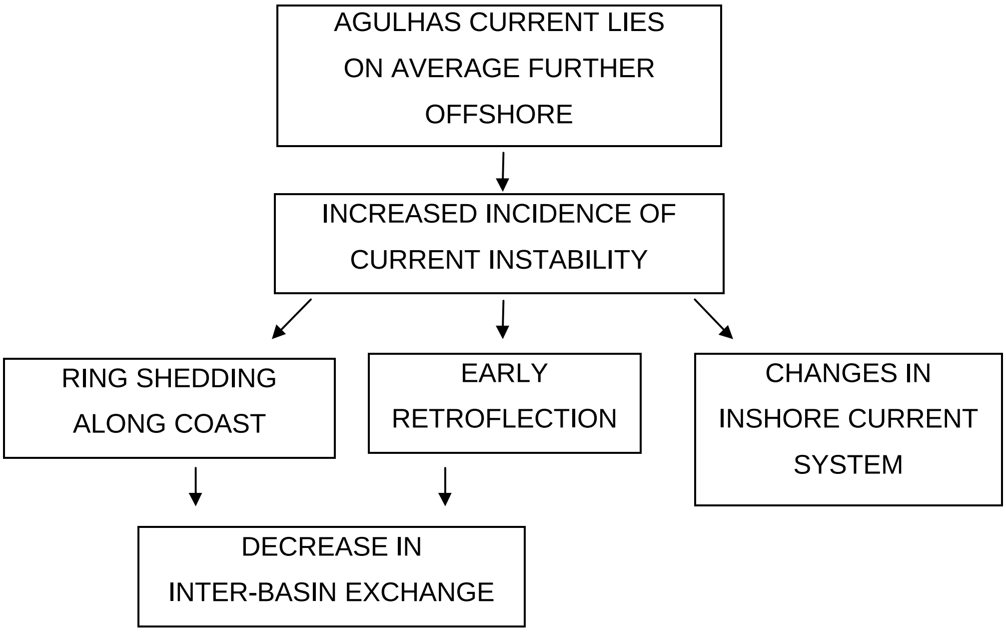

Fig. 3. Flow diagram of a thought-experiment on the possible increase of the Natal Pulse (modified after Lutjeharms & de Ruijter 1996)

On the other hand, other scenarios suggest that the volume of the water transported by the Agulhas Current may decrease, which would then result in an increase of the leakage of Agulhas water into the South Atlantic and, dependent on the intensity, in an increase of ‘Agulhas intrusion’ events (Shannon *et al.* 1990b, Siegfried *et al.* 1990). However, both scenarios predict possible substantial changes in the nearshore oceanography along the east and south coasts of South Africa and as well as for the west coast due to the likely change of the amount of Agulhas water leakage into the South Atlantic.

Longshore winds are important for barotropic processes on the shelf, surface drift, stratification, and for the development of upwelling and frontal systems. Records of pseudo wind stress data depict substantial intra- and interannual changes in regional longshore wind fields over the last century (Shannon *et al.* 1990b). The principal mechanism modulating longshore winds at sea level off the southern African west and south coasts are the eastward passage of cyclones in a belt between 35°S and 45°S and their attenuation of the South Atlantic High (SAH) Pressure Cell. An alteration of the location of the SAH is likely to change the position and intensity of fronts and currents on the west coast, in part due to the increased ridging of the SAH and to alterations in the trajectory of the approaching cyclones (Shannon *et al.* 1990b).

The scenarios of changes in the frequency of Benguela Niños, of possible alterations of the passage and the volume transport of the Agulhas Current, of changes in the intrusion of Agulhas water into the South Atlantic and of modifications in the position of the SAH all imply possible drastic alteration in inshore currents around the whole of the South African coast. At present, the greatest uncertainties about possible global warming induced changes relate to future wind direction and speed and there is no indication at this stage as to how they might change (Shackleton *et al.* 1996). It is therefore not possible to predict whether and where there will be an increase or a decrease in the strength of currents or changes in directions. However, data from studies of the South African coast and elsewhere in the world have shown that nearshore oceanographic conditions have an important influence on recruitment patterns over the whole range of scales (e.g. Harris *et al.* 1998, Connolly & Roughgarden 1998). Any changes in the existing nearshore oceanography will therefore have important consequences for the community structure of rocky shores. Alteration in the amount of larvae arriving at a particular stretch of shore not only implies a direct impact through higher or lower settlement rates, but will also have an indirect impact in changing the existing strength of biological interactions such as competition and predation (Menge & Sutherland 1987). Alteration of currents on local or larger scales could as well have an impact on the nutrient and phytoplankton supply to rocky shores (Menge *et al.* 1997b). A change in the onshore transport of phytoplankton would affect filter-feeders, especially at the south and east coasts, where there is no subsidy from kelp detritus. But changes in the production rates of this subtidal community, due to differences in nutrient availability, may also affect the west coast rocky shore filter-feeders. In the Pacific, El Niño-generated storm swells are reported to have caused extensive damage to kelp forests through physical damage and low nutrient levels that interfered with growth and reproduction (Glynn 1988). If a global warming increases the occurrence and intensity of Benguela Niños, such damage might well happen to the west coast kelp forests. Since kelp forests are an important food source for filter-feeders (Bustamante & Branch 1996a), a reduction in kelp and kelp detritus availability would have a negative effect on filter-feeders and kelp-dependent grazers. A change in bottom-up factors, i.e. larval transport and nutrient supply, may thus have far reaching consequences influencing all levels of the food web along the rocky shore.

4.5. SAND INUNDATION

One of the significant features on the east coast is the shifting of vast amounts of sand that can alter the profile of beaches within a few days and influences the adjacent rocky shores. The Agulhas Current itself is responsible for this massive transport along the coast and extensive southward migrating dune-fields below 50 m depth and up to 8 m high have been recorded (Heydorn 1978). The regular alternation of northeasterly and southwesterly winds has a strong influence on the coast and inshore waters of Natal. Surf action originating from the south-west swell is powerful enough to set up pronounced sand scour patterns which results in high turbidity and cyclical covering and uncovering of inshore reefs with sand (Jackson 1976, Heydorn 1978). During the summer months the turbidity of inshore waters is additionally increased when flooded rivers carry heavy silt loads into the ocean. Inshore counter-current water movements oppose the southward flow at certain sections of the coast and river input is often first reflected to the north before dispersal over large areas.

Inundation of rocky shores by sand is viewed to be a natural catastrophe, reducing the abundance of the rock-living organism by smothering and abrasion (e.g. Daly & Mathieson 1977). But monitoring of inundated rocks has shown that a variety of species e.g. the mussel *Perna perna*, the ascidian *Pyura stolonifera*, the oyster *Saccostrea margaritacea* and some macroalgae seem to be able to survive burial for considerable periods (Jackson 1976, Berry 1982). Moreover, some species (e.g. *S. margaritacea*) seem to prefer sandy areas and some macro-algal turfs have been found to survive better when buried under sand, since this reduced grazing, heat stress and desiccation (Norris 1983). This suggests that the physical disruption of sand inundation on the existing community can be critical for the maintenance of diversity and may lead to the development of highly specialised communities of sand favouring species and species which are usually inferior but may now be able to dominate over sand intolerant species (Bally *et al.* 1984). Littler *et al.* (1983) suggest that sandstressed rocky intertidal habitats are important refuges for stress-tolerant and opportunistic species. They described a sub-climax community consisting of opportunistic algae and fast growing macroinvertebrates (e.g. barnacles) while long-lived species (e.g. mussels) are restricted to elevated structures such as pinnacles and turrets.

A rise in sea level could increase the erosion of coastal dunes and the mobilisation of sand, while a drier climate may even enhance this through reduction in moisture in coastal dunes and a sparser vegetation cover (Shackleton *et al.* 1996). Changes in the wind stress curl over the Indian Ocean and the possible consequences for the Agulhas Current and the associated oceanographic conditions (Shannon *et al.* 1990b, Lutjeharms & de Ruijter 1996) may lead to a change in the sediment transport. The combination of these factors may result in changes in the frequency and length of sand inundation and in the amount of sand involved. An increase in inundation could surpass the tolerance threshold of sand-favouring species, and in extreme cases, may render some shores uninhabitable. A decrease in sand inundation may on the other hand result in a loss of the specialised communities since sand intolerant species will outcompete the sand-specialised species.

4.6. RADIATION

Photosynthetic processes on earth are only possible due to sunlight. However, aspects of sunlight, such as the ultraviolet light spectrum, are highly energetic and can cause damages to living organisms. The stratospheric ozone shields the Earth from much of the solar UV radiation, but the introduction of man-made ozone depleting gases such as chlorofluorcarbons and halone into the atmosphere has resulted in a reduction of the ozone layer. Decreased ozone concentration will result predominantly in an increase of UV-B radiation incident (Helbling *et al.* 1992). Much concern has been expressed since the discovery of the ozone hole over Antarctica and its possible impact on the marine ecosystem, but changes in ozone are not confined to Antarctica (Shackleton *et al.* 1996). The mid-latitudes may experience a significant increase in UV-B radiation in the next decades, due to a combination of possible decreasing cloud cover and continued depletion of the ozone shields (Pittock 1991). Estimations for ozone decrease over South Africa by the year 2025 range from 13% for Durban to 17% for Cape Town (Human 1992).

It is well known that solar UV radiation can have many diverse deleterious effects on living organisms, even under ‘normal conditions’. Solar UV-B has been found to affect DNA, to impair photosynthesis, affect nutrient uptake, enzyme activities and nitrogen incorporation, to bleach cellular pigments and to inhibit motility and orientation in phytoplankton (Döhler *et al.* 1991, Worrest & Häder 1989, Häder & Worrest 1991, Larkum & Wood 1993, Behrenfield *et al.* 1995). Field studies conducted under the Antarctic hole demonstrated some detrimental impacts of UV light on phytoplankton primary production (Smith *et al.* 1992, Helbling *et al.* 1992), but since depletion of the ozone layer is expected to continue at all latitudes, such effects may also be of relevance outside polar regions. Calkins & Thordardottir (1980) have found that tolerance and exposure of organisms to present solar UV are approximately equal, which implies that UV radiation is a significant ecological factor influencing the distribution of species. It further suggests that no large reserve of resistance is available that could cope with an increase in UV radiation without requiring modification of physiology and behaviour. Several mechanisms have been found that diminish the harmful effects of ultraviolet light. These include migration, production of absorbing organic matter and development of repair functions (see review of Vincent & Roy 1993). Different species have different sensitivities towards UV radiation and a shift in species composition is therefore a likely consequence of increased UV radiation. Smaller organisms such as bacterioplankton and microplankton seem to be generally more effected than larger phytoplankton (Kramer 1990, Häder *et al.* 1995). This could have an effect on the subsequent links in the trophic food web. Negative effects of UV-B light were also found for the early developmental life stages of fish, shrimps, crabs, amphibians and other animals. The most severe effects are decreased reproduction and impaired larval development (see review of Kramer 1990, IPCC 1996). Only a few studies have been carried out on macroalgae (see review of Franklin & Foster 1997, Beardall *et al.* 1998). Benthic macroalgae are restricted to the intertidal and to certain depth zones below it, caused by the penetration depth of visible light, and to the resultant exposure to radiation at their specific growing site. An increase in UV-B will subject the algae to enhanced short-wavelength light to which they may not be adapted. Recent studies have found no effect on respiration, but inhibition of photosynthesis in many red, brown and green benthic algae was recorded (Larkum & Wood 1993, Maegawa *et al.* 1993, Häder & Schäfer 1994). Deep-water species were at least twice as sensitive as intertidal dwellers and red algae were in general less sensitive than green algae (Polne & Gardner 1982). Organism may be able to adapt to an increase in UV radiation in developing repair mechanism but it could be that the time frame of the predicted changes in the ozone layer is not sufficient enough for any genetic adaptation (Häder *et al.* 1995).

The structure of the marine ecosystem is very complex and dynamic and although there is clear evidence that increases in UV-B exposure are harmful to specific species, potential effects on aquatic ecosystems can only be made very roughly at the present state of knowledge (Kramer 1990, Häder *et al.* 1995). Especially little is known about the effect of increased solar UV radiation on rocky shore communities and any scenarios developed are therefore purely speculative. Most intertidal organisms will probably be barely directly affected by an increase in UV light owing to their protective shells. The dense matrix of mussel beds and the algae canopy could suffice as protection for animals such as amphipods, isopods and polychaets. Eggs and larval stages of invertebrates and fish have been shown to be sensitive to UV-B exposure and an increase of larval mortality could follow. But larvae of intertidal species are presumably primarily in coastal waters which is significantly less penetrable for UV-B light due to the amount of particulate matter and gelbstoffe compared to oceanic waters (Smith *et al.* 1992, Häder *et al.* 1995). The algae community would probably experience the most damaging effects, although intertidal macroalgae have shown do be less sensitive to UV-B light than deeper living algae species. However, a decrease in the photosynthetic capacity could result in a reduced standing stock, and/or a shift towards certain more resistant species. Rocky shore tidepools may experience the greatest impact due to increased UV radiation, since their community is dominated by seaweed. Considering that UV-B light has proven to have deleterious effects on bacterioplankton, phytoplankton and macroalgae (review of Kramer 1990, IPCC 1996), it is likely that there will be also an effect on the *in-situ* microalgal production. A change in the biomass and the composition of the micro- and macroalgal community could influence the abundance and distribution of grazers. An indirect effect of an enhancement of UV radiation on rocky shores could come from changes in offshore communities. Estimations are made that a 16% ozone depletion may result in a 5% loss in phytoplankton (Nixon 1988). Such a reduction of primary production could have an impact on filter-feeders, which depend on phytoplankton as an ‘imported’ food source. Filter-feeders at the west coast may be less impacted due to the supply of detritus from the kelp forest but an increase in UV-B radiation might have a negative effect on the photosynthesis capacity of the kelp and thus diminish their subsidy potential. Since all organisms in a community are somehow linked through the intricate food web, changes in one level will have more or less severe consequences for the other trophic levels.

4.7. STORMS

An increase in tropical sea-surface temperature may result in a southward movement of tropical cyclones along the east coast of South Africa and in an increase in their intensity (Shackleton *et al.* 1996). A possible climate-related westward extension of the Agulhas Current and the linkage of the intensification of atmospheric depression to this, may increase the frequency and intensity of storm events at the western and southern coastal regions of South Africa (Brundrit & Shannon 1989). Storms are one of the main causes for disturbances in intertidal populations. Disturbances have an important ecological impact on rocky shore communities in creating patches of different ages and stages of succession (Sousa 1985) and preventing dominant species from monopolising the shore (Paine 1966). After a disturbance event a cycle of recovery follows which involves a suite of different species usually starting with fast growing opportunistic species. At the end of such different stages of succession an end phase with long-living, dominant species prevails until the next storm appears. An increase in storm frequency will shorten the time available for the recovery of the created patch. This could result in reducing the abundance of longer living species by favouring short living, fast growing species.

5. CONCLUSION

South African rocky shores are an ecologically and economically important coastal ecosystem. They support a wide range of marine organisms and are used for a broad range of activities including recreational usage, and subsistence and commercial exploitation (Branch & Branch 1981, Field & Griffiths 1991). It is very likely that global warming and its associated environmental changes will have vast impacts on this ecosystem (IPCC 1996). Long-term monitoring data sets from rocky shores elsewhere in the world support this possibility (Barry *et al.* 1995, Southward *et al.* 1995). At present, regional climate change scenarios are based on evidence from current GCMs and little confidence is given to their predictive power on a regional scale (Shackleton *et al.* 1996, IPCC 1996). This limitation allows only for the development of 'what-if' scenarios rather than predictions.

Scenarios of possible impacts on rocky shores include that a rise in sea level would probably have little effect on rocky shores other than moving zones up the shore or, in extreme cases, displacing zones off the rocks. Sea surface temperature changes might affect the geographic distribution of species along the coast by shifting warm-water species from the east to the west and northern tropical species down south. On a local scale, SST changes may also alter the strength of biological interactions such as predator-prey interactions. The perhaps greatest impacts could result from increases in frequency and intensity of upwelling events and alteration of nearshore currents by affecting the nutrient and larval supply to the coast, which in turn would strongly influence the current community structures around the coast. Increases in 'red tide' events would negatively influence the rocky shore communities at the west coast, while at the east coast changes in sand inundation could modify the existing species composition towards either more or less sand tolerant species. A rise in UV-B radiation might change the algal community around the whole of the coast towards more UV resistant species, which would have an influence on the food web. An increase in storm events would accelerate the rate of disturbance, which could favour short-living over long-living species.

The described scenarios all involve a great amount of uncertainties due to the uncertainties in the climate change predictions, but there is hope that the accuracy of GCMs will improve with time. The first step towards better predictions of the future course of South African rocky shore communities would therefore be the development of more precise climate change predictions, especially in the field of wind stress changes and nearshore current alterations. Another major problem facing scientists investigating the issue of impacts on rocky shore systems is the scarcity of long-term monitoring data sets in South Africa. To the best of the author's knowledge only two published studies exist concerning one long-term data set from three sites on the east coast of South Africa (Dye 1998a, 1998b). Long-term data are of great importance to determine changes in community structure because many important processes and changes may occur over such long periods that they would never be detected without comparison with historical data from the same sites (Dye 1998b). Hence, it is imperative to continue with existing and to start with new 'long-time-series-studies', to be able to detect ongoing changes and improve predictions.

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POSSIBLE EFFECTS OF CLIMATE CHANGE ON SOUTH AFRICAN ESTUARIES

B.M. Clark

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2. INTRODUCTION

The southern African coastline is well endowed with estuaries. They lie at the interface between terrestrial drainage systems and sea, but are neither riverine nor marine environments. They constitute a unique habitat type of their own, and include many species of fauna and flora found nowhere else. Where they occur, they fulfil a variety of important roles, including ecological, economic and cultural functions. They are used by man for transport, harbours, mariculture, marina development, fishing, watersports and even an outlet for industrial and domestic waste. They are used extensively by migrant birds, fish and prawns as important feeding and nursery grounds. Their role in this respect in southern Africa is thought to be particularly important, as they contain much of the only suitably sheltered habitat along our coastline, due to the highly exposed, almost linear nature (Beckley 1984, Field & Griffiths 1991).

Lying at the interface between rivers and the sea means that they are extraordinarily vulnerable to and easily destroyed by human activities. They are susceptible to changes that take place in the ocean as well as those occurring far into the hinterland, and thus the characteristics of these systems tend to vary enormously both in space and time. This fluctuating character lies at the heart of estuarine ecology, and plant and animal species inhabiting or frequenting these environments generally require special adaptations in order to do so. Those that can survive here, thrive on the nutrients and food provided by both rivers and the sea that make these habitats amongst the most productive in the world. They represent the conduit through which all accumulated inputs into a river system must travel before reaching the sea.

This report explores some of the threats posed by potentially changing climatic conditions on estuaries in southern Africa. It starts by outlining the essential physico-chemical characteristics of estuaries in southern Africa and describing the basic elements of their biota. It goes on to examine the likely effects of climate change on the structure and functioning of these systems and the likely effect these changes will have on the biota and biotic interactions. Finally, some recommendations are provided for researchers and policy makers to monitor, lessen and/or adapt to the negative consequences of climate change for estuaries in southern Africa.

3. HYDRODYNAMIC CHARACTERISTICS OF SOUTH AFRICAN ESTUARIES

3.1 WHAT IS AN ESTUARY?

Not all rivers entering the sea possess true estuaries. The number of estuaries in South Africa varies thus according to what types of systems are included in the definition of an estuary. During the first international conference on estuaries in 1964 wide support was received for the following definition: “An estuary is a semi-enclosed body of water which has a free connection with the open sea and within which sea water is measurably diluted with fresh water derived from land drainage” (Prichard 1967). While this definition is still widely accepted in the Northern Hemisphere, Day (1980) pointed out that several problems arise when this definition is applied to estuaries in southern Africa. Sand bars form at the mouths of many estuaries in this part of the world during the drier periods of the year. These systems remain closed until their mouths are breached by high riverine discharge or by artificial methods. These so-called “blind” estuaries can undergo lengthy periods during which they have no free connection with the open sea, considered to be crucial in Prichard’s definition. Indeed, according to Reddering & Rust (1990) only 37 or 12.8% of the 289 South African river mouths maintain permanent tidal inlets with the sea. In order to accommodate the peculiarities of these systems, Day (1980) developed a modification of the above definition that is now widely accepted in southern Africa. He defined an estuary as “a partially enclosed coastal body of water which is either permanently or periodically open to the sea and within which there is a measurable variation of salinity due to the mixture of salt water with fresh water derived from land drainage”. Even under this definition, many river mouths in southern Africa are still not considered to form true estuaries. Those that are excluded include mostly those systems that have very steep profiles or very high levels of discharge that prevent sea water from penetrating a significant distance upstream and those that discharge into permanently open bays where there is no measurable dilution of sea water.

3.2 INFLUENCES OF RIVER FLOW AND SEA WATER EXCHANGE

The characteristics and behaviour of estuaries are directly related to the catchment and coastal environmental characteristics in which they are located. Many of these in turn are influenced or controlled by global climatic processes. The South African west coast (west of

Cape Point) borders on the South Atlantic, which is driven by sporadic upwelling of cool, nutrient rich waters characteristic of the Benguela Current regime. The east coast borders on the Indian Ocean and is dominated by the warm Agulhas current. This warm current follows the coast closely as it moves southwards along the east coast but moves progressively further offshore as it moves around the southern part of the country. This results in a temperature gradient extending from subtropical in the east to warm temperate in the south. East coast waters are generally characterized by great biotic diversity, whereas the more productive waters of the west and south coast have fewer species but in greater profusion (Heydorn & Flemming 1985).

The characteristics of the drainage basin that feeds an estuary also has an important influence on the estuarine environment. Differences in the rainfall patterns in the various catchments around the country have had a profound influence on the development and maintenance of estuaries in different parts of the country. Climate along the coast of South Africa ranges from near arid on the west coast, to Mediterranean along much of the south coast, to subtropical along the Natal east coast. Rain falls mostly during summer on the east coast, during summer and winter on the south coast, during winter along the southwest coast and hardly at all on the northwest coast. As a result of this, estuaries in different parts of the country tend to look and function in very different ways. Estuaries on the west coast are generally stunted in their development due to low average river discharge and infrequent floods. Some are little more than dry riverbeds for most of the year, only linking up to the sea during periods of exceptional rainfall. Estuaries on the south coast are better developed both in terms of size and function than those on the west coast. They are fed by rivers that receive more rain and flood more frequently. Rivers in this region tend to be short and steep, but drain sandstone/quartzite formations with little unbound soil cover and therefore carry low silt loads (Whitfield 1998). In the eastern part of the country the hinterland has a higher relief than elsewhere, rivers have a high discharge rate and deliver substantial volumes of sediment to the estuaries in this part of the country (Reddering & Rust 1990).

The size and area of a drainage basin also play an important role in the dynamics of an estuary, as it controls the extent or volume of the normal and flood discharges reaching the estuary. An estuarine channel is normally cut into a bed consisting of unconsolidated sediment. Floods tend to scour the channel to the cross-sectional area required to accommodate the increased discharge, which is then back-filled during periods between floods (Reddering & Rust 1990). Estuaries with large drainage basins tend to be large, containing a substantial volume of water, while those with small drainage basins tend to be small and encompass smaller bodies of water.

The configuration of the coastline and the prevailing wave climate play an important role in controlling the structure and dynamics of an estuary mouth. Sediment suspended by waves in the sea near an estuary mouth tends to be carried into the system by flood tidal currents. This material then settles in the calmer waters of the estuary and is only partially removed by the ebb tidal currents. This results in an accretion of sand inside the estuary mouth and may eventually form a flood tidal delta. River flow, particularly during flood periods, tends to scour out this accumulated sand, carrying it back out to sea. This dynamic balance between the supply and removal of marine sediment tends to be very variable because of the intermittent nature of large floods. The natural pattern is often one in which sediments accumulate at the mouth of an estuary over a number of years and are then rapidly depleted during episodic floods (Rossouw et al. 1991). If the tidal exchange and/or river discharge is insufficient to maintain mouth depth, a sand bar forms. The bar will increase in size until it eventually cuts off all tidal exchange of water, and will remain this way (even for several years) until renewed freshwater flow is able scour the mouth open and starts the process again.

3.3 VARIATION IN TEMPERATURE AND SALINITY

Since an estuary is an area of mixing between river water and the sea, the temperature and salinity of estuarine waters are determined by a combination of river discharge and tidal inflow, which in turn are modified by solar heating and evaporation. Mean monthly sea surface temperatures along the South Africa east coast range from 22°C in winter to 27°C in summer, from 15-22°C along the south coast and 14-15°C along the west coast (Field & Griffiths 1991). Rivers are usually cooler than the sea in winter and warmer in summer, except for those that arise in high mountains, which they may remain cooler than the sea throughout the year. In the southern and western Cape, river temperatures may vary between 9 and 27(C; while those in the KwaZulu-Natal show less variation, usually in the range of 20-25(C (Day 1981a).

Estuaries that are open to the sea will usually display a gradient in salinity and temperature. Readings approximate those of the river and sea at the upper and lower reaches, respectively, while these grade into one another along the length of the system. Those that close for any period of time become divorced from the moderating influence of the sea and come under greater influence of the overlying air masses. Cool temperate estuaries along the west coast typically display a temperature range of 10-24(C, warm temperate estuaries along the south coast are usually within the range of 12-26(C and those subtropical estuaries on the east coast usually in the range of 14-28(C (Day 1981b, Whitfield 1998). Rivers usually carry little or no salt at all and thus in almost all cases it is justifiable to assume that the salt content of estuarine waters is of marine origin. The salinity usually increases from very low values in the river water at the head of the estuary to about 35 ‰ in the sea near the mouth. In an estuary that is open to the sea, the salinity at any point will rise and fall with the ebb and flow of the tides as seawater pushes in and out of the mouth of the system. Evaporation during the dry season raises salinity levels in the estuary, sometimes even to a point where it exceeds that of seawater (i.e. hypersalinity). This phenomenon is usually, but not only, confined to periods when the estuary is closed to the sea.

3.4 THE CLASSIFICATION OF ESTUARIES

There exist an infinite variety of different estuaries and it is only for convenience that they are grouped into a few classes. Geologists, physicists, chemists and biologists have classified estuaries according to their own particular interests; thus there also exists a large number of different classification systems. Day (1981c) recognizes three basic types of estuaries that are also recognized by most other authors:

3.4.1 Normal estuaries

Most estuaries are normal or “positive” in the sense that there is an increase in salinity from the head where the river enters, towards the sea. There is also a net flow of water seawards over a full tidal cycle. The catchments of these estuaries are usually larger than 500 km2 and rivers have a perennial flow in their natural condition. Average salinities in the estuary itself usually fluctuate between 15 and 35‰, but are usually greater than 25‰. Water temperatures are highly variable; they tend to reflect riverine conditions during floods and sea conditions during periods of normal river flow or drought.

3.4.2 Closed or blind estuaries

These are estuaries that are blocked off from the sea for varying lengths of time by a sand bar that forms across the mouth. At such times there is no tidal range and no tidal currents. Most of these estuaries have small river catchments (<500km2) and river flow is minimal of stops altogether for long periods at a time (several months). Salinity in these systems varies according to the ratio between evaporation and overwash over or seepage of seawater through the bar on one hand, and freshwater inflow and precipitation on the other. During episodic floods river conditions may prevail briefly, but during droughts conditions can become hypersaline (>40‰).

3.4.3 Hypersaline estuaries

These estuaries have a reversed or “negative” salinity gradient with salinity increasing from seawater values at the mouth to hypersaline conditions in the upper reaches. The water level in the upper reaches is below mean sea level and net flow is towards the head of the estuary. Such conditions usually occur during droughts or long periods of no rainfall (e.g. along the South African west coast).

4. BIODIVERSITY AND TROPHIC FUNCTIONING IN SOUTH AFRICAN ESTUARIES

Estuaries are highly variable environments but richer in nutrients than either freshwater systems or the sea. Flora found in estuaries are usually highly productive and the animal life prolific. The extremely variable conditions found in estuarine environments (e.g. rising and falling tides, changes in salinity and temperature), however, require that organisms living here have special adaptations in order to survive. Both the flora and the fauna of estuaries are usually made up of relatively few species; the number of species inhabiting estuaries being smaller than either the sea or freshwater alone. Estuaries in a large part owe their high productivity to the fact that they act a "nutrient traps" gaining nutrients both from river and the sea. Organic particles as well as larger items carried down by rivers or brought in by the sea settle in the relatively still and calm water of estuaries where they are decomposed by bacteria, releasing nutrients that in turn fertilise plant growth. Fauna and flora of estuaries include representatives from a number of basic groups of organisms, each of which are expanded on below.

4.1 BACTERIA

The water and mud of estuaries are extremely rich in bacteria. They live in the water column as well as in the interstitial spaces between the particles or on the surfaces of the particles themselves. Most bacteria are aerobic (i.e. use oxygen for respiratory processes) and place a heavy oxygen demand on the interstitial waters. In the absence of free oxygen, some bacteria are able to use the abundant sulphate in seawater as their source of oxygen. The reduction of sulphate results in the release of hydrogen sulphide that accounts for the sulphurous nature of most deeper-lying estuarine muds.

Bacteria make an extremely important contribution to estuarine trophic functioning by breaking down and assimilating detritus thereby making it available to other estuarine fauna. Indeed, it has been suggested (Fenchel 1972) that the only significant primary decomposers of plant material in the sea (and by association estuaries) are bacteria. Their role may be compared to that of micro-organisms living in the guts of herbivores, since the bacteria living on the particulate and dissolved organic matter make the primary production available for consumption (McLusky 1981).

4.2 ESTUARINE FLORA

4.2.1 Phytoplankton and microalgae

Phytoplankton are at somewhat of a disadvantage in estuaries and seldom form dominant components of the flora. Several reasons have been postulated to explain this. Many estuaries are simply flow-through systems and phytoplankton are constantly in danger of being washed out to sea. Many estuaries are also so muddy that only the top few centimetres of water enjoy sufficient sunlight for photosynthesis. Large rooted plants (macrophytes) frequently inhibit the growth of phytoplankton through competition for nutrients or by releasing tannins into the water (e.g. mangroves). Phytoplankton is able to grow very fast, however, faster than any of the larger macrophytes, and can double its mass in as little as one day if conditions are suitable. Low levels of phytoplankton can thus still contribute significantly to the productivity of an estuary.

High numbers of diatoms are also found resting on the surface of estuarine muds and sands. Many have the ability to migrate up and down through the top few millimetres of sand. In estuaries where the waters are turbid or muddy these diatoms colonise intertidal sand and mud banks, and only remain on the surface when the tide is out. They migrate down into the sediments as the tide rises over them, presumably to avoid being eaten by fish and other predators.

4.2.2 Macrophytes and macroalgae

Few seaweeds (algae) can tolerate low salinities and most are thus excluded from estuaries. Those that do occur in estuaries are able to withstand the turbidity, deposition of silt and the absence of wave action. These are usually confined to rocky outcrops, quays or piers near the mouth of the estuary.

Vascular plants or macrophytes found in estuaries in southern Africa include only giant ferns, sea grasses, salt marsh plants and mangroves. Sea grasses are adapted to complete submergence at or below low tide, while salt marsh plants and mangrove grow at or above mid-tide, and are adapted to varying periods of emergence. Mangrove trees are naturally perennial but somewhat surprising so are most sea grass and salt marsh species, having recorded life spans of 10-40 years (Day 1981d).

The depth-distribution of sea grasses in estuaries is severely restricted by light penetration. They are usually limited to the shallower banks within a few meters of the surface. They all have well-developed rhizomes in the sediment that give rise to stems of variable length which bear long flexible leaves. At the end of the growing season most of the food reserves of the sea grasses are translocated to the rhizomes, and the old leaves are attacked by fungi and bacteria. Eventually they disintegrate and add to the drifting organic detritus in the estuary. New leaves appear at the beginning of spring each year.

Salt-tolerant plants form broad salt-marshes around the edges of most estuarine lagoons. They include a wide variety of grass, sedge and succulent species and have long been recognised as being amongst the most productive ecosystems in the world (Odum 1959). Relatively little salt marsh vegetation is consumed directly by animals. As is the case with sea grasses, most of the primary production reaches the estuarine ecosystem in the form of fragments, which break off and are decomposed by bacteria. Salt marsh vegetation also plays a very important role in reducing the rate of flow of tidal and riverine waters, and in so doing accelerate the rate of sediment deposition in estuaries. They consolidate the soil and act as giant filters trapping silt and extracting nutrients from the water thereby keeping the estuary clean and preventing excess fertilisation.

Mangrove swamps are associations of halophytic trees, shrubs, palms and occasional creepers that replaces the temperate salt marshes on tropical and subtropical shores. They are limited to calm waters and grow best grow best on muddy shores of sheltered bays and estuaries where rainfall exceeds 1 500 mm per annum and temperatures do not fall below 20°. Their distribution in South African estuaries extends about as far south as the Mbashe River estuary (32° 17'S).

Mangrove trees can reach up to 40 m in height, but have surprisingly shallow roots because they grow in anoxic soils. They have pneumatophores or prop-roots that function to absorb oxygen from the air. Mangroves are highly productive and shed large quantities of leaves that are either eaten directly or (more commonly) add to the general detritus pool in estuaries. Mangroves also have a tremendous capacity for trapping silt because their rootlets form a dense web, which stabilises mud banks and cleanses the water of silt.

Taken together, sea grasses, salt marsh plants and mangroves, are by far the most important plant life in estuaries. They form the major source of food that sustains the prolific fauna found in these systems. Salt marshes and sea grass account for 60-90% of plant production in temperate south and west coast estuaries in South Africa (Branch &Branch 1981), and are only eclipsed by the dense mangrove forests in the subtropical estuaries of the east coast.

4.3 ESTUARINE FAUNA

4.3.1 Zooplankton

Estuarine zooplankton of include a wide variety of forms including holoplankton (organisms with an entirely planktonic life history) and meroplankton (temporary planktonic organisms including the larvae of benthic invertebrates and fish). These are further subdivided on the basis of their salinity tolerances to include a stenohaline marine component (marine species with a narrow salinity tolerance found only at or near the mouth), a euryhaline marine component (marine species with a wide salinity tolerance that penetrate further up into estuaries), a true estuarine component (species confined to estuaries) and a freshwater component (comprising species normally found in fresh water).

As with phytoplankton, zooplankton are not particularly abundant in estuaries. This is partly because there is a limited amount of food available to zooplankton (due to the low phytoplankton biomass) but more importantly because these organisms also tend to be carried out to sea by the net flow through estuaries. Most zooplankton have, however, developed strong vertical migration patterns to compensate for this. Hardly any zooplankton can be found in the water column during the hours of daylight; most species rise after dark, reach peak concentration at the surface near the middle of the night and descend again before dawn. Most estuaries are stratified to some degree, with net surface flow being generally seawards (as freshwater is less dense and “floats” on seawater) whereas there is a net influx of saline water along the bottom. By migrating vertically on a daily basis, zooplankton are able to maintain their position in the estuary by alternately drifting up and down.

The greatest number of zooplankton species are usually found near the mouth of an estuary, while greatest biomass is usually found somewhat further up. Some seasonality is usually evident in their abundance, peaking during late spring and summer (immediately following the phytoplankton peak) but this is often disrupted by flooding or the opening and closing of estuary mouths.

4.3.2 Benthic macrofauna

For practical purposes benthic fauna are commonly divided into different groups. Animals that are retained in a sieve with meshes of 1.0 mm are referred to as macrofauna; those that pass through this mesh but are retained on a mesh of 0.1 mm are termed meiofauna and those that pass through this mesh are termed microfauna. This convention has no functional significance and has simply been adopted for practical purposes. Microfauna generally includes the Protozoa; while meiofauna includes groups such as the nematodes, ostracods and harpacticoid copepods; and macrofauna includes polychaetes, amphipods, molluscs and the larger crustacea. Macrofauna are also frequently further subdivided into the same groups as the zooplankton based on their salinity tolerances (stenohaline marine, euryhaline marine, true estuarine and freshwater species).

Benthic macrofauna form the principal primary consumers in estuaries, feeding principally on the abundant supply of bacteria-rich detritus. Some are suspension or filter feeders extracting fine particulate matter directly from the water column, while others rely on the detritus within the muddy estuarine deposits. Some of these live and feed from within burrows (infauna) while other live and/or feed on the surface (epifauna).

4.3.3 Fish

Fish enter estuaries in large numbers to take advantage of the ideal conditions found within these environments – highly productive, warm, shallow waters that are mostly free of large predators. Few species live permanently in estuaries or even complete their entire life cycles in these environments, largely because of the highly variable and often unpredictable nature of prevailing conditions. Most species have the advantage that they are highly mobile and sufficiently large that they can come and go as they please, enjoying the good times whilst avoiding the bad. These species are termed migrants and include mostly marine species that enter estuaries from the sea but also a few freshwater species that enter from rivers.

The main feature of the life cycle of most marine species entering Southern African estuaries is the division into a juvenile phase that is predominantly estuarine and an adult phase that is predominantly marine. Adults of the marine species spawn at sea, and the juveniles enter estuaries shortly after metamorphosing from larvae when they are between 10 and 60 mm in length. The proportion of juveniles entering estuaries varies among species, and ranges from those species that are seldom found in estuaries, to those species that are entirely dependent on estuaries during the juvenile phase of their life cycles (Wallace et al. 1984). Whitfield (1994) has identified a set of 37 species in southern Africa whose juveniles he considers entirely dependent on estuaries as nursery areas and that are liable to go extinct if denied access to these systems. Most of these species will spend between one and three years in the estuarine environment before returning to the sea to join adult stocks.

Some species, termed estuarine species, have evolved the necessary adaptations in order to breed within estuaries. These are mostly small species that mature at less than 70 mm in length (by contrast most marine taxa only mature above 200 mm length) and have specialised reproductive traits that reduce the mortality of the more sensitive egg and larval stages and/or facilitate the retention of their eggs and larvae within the estuarine environment. It has been suggested that the small size of these species reduces their physical ability to undertake migrations to and from the marine environment (Wallace 1975). Some estuarine species are also able to breed in the sea and are found in abundance there, but most have become entirely dependent on estuaries and cannot survive for long outside of these systems.

Another group of fishes occasionally found in estuaries are the diadromous species – those that migrate between rivers and the sea for breeding purposes. The African subcontinent has four catadromous species (freshwater species that breed in the sea) and no anadromous species (marine species that spawn in fresh water). Only one of catadromous species (freshwater eel Anguila mossambica) is abundant and widespread in southern Africa. This species is dependent on the availability of open estuaries as a migratory route for its survival.

4.3.4 Other nekton

Nekton is a termed used to describe swimming organisms and in the case of estuaries in southern Africa includes the likes of swimming crabs, penaeid prawns, palaemonid shrimps, crocodiles, turtles and of course fish. Penaeid prawns commonly found in southern African estuaries include several species belonging to the genera Penaeus and Metapenaeus, while several species of palaemonid shrimp from the genera Macrobrachium, Palaemon and Nematopalaemon and only one species of swimming crab (Scylla serrata) (Forbes 1999). With the exception of one species of the genus Palaemon, all are tropical Indo-Pacific species that extend down the east coast becoming progressively less common southwards. Most are found only in KwaZulu-Natal while some extend as far south as the Knysna estuary (34°04'S). Like many of the fish species frequenting estuaries in southern Africa most of these invertebrates use estuaries as nursery areas, and migrate between them and their offshore spawning grounds that are occupied by the adults and larvae.

4.3.5 Birds

Many species of birds take advantage of the abundant food resources in estuaries. They are exceptionally mobile animals capable of travelling large distances in relatively short periods. This allows them to exploit the temporally and spatially fluctuating resources available in estuaries that are outside of the reach of many other animals. One hundred and sixty-two bird species are thought to occur regularly in South African estuaries (Hockey & Turpie 1999). Temperate estuaries characteristically support mainly migrant populations of birds while tropical estuaries also support large populations of resident birds (Siegfried 1981).

Migrant birds frequenting estuaries are drawn chiefly from two taxonomic groups – Charadriiformes (waders or shore birds) and Anatidae (ducks, geese and swans). The Charadriiformes (plovers, sand pipers and terns) are mostly Palaearctic migrants which breed mainly in the northern tundra but visit southern African estuaries during austral summer to feed. Resident birds mainly belong to the Ciconiiformes and Pelacaniformes (herons, storks, ibises, cormorants and pelicans).

The number of birds frequenting estuaries around the South African coastline decreases from east to west, with tropical and subtropical estuaries on the east coast supporting many more bird species than their temperate counterparts on the west coast. Dividing the coast into 200 km sections, Hockey et al. (1983) found that species richness north of Durban average 145; this decreased rapidly to 123 between Durban and Port Elizabeth and to 111 between Port Elizabeth and St Helena Bay. North of St Helena Bay, the average species richness per 200 km section was only 85, 57 of which were species that occur around the entire South African coast.

Hockey & Turpie (1999) have identified 15 bird species they consider to be highly dependent on South African estuaries (their national populations occurring predominantly or entirely within estuaries for at least part of the year) and 39 species that are partially dependent on estuaries (a relatively large potion of their populations are thought to occur in estuaries although they do make use of other wetland and intertidal habitats). The decline in overall species richness by 41% from east to west in South African estuaries observed by Hockey et al. (1983), is mirrored by a similar decline in the number of estuarine dependent species (a decrease of 38%). The proportion of estuarine dependent taxa, however, in each 200 km section remained remarkably constant, ranging from 33-39%.

4.4 TROPHIC FUNCTIONING IN ESTUARIES

In the past, organisms within the estuarine ecosystem have all be assigned to specific trophic (or feeding) levels. These are the groups of organisms, which share a common method of obtaining their energy supplies. They are usually arranged hierarchically as the organisms in one level usually form the basis of the food supply in the following level. Within an estuary, the phytoplankton, algae and macrophytes, or primary producers form the base level of the pyramid, utilising energy from sunlight to produce living biological material. Primary consumers, mainly invertebrates, feed on this living plant material as well as the non-living detritus and are in turn preyed upon by the secondary consumers or carnivores (mostly birds and fish). A very simply estuarine food web, showing the basic trophic levels, is depicted in Figure 1.

Several things are immediately obvious from the simplified estuarine food web outlined in Fig. 1. Firstly, all organisms making up the estuarine food web are ultimately dependent on the input of energy from two sources: sunlight and the transportation of organic matter into the estuary by rivers and tides. At this stage it is important to note that the term detritus is used to describe not only the decaying organic debris but also the vast numbers of micro-organisms (fungi and especially bacteria) responsible for its decay, as well as other microscopic organisms such as heterotrophic flagellates, ciliates and nematodes which feed on the agents of decay. These micro-organisms convert the plant material, much of which cannot be digested by animals, into a highly nutritious nitrogen-rich food source. Secondly, some recycling of material does occur (as can be seen from the lowest loop where animals and plants that die are incorporated within the detritus pool). This is generally a small component, however, as a great deal of the energy (or organic matter) from estuaries is simply carried out to sea with the net flow of water or is actively removed by migratory species such as fish and birds. Thirdly, not all species (or in this case groups of species) fit comfortably within the trophic levels to which they have been assigned. Some consumers feed on animals at the same level as themselves as well as those in lower levels, others feed on both producers and consumers and others change their diets seasonally in response to the availability of different food sources.

For the reasons outlined above (and others) it is more common nowadays to draw up food webs without strict trophic levels. Members of the estuarine community are simply assigned to compartments which are joined using the appropriate links which represent the flux of energy or (more often) carbon between them. Figure 2 shows examples of carbon flow networks from the Swartkops (southern Cape) and the Bot estuaries (western Cape) developed by Baird (1999). Although there are considerable differences in the composition of the species in the various communities or compartments, structurally they are very similar. It is thought that essentially the same trophic guilds e.g. suspension feeders, deposit feeders etc., occur in virtually all estuarine systems.

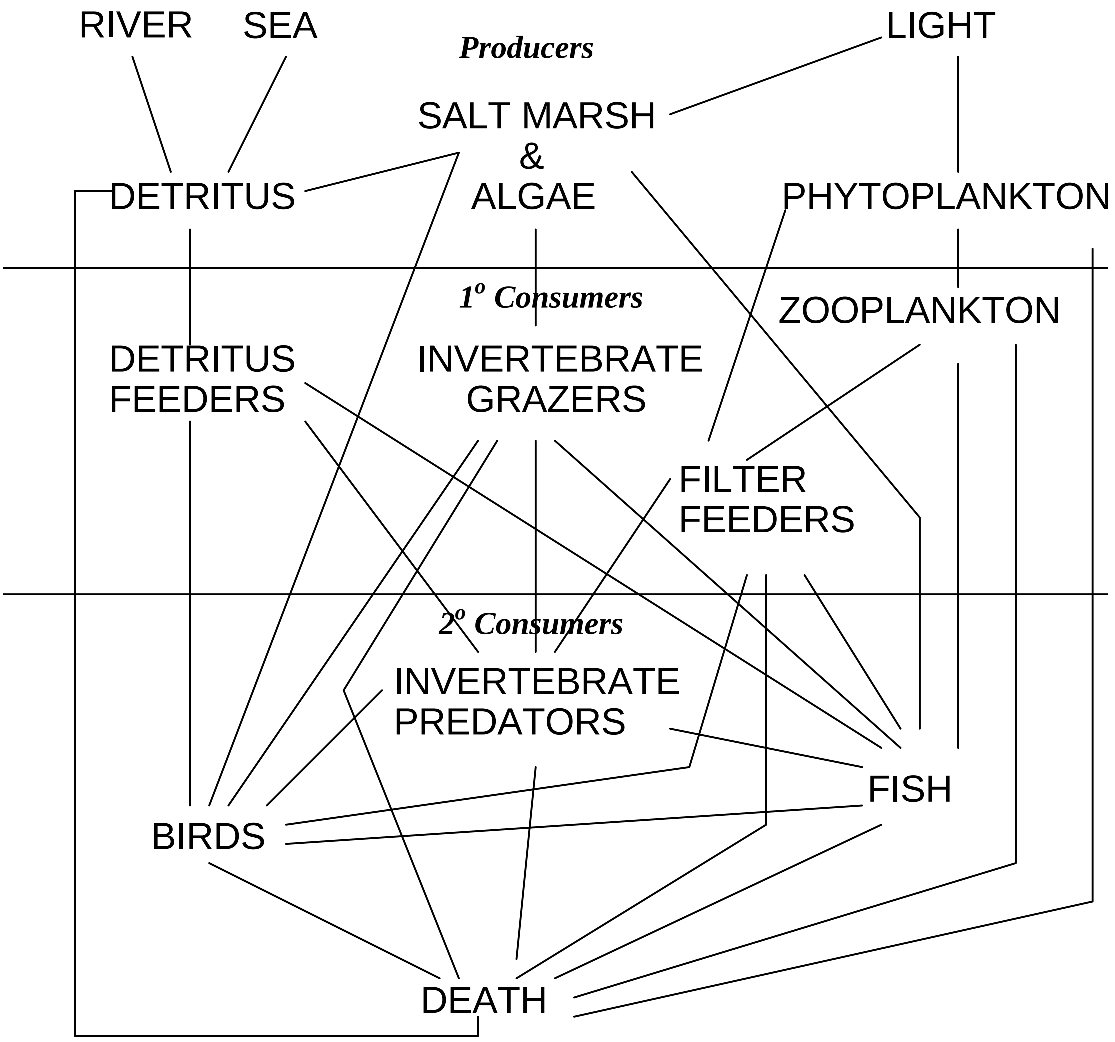

Fig. 1. A generalized model of an estuarine food web. The arrows indicate feeding relationships and the dotted lines the approximate division into producers, primary consumers and secondary consumers.

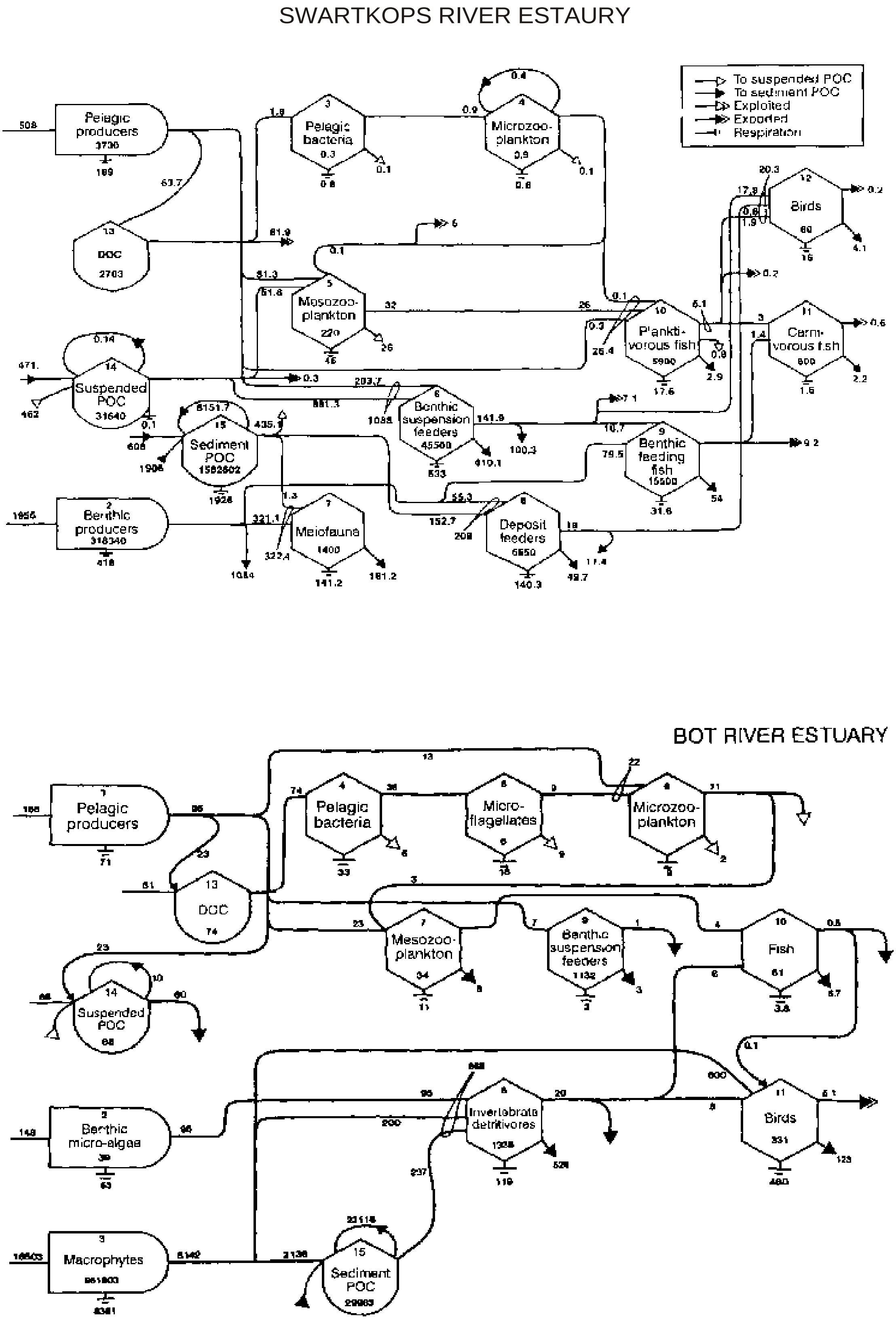

Fig. 2. Carbon flow networks from the Swartkops and Bot estuaries. After Baird (1999).

5. THE CURRENT STATE OF SOUTH AFRICAN ESTUARIES

World-wide the demands of a burgeoning population are placing ever increasing demands on the resources of the planet. South Africa is no exception. Much of the country is semi-arid or prone to severe droughts. This has necessitated the construction of dams on most of the larger rivers as well as large inter-basin transfer schemes to satisfy the extreme demands for freshwater in certain areas. When faced with the task of feeding and improving the living conditions of its people, the needs of the environment generally take second place. Water allocated for environmental purposes is viewed by many as water wasted. This is extremely unfortunate as the damming and abstraction of water from river systems in South Africa has had a profound effect on the estuaries downstream. Apart from simply reducing the volume of fresh water entering estuaries, dams also disrupt an essential element in their natural cycles – namely the normal flood events. Dams cause a decrease in the overall number of floods, the volume of water per flood and also increase the time between flood events. Floods are the principal means by which accumulated sediment is removed from the mouths of estuaries thereby maintaining or re-establishing their connection with the sea. By damming a river, the estuary downstream opens to the sea with reduced frequency and for shorter periods, reducing opportunities for biota to move between estuaries and the marine environment.

Fortunately views on freshwater requirements of the environment and estuaries in particular have changed in recent years. Following on from its original introduction by Roberts (1983), the concept of allocating a portion of river runoff to environmental management is now widely accepted by researches and managers alike. The Department of Water Affairs (1986, 1991) now recognises estuaries as “valid” users of water. Commitment to this philosophy has been reaffirmed through the allocation of funds for the estimation of what the regional freshwater requirements for estuaries might be (Jezewski & Roberts 1986) as well as those for specific estuaries (e.g. CSIR 1992 a, b, c). Such assessments have only been completed for a very small number of systems, however, and the recommendations emanating therefrom have been implemented in even fewer cases.

The reduction of freshwater flow into estuaries may have had the single greatest impact on estuaries, but it is not the only one. Estuaries have also long been popular growth points for coastal developments and holiday resorts. This has resulted in the construction of bridges, causeways, jetties, marinas and the artificial opening and closure of mouths, all considered essential for human recreational activities. Pressure on estuarine areas in South Africa has been particularly great because of the rugged nature of our coastline; a coastline that has few truly sheltered embayments and is dominated by high wave energy regime and strong winds throughout the year (Field & Griffiths 1991, Morant & Quinn 1999). Artificial breaching of estuary mouths is usually undertaken to safeguard properties built below the normal breaching levels of a particular system. This can have serious long-term implication for the sediment dynamics and biota of a particular system. Breaching the mouth artificially when the water level is below that when breaching would occur naturally results in reduced scour potential and in the long term, accumulation of sediments in the estuary mouth. Following breaching, water levels drop dramatically exposing large areas of the estuarine basin to desiccation; macrophyte vegetation previously submerged becomes stranded and dies along with the associated invertebrate fauna; water birds desert the area, taking many years before they return again.

Poor agricultural practices, leading to soil erosion and pollution, have also had a major impact on estuaries in South Africa. Soil erosion leads to siltation, which is considered to have had the greatest impact on estuaries in KwaZulu-Natal than any other single factor (Begg 1978). Modern rates of sediment supply to estuaries in this part of the country are considered to be 12-22 times greater than the geological average (Martin 1987). The consequences of high sediment yield for estuaries is an increase in sedimentation resulting in a shallower estuarine basin which affects the temperature regime of the water column and encourages the encroachment by reeds and other marginal vegetation.

In metropolitan areas the local effects on estuaries have almost invariably been severe to extreme, and include pollution, canalisation and profound modification of the natural circulation. By far the greatest volume of effluent discharged into estuaries is domestic waste, the main constituent being organic matter. The decomposition of organic material is a natural process that occurs in all estuaries. Bacteria and other micro-organisms are able to metabolise most of the organic compounds, using oxygen and releasing nutrient salts, particularly nitrogen compounds and phosphate. So long as there is sufficient oxygen available, estuarine communities flourish. However, when organic matter is supplied at a rate which exceeds the oxygen supply (e.g. an estuary receiving sewage effluent) anaerobic bacteria begin to flourish. This normally occurs only in subsurface mud, but when pollution becomes serious, the overlying water also becomes anoxic and first nitrates then sulphates are reduced and hydrogen sulphide is liberated. Hydrogen sulphide is toxic and leads to the death of submerged plants and animals which add to the pollution load. Oil, surfactants and heavy metals such as mercury, chromium, arsenic, cadmium and copper are commonly found in industrial effluents that discharged into metropolitan estuaries. These chemicals are all toxic to plants and animals to vary degrees and tend to become concentrated in their tissues.

Many of the organic pesticides and fertilisers used for agriculture in catchment areas often find their way into estuaries. These chemicals have the effect of increasing nutrient concentrations in estuaries. In small quantities these can be beneficial, acting as a fertiliser and increasing the productivity of the system. In large quantities, however, they can operate in a similar manner to sewage pollution, leading to eutrophication and the eventual loss of biodiversity.

Assessments of the biological health of estuaries in South Africa indicates that the overall status of these systems is very low. Rating estuaries on the west, south and KwaZulu-Natal coasts, Heydorn (1986) found most estuaries to be in fair (46%) or poor condition (26%) . Only 28% of the estuaries rated were considered to be biologically in good condition. Results were similar in all three sectors of the country sampled, with the west coast having the smallest proportion of biologically healthy estuaries (22%). The situation has undoubtedly declined since this time, which is reflected in the results of Cooper (1994) and Harrison et al. (1994, 1995) . These authors also rated 109 estuaries on the west, south and KwaZulu-Natal coasts, but this time on a scale of 0-10. Only 7% or 8 of these estuaries received a score or 7.0 or more, with the majority receiving scores of 4.0-6.9 (55%) or less (0.0-3.9, 38%). If we assume that these groupings are even remotely similar to those of Heydorn (1986) (accepting that the ways in which these were calculated are completely different – see footnotes below), this implies that a massive decline has taken place in the health of South African estuaries in the intervening years. Not only is the overall health of South African estuarine systems low, but it appears to be declining at an alarming rate.

[1] Heydorn (1986) rated estuaries as being “Good” which implied that the catchment was not overly disturbed by erosion or river regulation nor was it subject to serious inputs of organic or toxic waste (or any combination thereof); as “Fair” if there was a noticeable degree of degradation in the catchment through any of the above, and “Poor” if the estuary in question had been severely altered (by canalization for example) or were so heavily eutrophied that sediments had become anoxic.

[2] The rating system used by Cooper (1994) and Harrison et al. (1994, 1995) was based on a comparison of fish species fish present in each estuary to hypothetical or historical list of species that would have been present in the absence of or prior to degradation. It assumes that any major differences between the potential and existing communities are due to habitat degradation.

Biological health indices for estuaries on the west, south and KwaZulu-Natal coasts as calculated by Heydorn (1986) and Cooper (1994) and Harrison *et al.* (1994, 1995). The proportion in each category as well as the actual number (in brackets) are presented for each region.

	Heydorn (1986)			Cooper (1994), Harrison et al. (1994, 1995)		
	Poor	Fair	Good	0.0-3.9	4.0-6.9	7.0-10.0
West	34 (11)	44 (14)	22 (7)	64 (7)	36 (4)	7 (4)
South	17 (19)	56 (63)	27 (30)	38 (15)	50 (20)	0 (0)
KwaZulu-Natal	26 (19)	46 (33)	28 (20)	32 (19)	61 (36)	7 (4)
Total	26 (49)	46 (110)	28 (57)	38 (41)	55 (60)	7 (8)

6. LIKELY EFFECTS OF CLIMATE CHANGE

Climate scenarios currently represent the best methods available for predicting future climate change (Tyson 1990). Several such scenarios of climate change in southern Africa exist in the literature (e.g. Tyson 1990, Tyson 1993, Schulze & Kunz 1993, Shackleton et al. 1996, Perks et al. 1999), but confidence in their regional predictive power remains low, given the uncertainties involved (Tyson 1993, Shackleton et al. 1996, IPCC 1996). Several methods are available for developing these scenarios, the most favoured of which use results from large scale atmospheric models, know as General Circulation Models (GCMs).

Due to the limitations in our knowledge regarding future climate change at a regional scale as well as the likely responses these will elicit in the biota. I have no intention of trying to formulate clear predictions regarding the impact of future climate change on estuaries in South Africa. I will endeavour rather to explore some of the potential consequences of the current climate change scenarios on estuaries in this country. Effects of changes in five environmental variables likely to have the most profound consequences for South African estuaries are examined here. These include changes in the influx of freshwater into estuaries, temperature, sea level, atmospheric CO_2 and ultraviolet radiation. Very little is known about the potential additive effects of changes in these variables and thus are only really considered in isolation here. Wherever possible, climate change predictions were taken from results generated by recent runs of a variety of General Circulation Models.

6.1 FRESHWATER INFLOW

The most important variable that induces changes in volume of water in a particular catchment (and thus entering the estuary) is precipitation (Schulze & Perks 1999). Given that river inflow is one of the most critical factors influencing estuaries on the subcontinent, knowing how precipitation is likely to change on spatial and temporal scales in southern Africa in the future is critical for understanding what the future status of estuaries in this region will be. Predicted changes in both annual and seasonal precipitation over southern Africa vary widely. Even the outputs from high resolution GCM output show large discrepancies (Perks et al. 1999). For example, under a double CO_2 scenario the Genesis GCM predicts an increase in annual precipitation over the whole of southern Africa, while the CSM model predicts decreases of 5-15%. Both Hadley models (with and without sulphate forcing), on the other hand, predict a decrease in annual rainfall only in western and central parts of the country. Predicted seasonal changes in rainfall also show wide discrepancies. Attempts to validate the output from these models indicate that their ability to predict current and historical rainfall patterns is poor (Perks et al. 1999). However, Perks et al. (1999) argue that although significant errors have been identified in the output from GCMs for present (and historical) climatic conditions, they are still useful as an index of relative change in precipitation. This, they argue, is because there will be little or no relative change in the magnitude of the error for a 2x CO_2 climate scenario versus a 1x CO_2 scenario for the same model. Thus, the ratio between 1x CO_2 versus 2x CO_2 predictions can be used as a plausible scenario of relative change.

This is exactly what was attempted in this study. Dynamic simulations of runoff from 23 catchment systems from around the country (Fig 3) were generated using the ACRU agrohydrological modelling system (Schulze 1995). The ACRU models was presented with precipitation data for present and future (2x CO_2) climates predicted by the Hadley GCM excluding sulphate forcing. Only the relative changes in runoff for each catchment are presented here (expressed as a percentage) as absolute changes in runoff were not considered valid for the reasons outlined above. Detailed methodology for these assessments are provided in Perks et al. (1999) and Schulze & Perks (1999), respectively.

Using results from only one GCM is an obvious pitfall but was unavoidable as these were the only results available at the time of writing. The reader is thus cautioned to treat these results with extreme scepticism especially considering the variation in future precipitation patterns predicted by the various GCMs (see Schulze & Perks 1999 for full details). The magnitude and direction (i.e. positive or negative) of the changes in precipitation predicted by the various GCMs differs widely and this will obviously have a direct bearing on the resultant runoff from each catchment system.

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[3] All data on simulated flow changes were provided by Greg Kiker of the School of Bioresources Engineering and Environmental Hydrology, University of Natal on the basis of estuarine mouth coordinates supplied by the author.

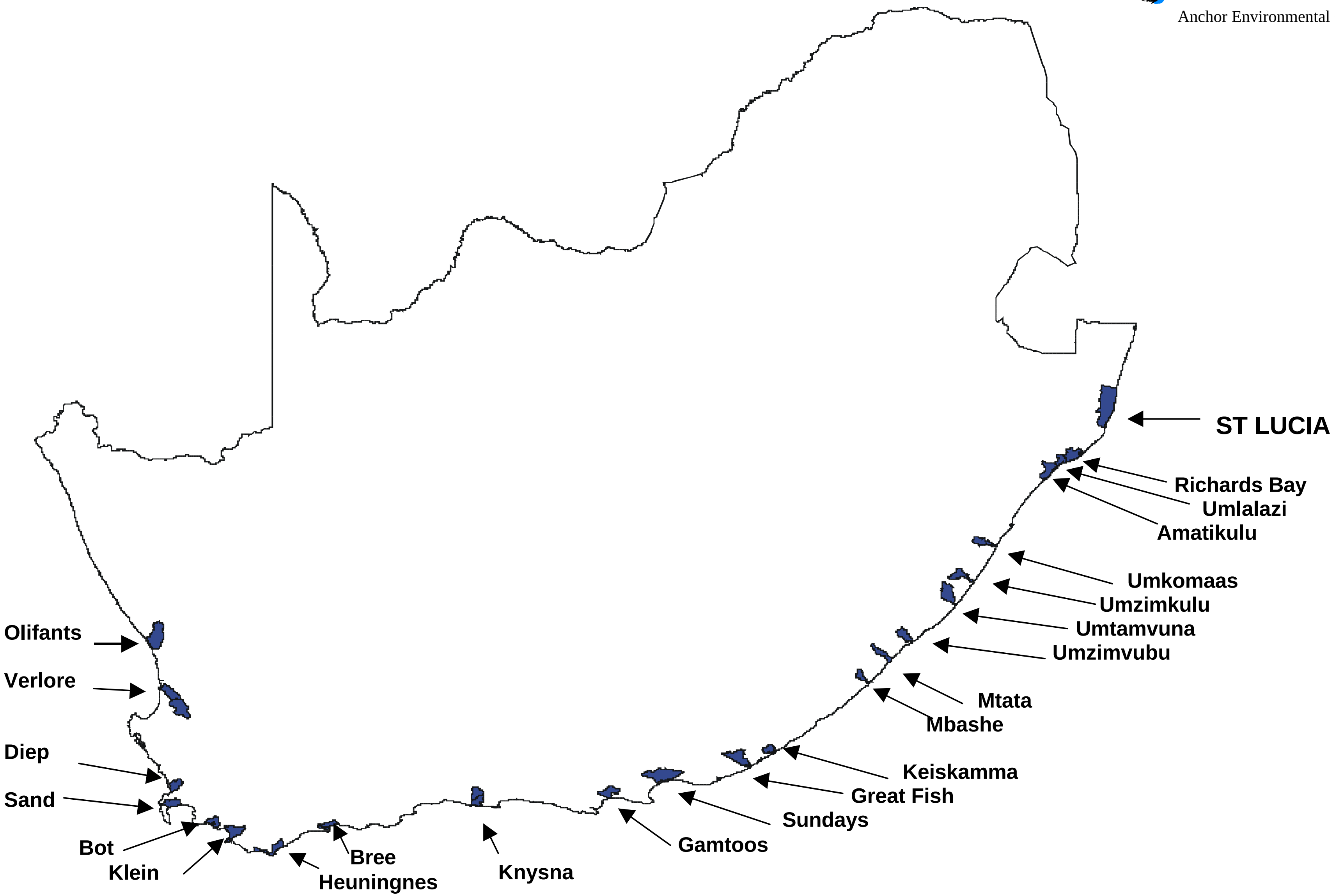

Fig. 3. Map showing the location of the catchment areas of the 23 estuaries for which changes in runoff were simulated in this study

The Hadley GCM excluding sulphates simulated a reduction in rainfall across most of southern Africa of between 5 and 15%, coupled with a general reduction in mean annual runoff (MAR) of 0-15 mm for most areas. Small increases in MAR could, however, be expected along the eastern coastline according to this GCM. These predictions are mirrored by reductions in total annual runoff from almost all-23 catchments examined, bar two (Fig. 4).

The model predicts that estuaries on the west coast (Olifants-Diep) and south coast (Sand-Keiskamma) will be hardest hit, experiencing reductions in flow between 11 and 84%. Those on the east coast are likely to less severely affected, some experiencing reductions in flow from 2-21% while others (the St Lucia and Mtata estuaries) will even receive more water in the future (increases of 2 and 10% respectively). There also appears to be a gradient in flow reduction, extending across the whole of the south coast from the hardest hit estuary (the Diep just outside Cape Town in the south-western Cape) right through to the Mbashe estuary on the east coast.

Seasonal changes in rainfall predicted by the Hadley GCM without sulphates widespread decreases in both summer and winter rainfall across the country. Summer rainfall is expected to decrease by as much as 25% or more in some areas (e.g. the Eastern Cape and the western tip of the country) while changes in the rest of the country are expected to be much more modest. Seasonal changes in streamflow projected from these changes in rainfall are shown in Fig. 5. Estuaries on the west and south coast estuaries as far east as the Knysna estuary can expect considerable reductions in streamflow during most months of the year. Modest increases can be expected for some of these systems in Autumn, however. Estuaries on the remainder of the south coast (Gamtoos-Keiskamma) and the whole of the east coast can also expect modest decreases in flow for most of the year, except during late winter and Spring where streamflow is predicted to increase substantially above existing levels for most systems (by as much as 180%).

Any reduction in flow will be felt most severely at the lower end of the river system. People will find it extremely difficult, if not impossible, to reduce their current levels of freshwater offtake. This means that the full effects of any flow reduction are likely to be passed directly onto estuaries around the country. Further reductions in flow can only exacerbate the dire situation in which many estuaries already find themselves, drastically altering their physico-chemical environments and impacting upon their ability to support biological communities.

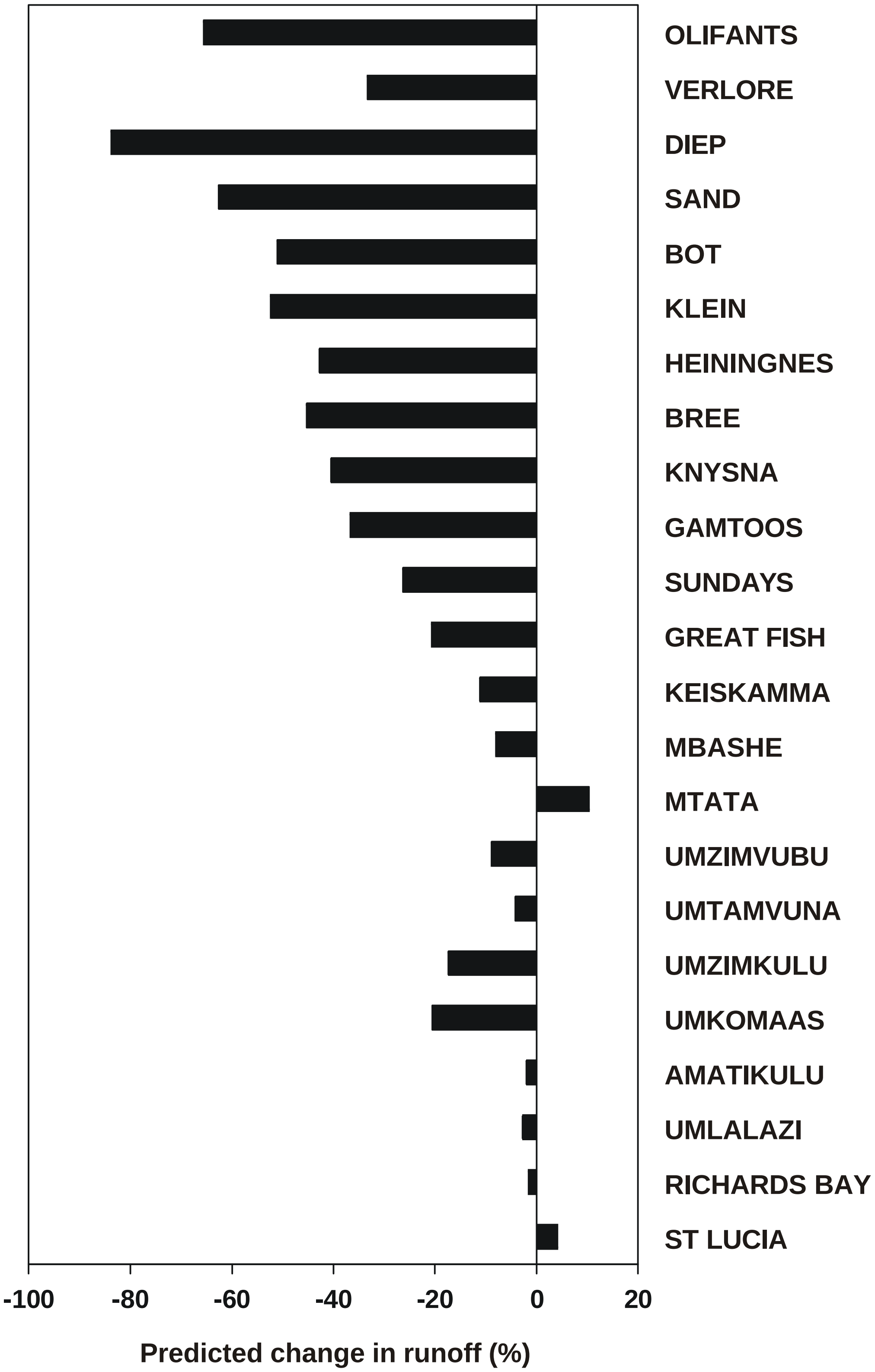

Fig. 4. Annual changes in the total volume of freshwater reaching a selection of estuaries in South Africa simulated by the ACRU agrohydrological modeling system using data from the Hadley GCM without sulphates (present vs. $2xCO_2$ scenario).

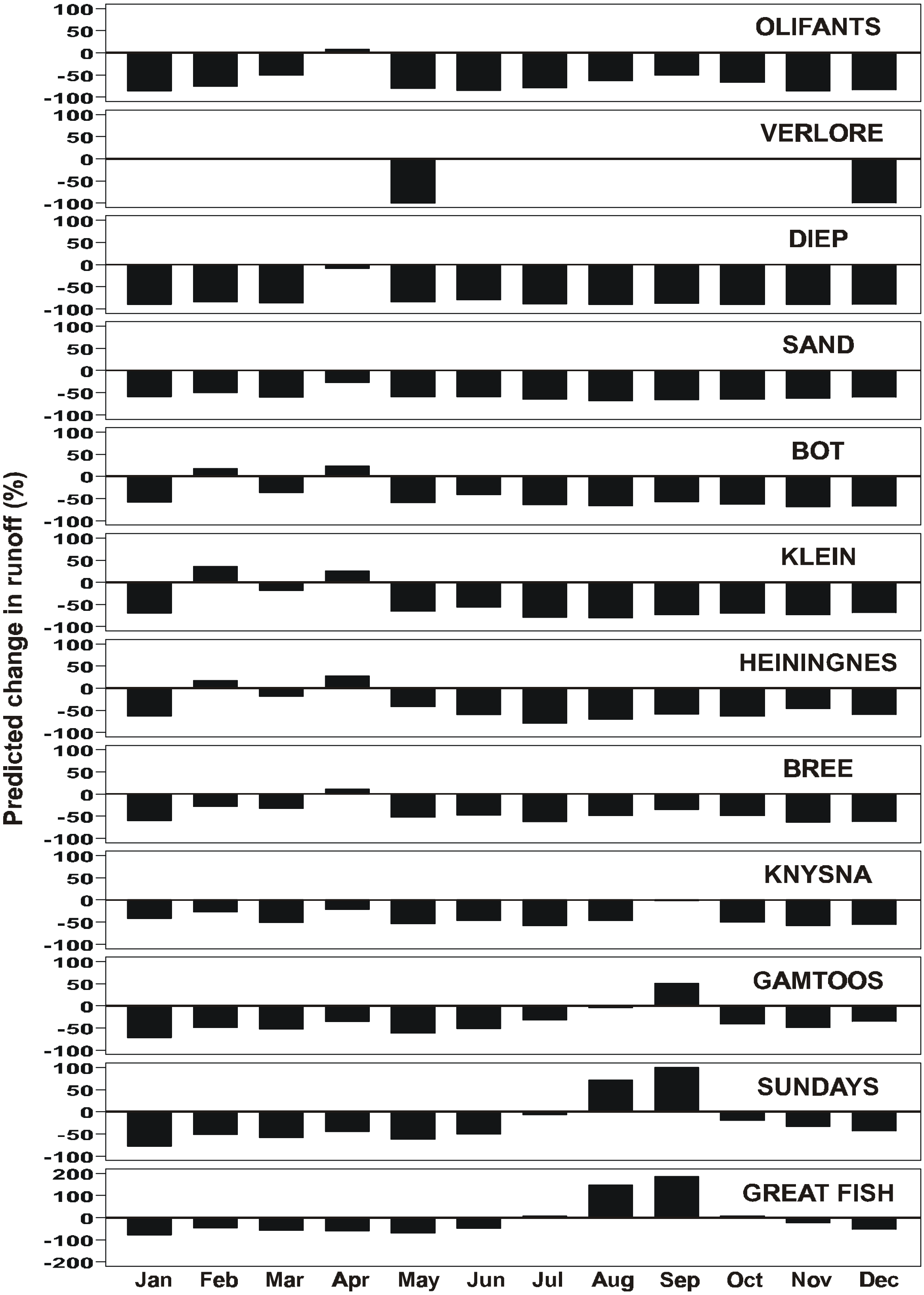

Fig. 5. Monthly changes in the total volume of freshwater reaching a selection of estuaries in South Africa simulated by the ACRU agrohydrological modeling system using data from the Hadley GCM without sulphates (present vs. 2xCO_2 scenario).

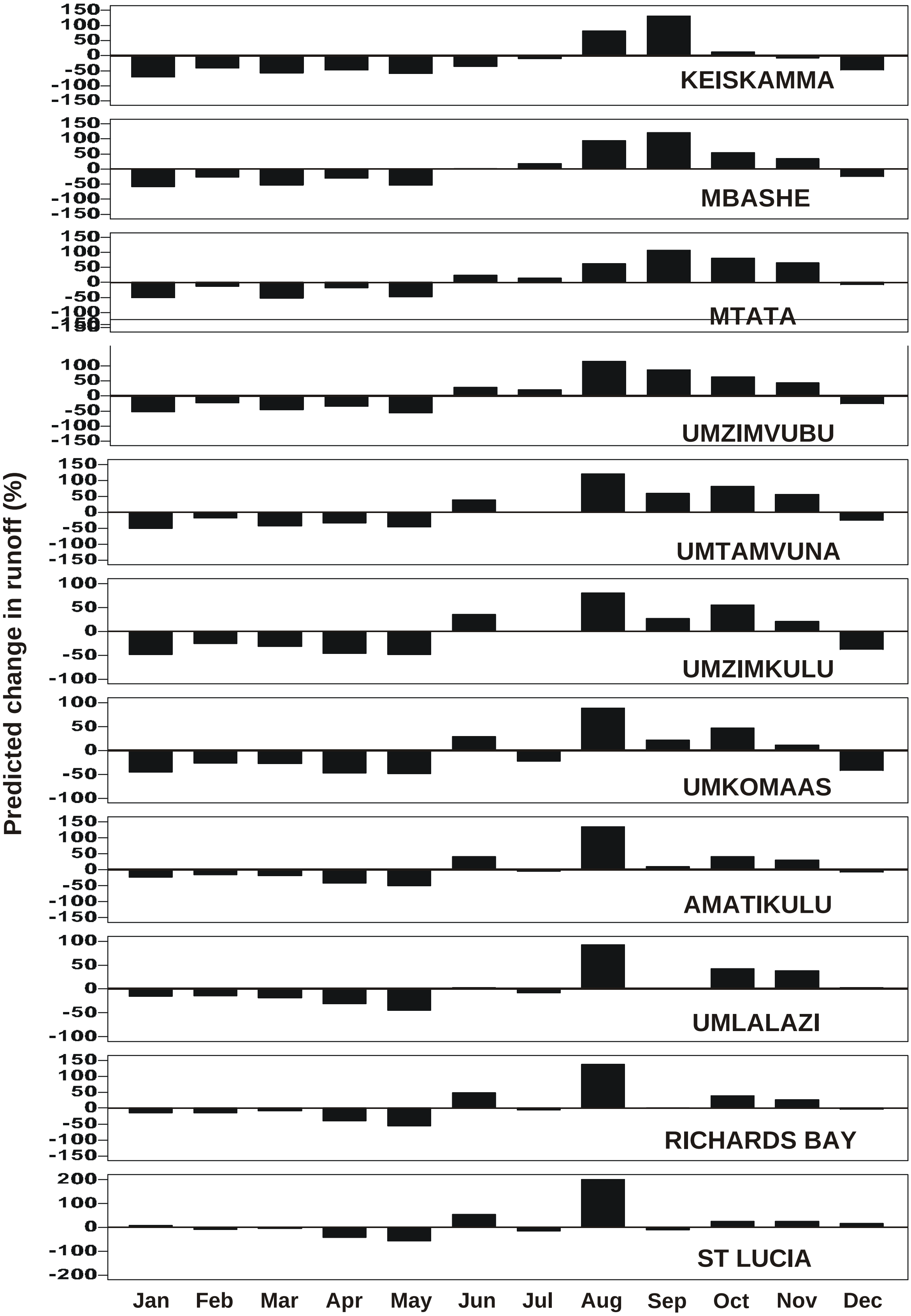

Fig. 5. cont. Monthly changes in the total volume of freshwater reaching a selection of estuaries in South Africa simulated by the ACRU agrohydrological modeling system using data from the Hadley GCM without sulphates (present vs. 2xCO_2 scenario).

A reduction in flow, particularly in the frequency or intensity of flooding, has several major consequences for an estuary. These include changes in the erosional capacity and other sedimentary processes, depth profiles, mouth configuration, duration of the open phases and tidal prism within an estuary. Sand shoals situated in the mouths and lower reaches of estuaries will grow larger, constricting the channel and reducing tidal exchange with the sea. Ultimately this will have the effect of increasing the frequency and length of time for which the mouths will close or remain closed. A change in flow may also be accompanied by changes in nutrient levels, suspended particulate matter, temperature, conductivity, dissolved oxygen and turbidity (Drinkwater & Frank 1994), all of which play a role in structuring biological communities in estuaries. Many estuaries will simply remain closed for much of the year or for several years at a time resulting in massive reductions in biodiversity in these systems. Many marine fish and invertebrate species have adapted their breeding habits to take advantage of the seasonal opening and closure of river mouths which varies around the country. Seasonal changes in river flow are likely to alter the timing of the open and closed phases which will impact negatively on recruitment into these systems. This and the permanent loss of many estuaries will result in the collapse of stocks and potential extinction of many estuarine species. Turbidity gradients established by the flow of freshwater through estuaries provide olfactory cues that certain species use as navigational aids when entering these systems (Cyrus & Blaber 1997). Any reduction in flow will make it more difficult for these organisms to correctly orientate to and navigate into estuaries. The interaction between tidal and river flow is thought to promote estuarine phyto- and zooplankton stocks, which when absent or reduced, leads to a reduction in the productivity of the water column and an increase in dependence on rooted macrophytes (Allanson & Read 1995). This will result in further reductions in biodiversity as filter feeding species dependent on phyto- and zooplankton stocks are deprived of essential food supplies. Reduction in the abundance of zooplankton in certain Eastern Cape estuaries in response to reduced freshwater inflow is believed to be responsible for the only extinction known for a marine species (the river pipefish) in southern Africa (Whitfield & Blaber 1996). A reduction in freshwater runoff is also likely to result in a reduction in the extent to which wastewater discharges are diluted before reaching estuaries. The concentration of pollutants in estuarine waters will increase while levels of dissolved oxygen will decrease, reducing the capacity of these environments to support biological communities.

The effects of freshwater deprivation will vary according to estuary type and locality. Estuaries in regions of low rainfall and high evaporation rates are likely to be more severely affected by a reduction in freshwater runoff than those in high rainfall regions. This is reflected in the virtual absence of hypersaline conditions in KwaZulu-Natal estuaries, when compared with those in the more arid Eastern and Western Cape (1981b). Hypersaline conditions (salinity >40 ppt) develop when evaporative water loss exceeds freshwater inflow into an estuary. The water in the estuarine basin becomes saltier to the extent that the salinity of the estuarine waters significantly exceeds the sea. This phenomenon usually only occurs in seasonally or normally closed estuaries, but is not uncommon in the upper reaches of permanently open estuaries, especially where freshwater runoff has been severely depleted for whatever reason. When hypersaline conditions develop in an estuarine basin, the water tends to become stagnant and unsuitable for occupation by most species. These conditions often result in mass mortalities among species unable to avoid them.

6.2 TEMPERATURE

One of the principal effects associated with an increase in greenhouse gasses in the atmosphere will be an increase in mean global air temperature (IPCC 1996). The most recent estimates suggest that annual global air surface temperatures have already warmed by 0.57°C over the period 1861-1997 (Jones et al. 1999). The warmest years on record have all occurred during the 1990s; the four warmest in descending order being 1998, 1997, 1995 and 1990. Placing this in perspective within the last millennium is difficult owing to absence of instrumental data, but can be done using proxy climatic sources such as tree ring densities and widths, ice core and coral records. A number of such proxy records of temperature changes over the last millennium have been assembled (see for example Mann et al. 1998, 1999, Briffa et al. 1998, Jones et al. 1998) and several striking features are evident therein. The twentieth century emerges as the warmest of the millennium, the warming during this century being unprecedented. The warmest years on record (see above) are the warmest since 1400, and probably since 1000 (Jones et al. 1999). High resolution GCMs predict that this warming trend will continue, with mean surface air temperatures over southern Africa expected to rise by as much as 2.5-3.0°C with a doubling in atmospheric CO_2 concentration (Perks et al. 1999). Similar models predict that maximum and minimum temperatures over southern Africa will increase by 0.5-4.5°C for the months of January (typical summer month) and July (typical winter month), respectively. Importantly, predicted increases in maximum temperatures are higher than the minimum temperatures, resulting in an increased temperature differential in most areas.

No firm predictions are available for changes in sea surface temperatures, but it is felt that these are likely to lag behind the rise in air temperature by about 20 years (Shannon et al. 1990, IPCC 1996). Long-term sea-surface temperature (SST) records from around southern

Africa (and elsewhere), however, already show an increasing trend. Off southern Africa, this has taken the form of an increase amounting to around 0.25°C per decade (Schumann et al. 1995) or 1°C since World War II (Taunton-Clark & Shannon 1988). Being much smaller bodies of water, estuaries are likely to respond much faster than the sea, and will probably mirror changes in surface air temperature much more closely than the sea.

Temperature is generally considered to be one of the most important physical variables controlling the life of all aquatic organisms. Changing global temperature thus have far reaching consequences for these organisms. The vast majority of aquatic organisms are thermoconformers; that is, they cannot maintain body temperatures much different from the water in which they occur. For many species, temperature is the master switch controlling many important behavioural and physiological responses, such as feeding growth, migration and reproduction. It controls the rates of metabolism and development and often governs distribution patterns. The most obvious changes that can be expected with increasing sea surface temperatures around the country, is that individual species or species assemblages will shift their distribution patterns in response to changing temperature regimes. This is likely to be most pronounced in those species that are most temperature sensitive or whose distribution patterns are strictly governed by temperature. With regard to the marine environment, some of the cold-tolerant species typically found only on the cool temperate west coast may be intolerant of increased temperature and will become more restricted in their distribution in the face of increasing temperatures. They may retreat to greater depths or become restricted to the immediate vicinity of the stronger upwelling cells. Meanwhile, some of the warm-tolerant species from the east and south coasts may expand their ranges southwards and westwards, possibly even moving around Cape Point onto the west coast. Indeed, such changes have already been observed in the face of major temperature anomalies both locally and abroad (see for example Crawford et al. 1990, Southward et al. 1995, Bhaud et al. 1995). Branch (1984) noted several such changes in South Africa during an unusually warm even that occurred during the summer of 1992/1993. Several “warm water” species extended their ranges much further into cool or cold waters than normal; mass mortalities in excess of those normally experienced were observed in certain “cold water” species; and atypical recruitment patterns (including both marked increases in recruitment and recruitment failure) were observed for certain species at the extreme edges of their ranges.

Examples such as the one above, which deals with strictly marine species or at least marine populations, abound in the literature. Few if any such examples have been reported for estuaries. Two principal reasons are probably responsible for this. Firstly, populations of estuarine organisms naturally tend to be highly variable in space and time and small changes are thus difficult, if not impossible, to pick up. Secondly, estuaries do not form a contiguous environment right along the coast which makes simple range extensions more difficult. Many estuarine species (particularly the resident species) may not be able to survive the prevailing conditions in the intervening marine environment between their home and target estuaries, even if they are suitably mobile. Other species, particularly invertebrates dependent on larval life history stages for dispersal, may not be capable of extended travel. Thus, although small incremental changes may not pose a major threat to marine biota, they may be significant for estuarine organisms in the long term. The magnitude of the overall change is probably more important than the rate of change itself, considering that animals (and plants) in the sea normally experience seasonal changes in temperature.

Fortunately most species frequenting estuaries in southern Africa are marine migrants (i.e. have the capacity to colonise new estuaries), they utilise estuaries on a facultative basis only (i.e. are not dependent on these systems for their survival) and/or are fairly widespread (i.e. inhabit a number of estuaries spanning a fairly wide area). Few extinctions or catastrophes can thus be expected as a direct consequence of temperature change, but we can still expect certain small changes as a direct response to increasing air and sea temperature. Over the long term, the fauna and flora of our “cool-water” estuaries will probably come to resemble neighbouring estuaries that are currently situated in warmer waters, albeit with somewhat reduced diversity.

Several species (including some important fish and invertebrates) are entirely dependent on estuaries for their survival or are restricted to a small number of estuaries (e.g. less than five). These are obviously the most vulnerable as many of them are already severely depressed or threatened as a result of existing degradation, and may not survive further change. Other effects that can be expected as a consequence of increased temperatures may include increased growth in certain species. Higher temperatures will favour higher rates of food digestion and assimilation (Costa 1990), provided of course that sufficient food resources are available to sustain this growth. It has been argued that because estuarine temperatures are generally warmer than the adjacent sea, marine organisms in these environments are already close to their physiological tolerance limits (Odum 1970). Even a small increase in temperature may thus have drastic consequences. Many animals require specific temperatures for spawning, sometimes preceded by a temperature increase or decrease (Costa 1990). Increased temperatures may thus result in a broadening of the spawning period of these organisms, and increased opportunities for survival. Changing temperatures may also result in changes in competitive interactions. For example, several authors believe that increases in sea surface temperatures off southern Africa may have been partly responsible for initiating a switch over from an anchovy to a sardine dominated system (Crawford et al. 1990, Shelton et al. 1985). Sardine is thought to have been offered a competitive advantage because of reduced spawning activity among anchovy, brought on by low survival of larvae in excessively warm waters. A similar explanation has been offered for changing dominance by the herring-pilchard pair in the English Channel (Southward 1963).

Not only will the effects of increasing global temperatures on estuaries be felt directly, but also indirectly through mechanisms such as an increase in evaporation, which, if are not balanced by increases in rainfall or freshwater runoff will result in increases in the salinity of estuarine waters in general as well as an increase in the occurrence of hypersalinity (i.e. salinities above 40 ppt). Hypersalinity is a drastic event responsible for the mass mortality of many estuarine organisms, and is dealt with in more detail in changes in freshwater inflow (Section 5.1 above).

6.3 SEA LEVEL

It is now generally accepted that as global mean temperature continues to rise, global sea level is expected to rise as well (Gornitz et al. 1982, Thomas 1987, Lutjeharms & Valentine 1991). This has in fact already begun, with measured increases of between 10 and 15 cm having taken place over the last century (Gornitz et al. 1982, Barnett 1983, Brundrit 1995). Whether sea levels will continue to rise at this rate is open to speculation, but considering that there is a fairly close correlation between global surface air temperature and sea level most authors accept that this trend is likely to accelerate in the future (Brundrit 1995). The Intergovernmental Panel on Climate Change (IPCC) has estimated that by the year 2030 global mean sea level will be 8-29 cm higher than in 1990 with a best estimate of 18 cm, and by 2070 it will have risen by 21-71 cm with a best estimate of 44 cm.

The effects of rising sea level on estuaries is likely to be complex, with both positive and negative consequences expected. Geological evidence suggests that estuaries have been an integral part of the South African coastline for at least the last 150 million years (Reddering & Rust 1990, Rust & Reddering 1990), in spite of several changes that have taken place in sea level. This suggests that estuaries are naturally able to re-establish themselves over geological time-scales as new sea levels develop (Reddering & Rust 1990). Rising sea levels are actually considered to promote the development of estuaries; estuaries tending to be relatively large and abundant after periods of rising sea level (Schubel &

Hirschberg 1978, Reddering & Rust 1990). Thus, from a physical viewpoint, a rise in sea level is likely to be beneficial, as it has the potential to improve the dynamic operation and size of most estuaries (Reddering & Rust 1990). Tidal waters are likely to flood a wider section of most river valleys and their estuaries, and increase the size of the tidal prism moving in and out of their mouths. Estuaries that are seasonally or even normally closed are likely to become permanently open. Whether this will be sufficient to counter balance the effects of reduced freshwater inflow on inlet dynamics is completely unknown.

Increasing sea levels will also result in an increase in coastal erosion particularly in areas where soft sandy sediments predominate (Bruun 1962, Gornitz & Kanciruk 1989, Lutjeharms & Valentine 1991). Sea-level rise will result in net erosion of beaches, salt-marshes and estuarine areas, as it will allow storm waves to strike further inland and will decrease the ability of small waves to rebuild beaches. Salt-marsh and mangrove habitats exist in a dynamic balance between the accumulation and loss of sediment. During normal conditions, standing vegetation reduces the velocity of water moving through it or past it, resulting in the deposition of sediment and vertical or horizontal accretion of the marsh area. During storm or flood conditions, sediment and vegetation is scoured from the marsh area reducing its aerial extent. Research has shown that most coastal wetlands can withstand considerable increases in sea level provided that the vertical accretion of the wetland surface is equal to the water level rise (see for example Beeftink 1979, Bauman et al. 1984). In the absence of a strong supply of sediment, marshes rapidly become water logged or completely inundated and species unable to tolerate these conditions or the increased salinity from marine waters, die back and expose the underlying sediments to further erosion (Beeftink 1979). Estuaries are fortunately sediment sinks and are usually sites of marsh accretion. Thus, they are likely to be buffered to a certain extent from sea level rise. However, even where salt marshes are able to accrete or migrate inland fast enough, investigations both locally and abroad have shown that the area just above the present sea level, available for wetland creation, is far smaller than that which would be lost to predicted increases in sea level (Titus 1987). Human responses to sea level rise will most likely be to build hard structures to hold the sea back, thereby protecting coastal properties. This would further limit the extent to which marshes can retreat in a landward direction, as sea level rises.

Overall, it is considered unlikely that all estuarine salt marsh and mangrove areas will be able to keep pace with rising sea levels through the natural processes of sedimentation and vegetation growth, particularly in the face of reduced freshwater input to these systems (Stevenson et al. 1985, Day & Templet 1989, Dijkema et al. 1990). Widespread destruction of salt marsh and mangrove habitat is expected in certain areas, with losses between 30 and

80% predicted by case studies in the USA (Lutjeharms & Valentine 1991). Salt marsh and mangrove flora constitute the most important plant life in estuaries, forming an integral part of the estuarine environment. They are the most important source of detrital material in estuaries, a major source of food for invertebrates and fish, important structural habitat and a major nutrient sink. The loss of this marginal vegetation would deprive many of the detritus based food webs of essential nourishment, many species of essential nursery, breeding and/or feeding grounds. In time lost vegetation may be replaced by beds of submerged aquatic vegetation such as sea grasses, but this at best would only support a completely different suite of organisms with much lower diversity.

6.4 ATMOSPHERIC CO_2

Aside from the indirect effects brought about by increases in atmospheric temperature, increasing levels of CO_2 in the atmosphere are also likely to have certain direct effects on estuarine biota. Since the atmospheric concentration of CO_2 is limiting to plant growth and photosynthetic rate, both processes are expected to increase with elevated atmospheric carbon dioxide (Rozema et al. 1990). Surveys with a variety of crop plants suggest that doubling the present atmospheric CO_2 level is likely to increase yields by about 30% on average (Kimball 1983). Effects on marine and estuarine flora are more difficult to predict. Almost all marine plant species fall into a group know as C_3-plants, which are expected to respond more strongly to increased CO_2 levels than their C_4 counterparts (Gates et al. 1983). Photosynthetic processes in most intertidal macroalgal species are Ci saturated, however, whereas this is not the case for subtidal macroalgae or seagrasses (Beardall et al. 1998). Responses in the latter two groups can thus be expected to be relatively strong, while little response is expected in the former. A note of caution must be voiced here, however, as certain authors feel that plant growth in salt marsh environments is limited primarily by salinity and anaerobic waterlogging conditions, rather than CO_2 concentration (see Rozema et al. 1990 for citations).

6.5 ULTRAVIOLET RADIATION

There is considerable evidence that the flux of UV-B radiation from the sun is increasing at certain locations, notably the Antarctic and Arctic regions (Crutzen 1992). The principal cause of this is thought to be anthropogenic ozone depletion, which is most severe in the polar regions (Vincent & Roy 1993). Even under “normal” conditions UV-B radiation is known to have inhibitory effects on photosynthesis and nutrient uptake and can cause damage to DNA in aquatic plants (Larkum & Wood 1993, Behrenfield et al. 1995, Gieskes & Buma 1997). Plant responses to UV-B radiation are very specific, however, and many species have evolved strategies for coping with the deleterious effects of this radiation (Vincent & Roy 1993). Intertidal species generally show less inhibition of photosynthesis by UV-B radiation than their subtidal counterparts, and it is thought that this may exert some sort of control over species' distribution patterns (Larkum & Wood 1993, Beardall et al. 1998). A corollary to this is that increasing UV-B fluxes may well change the species composition of seagrasses, phytoplankton and other aquatic plant communities, favouring those with UV tolerance or repair mechanisms (Dawson & Dennison 1996, Beardall et al. 1998). The full extent of these effects is still open to speculation at this stage, however.

UV-B radiation can also negatively affects animals as well as plants. It has been found to cause damage to early developmental stages of fish, shrimp, crab and other species (Häder et al. 1995). The most severe effects are considered to be decreased reproductive capacity and impaired larval development (USEPA 1987). Similar to plants, marine invertebrates also differ greatly in the sensitivity to UV-B radiation. Some species show no effects under a 16-fold increase while others suffer mortalities up to 50% at current UV-B levels at the sea surface. Fortunately, relatively high concentrations of suspended particulate matter typically found in estuarine waters limit the transmission of UV-B to the surface layers (<0.5-1 m, Kramer 1990). Thus, biological effects of increased UV-B radiation on estuaries is expected to be limited the surface layers and exposed vegetation and mudflats.

7. CONCLUSIONS

South African estuaries are important as ecological, economic and cultural resources. They exist in this transition zone between riverine environments and the sea, supporting rich and diverse plant and animal communities. They are highly productive and extremely variable both in space and time, responding to changes in the terrestrial environment above and the marine environment below. Their structure and the manner in which they function depends on complex interactions between the underlying geology and environmental influences such as rainfall, waves, winds and tides. This dynamic nature and dependence on both terrestrial and marine influences makes them extremely vulnerable to change.

The effects of climate change on these environments is extremely difficult to predict, and is likely to be far reaching. Changes in rainfall patterns over southern Africa, for example, are likely to have a major effect on the amount of freshwater entering our estuaries. This in turn is likely to drastically alter the chemistry of estuarine waters, the amount of nutrients entering these systems and the duration, timing and frequency of the opening and closure of their mouths. This in turn will alter the suitability of these environments for certain species and their accessibility to others. Current predictions indicate the potential for both increases and decreases in rainfall in different parts of the country, with corresponding changes in runoff entering the various catchment systems. Considering the rate at which the human population in this country is expanding and with it a need for additional freshwater, it is considered highly unlikely that any increased flow will ever reach the estuaries at the end of the line. At best, we can hope that this will ameliorate the reduction in flow for some systems. In the same vein, we can be fairly sure that those systems projected to experience a decrease in runoff are almost certainly doomed to extinction. The effects of an increasing global air temperature on estuarine environments is more difficult to predict. Simple latitudinal shifts in the distribution patterns of affected organisms as is predicted for parts of the marine environment, is unlikely to happen on a large scale with estuarine organisms. Estuaries do not form a continuous environment around southern Africa, and those species not capable of extended travel or not able to survive prevailing conditions in the marine environment, are likely to perish before reaching or colonising suitable new habitats. In the long term, as global air temperature continue to increase, we can expect an overall reduction in the diversity of estuarine fauna, with eurythermal and warm water species prevailing over stenothermal and cool water forms. Changes in the height of mean sea level, projected to increase in the future, offer some small hope for estuaries. A rise in sea level offers both benefits and drawbacks for most systems. It has the potential to improve the dynamic nature of estuaries by increasing the size of the tidal prism moving in and out of the mouth, but at the same time will wipe out large tracts of marginal vegetation that provide the major source of nutrition for the estuarine fauna. The influences of increasing atmospheric CO_2 and incident UVB radiation were also considered in this report, but are mostly speculative and not worth repeating here.

Our ability to predict reliably the consequences of climate change on estuarine ecosystems in southern Africa is severely hampered firstly by our ability to predict with any degree of confidence what the effects of a changing global climate will have on weather pattern on a regional scale; and secondly by our poor understanding of how estuarine flora and fauna will respond to these changes. At present, the information available for both of these aspects is wholly inadequate. Knowing that the bulk of the fauna found in estuaries is of marine origin, helps little, as knowledge of physiological tolerance limits of marine organisms and the effects of environmental variables on biological processes and interactions in the sea, lags way behind that for terrestrial systems. What is clear, is that estuaries are likely to be very severely affected by changes in climatic conditions, most likely more so than the marine or terrestrial environments. The technology exists to provide precise predictions regarding changes in certain variables, such as the likely changes in stream flow in response to changing precipitation and temperature regimes, but before this can be optimally exploited major advances need to be made in our ability to predict future changes in rainfall patterns themselves.

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CONCLUSIONS AND RECOMMENDATIONS

B.M. Clark

Several conclusions can be drawn from the preceding studies on the likely effects of climate change on the marine environment. In the first instance, it is clear that our ability to predict how marine ecosystems are likely to respond in the face of a changing climate is extremely poor. Most of the scenarios regarding the impact of climate change on the respective marine ecosystems described, were 'what if' scenarios. In very few instances was it possible to provide a definitive prediction about a cause and effect relationship.

Our ability to predict future changes in the atmosphere has increased enormously over the last decade but our understanding and hence our ability to predict what effect this will have on oceanic processes remains mostly speculative. Huge advances have been made in our understanding of how pressure systems and hence wind fields are likely to change over time, but our understanding of how this might affect currents and other oceanic processes (which are really important for marine biota) is almost non-existent. Improving our understanding of the processes that couple the ocean and atmosphere, particularly those that influence the transfer of heat, momentum and greenhouse gases between these two entities is of paramount importance. The worlds ocean covers over 70% of the earth's surface and exerts a powerful influence on the earth's climate and vice versa. It is also important to improve our understanding of how marine organisms, communities and ecosystems are likely to respond to future changes. Emphasis should be placed on examining responses to scenarios that most accurately describe ocean atmosphere changes. Reconstruction and analysis of ecosystems associated with past climates can assist greatly in this field. Monitoring of marine ecosystems can also make an important contribution toward understanding and evaluating the impacts of global climate change. Simple monitoring should focus on the continuation and/or initiation of long-term studies to discriminate direction change vs. year to year variability.

The marine environment is extremely robust, being able to absorb an enormous amount of punishment with little or no apparent change, before major changes start to occur. Many of the changes we are likely to experience as a result of changing climates will be relatively small. A few changes of colossal proportions can be expected, however, and it is these that we should concern ourselves with. We simply need to consider what happens during an El-Nino event in order to be convinced of this. Contraction or expansion in the range occupied by a few species is unlikely to have a great impact on a global or even regional scale unless these species are of great economic value or social importance. A change in the passage or volume transport of the Agulhas current on the other hand, is likely to have enormous implications for marine biota living along the whole of the east, west and south coasts of South Africa, and potentially much further afield. The species composition and trophic functioning of rocky shore, sandy beach, estuarine and subtidal communities along these shores is likely to be altered dramatically. It is imperative that we are able to anticipate these changes before they occur or at least identify them in their early stages. This will assist both in developing effective mitigation but also in convincing those in authority of the magnitude of the problem we are facing. Coastal communities in southern Africa depend heavily on the harvesting and sale of marine resources for their livelihood and/or income. The collapse of the sardine stock off Namibia in the 1960s had an enormous impact on the people living along the coast. Coastal towns were literally abandoned as people were forced to move on or starve.

Regrettably, in this case much of the damage has already been done. In many instances there is virtually nothing that can be done at this stage to halt the change in climate. Sea level rise is a case in point. An immediate and complete cessation in the production of greenhouse gases probably would not even fully avert the crisis we find ourselves in. At best we can attempt to minimize the effects of climate change by, for example, reducing outputs of greenhouse gases and through effective management of existing anthropogenic threats (a complete cessation in the production of greenhouse gases is not realistic). Slowing global warming and other forms of global change in the first place would do far more than any after-the-fact measures could do to conserve biodiversity in the long-term. Some effects of global climate change can still be mitigated, however. Consider the case of a potential reduction in freshwater runoff reaching southern Africa estuaries (which in many cases seems likely). This has greater implications for estuaries in southern Africa than any other single factor, and it can be mitigated to a certain extent at least. Consideration must therefore be given to identifying where and to what extent mitigation is possible, and then must be applied in the most appropriate manner.

Any system that is already compromised by existing impacts is less likely to be able to deal with new threats. Where it seems likely that existing threats will be exacerbated (e.g. in the case of volumes of freshwater runoff reaching estuaries), they need to be dealt with immediately rather than waiting until the problem becomes worse. We simply cannot afford to continue ignoring the problem because soon we will not be able to ignore it any longer.

APPENDIX

DATA REVIEW: DISTRIBUTION DATA AVAILABLE FOR SELECTED MARINE ORGANISMS AND PROTECTED AREAS IN SOUTH AFRICA

A.T. Lombard, Conservation Systems, July 1998

INTRODUCTION

A thorough examination of all available data regarding the distribution of marine biodiversity in South Africa was conducted. These data could be used in future research to monitor or predict the range extensions or contractions of selected species. This review describes the following data sets:

1. Marine Fish
2. Marine Invertebrates
3. Seaweeds
4. Corals
5. Bird Breeding Sites
6. Marine Protected Areas

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1. MARINE FISH

Title of database

The distribution of marine fish species that occur regularly on the South African coast and continental shelf.

Curator of database

Dr Jane Turpie, FitzPatrick Institute of African Ornithology, University of Cape Town.

Description

The entire South African coastline was divided up into 52 sections of 50 km each. Data were mapped by Turpie *et al.* (in lit.) using a GIS (ARC/INFO) format.

Only those marine fish species that occur regularly on the South African coast and continental shelf were included in the data set. Those species which occur in the open ocean, mostly at depths greater than 200 m, were not included, nor were those species which were recorded only once or twice in South African waters and are unlikely to occur regularly (i.e. vagrant fish). The data set includes a total of 1239 fish species (of the expected 2200 fish species which exist off the South African coastline). The taxonomic and distributional data are primarily from the work of Smith and Heemstra (1986, updated in 1993 and 1995). This data set was expanded with additional species: chondrichthyan by Compagno *et al.* (1989) and sciaenids by Griffiths and Heemstra (1995).

Based on distributional ranges, each species was recorded as being either present or absent in each of the 52 50 km sections of coastline. Where descriptions of distributional limits were vague, certain assumptions had to be made, because not all species distributions were at a fine enough resolution. Also, each species was placed in a category according to its world-wide distribution: global; Atlantic; Indo-Pacific; western Indian Ocean; endemic to southern Africa; or endemic to South Africa. The broad habitat preference of each species was also recorded as intertidal, demersal (sandy, rocky or coral reef) or pelagic.

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2. MARINE INVEREBRATES

Title of database

The distribution of marine invertebrates found off the South African coastline.

Curator of database

Prof. George Branch, Marine Biology Research Institute, Zoology Department, University of Cape Town.

Description

The data set was collected and collated Bruce Emanuel (Emanuel *et al.*, 1992). The geographic area covers the whole of southern Africa extending from the northern border of Namibia to southern Mozambique. Data were derived from three sources: University of Cape Town records which are kept in the South African Museum; available literature; and from data collected from field trips. Digital data are available in tabular form. Eleven subsets of data are included.

1. Amphipods of southern African rocky shores
2. Bivalve mollusks of southern African rocky shores
3. Echinoderms of southern African rocky shores
4. Characteristic macrobenthic Fauna of southern African rocky shores
5. Prosobranch gastropods of southern African rocky shores
6. Opisthobranch gastropods of southern African rocky shores
7. Littoral invertebrates of southern African sandy beaches
8. Chitons of southern African rocky shores
9. Pulmonate gastropods of southern African rocky shores
10. Scaphopods of southern African rocky shores

An example of each subset of data is provided below. For each species, the family, genus and species are provided. A "Y" refers to the number of sites where the species was actually recorded. An "X" refers to the inferred number of sites recorded. A "T" refers to the sum of the two which enables one to determine how ubiquitous the species is. The coastline is divided up into 48 sections of 100 km which are coded as the letters A-Z and a-v. At each of these sites, all present species have been recorded and are represented in the table as either a 1; a 2; or a space, which represents respectively that there is either a definite record of the species, that it has been extrapolated or that the species is absent.

Family:	Aeginellidae
Genus:	*Pseudaeginella*
Species:	*tristanesis*
Y:	3
X:	14
T:	17

Reference

Emanuel, B.P., Bustamante, R.H., Branch, G.M., Eekhout, S. and Odendaal, F.J. 1992. A zoogeographic and functional approach to the selection of marine reserves on the west coast of South Africa. *South African Journal of Marine Science* **12**: 341-354.

3. SEAWEEDS

Title of database

The distribution of seaweed species along the coastline of South Africa.

Curator of database

Assoc. Prof. John Bolton, Botany Department, University of Cape Town.

Description

The entire South African coastline was divided up into 59 sections of 50 km each.. Within each section , the presence (or absence) of 937 seaweed species has been recorded. For each of the species the phylum, order, family and genus is provided. All species fall under the three main algal groups: Phaeophyta, Chlorophyta and Rhodophyta (Bolton and Anderson, 1997). Species endemism is also recorded (i.e. species are listed as endemic to Namibia; South Africa; South Africa and Namibia; South Africa and Mozambique; South Africa, Mozambique and Namibia; or other). Digital data are available in tabular form.

For each species, the scale of available distribution data are recorded. Scales are either coarse (i.e. simply the names of landmarks), or more specific (lat-long co-ordinates as well as place names, and names of familiar places found within the co-ordinates). In addition, the resolution of the data (i.e. the occurrence of each species is described as collected, a vague description, an extrapolation, or the literature records occurrence), and the source of the literature from which the species information has been cited, is provided.

Data were collated from various sources. West Coast species were collected by Stegenga *et al.* (1997). Herbarium specimens were mostly from the Bolus herbarium in Cape Town and Pocock's herbarium in Grahamstown. Outside the West Coast, detailed collections have been made from places such as De Hoop, Tsitsikamma, Hluleka *etc*. The West Coast data are far more reliable and complete than the South Coast and KwaZulu-Natal data (pers.

comm., Assoc. Prof. John Bolton). All additional data available in the literature were also collated.

Details of each field of data

An example of a species record is given below:

Record number:	104
Phylum:	Phaeophyta
Order:	Laminariales
Family:	Alariaceae
Genus:	*Ecklonia*
Species:	*radiata*
Endemic:	6 (a code)
Coarse scale distance:	From Koppie Alleen into southern Natal
Geographic co-ordinates:	24 west; 48 east
Resolution of Data:	Collected
Source:	Seaweed Flora
Other name for species:	*Laminaria radiata* C. Agardh 1820a: 113

References

Bolton, J.J. and Anderson, R.J. 1997. Marine vegetation. In: *Vegetation of Southern Africa*. Cambridge University Press. Pp. 348-370.

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Acknowledgements

I thank Rauri Bowie and Colleen Seymour for extensive updating of the seaweed database.

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4. CORALS

Research on the effects of climate change on corals in South Africa is currently underway at the Oceanographic Research Institute (ORI) in Durban (Dr Michael Schleyer), and additional coral research at the University of Natal (UN) (Professor Michael Samways). Consequently, the Marine Biodiversity Section of the South African Country Study on Climate Change (SACSTUDS) will not attempt to analyse the coral data, but will report on any results produced by ORI or UN in time for the submission of the Marine Biodiversity Section final documents.

Title of ORI project

The effects of climate change on South African coral reefs

Description of project

The Oceanographic Research Institute (ORI) has been intensively involved in coral reef research in the present decade, both in South Africa and elsewhere along the East African Coast. The studies have been wide-ranging and some aspects are of interest in terms of monitoring the effects of climate change.

South African coral reefs represent the southernmost extension of this fauna on the African coast. The coral fauna is thus marginal in nature but the reefs also fall in a subtraction zone in the distribution of more temperate sponges and tunicates. The ORI work is partially taxonomic in nature and is providing an elaboration of the level of endemism in the area. Far from being impoverished in terms of species richness, the reefs manifest a peak in biodiversity and a biogeographic pattern is emerging.

The first aspect of ORI coral research of direct relevance to climate change is a monitoring study which is being undertaken at Nine-mile Reef at Sodwana Bay. A long-term monitoring site was established on this reef during a study on the ecology and management of the KwaZulu-Natal coral reefs. As the level of sport-diving is low at this site, it was felt that Nine-mile Reef provided a good comparative reference for monitoring natural and anthropogenic damage as well as to assess the effects of climate change. The objectives of this study are thus to determine:

1. Long-term changes in coral community structure and sea temperature at Nine-mile Reef.
2. Correlations between these changes.
3. The comparison between the community structure at Nine-mile Reef and more heavily dived sites.

Beacons were installed at the site to mark 80 fixed quadrats totalling 20 m^2 and these have been photographed annually since 1993. A temperature recorder was installed in 1994. Five years of quadrat photographs have been subjected to image analysis and the data are presently being used to assess changes in community structure on the reef as well as the growth of individual organisms. The temperature data comprise an unbroken record of hourly means since the date of installation and are showing a clear upward trend in sea temperatures. A change in the reef community structure is anticipated with the shift in temperatures owing to the marginal nature of the biota.

The study has been very demanding and challenging at every stage of its progress but the results should constitute a breakthrough in long-term coral monitoring according to international reef specialists.

The other research site which could be of interest is Aliwal Shoal. The intrusion of temperate fauna is more marked here as the shoal is about 40 km south of Durban. Corals are more marginal and are of reduced importance. Pulp effluent has been discharged in the vicinity of Aliwal Shoal for decades and is believed to have had a deleterious effect on its the benthos. The effluent pipeline is to be extended and a programme is being recommended to monitor community changes on the reef. Changes related to a reduction in the effluent will be sought but the temperature effects of global warming could also be encountered.

Title of UN project

Conservation of coral reefs, with special emphasis on the Western Indian Ocean.

Description of project

Projects include:

1. Monitoring for sustainable use of South African coral reefs
2. Monitoring for sustainable use of Seychelles coral reefs
3. Coral disease assessment in the Gulf
4. Macroecology of reef systems

Networks/Linkages:

KwaZulu-Natal Nature Conservation Service, Oceanographic Research Institute, Marine Parks Authority (Seychelles), Global Coral Reef Monitoring Network (Australia), National Oceanic and Atmospheric Administration (USA), Commission de l'Ocean Indien (Europe and Indian Ocean).

Acknowledgements

I thank Dr Michael Schleyer and Prof. Michael Samways for the above project descriptions.

5. BIRD BREEDING SITES

Title of database

A list of coastal breeding bird species that could be affected by a rise in sea level along the South African coastline.

Description

The irregular coastline of southern Africa has few offshore islands, yet has a high degree of coastal bird endemism. Those species that breed in coastal areas or on offshore islands are most likely to be affected by climate change, particularly a rise in sea level. Sea level rise will reduce the area of the offshore islands and thus reduce the available area for bird breeding sites. Migrant birds are not directly affected by a rise in sea level, but may be affected by a change in currents as this might alter the food availability in the oceans (pers. comm., Dr Peter Ryan, FitzPatrick Institute of African Ornithology, University of Cape Town).

The southern African coastline has a series of rocky islands which are scattered offshore extending from Hollam's Bird Island north of Lüderitz to Bird Island in Algoa Bay. These islands provide platforms for seabird breeding colonies (Berruti *et al.*, 1989). The majority of the global populations of six southern African endemic seabird species breed on these offshore islands: the Jackass Penguin, Cape Gannet, Cape Cormorant, Bank Cormorant, Crowned Cormorant and Hartlaub's Gull. The Cape Gannet will probably be affected the most by a rise in sea level, because it breeds on flat ground at only six coastal islands off South Africa and Namibia. There are only between 80 000 and 100 000 breeding pairs left (Berruti, 1987). Shorebirds such as the African Black Oystercatcher will also be affected, because over 50% of this species' population breeds on these islands (Harrison *et al.*, 1997). Other non-endemic seabirds which could be affected by a rise in sea level include the White Breasted Cormorant, Kelp Gull and Swift (Crested) Tern (pers. comm., Dr Peter Ryan).

A rise in sea-level will also affect bird species which occur in estuarine environments. Sea level rise may not necessarily have a negative effect on these species because an inundation of sea water may provide a larger estuarine area and therefore a larger breeding and feeding site area. Coastal feeders might also be affected by a change in the climate if the upwelling regime in water alongside the coast is altered, thereby affecting the concentrations of plankton and thus food sources in the surface layers of the ocean.

References

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6. MARINE PROTECTED AREAS

Title of database

The distribution of marine protected areas in South Africa

Curator of database

Prof. George Branch, Marine Biology Research Institute, Zoology Department, University of Cape Town, and Mr Muller Coetzee from Kapp, Prestidge and Retief.

Description

The database forms part of the second phase of the Cape Coastal Conservation Plan carried out by Scientific Services Ecological Investigations (pers. comm., Prof. George Branch). The plan makes reference to all coastal areas which are defined as being that part of the land/sea interface whose characteristics are, or have been, determined by the marine environment. The database includes 53 maps which cover the coastline from Oranjemund on the west coast to Nature’s Valley on the south coast. The maps are complied from base maps at scales of 1:50 000, 1:30 000 or 1:45 000. The contour interval on each map is 20 m. For each of the maps the following categories have been highlighted using different colours:

1. Reserve areas (purple)
2. Conservation areas (red)
3. Areas of conservation with development (green)
4. Areas of development with conservation (yellow)
5. Areas of development (brown)

A digital copy of the data is also available from Dr Niel Malan of the Department of Environmental Affairs and Tourism, Cape Town.

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