RHODES UNIVERSITY

GEOGRAPHICAL VARIATION IN EFFECTS OF NUTRIENT LEVELS AND GRAZING INTENSITY ON COMMUNITY STRUCTURE BETWEEN UPWELLING AND NON-UPWELLING REGIONS OF SOUTH AFRICA

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ABSTRACT

The aim of this thesis was to assess the influence of upwelling on alga-grazer interactions in rocky shore communities along the south coast of South Africa using grazer exclusion treatments with controls and procedural controls set out in a block design and monitored for algal cover roughly monthly for one year. In the first experiment grazers were excluded from treatment plots at two upwelling and two non-upwelling sites and the rates of algal biomass accumulation were then compared. The upwelling sites showed significantly faster algal colonisation rates, with *Ulva rigida* being the first species to colonise the rocks. Final algal cover and biomass did not differ significantly between upwelling and non-upwelling sites in control plots open to grazers, but were significantly higher in grazer exclusion plots at upwelling sites indicating stronger grazing effects. This was confirmed by estimating the intensity of grazing using the log-response ratio (LRR), which was calculated from treatment and control plots. Upwelling sites had significantly lower LLR values indicating stronger grazing effects, than at non-upwelling sites, despite no difference in grazer abundances.

The second experiment examined the effects of nutrient addition on algal growth and community composition by comparing high nutrient enrichment plots with low enrichment plots at one upwelling and one non-upwelling site. ANOVA indicated faster growth rates and significantly higher final algal biomass in high enrichment plots compared to low enrichment and control plots at both upwelling and non-upwelling sites. A two-way ANOVA indicated significantly higher algal cover in high enrichment plots compared to the data from the grazer exclusion plots in experiment 1 at both sites, suggesting that nutrient addition plays a major role in algal growth and community composition.

The findings of these studies have shown significant differences between treatments, sites and seasons, with significant differences not only occurring in algal cover but also accumulation of algal biomass and recruitment patterns between treatments. The small scale local processes acting within a few centimetres (plots) or tens of meters (among blocks) can also be reflected over larger scales such as sites (upwelling/non-upwelling shores). Further, these studies have demonstrated that various factors such as the effects from increased nutrients at upwelling cells and the change in grazing effects due to enhanced nutrients can determine the abundance and diversity of the community structure, including an increase in the abundance of the fast growing algae *Ulva rigida*, and a slow recovery of the brown and red algae.

Keywords: Grazing, algae, upwelling, recruitment, top-down control, bottom-up control

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CHAPTER 1 – General Introduction

1.1 GENERAL INTRODUCTION

One of the key questions is ecology is what factors determine the community assemblages in an environment? The relationship between top-down and bottom-up control has been analysed in many previous studies of marine benthic systems to determine which form of regulation is key in controlling community composition (Menge and Sutherland 1987; Menge 2000; Blanchette *et al*. 2009). Top-down models refer to how higher trophic levels control lower ones. For example, how or whether predators control the abundance of grazers and thus the effect of grazing on the plant communities (Burkepile and Hay 2006; Vinueza *et al*. 2006), while bottom-up models refer to the role of resources which do not affect higher trophic levels (Hairston *et al*. 1960; Dayton 1971; Underwood 1981; Worm *et al.* 2002; Vinueza *et al*. 2006). Rocky shore ecosystems provide ideal habitats for ecologists to study such questions as they are diverse and the organisms and resources can be easily manipulated. Such studies can also take place over a range of spatial and temporal scales resulting in a better understanding of the functioning of the ecosystem.

Physical factors experienced at different rocky shores such as wave exposure, desiccation, temperature and light intensity exert a number of both harmful and beneficial effects on the rocky shore community (Dayton 1971; Bustamante *et al.* 1997). The physical changes experienced during changing tides play a crucial role in determining the distribution and community structure of the intertidal algal assemblages (Underwood 1980; Hawkins and Hartnoll 1983). For example, Dayton (1971) found that several species of algae are highly sensitive to desiccation and can only survive in moist conditions or under the canopy of other algal species in the intertidal zone, where grazing effects are often reduced as the growth rate of algae increases in the favourable conditions (Arrontes *et al.* 2004). The tolerance levels of organisms to stress vary from species to species and "environmental stress gradients" can range from innocuous to harmful to lethal, thus limiting the vertical distribution range of a species on the shore (Benedetti-Cecchi 2000). For example, filter feeders have increased growth rates on wave exposed shores (McQuaid and Branch 1985, McQuaid and Lindsay 2000), while Underwood and Jernakoff (1984) showed that reduced physical stress had positive effects on the growth and survival rate of a number intertidal algal species.

1.1.1 ROCKY SHORE ZONATION

Rocky shores are characterised by continually changing physical conditions such as temperature, salinity, air and wave exposure (Johansson 2003) and are hence some of the harshest environments for organisms to survive (Branch and Branch 1988). Rocky shores are commonly divided into three broad zones based on their characteristic biological communities, which are largely a result of the different exposure times to air (Menge and Sutherland 1987). The three zones together form the eulittoral zone, which extends from the spring high tide mark down to below the low tide mark below which the seabed is covered by seawater at all times (Bustamante *et al.* 1997).

The Supralittoral zone, or Littorinind zone, although regularly splashed, resembles the terrestrial habitat in that it is dry for prolonged periods. Organisms such as barnacles, semi-terrestrial isopods and littorinids (Stephenson and Stephenson 1949) are well adapted to living in the harsh dry conditions experienced in this region (Branch *et al*. 2010). Very little macrophyte vegetation grows in this area, though macroalgae such as *Porphyra capensis* can be present in winter when conditions are less harsh (Lubke and De Moor 1998).

The true intertidal zone, extends from the spring high tide mark to the spring low tide mark. The intertidal zone is exposed to strong wave action and turbulence by cyclical tides (Stephenson and Stephenson 1949) and potentially has increased primary productivity levels compared to the supralittoral zone (Diaz 2008). The main determining factor of algal community structure in the intertidal zone is considered to be grazing as stronger ecological interactions are shown in this zone (Menge and Sutherland 1987). The organisms found in the eulittoral zone have adaptations to cling onto the rocks to withstand the pounding of waves. Species found in this region include barnacles, limpets, mussels and urchins, though the latter are often restricted to tidal pools. The eulittoral zone normally exhibits regular patterns of dominance of space by conspicuous species that differ at different tidal heights.

The Sublittoral zone, or subtidal zone, is directly below the eulittoral zone and is permanently covered by seawater. Marine algae are the dominant organisms found in this region, which has high rates of primary productivity (Stephenson and Stephenson 1949).

1.1.2 HORIZONTAL SPATIAL DISTRIBUTION

Although zonation limits the vertical distribution of the species on a shore, it does not determine the horizontal spatial distribution of species; this is largely determined by complex predator-prey and consumer-producer interactions as well as large scale processes such as upwelling, recruitment (Menge and Sutherland 1987) and wave exposure (Jenkins *et al*. 2008). These interactions and processes can have impacts across different scales, and unless previous studies present congruent results, the understanding of these patterns and processes remain unclear (Underwood 2000).

A study carried out on South African shores found that primary productivity has a strong influence on the biomass of grazers and filter feeders along a gradient of increasing nutrient levels from east to west (Bustamante *et al*. 1995). However, there was no change in algal biomass between the nutrient rich west coast and the nutrient deficient east coast, despite the higher intensity of grazing on the west coast. This indicates that the bottom-up control from nutrients is offset by the strong top-down control from grazers, on the west coast (Bustamante *et al*. 1995). Similarly Lotze *et al.* (2001) found greater biomasses of grazers in eutrophic habitats in the Baltic Sea dominated by perennial algae, compared to oligotrophic habitats in the north-west Atlantic Ocean dominated by annual algae. These studies demonstrate the importance of both top-down and bottom-up factors in nutrient rich waters such as those found in upwelling regions and how they can contribute to the horizontal spatial variability of species distributions and abundances.

The ecological interactions taking place on rocky shores are largely the same at tropical and temperate latitudes, with competition being an important factor in determining the abundance and distribution of basal sessile species, particularly algal species, on both temperate and tropical rocky shores (Williams *et al*. 2000), but the balance among factors influencing community structure tend to differ across latitudes. Some studies have shown consumers to be primarily responsible for algal distribution patterns on tropical rocky shores (Menge *et al.* 1986; Menge and Sutherland 1987), but others show that the extreme conditions of tropical summers can over-ride grazing effects (Hutchinson and Williams 2005). Variation in herbivore density and distribution patterns also has an influence on algal distribution patterns and often results in patches of different algal species that are either resistant to grazing or are facilitated by grazing pressure (Williams *et al*. 2000). Rock crevices and holes are often left bare of algae as these provide shelter and homing areas for the grazers when at rest and contribute further to the patchy distribution of algae (Hawkins and Hartnoll 1983).

The degree of wave exposure and slope of the shore also play major roles in determining community composition (Benedetti-Cecchi *et al*. 2000; Zamprogno *et al*. 2012). Ordinarily, more sheltered shores support a diverse, low biomass faunal community, whereas the exposed shores support a high biomass of lower species diversity (Bustamante *et al.* 1997), though some studies show the reverse (Zamprogno *et al*. 2012), possibly because greater water movement increases variability in the supply of larvae (Bulleri 2005), sometimes offset by reduced recruitment due to the harsher conditions experienced at exposed than sheltered shores (Branch and Steffani 2004). Zamprogno *et al*. (2012) found that, while exposed shores support greater richness, the sheltered shores exhibited higher values of evenness, suggesting that there is less dominance by a few species compared to exposed shores.

1.1.3 ROLE OF DISTURBANCE

Disturbance can be caused by physical actions such as wave exposure, battering by drifting logs and environmental stressors such as desiccation and light intensity, or biological factors such as grazing and predation (Dayton 1971). Disturbance can influence organisms through different trophic levels, for example, sea ice can detach a patch of mussels or a stand of macroalgae from the rocks leaving a bare patch. Depending on its intensity, a disturbance can either enhance or reduce biomass and diversity within an ecosystem such that at moderate levels of disturbance species richness will reach a peak, whereas at very weak or very strong disturbance levels species richness will decrease (Kondoh 2001), as indicated by the intermediate-disturbance hypothesis described by Connell (1978).

The intermediate-disturbance hypothesis has, however, been questioned by marine scientists as it is inconsistent with the model proposed by Menge and Sutherland (1987) that incorporates competition, predation and disturbance in shaping the diversity of a community. For example, when disturbance is low, predation pressure would increase, while high disturbance would lead to low predation, causing competitive exclusion between species. Predation and grazing have been considered important forms of disturbance that can alter the productivity of ecosystems and their species richness (Proulx and Mazumder 1998). Studies have, however, found varying effects of grazing and predation, with some studies finding increased diversity with an increase in predation or grazing pressure, while other studies have found the reverse. There have also been studies that have reported no relationship between diversity and predation or grazing pressure (Proulx and Mazumder 1998).

The disturbance of algae through grazing can indirectly influence the abundance of sessile invertebrates by affecting the habitat they require to settle on, as well as directly affecting the abundance of the sessile invertebrates through bulldozing (Williams *et al.* 2013). For example, limpets can directly dislodge barnacle recruits with the edge of their shell as they graze and move over the rocks, thereby reducing barnacle abundances (Dayton 1971). This effect will vary with limpet size, abundance and species and may result in barnacle recruitment variation. Another example is the indirect effect of grazers on mussel recruitment rates by reducing the cover of the algae on which the mussels settle (Menge *et al.* 1997). This form of disturbance will ultimately influence the community composition, structure and abundance.

Disturbance can also be linked to a change in nutrient availability within the system, for example nutrient inputs from coastal upwelling events (Menge *et al.* 1997). These upwelling events can cause a shift in the diversity of a system due to changes in the grazing intensity and nutrient uptake rates of specific algae species. For example some *Ulva* species have rapid nutrient uptake rates and increased growth rates in nutrient rich water and are therefore more resilient to grazing effects (Worm *et al.* 2002; Williams *et al.* 2013).

1.1.4 BACKGROUND TO THIS STUDY

Numerous studies have examined the effects of grazing on algal assemblages (e.g. Menge *et al.* 1997; Benedetti-Cecchi *et al*. 2001; Worm *et al.* 2002; Arrontes *et al.* 2004; Jenkins *et al*. 2005), as well as the effects of enhanced nutrients on community composition (Bosman *et al.* 1987; Fridley 2002; Burkepile and Hay 2006; Hillebrand *et al*. 2007), while a few studies have examined the combined effects of grazing and nutrient effects (Hillebrand 2003; Eriksson *et al.* 2006; Masterson *et al*. 2008). A limited number of studies have been conducted along the South African coastline, with a focus on particular species. For example, Carter and Anderson (1991) looked at the grazing of the limpet *Cymbula oculus* feeding on *Gelidium pristoides,* while McQuaid and Froneman (1993) looked at the effect of the limpet *Scutellastra longicosta* grazing on *Ralfsia verrucosa.* These studies reported the effects of grazing on the specific algal species, however they were unable to conclude anything regarding grazing effects on the whole algal assemblage. The effects of grazing are suggested to vary according to the proportions of algae groups on the shore, which can differ along the coastline (Steneck and Dethier 1994). For example, Bustamante *et al*. (1995) found that encrusting corallines dominate over turf and foliose algae on the east coast of South Africa, whereas foliose algae dominate on the west coast. For this reason, in this study grazing effects were assessed on the whole algal assemblage and at low and high nutrient levels across the south coast.

1.1.5 AIMS AND OBJECTIVES

Identifying the scales at which variability occurs on shores and the processes that generate and maintain rocky shore ecological systems are among the key objectives of marine ecologists (Menge and Sutherland 1987, Benedetti-Cecchi 2001, Boaventura *et al.* 2002, Cole and McQuaid 2010). Rocky shores along the southern coast of South Africa experience an extensive range of environmental conditions, prompting research to assess similarities and differences in the composition and functioning of rocky shore communities (Blanchette *et al*. 2009). In this thesis I manipulated grazer presence as well as small scale nutrient levels to investigate the macroalgal response at the community and species levels. In particular, I aimed to investigate geographical variation in the effects of nutrient levels and grazing intensity on the algal community by comparing upwelling and non-upwelling regions.

This study was divided into two experiments with the goal of determining if there is a difference between upwelling and non-upwelling regions in the effects of grazing on the development of algal standing stocks along the south-east coast of South Africa.

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CHAPTER 2 – The effects of grazer exclusion on algal community structure

2.1 INTRODUCTION

2.1.1 WHAT DETERMINES COMMUNITY STRUCTURE?

Rocky shore community structure is determined by a complex interaction of large-scale and small-scale factors. Large-scale factors include, but are not limited to, physical conditions of the environment, including climate, storms, wave exposure (Dayton 1971), upwelling conditions (Menge and Sutherland 1987; Bracken *et al.* 2011) and nutrient availability (Bustamante *et al.* 1995), while small-scale biological factors include, local grazing intensity (Menge *et al.* 2002), interspecific and intraspecific competition (Creese and Underwood 1982) and recruitment (Freidenburg *et al*. 2007).

Physical and biological factors act simultaneously to shape the composition, biomass and diversity of marine, freshwater and terrestrial plant communities (Hillebrand *et al*. 2007). The rate at which the producers use resources is influenced by the availability of nutrients, the degree of physical stress, light availability and the intensity of herbivory. For example, the top-down effects of herbivory may affect the biomass and diversity of algal species, while the bottom-up effects of nutrient availability and levels of physical stress can interact to determine plant quality and the level of herbivory (Menge and Sutherland 1987).

The level of stress experienced by a herbivore can alter its feeding behaviour from marginal effects to completely changing its feeding distribution patterns as it escapes the environmental stressor (Menge and Sutherland 1987; Williams *et al.* 2000). A general pattern of this can be seen on tropical rocky shores where seasonal conditions such as temperature and light intensity act as stressors on both the algal and grazer communities. In the hot summers the macroalgae die off and herbivores have to forage further and feed lower on the shores for shorter periods of time, whereas in winter the macroalgae flourish and herbivore foraging periods and ranges are extended (Williams *et al.* 2000).

All factors such as herbivory, tidal height and nutrient availability have to be taken into consideration when determining the effects of nutrient availability on algal communities as these can have effects at both the individual and whole community level and across large spatial and temporal scales (Bracken *et al.* 2011). In order to determine what factors influence algal community structures along South African shores, this study looks at both bottom-up control, through recruitment and nutrient supply through upwelling, and top-down control through grazing.

2.1.2 BOTTOM-UP FACTORS

Bottom-up control is the regulation of community structure either directly or indirectly through dependence on the lower trophic levels, such as primary nutrient resources for plants or herbivores as prey for the higher trophic levels (Menge 2000). Environmental stresses caused by characteristics of the physical environment, such as the mechanical forces acting on an organism and biochemical reactions within the organism, play a key role in determining the community structure in all habitat types (Menge and Sutherland 1987).

Until recently, top-down effects were thought to be the main contributor to rocky shore community structures and bottom-up effects were thought to be secondary (Menge 1992). It was previously assumed that oceanographic conditions would have little effect on the variation in communities as they were thought to be consistent over very large scales (Menge *et al*. 2002). However, variations in oceanographic conditions, such as sea surface temperature and chlorophyll, have been noted via remote sensing and have led researchers to believe that these factors may play critical roles in coastal environments. Subsequently, studies in South Africa, Oregon, New Zealand and Chile have shown bottom-up effects on intertidal communities (Menge 2000).

Experimental studies in which nutrients are artificially enhanced (Bustamante *et al.* 1995) and observational studies on natural systems (Nielsen 2001) have both shown bottom-up control of nutrients on algal development and primary production on rocky shores (Masterson *et al*. 2008).

These are reflected in fluctuations in algal cover and primary production and can have effects through the trophic levels causing changes in overall community structure and/or diversity, through enhanced algal growth, increased grazing or increased grazer abundance as prey for predators (Worm *et al*. 2002; Masterson *et al*. 2008).

However, nutrient availability can also be divided into the input of new versus regenerated nitrogen. Regenerated nitrogen input is often less important in allochthonous systems exposed to strong waves and currents, whereas regenerated nitrogen plays more of a role in autochthonous systems (Aquilino *et al*. 2009). Nitrogen availability and limitation are therefore fundamental in controlling primary production and hence algal species composition (Kudela *et al*. 2008). While nitrogen is the principal limiting nutrient, iron and phosphorus also influence primary production rates and can be equally important in controlling primary producer community composition (Kudela *et al.* 2008).

Recruitment and Succession

Mobility of organisms plays a large role in determining rocky shore community structure. Recruitment patterns of sessile species such as barnacles and sedentary species such as mussels, are pivotal to the dynamics of the community as such species act as both competitors for space and as prey for other species (Menge *et al*. 2010), apart from acting as ecological engineers that provide habitat for other species. Ecological processes such as competition, predation and disturbance create a balance between the sessile and mobile organisms occupying space on the rocky intertidal shores (Bosman *et al*. 1987), as well as playing a key role in determining the amount and type of algae that will colonise the shore (Dye 1993). Settlement of grazers and algae has varying impacts on the overall community structure with regards to abundance, density and diversity, which in turn play a key role in the dynamics of the ecosystem (O’Connor *et al*. 2011).

Foster *et al.* (2003) found that abiotic site characteristics and seasonality have a more significant effect on reproduction, dispersal, recruitment and growth of algae than biotic factors such as grazing and competition. The intensity of recruitment can vary across small to large spatial and temporal scales due to local and non-local process (Kinlan and Gaines 2003). For example, current effects can cause variation in recruit densities in the water column, which in turn further leads to differing settlement patterns among shores (Hutchinson and Williams 2001; O'Connor *et al*. 2011). Propagule dispersal is also largely dependent on the taxa considered and their specific life cycles. For example, algal propagule dispersal distances range from a few meters to less than 5km, whereas invertebrate propagule dispersal ranges can extend from tens of meters to hundreds of kilometres (Kinlan and Gaines 2003).

Propagule survival is highly variable and is affected by a number of different physical and biological factors (Hutchinson and Williams 2001), including large scale physical factors such as wind, upwelling, linear oceanographic features and the vertical distribution of larvae in the water column (Hunt and Scheibling 1997), while small scale biological factors include factors such as life histories (Hadfield and Strathmann 1996) and differences in grazing intensity on recently settled sporelings (Benedetti-Cecchi 2000b). Although algal recruit survival rate is highly variable, it remains a key factor influencing rocky shore community assemblage.

Upwelling

The coastal oceanography of South Africa is dominated by two major currents, namely the Benguela Current along the Atlantic coast and the Agulhas Current along the Indian Ocean coast (Griffiths *et al*. 2010). The cold, eastern-boundary Benguela Current that dominates the west coast of the country exhibits dynamic wind-driven upwelling which is largely controlled by local weather systems and results in short-term upwelling cells. Coastal upwelling along the Atlantic Coast occurs when Coriolis force diverts wind-driven surface currents to a 45° angle to the wind direction. This diversion is known as the Ekman Spiral and with winds from the appropriate direction, results in Ekman transport of the warmer, nutrient poor surface waters away from the coast and the replacement of these surface waters with colder, nutrient rich deep water. This upwelling is focussed within upwelling cells and generally occurs in the austral spring and summer (Lutjeharms *et al*. 2000).

Different upwelling regions have been found to differ in their potential for biological production and have been separated according to whether upwelling is driven by local forcing or large-scale circulation related factors (Lachkar and Gruber 2011). Various hypotheses have been formed regarding the differences in potential for biological production, namely differences in iron limitation, biomass retention and community structure in these regions (Lachkar and Gruber 2011). Recent studies have led to the belief that local intertidal community dynamics are strongly influenced by the upwelling of nutrients and chlorophyll, while offshore Ekman transport is a pivotal process in determining the spatial and temporal rates of recruitment (Broitman *et al*. 2001). One such study conducted by Blanchette *et al*. (2007) identified the negative impact of upwelling on recruitment due the colder temperatures and advection of larvae offshore during upwelling events.

Intense upwelling along the west coast of South Africa results in surface waters being rich in inorganic nutrients, with the major nutrients being various forms of nitrates, phosphates and silicates (Griffiths *et al*. 2010). These waters are highly productive and support a large biomass of biological stocks (Griffiths *et al*. 2010). The reductions in oxygen in bottom waters, caused by the decay of sinking organic matter, can often result in mass mortalities of fish, rock lobster and other invertebrates and can have persistent effects on coastal ecosystems (Pitcher and Calder 2000). Upwelling is therefore associated with dramatic changes in the physico-chemical and biological systems on the west coast where upwelling occurs.

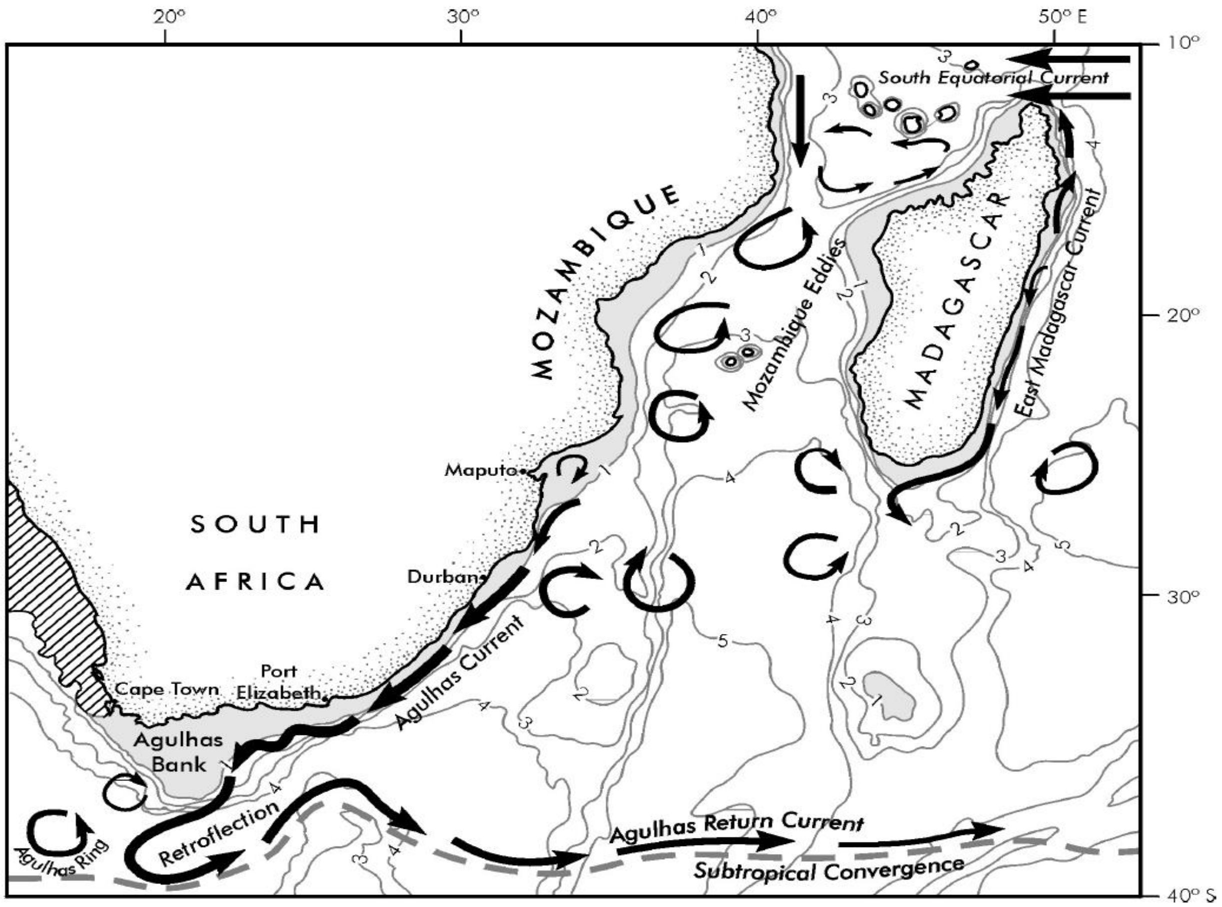


Figure 1.1: The flow patterns of the Agulhas Current showing the retroflection off the Agulhas Bank (from Lutjeharms 2006b).

The east coast of South Africa is very different from the west coast. The Agulhas Current is fed by the Mozambique Current and a tributary of the East Madagascar Current flows poleward along the shelf edge of southern Africa (Figure 1.1). At Durban, however, the Agulhas current is offset over the edge of the wider shelf, forming sheer edge eddies (Lutjeharms 2006a). South of Port Elizabeth the continental shelf widens to form an extensive bank, known as the Agulhas Bank, which causes the fast-flowing current to deflect offshore at the edge of the Agulhas Bank (Lutjeharms *et al*. 2000). This offshore deflection is termed the Agulhas Current retroflection. It is found between 16° and 20°E and has a loop diameter of 340 km. Agulhas rings are shed off the western extent of the retroflection allowing inter-oceanic exchanges between the Indian and Atlantic Oceans (Dencausse *et al.* 2010).

The deflection of the Agulhas Current off the Agulhas Bank allows the Benguela Current to flow inshore and occasionally the south coast experiences local, wind-driven upwelling of this cool bottom water (Lutjeharms 1998). The frequency and intensity of this upwelling varies seasonally and has been linked to changes in sea temperature along the south coast, with the local dominant wind pattern being the key determining factor triggering upwelling (Goshen and Schumann 2011).

However, a distinct semi-permanent upwelling cell occurs off the inshore edge of Port Alfred (Figure 1.2) where along-current winds create a thermal front (Lutjeharms 2006b). This upwelling cell may have considerable ecological implications, as the cold water from this upwelling cell may extend up to 300km northward, inshore of the Agulhas Current. Nutrient values and primary productivity are elevated in the region of the upwelling cell at Port Alfred, such that nutrients can exceed 20 µmol/ℓ compared to less than 5 µmol/ℓ of the adjacent shelf and primary production rates can reach 888 mg/m^2/h compared to 104 mg/m^2/h on the adjacent shelf (Lutjeharms 2006b). There are other sites along the south coast that experience divergent, topographically induced upwelling that is more sporadic and localised and that is associated with the effects of headlands on coastal circulation (Cole and McQuaid 2010; Reaugh-Flower *et al,* 2011).

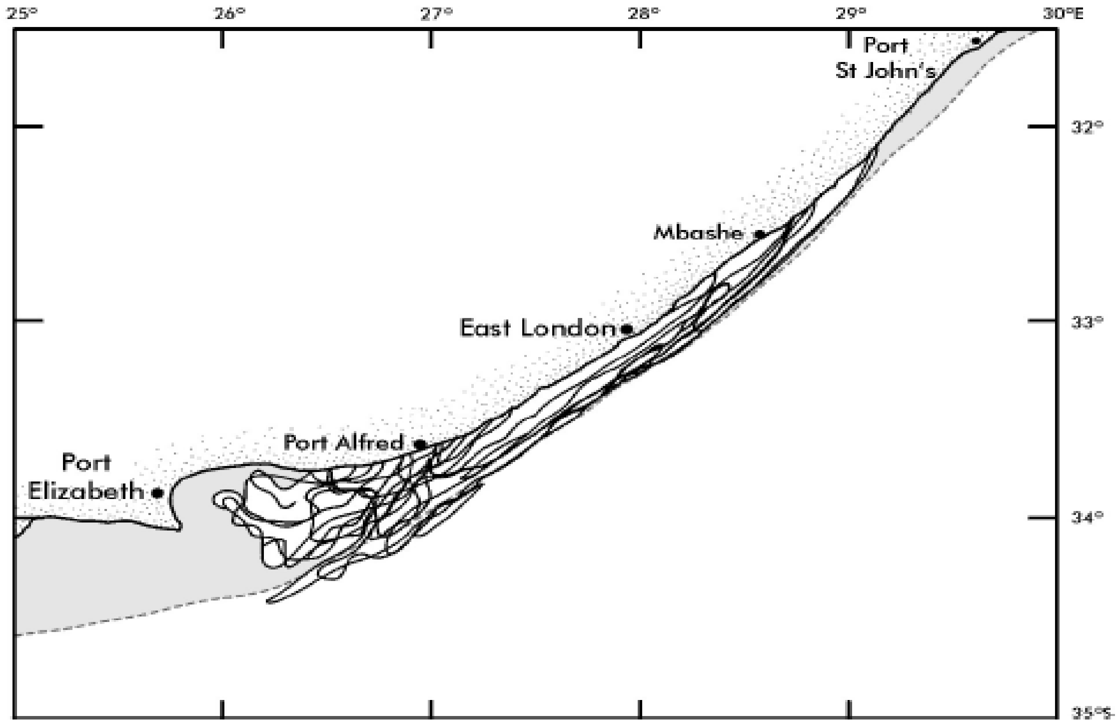


Figure 1.2: Location of the Port Alfred upwelling cell on the wider continental shelf (Source: Lutjeharms 2006b).

Productivity levels influence the relationships of organisms through all trophic levels and factors that enhance rates of primary production may alter community structure and trophic relationships

(Bosman *et al.* 1987). Previous studies performed by Bosman *et al*. (1987) found that rocky shores in upwelling zones had significantly greater algal cover and herbivore biomass than non-upwelling zones; however the sessile filter-feeding organisms had greater ground cover in non-upwelling zones. These findings by Bosman *et al*. (1987) along with studies conducted by McQuaid and Branch (1984, 1985) suggest that algae and filter-feeders compete for space, with algae outcompeting filter-feeders on upwelling shores. Conclusions such as these suggest that rocky shores found in upwelling and non-upwelling regions support different community structures due to the impact that nutrients levels play on the organisms. The upwelling cells along the southern coast have lower productivity than those on the west coast, which can often result in coastal marine resources being less able to sustain human exploitation (Lutjeharms 1998).

2.1.3 TOP-DOWN CONTROL

Top-down control implies that the distribution, abundance and diversity of lower trophic levels are structured either directly or indirectly through predation or herbivory from the higher trophic levels (Menge 2002). Top-down effects are generally only directly felt one or two trophic levels lower than the herbivore or predator (Seitz and Lipcius 2001). For example a predator in the third trophic level will influence the number of the herbivores in the second trophic level, but will have very little influence on the primary producers in the first trophic level. An exception to this pattern occurs when an increase in predator density causes an increase in the primary producer density due to the removal of a greater number of herbivores. A classic example of such a trophic cascade is seen on the Alaskan coast where increased killer whale predation caused a major decline in the sea otter population and a coinciding increase in sea urchin density with the consequence of kelp bed deforestation (Estes *et al*. 1998).

Three alternative succession patterns have been characterized by Connell and Slatyer (1977) whereby the early colonisers either “facilitate,” “tolerate” or “inhibit” the later colonisers. These succession patterns determine whether early or late successional species dominate a rocky shore at any given time, and influence whether grazers move into or out of neighbouring habitats in the search for suitable food sources (Benedetti-Cecchi 2000b). As the number of grazers reduces early successional colonies, late successional species are given the opportunity to establish and form assemblages (Benedetti-Cecchi 2000b), highlighting the importance of consumers in regulating succession.

The distribution and succession of algal species are largely determined by grazing effects, which can either facilitate or inhibit algal succession on the shore by providing additional open substratum to facilitate recruitment, or by inhibiting algal growth through overgrazing and removing spores (Hawkins and Hartnoll 1983; Benedetti-Cecchi 2000a). Experiments on nutrient-enrichment carried out by Worm *et al*. (2002) showed that, when grazers were introduced into a nutrient-enriched plot, algal cover was significantly reduced compared to situations where no grazers were present in the nutrient-enriched plots. This indicated a strong top-down control from consumers on primary producer's diversity and abundance.

Grazing intensity determines the level of top-down stress experienced by algae, which in turn determines algal growth rates and nutritional value (Menge 2002). Furthermore, grazers can modify the whole community structure by accelerating or reducing the rate of succession by affecting early or late successional species (O'Connor *et al.* 2011). For example, grazers have also been known to impede barnacle recruitment by directly consuming the recruits or to facilitate their recruitment by eliminating algal competitors (O'Connor *et al.* 2011), thereby affecting the dynamics of the whole ecosystem.

The influence of top-down effects therefore appears to vary with time and space and the large variability in grazing effects is influenced by a number of factors such as nutrient status (Worm *et al*. 2002) and oceanographic conditions (Bustamante and Branch 1996; Menge *et al*. 2010), as well as the life stages and life histories of the species considered (Korpinen *et al*. 2008).

By looking at studies such as Menge (2000), Nielsen (2001), Worm *et al*. (2002) and Freidenburg *et al*. (2007), it is clear that top-down and bottom-up controls work simultaneously to influence rocky shore community structure, biomass and diversity. These studies have successfully explained the differences in patterns of distribution of organisms at particular locations and times and have created general ecological models as a foundation for further studies. However, since all ecosystems are subject to scale and context-dependant factors, one cannot generalise results for individual shores from the results of ecological models (Benedetti-Cecchi 2001).

2.1.4 AIMS AND OBJECTIVES

The goal of this study was to determine if there is an influence of upwelling on the effects of grazing on rocky shores along the south-east coast of South Africa. A further objective was to identify if there were any differences in algal production between the two regions (upwelling vs. non-upwelling). The questions below were identified in order to a gain a better understanding of the balance between the effects of top-down and bottom-up factors on algal assemblages.

This study centred on the following questions:

- Does upwelling affect the densities of grazers?
- How do the top-down effects of grazing, differ on spatial scales from 10s of centimetres, to 10s of meters, to 100s of kilometres and how is this influenced by nutrient supply?

Hypotheses

Two hypotheses were derived from the general model that grazers influence the structure of community assemblages in different ways in upwelling and non-upwelling regions:

(1) Algal cover increases more rapidly in exclusion quadrats under upwelling conditions than in exclusion plots with no upwelling

(2) The effects of grazing are stronger in upwelling regions compared to non-upwelling regions.

2.2 METHODS

2.2.1 SITES

Grazer exclusion experiments were set up at the midshore level on two upwelling shores interspersed with two non-upwelling shores on the south-east coast of South Africa. The upwelling shores are located at Cape St Francis (34°11’20.0” S, 24° 51’31.4”E), and Port Alfred (33° 36’ 52.0’S 26° 53’ 18.4’ E) while the non-upwelling shores are located at Jeffery’s Bay (34° 01’39.2”S, 24° 55’54.3”E) and East London (32° 58’24.2’S 27° 58’13.2”E). The main criteria in shore selection were moderate exposure to wave action, topographical simplicity, a gentle slope (<30°) and domination at mid-tide level by an extensive cover of barnacles and patellid limpets (Jenkins *et al.* 2005).

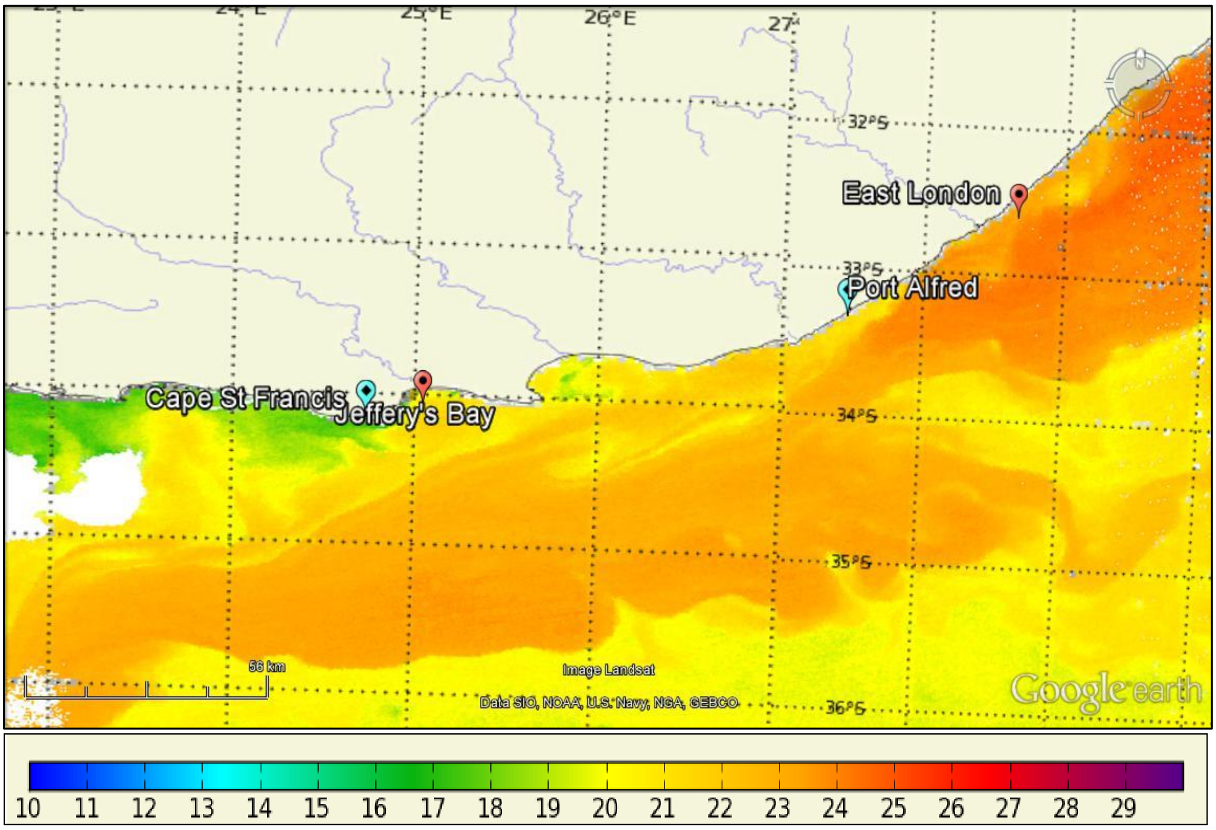


Figure 2.1: Google Earth overlay of Sea Surface Temperature indicating the two upwelling sites by blue markers and the non-upwelling sites by red markers. (Data source: Marine Remote Sensing Unit, http://www.afro-sea.org.za).

The shores all differed in rock formation and structure (Figure 2.2). St Francis is characterised by boulders of the Table Mountain Group formation made from small grains of creamy white to ash grey quartz sandstone (Lubke and De Moor 1998). Jeffery's Bay is underlain with the Bokkeveld Group formation which consists of black shale, compact siltstone and olive-grey sandstone. The shale rock weathers into jagged parallel formations separated by deep gullies (McQuaid and Branch 1984). The Witteberg Group comprises quartzite rock formations of incised gullies which underlie the Port Alfred area, while East London is made up of the Karoo Supergroup, consisting of dolerite dykes and sills (Lubke and De Moor 1998). The intertidal communities of all the shores were similar in nature with a clearly visible margin between the limpet and barnacle zone and the region dominated by a red algal turf. The maximum tidal range is approximately 2.0m for all sites.

The mid-intertidal region at all sites is dominated by barnacles, *Tetraclita serrata,* interspersed with limpets of varying sizes and species, with the dominant species being *Cymbula oculus*. The red alga, *Gelidium pristoides* and the green alga*, Ulva rigida* are found in patches along the mid-intertidal region. Encrusting coralline species *Lithothamnium* sp. and *Lithophyllum* sp. occur in small patches.

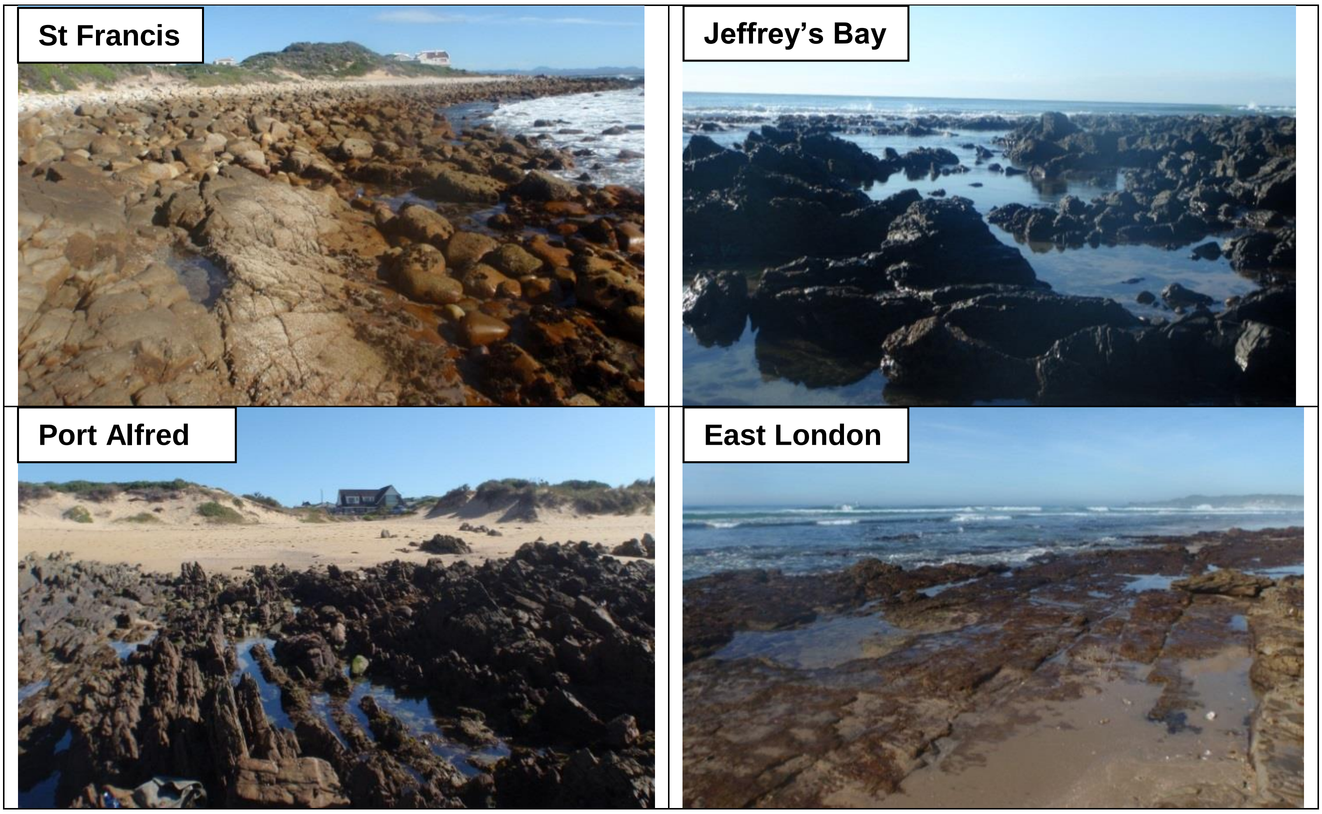


Figure 2.2: Rocky shore structures at the four sites

2.2.2 GRAZER EXCLUSION EXPERIMENT

Five blocks at each study site were randomly selected to set up the experiment. Three treatments were set up in each block and blocks were separated by between three and five meters. The experiment commenced in May 2012 (austral autumn) and was run for one year.

The experiment consisted of three treatments in each block: (1) complete exclusion of limpets using anti-fouling paint in 25 x 25 cm plots, hereafter named exclusion treatments (E), (2) a procedural control (PC) or semi-exclusion plot using anti-fouling paint to paint an L-shape in two corners of the plot and (3) a control treatment (C) where only the corners of the plot are marked by screws and the plot was otherwise unaltered. The screws were fixed in holes in the rock drilled by a battery-operated Hilti drill. Copper based anti-fouling paint was used as it has been shown to effectively impede limpets and chitons in experimental plots (Freidenburg *et al*., 2007; Guerry *et al*., 2009; Menge *et al*., 2010). The procedural control tests for experimental artefacts other than the effects of exclusion of grazers, such as an effect on algal growth due to the presence of the anti-fouling paint in the exclusion treatment (Jenkins *et al*. 2005).

Control and experimental plots were scraped clear and burnt with a blowtorch to remove all living organisms, with the intention of starting all plots with 0% algal cover. Plots were then left for one month, after which sites were revisited monthly during spring low tides.

The experimental treatments were replicated at two spatial scales: between locations (separated by 10s - 100s of kilometres) and among patches (blocks) within each shore (separated by meters). Succession was assessed over a 12 month period by sampling monthly to determine the effects of grazing by molluscs along the coast during different seasons to determine the interaction of nutrient supply and grazing (Jenkins *et al.* 2005).

Experimental block at St. Francis

Experimental block at Jeffrey’s Bay

Experimental block at Port Alfred

Experimental block at East London

Figure 2.3: Experimental design shown at the four sites

2.2.3 MAINTENANCE AND SAMPLING OF THE EXPERIMENTS

Following establishment of the experiment, sampling was undertaken during spring low tides, monthly for the first 3 months and then bimonthly until the conclusion of the experiment at 12 mo. At each sampling date, the experimental plots were photographed and percentage algal cover was estimated using the point intercept method with a quadrat sectioned into 5 x 5cm quadrats and 30 point intercepts. Algae were further identified to the functional group level. The abundance of grazers was recorded monthly at each site by counting the number of individuals in 10 randomly placed 25 x 25cm quadrats along the intertidal zone. The density of meso- (<20mm) and macro-grazers (20- 100mm) was quantified by dividing the number of grazers by the area of each quadrat (0.0625m^2). Repairs were made to any damaged paint in the experimental plots and any limpets that had entered the exclusion treatments, roughly 1 limpet per site, were removed at each sampling date (Jenkins *et al*. 2005). Temperature was recorded using iBbuttons that recorded temperature with a precision of 0.5°C, every five minutes at each location to determine the frequency of upwelling events. Upwelling occurrences in this region are defined as events when sea water temperature reached below 15°C (Lutjeharms 2006b). In this study they were defined as events when intertidal temperatures fell below 15°C.

2.2.4 FUNCTIONAL GROUPS OF BIOTA

After the 12 month duration of the grazer exclusion experiment, the surface of each plot was scraped to determine the total biomass (measured as wet mass) of all algae present. Mean biomass values for all algae from upwelling and non-upwelling sites were then compared using ANOVA (see below). The common species of algae found at all four sites are listed in Table 3.1 below.

Although there are herbivores in the study area that would not be excluded by my treatments, such as the littorinid snail, *Afrolittorina* spp, and various small fish species at high tide, my experiments focused mainly on limpets, as these formed the bulk of the herbivore biomass at all sites (*pers. observation*; McQuaid and Branch, 1984).

Table 2.1: Common species found at all sites (Branch *et al.* 2010).

Algal Species			
Green	Red	Brown	Coralline
Ulva rigida	*Gelidium pristoides*	*Sargassum elegans* *Ralfsia verrucosa*	*Arthrocardia sp.* *Jania sp.*
Grazer Species			
Limpets	False Limpets	Periwinkles	
Cymbula oculus *Scutellastra granularis* *S. cochlear* *S. longicosta*	*Siphonaria capensis* *S. oculus*	*Afrolittorina africana* *A. knysnaensis*	
Filter Feeders			
Barnacles	Mussels		
Chthamalus dentatus *Tetraclita serrata*	*Perna perna*		

2.2.5 DATA ANALYSES

Statistical analysis of the data took place in the form of several Analysis of Variance (ANOVA) tests to determine the interactions among the elements: upwelling and grazer exclusion.

Grazer density (using the mean annual grazer density) was compared between upwelling and non-upwelling sites using two two-way nested ANOVAs, with upwelling as a fixed factor with two levels and site as a random factor with four levels nested within upwelling. The densities of meso and macrograzers were dependent factors, analysed separately.

Algal cover and biomass were analysed for the last month of the experiment using two three-way nested ANOVAs. The three factors were site (4 levels, random) nested in upwelling (fixed, two levels) and treatment (fixed 3 levels).

Log Response Ratio

The effects of grazing, as either an interaction or a main effect, were estimated using the Log Response Ratio (LRR), comparing the two control plots (i.e. procedural control vs. control) and then comparing the Exclusion plots with the control plots (Arrontes *et al*. 2004). This tested for any experimental artefacts and effects of grazer exclusion respectively.

The Log Response Ratio (LRR) was calculated from data for the exclusion treatment and control treatments after testing for experimental artifacts (Diaz, 2008). Mean percentage algal cover at month 12 was used for all of the experimental sites. The LRR was calculated for each block by using the equation below.

$$\text{LRR} = \text{In } (\%\text{ algal cover}_{\text{control}} / \%\text{ algal cover}_{\text{treatment}})$$

In this instance LRR was used to calculate the grazer influence at each of the sites. Positive values show that grazers promote algal growth, whereas negative values show that grazers reduce algal growth (Diaz and McQuaid, 2011).

The LRR was analysed using data from month 12 of the experiment using a three-way nested ANOVA. The three factors were site (4 levels, random) nested in upwelling (fixed, two levels) and month (fixed 8 levels).

2.3 RESULTS

2.3.1 GRAZER DENSITY

For all sites, mesograzer densities changed considerably during the experiment, suggesting strong seasonality (Figure 2.4b). Grazer density in the first half of the experiment (June – October, i.e. winter-spring) was approximately double that of the second half (October – May). Within-site variation in macrograzer densities showed no clear pattern (Figure 2.4c). The two-way nested ANOVAs for meso and macro grazer density were used to determine if there was a difference in abundance between upwelling and non-upwelling sites. Although mesograzers clearly had higher densities than macrograzers at all sites (Figure 2.4a), no significant differences (p>0.05) were found between upwelling sites and non-upwelling sites for the densities of either meso grazers or macro grazers (Table 2.1a, b) indicating that upwelling had no influence on the densities of the two size classes of grazers.

Table 2.1a: Two-way nested ANOVA of mesograzer density between upwelling and non-upwelling sites.

a) Effect	DF	MS	F	P
Site (Upwelling)	2	0.006032	0.3307	0.72
Upwelling	1	0.016928	0.9282	0.34
Error	28	0.018238		

Table 2.1b: Two-way nested ANOVA of macrograzer density between upwelling and non-upwelling sites.

b) Effect	DF	MS	F	P
Site (Upwelling)	2	0.005107	2.2391	0.12
Upwelling	1	0.002466	1.0809	0.31
Error	28	0.002281		

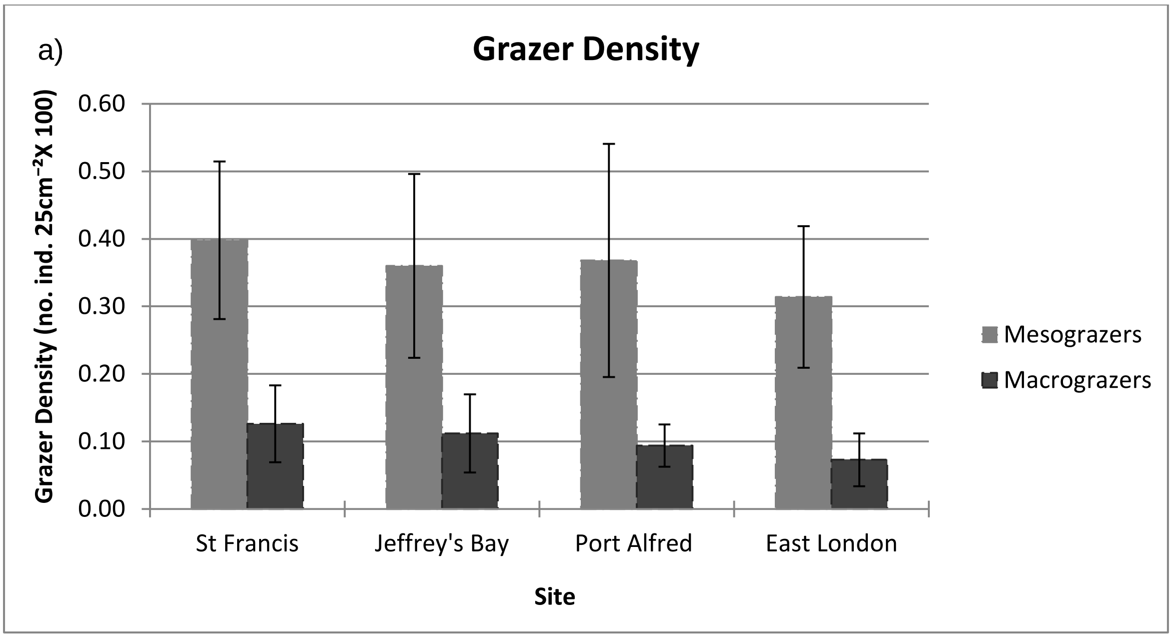
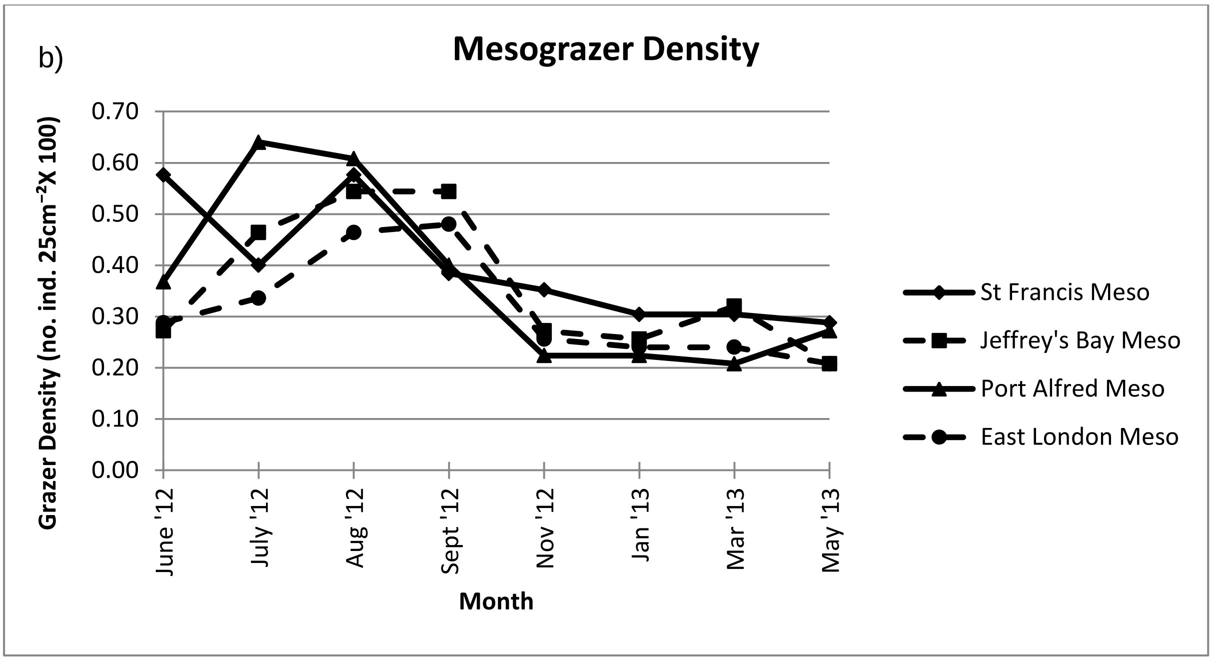


Figure 2.4: a) Annual average meso- and macrograzer densities determined for upwelling (St Frances, Port Alfred) and non-upwelling (Jeffrey's Bay, East London) sites.



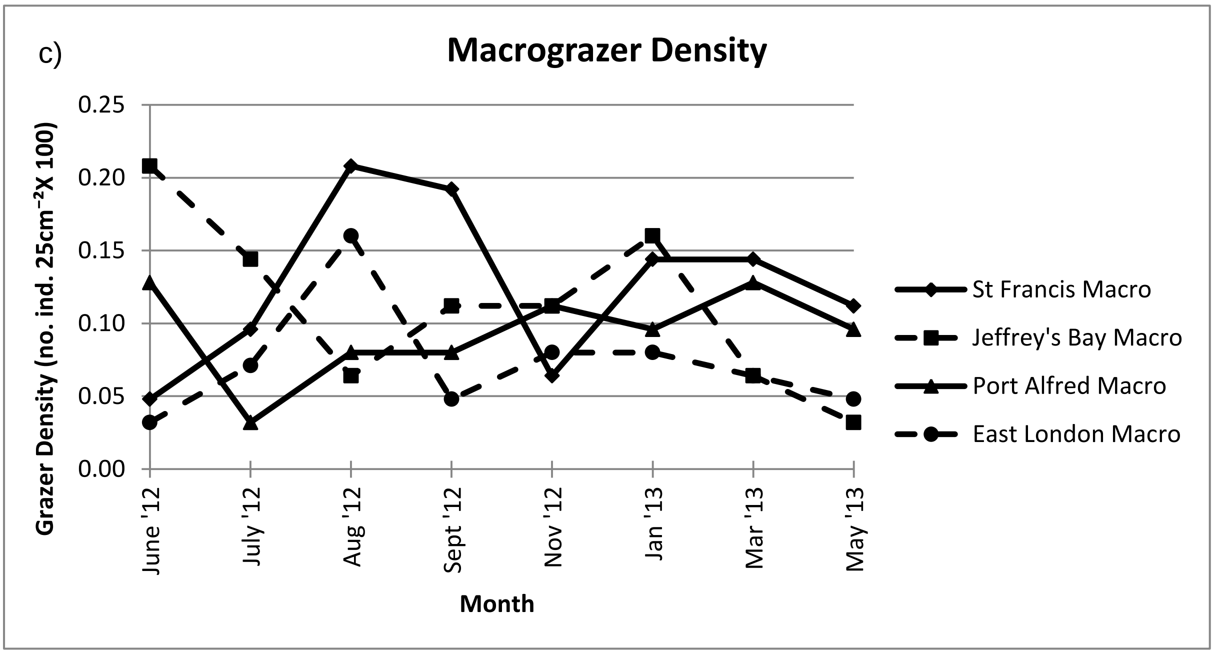


Figure 2.4: b) and c) Monthly average density of meso- and macrograzers determined for upwelling (St Frances, Port Alfred) and non-upwelling (Jeffrey's Bay, East London) sites. Error bars have been omitted for clarity.

2.3.2 ALGAL COVER AND BIOMASS

The rate of algal recovery differed between the sites with the two upwelling sites, St Francis and Port Alfred, reaching maximum recovery of 80-90% cover in 8 months, while algal recovery at Jeffrey's Bay and East London took considerably longer and had not reached 80% recovery by the end of 12 months (Figure 2.5).

Recovery rates were slower within the procedural plots and controls with a maximum cover of only 50% exhibited in the procedural plots at the St Francis site and a maximum cover of only 30% in control plots at Port Alfred.

Three-way ANOVA results indicated that, at the end of the experiment, there were significant differences in percentage algal cover between upwelling and non-upwelling shores and among treatments (Table 2.2) , however there was no significant interaction between treatment and either upwelling or site. The post-hoc Tukey HSD test indicated experimental artefacts due to the experimental procedure (i.e. cover was significantly higher in PC than C treatments) but both control plots had significantly lower cover than experimental plots ($p < 0.05$ in both cases), indicating clear reduction of algal cover in the presence of grazers despite this artefact.

Table 2.2: Three-way analysis of differences in algal cover. Significant values are shown in bold (p<0.05).

	SS	DF	MS	F	p
Upwelling	2333.8	1	2333.8	60.33	**0.01**
Site(Upwelling)	76.9	2	38.4	0.28	0.77
Treatment	39750.3	2	19875.2	144.31	**<0.001**
Upwelling*Treatment	786.1	2	393.1	2.85	0.17
Site(Upwelling)*Treatment	554.8	4	138.7	2.33	0.06
Error	5176.4	87	59.5		

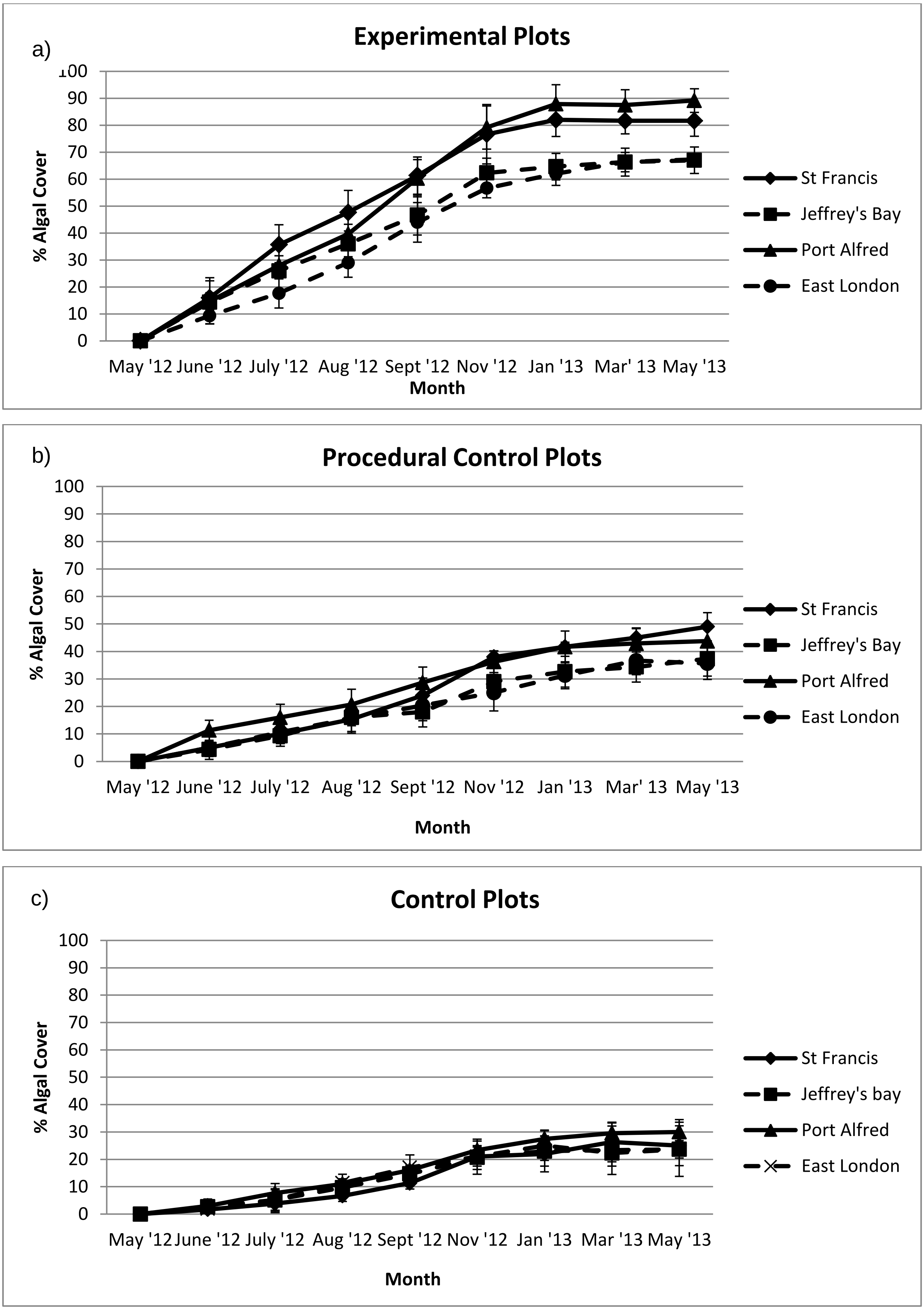


Figure 2.5: Percentage of algal cover at the a) experimental plots, b) procedural control plots and c) control plots at the two upwelling sites (St Francis, Port Alfred) and the two non-upwelling sites (Jeffrey's Bay, East London). In all cases, data are mean ± SD (N = 12).

Algal biomass at the end of the experiment was compared among exclusion plots, procedural control plots and control plots at the upwelling sites and non-upwelling sites using a three-way nested ANOVA on the wet algal mass (Table 3.3). Significant differences were found between upwelling and non-upwelling sites and among treatments, with no significant interaction. The post-hoc Tukey HSD test indicated that the algal biomass in the experimental exclusion plots was significantly higher in the upwelling sites compared to the non-upwelling sites ($p<0.05$), indicating that upwelling had an influence on algal biomass in the absence of grazers. No significant differences were found between the two upwelling sites or between the two non-upwelling sites Figure 2.6 indicates the average algal biomass found at the four sites and clearly shows that the upwelling sites had higher algal biomasses than the non-upwelling sites in the exclusion plots. The control plots however did not differ significantly suggesting that grazing intensity may have been stronger at the upwelling sites, resulting in similar final algal biomass in the control plots. Regarding the significant treatment effect, post-hoc tests between C and PC treatments revealed experimental artifacts at each site, with some enhancement of algal biomass due to the experimental procedure. Despite this, PC and exclusion treatments were significantly different at all sites, indicating clear reduction of algal biomass in the presence of grazers.

Table 2.3: Three-way ANOVA results on algal biomass between upwelling and non-upwelling sites. Significant values are shown in bold.

	DF	MS	F	p
Upwelling	1	2048.1	56.764	**0.02**
Site(Upwelling)	2	36.1	0.269	0.78
Treatment	2	11614.4	86.504	**<0.001**
Upwelling*Treatment	2	120.0	0.894	0.48
Site(Upwelling)*Treatment	4	134.3	1.028	0.41
Error	24	130.6		

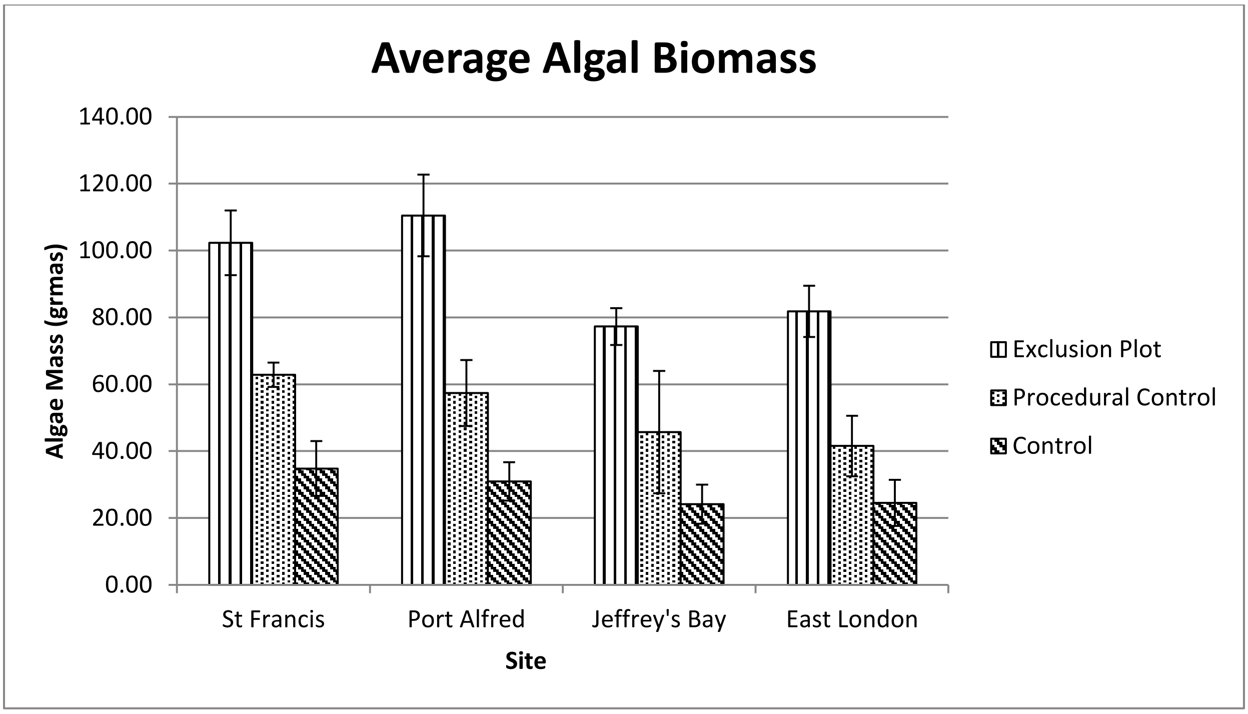


Figure 2.6: Average algal biomass at the two upwelling (St Francis, Port Alfred) and two non-upwelling (Jeffrey's Bay, East London) sites.

2.3.3 ALGAL MORPHOLOGICAL GROUPS

Algal recovery patterns in cleared plots were similar at all four sites with a thin biofilm layer (probably including benthic diatoms and juvenile algal stages) appearing soon after clearing the plots. The green algae, *Ulva rigida,* and the encrusting brown alga *Ralfsia verrucosa* were the initial colonisers thereafter. *Ulva rigida* was however the most abundant algal species in all experimental plots. Foliose corallines (*Arthrocardia* sp. and *Jania* sp.) started to recover after 10 months at only two of the Port Alfred experimental plots, and did not recover at any of the other sites.

2.3.4 LOG RESPONSE RATIO

The Log Response Ratio (LRR) was calculated for all four sites, with each site demonstrating negative values, indicating that grazers reduced algal growth at all sites (Figure 2.7). The three-way ANOVA conducted on the LRR indicated that there was a significant difference between upwelling sites and non-welling sites (Table 2.4, $p<0.001$) with upwelling sites indicating stronger grazing effects. The post-hoc Tukey test on the effect of Site indicated significant differences ($p<0.05$) between the two upwelling sites (i.e. St Francis vs. Port Alfred), however no significant difference ($p>0.05$) between the two non-upwelling sites (i.e. Jeffrey's Bay vs. East London). The ANOVA indicated that the upwelling sites had significantly lower LLR values than the non-upwelling sites indicating stronger grazing effects at upwelling sites, as well as a significant interaction between Site and Month suggesting that there is a stronger effect of grazing during the summer months at upwelling sites.

Table 2.4: Three-way ANOVA results on the LRR values for the upwelling and non-upwelling sites. Significant values shown in bold.

Effect	DF	MS	F	p
Upwelling	1	0.29248	16.935	**<0.001**
Site(Upwelling)	2	0.14151	8.194	**0.001**
Month	8	0.87987	50.946	**<0.001**
Upwelling*Month	8	0.3841	2.85	**0.02**
Site(Upwelling)*Month	16	0.2484	2.33	**0.04**
Error	24	0.01727		

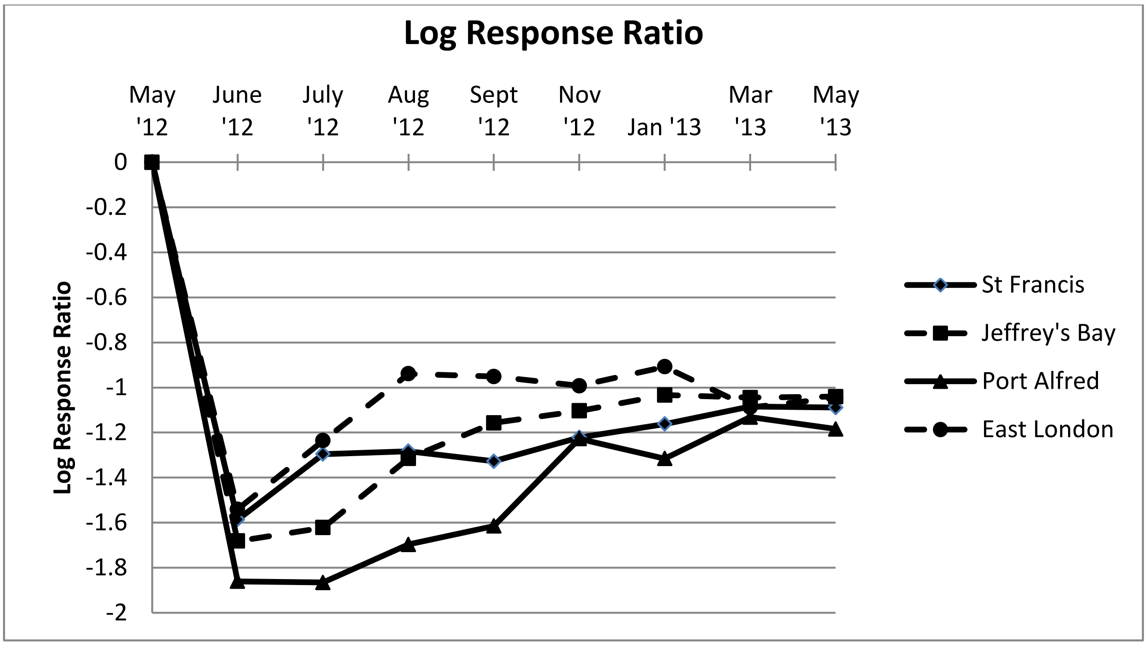
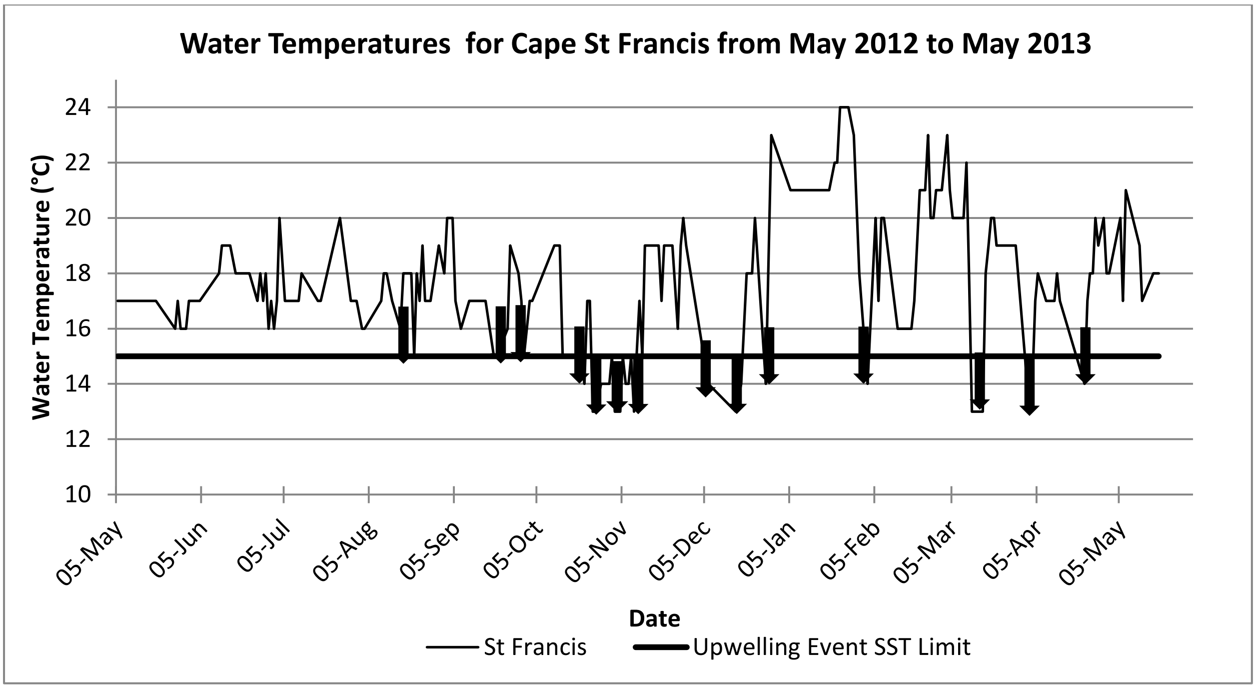


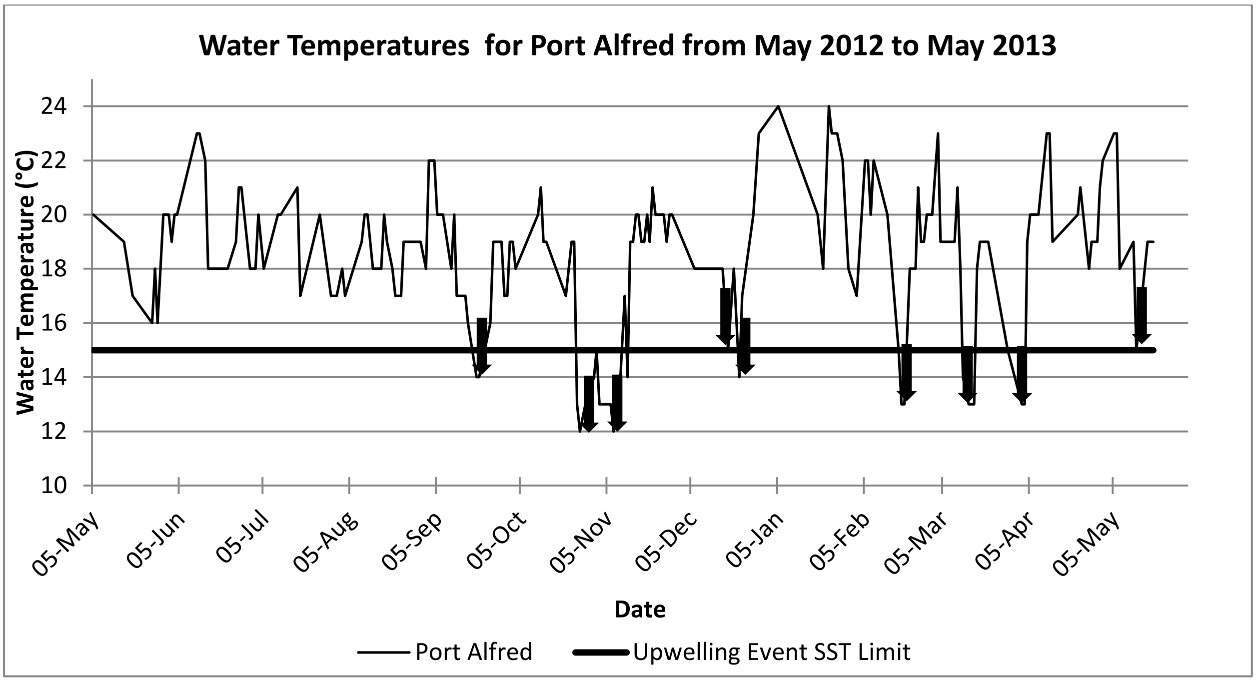
Figure 2.7 : Log Response Ratios for the four sites over the 12 month experiment duration.

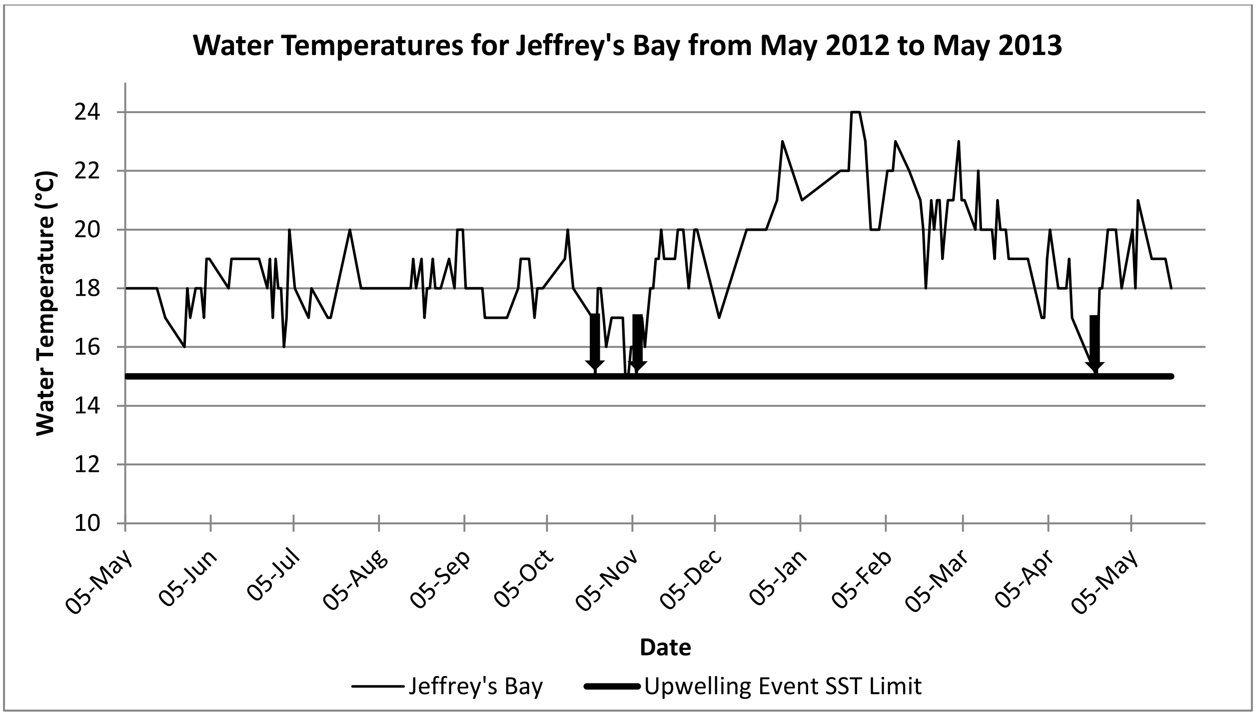
2.3.5 UPWELLING OCCURRENCES AND FREQUENCY

There was a significant difference (t-test, p=0.03) in the total number of upwelling occurrences between the upwelling sites and non-upwelling sites with St Francis and Port Alfred experiencing approximately 69 and 74 upwelling occurrences, respectively, while Jeffrey's Bay and East London experienced upwelling effects only 5 and 9 times respectively throughout the year from May 2012 to June 2013 (Figure 2.8). Upwelling occurrences were defined by events where water temperature reached below 15 ^{o}C (Lutjeharms 2006b). The non-upwelling sites, Jeffrey's Bay and East London, very seldom reached temperatures below 16^{o}C and East London only once had water temperature reach as low as 14 ^{o}C.

St Francis and Port Alfred tended to experience upwelling effects around the same days, with Port Alfred experiencing upwelling for either a slightly longer period or on additional days throughout the year. The summer months from October to December indicated lower water temperatures on average suggesting that temperature conditions at these sites are structured by the dominant easterly summer winds orientated approximately parallel to the coastline and resulting in upwelling (Goshen and Schumann 2011).


Water Temperatures for Cape St Francis from May 2012 to May 2013
Water Temperature (°C)
24
22
20
18
16
14
12
10
05-May
05-Jun
05-Jul
05-Aug
05-Sep
05-Oct
05-Nov
05-Dec
05-Jan
05-Feb
05-Mar
05-Apr
05-May
Date
St Francis
Upwelling Event SST Limit


Water Temperatures for Port Alfred from May 2012 to May 2013
Water Temperature (°C)
24
22
20
18
16
14
12
10
05-May
05-Jun
05-Jul
05-Aug
05-Sep
05-Oct
05-Nov
05-Dec
05-Jan
05-Feb
05-Mar
05-Apr
05-May
Date
Port Alfred
Upwelling Event SST Limit



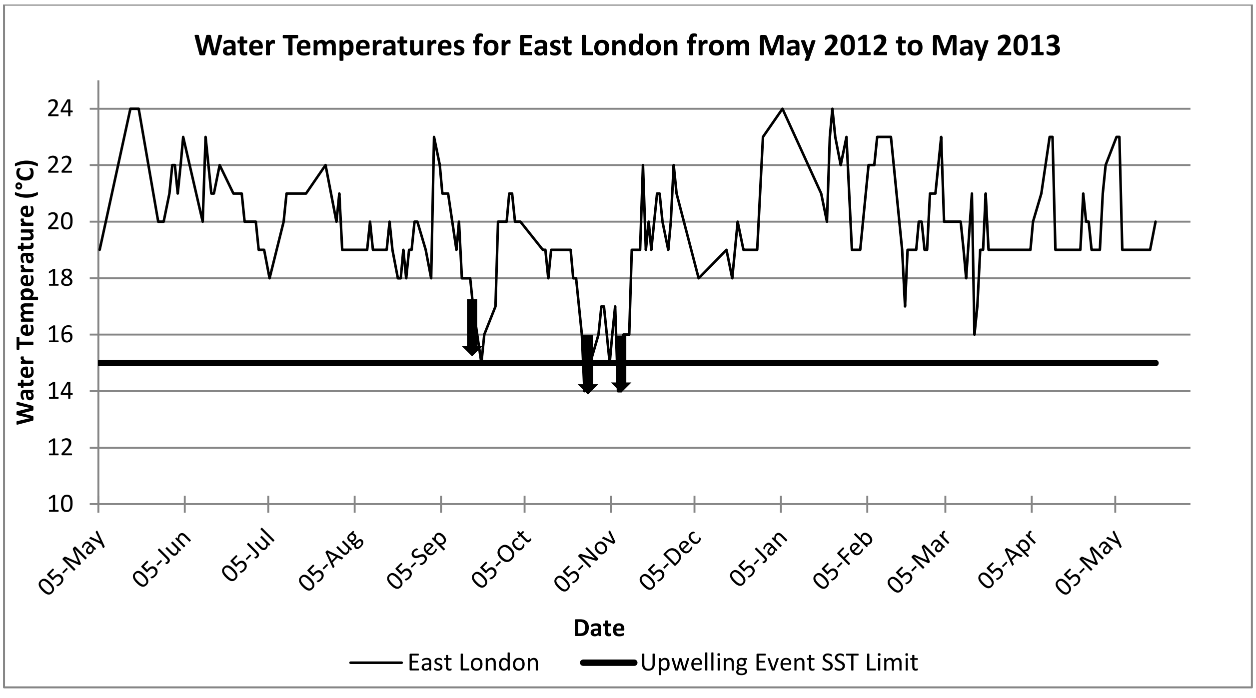


Figure 2.8: Sea Surface Temperature values for the four sites for the experimental year from May 2012 to May 2013. The arrows indicate possible upwelling events.

2.4 DISCUSSION

2.4.1 APPROACH

The experimental design and methodology applied in the above experiments have effectively shown that there is a complex interaction between grazing pressure and nutrient effects on algal communities on rocky shores. As expected in hypothesis 1, the exclusion plots at all four sites showed significantly greater algal cover percentage compared to both the procedural and control plots, thus indicating that grazers have a strong top-down effect on algal cover. The log response ratio confirms these results as all four sites demonstrated negative LRR values, indicating that grazers had a negative effect on the accumulation of algal biomass and reduced the algal cover and biomass at all sites.

Although there was no effect of upwelling on grazer abundances, hypothesis 2, which predicted that the effects of grazing would be greater in non-upwelling regions compared to upwelling regions, was rejected. By the end of the experiment, the exclusion plots exhibited higher average algal biomass at the upwelling sites than at the non-upwelling sites (Figure 2.3), while the control plots did not differ significantly and LRR values were significantly greater for upwelling sites, indicating that upwelling increased the effectiveness of grazing in reducing algal cover. This may be due to the algae being more tasty when they are higher in nutrient content and possibly lower in grazer detterents (Kraufvelin *et al*. 2006a).

2.4.2 GRAZER DENSITY AND ALGAL COVER

This study illustrates that grazer densities varied temporally and that their effects varied from small to large spatial scales. Figure 2.4a shows the average density of grazers at each site during the experimental year, while Figure 2.4b and c indicate the varying grazer densities during different times of the year, with winter and spring months showing a higher density of meso grazers than summer and autumn months, while the macro grazers exhibited irregularly fluctuating densities throughout the year.

Algal recovery rates (as indicated by the lines for cover in Figure 2.5), similarly showed a marked slow down after November, but little difference among sites. It is well known that different sizes and species of grazers have different effects on algal assemblages (Underwood and Jernakoff 1984; Arrontes *et al.* 2004; Diaz 2008) and hence grazing pressure will differ according to the abundance, size and species of grazers present on the rocky shore. Meso grazers such as *Siphonaria oculus* generally graze on the smaller algal spores and consequently limit recruitment, whereas larger territorial species such as *Scutellastra longicosta* are prudent predators and facilitate algal growth by limiting grazing by non-territorial grazers such as *Cymbula oculus*, which are highly destructive grazers (McQuaid and Froneman 1993). The density of meso grazers was found to be significantly higher than that of macro grazers at all sites, suggesting that algal recovery was limited by the meso grazers grazing on algal spores.

Meso grazers are highly effective at clearing algae off the rocks as they have a specially modified radula that allows them to graze on the algae spores on the rocks (Steneck and Watling 1982). Steneck and Watling (1982) studied the feeding efficiency of grazers by examining the anatomical structure of the radula of limpets. Their studies have shown that limpet radulas are very efficient at scraping algae off the rock surface, leaving the rocks almost bare. The study conducted by Steneck and Watling (1982) corroborates my results as even when there was a low density of grazers at a site, the algal cover exhibited in the procedural and control plots was also low.

Differences in the sizes and abundances of grazers between upwelling and non-upwelling sites must be taken into account when considering the recovery rates of algae at the four sites. The predominant species of mesograzers present at all sites was *S. capensis,* and considering the higher densities of meso grazers, it is suggested that *S. capensis* is the dominant species controlling algal recovery in terms of *Ulva rigida*. This finding is in contrast with findings from Maneveldt *et al.* (2009) who found that the macrograzer, *Cymbula oculus,* was the dominant factor controlling algae growth at Kalk Bay in the Cape of Good Hope. The significantly lower density of macro grazers along the Eastern Cape sites suggests that they have a lesser effect on *Ulva rigida* recovery as they predominantly graze on the larger red and brown algae (Raborg and Kautsky

2007, Korpinen *et al*. 2008, but see also Kraufvelin and Salovius 2004 for a broader perspective). These results are similar to those found in previous studies (Underwood *et al*. 1983; Dye 1993) which found that grazer abundance was a key determining factor for the type and extent of algal recolonisation.

2.4.3 RECRUITMENT AND SUCCESSION

The rate of recruitment plays a key role in determining which species will dominate the rocky shores after a disturbance event such as the artificial disturbance created in my experiments. The rapid colonisation of *Ulva* at all sites could possibly have prevented the succession of other slower growing species such as the red and encrusting coralline algae. A study conducted by Maneveldt *et al*. (2009) in Kalk Bay, South Africa, showed similar algal succession stages, with the green alga, *Ulva rigida* being the dominant species for the first year of the experiment. They found that there was an increase in algal diversity only after a year, with *Ulva rigida* being replaced by *Ralfsia verrucosa* and *Gelidium pristoides*.

Another study that exhibited similar results was that of Boaventura *et al*. (2002) who found that the composition of algal species in the experimental plots on European shores was dominated by a single green turf algal species for the first few months of the experiment. By the end of their experiment though, the algal composition had changed from green turf-forming algae to the red turf-forming alga, *Caulacanthus ustulatus.* These results indicate that succession plays a key role in determining the composition of the rocky shore community whereby fast growing and high tolerance level species will colonise first until the slower growing species have established themselves and slowly begin to take over and create a more diverse community structure ranging from early colonisers, such as *Ulva*, to late successional species such as encrusting corallines (Hunt and Scheibling 1997; Contardo Jara *et al*. 2008).

By reducing the amount of chlorophyll *a* content on a rocky substratum, grazers can affect the abundance and diversity of microalgae on the shore. Further selective grazing by limpets can result in a patchy distribution of the algae and cause early post-settlement mortality of algal spores (Hunt and Scheibling 1997).

Propagule supply, settlement and survival are key to determining the community structure and can often be very different among localised populations as the degree of connectivity of ecosystems can differ substantially over small scales (Schiel 2004; Bulleri 2005), even though macroalgae generally disperse over very small scales (Kinlan and Gaines 2003). Further influencing the rate of recruitment is the supply of propagules through upwelling events (Menge *et al*. 1997ab). Recruitment rates tend to be higher in areas where upwelling is intermittent, such as the events at Cape St Francis and Port Alfred, whereas in areas where upwelling is strong and continuous such as along eastern-boundary currents, the supply of propagules is generally low (Schiel 2004), resulting in differently structured shores.

Another factor linked to the survival of recruits is the ability to attach to the substratum in sufficient numbers in order to establish sustainable populations (Schiel 2004). Attachment plays a key role in community distribution and structure as many sessile species, such as barnacles and algae can only attach to open substratum, hence limiting space on the shore for colonisation by other species and may have consequences for later successional species (Bulleri 2005). Homing species such as many limpets, cause spatial patterns in grazing as the individuals forage for only short distances during high tide before returning to their home scars. The distribution patterns in which the home scars are situated will shape the grazing pattern and hence the algal growth patterns and patches (Hawkins and Hartnoll 1983), thereby having an influence on the community structure.

2.4.4 EFFECTS OF UPWELLING

This study has shown that upwelling has a major influence on the effects of grazing experienced at different sites, but its role in determining how the algal community is structured is less clear. Algal cover and biomass at the end of the experiment were significantly higher at upwelling sites but only in the exclusion plots, suggesting that grazing effects are stronger at upwelling sites. This was supported by the LRR values. Thus, there was more algal cover and biomass at upwelling sites in the absence of grazers, but with grazers, as in the control plots, there was no difference between upwelling and non-upwelling sites. Thus, grazers are removing more algae at upwelling sites resulting in the same amount of algal cover in the control plots. These factors could create a competitive relationship rather than a trophic interaction between algae and grazers at upwelling sites (Underwood and Jernakoff 1984). The competition for space will favour faster growing early colonising algae species. At the same time, the foraging range of limpets should theoretically be reduced, allowing higher densities of grazers (Arrontes et al 2004; Bulleri 2005), but this was not the case for my study sites, which showed no effect of upwelling on grazer densities.

Herbivore recruitment and life stages must also be considered when looking at the role of grazers at upwelling sites, as juvenile and adult herbivores will often graze on different species or life stages of algae and this can result in shifts in algae community composition (Nielsen and Navarrete 2004). Likewise if upwelling is persistent, the offshore advection of surface waters may result in limited recruitment of herbivores which can lead to reduced grazing pressure on the algae, consequently resulting in higher algal cover and biomass (Connolly *et al*. 2001; Nielsen and Navarrete 2004).

In conclusion, upwelling resulted in faster algal growth rates and higher algal biomass when compared to non-upwelling sites, but only in the absence of grazers.

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CHAPTER 3 – What are the effects of enhanced nutrients on algal production?

3.1 INTRODUCTION

The recent changes within the global oceans induced by climate change are among the main areas of present ocean research. Understanding the effects that these changes have on ecosystems is fundamental for managing these systems in the event of eutrophication, acidification or other modification by human activity (Nixon 1995; Borum and Sand-Jensen 1996; Downing *et al* 1999; Lachkar and Gruber 2011). Anthropogenic alteration of the global nitrogen cycle causes changes in primary productivity rates and can further affect factors driving ecosystem services (Borum and Sand-Jensen 1996; Antón *et al.* 2011).

3.1.1 EFFECTS OF ENHANCED NUTRIENTS

Nutrient enrichment is one of the major factors affecting global oceans as eutrophication can cause detrimental impacts on the ecosystems and alter the structural and functional traits driving ecosystem services (Antón *et al.* 2011). However, enhanced nutrients may also provide positive changes to the services such as enhancing the quality of the primary producers, thereby providing a higher quality food source for consumers (Oviatt *et al.* 1995; Teichberg *et al.* 2010).

Nitrogen and phosphorous have long been known to be the main nutrients limiting primary production rates (Kudela et al 2008), however nitrogen supply is the key factor in the control of algal growth and its levels of supply are a strong determinant of species composition in marine environments (Dugdale 1985; Nixon *et al*. 1986; Oviatt *et al*. 1995; Teichberg *et al.* 2010). The higher the supply of nitrogen, the lower the algal species diversity as many species grow optimally within a limited range of nutrient supply and can often be overshadowed and outcompeted by the faster growing, more generalised species, such as *Ulva* spp which are physiologically adapted to take up available nutrients rapidly (Valiela *et al*. 1997; Teichberg *et al.* 2010).

The effects of eutrophication have also been known to alter community structure by increasing the growth rates and dominance of filamentous algae, which have high nutrient uptake rates and requirements (Worm and Lotze 2006; Kraufvelin *et al.* 2010; Teichberg *et al.* 2010). These algal species flourish in nutrient enriched waters and consequently will compete aggressively for light and space and can eradicate perennial macrophytes and slow growing algal species (Borum and Sand-Jensen 1996, Kraufvelin 2007). This results in an ecosystem with much lower diversity and may be linked to the changes in ecosystem functions such as productivity (Kraufvelin *et al.* 2010). Examples of this can be seen in the Baltic and Adriatic Seas, where perennial macroalgal communities have largely declined and have been replaced by bloom-forming annual algae, with adverse effects on the coastal ecosystem (Vogt and Schramm 1991, Råberg and Kautsky 2007).

These algal blooms can, however, be reduced or hindered by grazers feeding on the early life stages, such as sporelings, to prevent further recruitment (Lotze and Worm 2000; Worm and Lotze 2006) and thereby to some extent reducing the adverse effects of eutrophication. Temporal patterns however must be taken into consideration when looking at grazing pressure at higher nutrient levels. For example, grazing effects were strong in spring but substantially weaker in summer months in the Baltic Sea (Worm and Lotze 2006). This can possibly be explained by an increase in predator abundance promoting stronger control of the grazer populations in the summer months (Worm *et al*. 2000) and reduced recruitment of bloom-forming green algae in summer, possibly limited by nutrients (Worm and Lotze 2006). These factors in conjunction will determine the extent of the algal blooms.

Another factor that can affect the size of an algal bloom is the intensity of upwelling driven by the strength of the wind (Kudela *et al*. 2008). Too much wind and insufficient relaxation period result in a decrease of nutrient draw down due to advection of nutrients and increased light limitation, while too little wind and longer relaxation periods result in low productivity due to decreased nutrient supply (Kudela *et al*. 2008).

3.1.2 EFFECTS OF INCREASED NUTRIENTS ON GRAZING

Grazing patterns are closely linked to the quality and quantity of food available such that the density of grazers may increase with eutrophication, but the diversity of grazers may decrease to only a few generalist species (Proulx and Mazumder 1998; Worm and Lotze 2006). These generalist grazer species are suited to grazing on fast growing algae with high nutrient values, whereas grazers in more oligotrophic waters must consume larger amounts of algae with low nutritious value to attain the same nutrient requirements (Russell and Connell 2007). Previous studies have found that species richness of grazers will often increase with increasing primary productivity until it reaches a certain level, and thereafter any increase in productivity will result in a decline of species richness (Proulx and Mazumder 1998; Russell and Connell 2007). However, even though grazers remain a key controller of algal biomass, often even with an increase in grazer abundance, the grazing pressure will remain constant, as they cannot compete with or reverse the effects of eutrophication (Worm *et al.* 1999; Worm and Lotze 2006).

Furthermore, grazing patterns differ according to the history of the nutrient conditions (i.e. whether long term nutrient conditions are low/ambient or high/enriched). In systems where nutrient conditions are predominantly low, gazers will respond strongly to nutrient enriched algae by increasing consumption, whereas in systems where nutrients are generally high, grazers do not react to a further increase in nutrients (Russell and Connell 2007). The timing of the change in grazing pressure also needs to be considered as different species often take different lengths of time to adapt to the changes in nutrient levels and to fully outcompete other species (Proulx and Mazumder 1998).

On the other hand, rocky shores have also been known to be partly resistant to algal blooms during eutrophic conditions, as waves and tidal action can moderate the recruitment of algal spores and thereby moderate the biomass of fast-growing algal species (Kraufvelin *et al.* 2006a). Physical conditions of the environment, such as wave exposure, water exchange rates, water currents, weather conditions and shore profiles must also be taken into consideration when trying to determine to what extent eutrophication can occur on a rocky shore (Kraufvelin *et al.* 2006a).

3.1.3 AIMS AND OBJECTIVES

This study assesses the impacts of locally increased nutrients, in the form of a fertilizer containing both nitrogen and phosphorous, on the rate of algal biomass increase on rocky shores in order to determine how these systems may be affected by possible ocean changes in the future. The questions below were identified in order to a gain a better understanding of the effects of upwelling on algal assemblages.

This study centred on the following question:

- What is the effect of locally enhanced nutrients on algal growth?

Hypotheses

One hypothesis was derived from the general model that nutrients influence the rate of algal growth differently between upwelling and non-upwelling regions:

(1) The effect of locally enhanced nutrients on rate of algal growth is stronger at a site that does not experience upwelling.

3.2 METHODS

3.2.1 SITES

Nutrient enrichment experiments were set up at the midshore level at one upwelling shore and one non-upwelling shore on the south-east coast in the Eastern Cape. The upwelling shore was located at Port Alfred (33° 36’ 52.0’S 26° 53’ 18.4’ E) while the non-upwelling shore was located at East London (32° 58’24.2’S 27° 58’13.2”E).

Shore selection was based on the same criteria as the grazer exclusion experiment in the previous chapter.

3.2.2 NUTRIENT ENRICHMENT EXPERIMENT

Three blocks at each study site were randomly chosen to set up the experiment, located approximately five meters apart. Three replicates of each treatment were set up within each block and replicates were situated approximately three meters apart. This was to minimise contamination of added nutrients among treatments. The experiment commenced in May 2013 (autumn) and was run for six months to determine the effects of local nutrient enrichment on algal growth at an upwelling and a non-upwelling site. I manipulated nutrient concentrations using a slow-release fertilizer (Plantacote-Plus 8M), manufactured by Aglukon, as this has shown to be effective in previous studies (Hillebrand *et al*. 2000; Worm *et al*. 2000).

The experiment consisted of two treatments, a procedural control and a control:

(1) Grazer exclusion, High enrichment treatment (HT) consisted of 1 bag of fertilizer, weighing 2kg;

(2) Grazer exclusion, Low enrichment treatment (LT) consisted of 1 bag of fertilizer, weighting 1kg;

(3) Procedural control (PC) or semi-exclusion plot using anti-fouling paint to paint an L-shape in two corners of the plot, no fertiliser

(4) A control treatment (C) where only the corners of the plot are marked by screws and left otherwise unaltered.

The screws were fixed in holes in the rock drilled by a battery-operated Hilti drill. Copper based anti-fouling paint was used to exclude limpets in the enrichment plots by painting a thick border (5 cm) around the 25 x 25cm plots, as in the previous experiment.

Control and experimental plots were scraped clear and blowtorched until white hot to remove all living organisms, with the intention of starting all plots with 0% algal cover. Plots were then established, with treatments assigned randomly, and left for one month, after which sites were revisited monthly during spring low tides.

3.2.3 MAINTENANCE AND SAMPLING

Following establishment of the experiment, sampling was undertaken during spring low tides, monthly for the first three months and then bimonthly until the conclusion of the experiment at 6 months. At each sampling date, the experimental plots were photographed and percentage algal cover was estimated using the point method. Repairs were made to any damaged paint in the experimental plots and any limpets that may have entered the exclusion treatments were removed at each sampling date (Jenkins *et al*. 2005). This occurred at a rate of approximately 1 limpet per month per site.

3.2.4 ALGAL BIOMASS

Algal biomass (measured as wet mass) was assessed after the 6 month duration of the nutrient enrichment experiment by scraping all algae from the plots, to determine if there was a difference in algal biomass among treatments. Biomass was then compared among treatments and between the upwelling and non-upwelling site.

3.2.5 DATA ANALYSIS

To determine the effects of treatment on algal cover and biomass, separate two-way ANOVA's were carried out on data for the last sampling occasion. Both involved site (random, 2 levels) and treatment (fixed, 4 levels), with either biomass or cover as the dependent variable.

As there were no controls for the effects of nutrients in the presence of grazers, data for the HT and LT plots in this experiment were compared with the results from the grazer exclusion plots in experiment 1 using a two-way ANOVA with site (random, 2 levels) and treatment (fixed, 5 levels) as the independent factor. This comparison is confounded by temporal effects as the two experiments were conducted at different times.

3.3 RESULTS

3.3.1 NUTRIENT ENRICHMENT EFFECTS

The two-way ANOVA indicated that there was a strong interaction between site and treatment with regards to algal cover. Cover in all treatments was greater at Port Alfred, but both sites exhibited the same pattern among treatments: an increase in cover ranked as C < PC < LT < HT. The interaction reflected the fact that the increase in cover between the PC and LT treatments was stronger at Port Alfred (Figure 3.1).

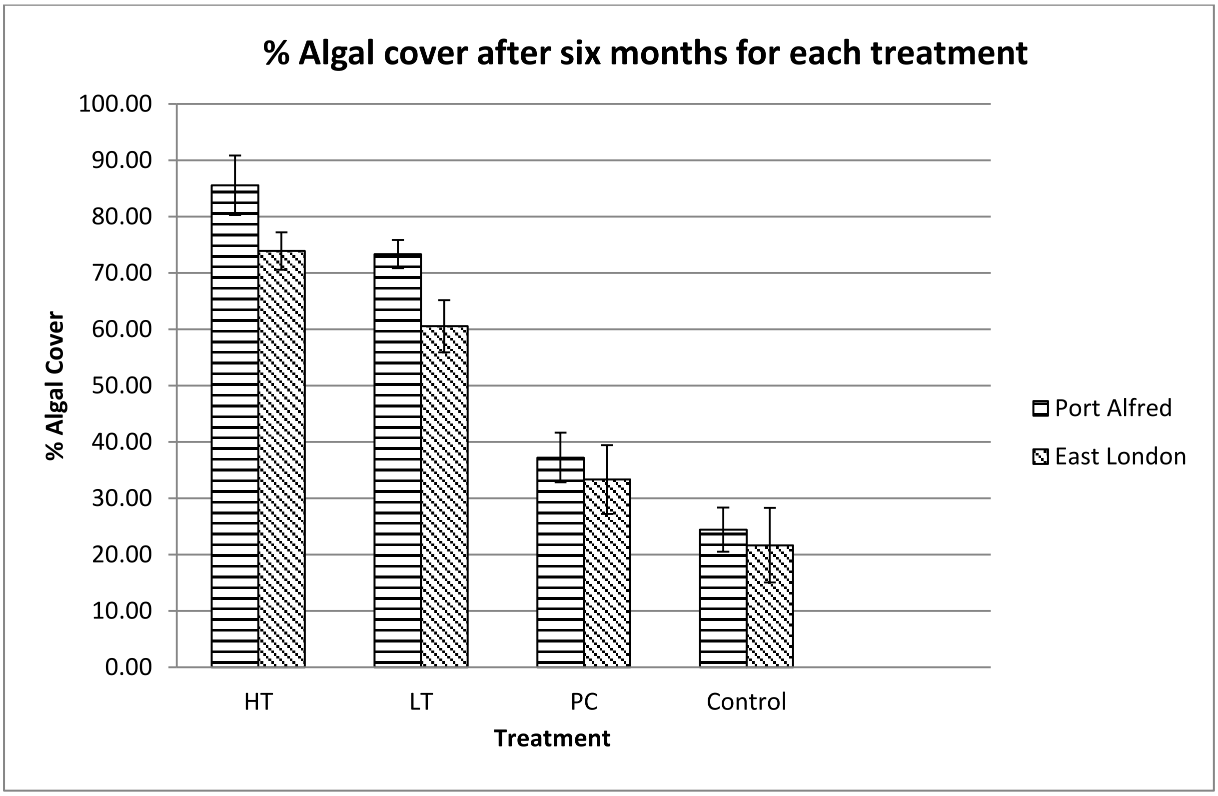

Figure 3.1: Percentage of algal cover (± standard deviation) established in the four treatment plots at the Port Alfred upwelling and East London non-upwelling site over the six month experiment duration.

Table 3.1: Two-way ANOVA conducted on effects of nutrients on algal cover between Port Alfred and East London sites. Significant values shown in bold (p<0.05).

	DF	MS	F	p
Site	1	362.96	9.04	0.06
Treatment	3	4214.04	105.02	**<0.01**
Site*Treatment	3	40.12	4.17	**0.02**
Error	16	9.61		

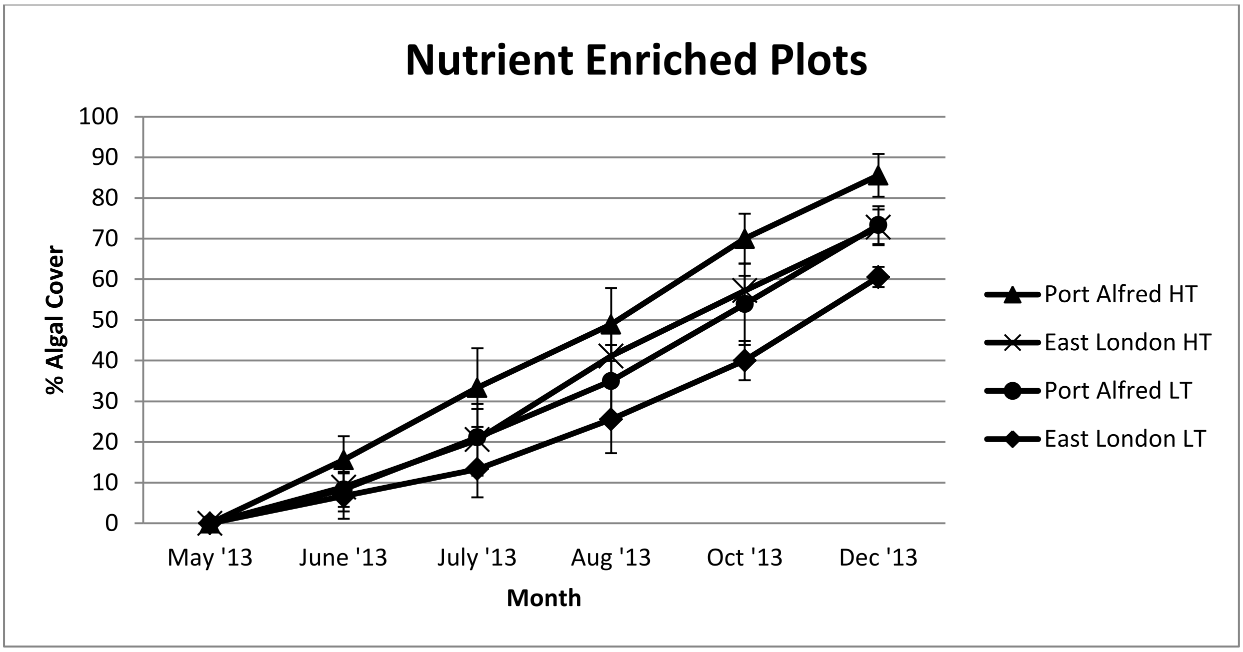

Figure 3.2: Percentage of algal cover established in the high and low treatment plots at the Port Alfred upwelling and East London non-upwelling site.

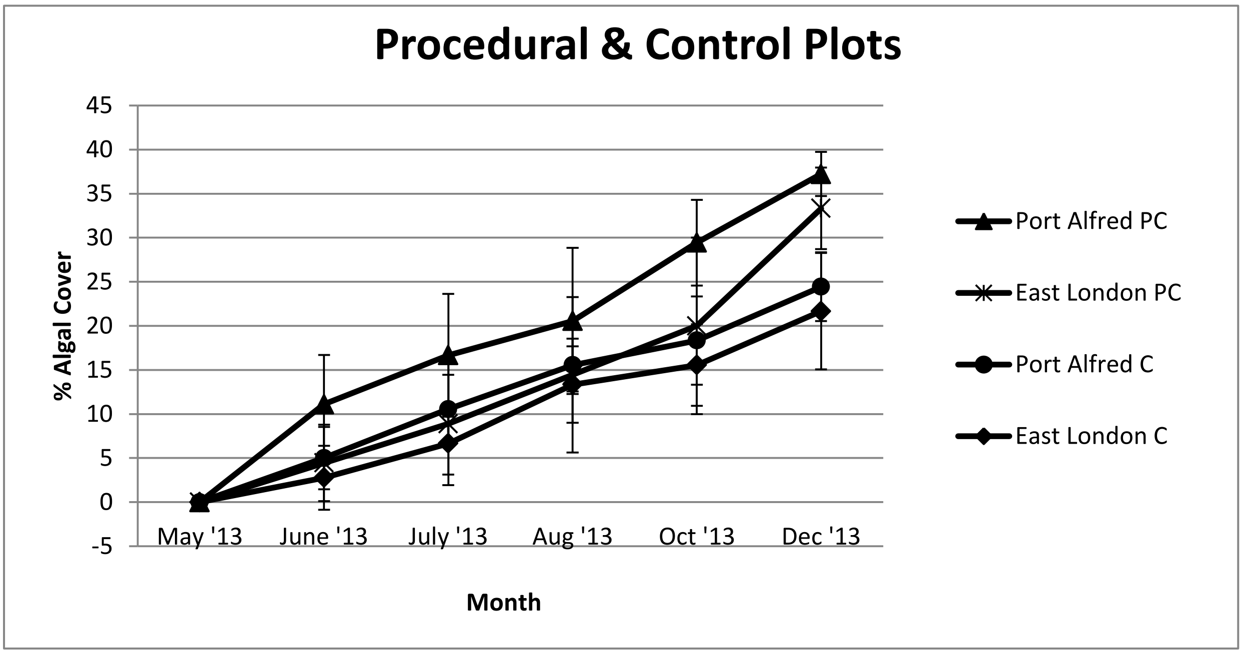

Figure 3.3: Percentage of algal cover established in the procedural and control plots at the upwelling and non-upwelling sites.

Results from the exclusion plots at East London and Port Alfred from the first six months of experiment 1 were compared with the high treatment (HT) plots from experiment 2 (the HT plots also excluded grazers) to further determine the extent of the effect of the enhanced nutrients on algal growth. For both sites, significantly higher algal cover was found in the HT plots than in the grazer exclusion plots (Table 3.2, $P < 0.01$ in both cases), suggesting that the nutrient enrichment had strong effects in increasing the algal growth rates (Figure 3.2). The post-hoc test indicated that there was no significant difference between the Port Alfred HT plot and the grazer exclusion treatment plot, however there was a significant difference between the East London HT plot and the grazer exclusion treatment plot. Moreover, the significant site x treatment interaction indicated that the within site difference between HT and grazer exclusion treatments was much greater for East London (Figure 3.4). These analyses were conducted after the six month duration of experiment 2 and the first six months of experiment 1, which were run during the same calendar months. It is possible that the effects of the enhanced nutrients could reach a plateau which could affect the difference in percentage of algal cover after one year. Differences between the two years in light intensity, temperature and background nutrient levels must also be taken into consideration as these factors will greatly influence the algal growth rate.

Table 3.2: Two-way ANOVA conducted on effects of the four treatments from experiment 2 plus the grazer exclusion from experiment 1 on algal cover between Port Alfred and East London sites. Significant values shown in bold (p<0.05).

	DF	MS	F	P
Site	1	963.33	7.71238	**0.04**
Treatment	4	3582.41	28.68050	**<0.01**
Site*Treatment	4	124.91	11.14876	**<0.01**
Error	20	11.20		

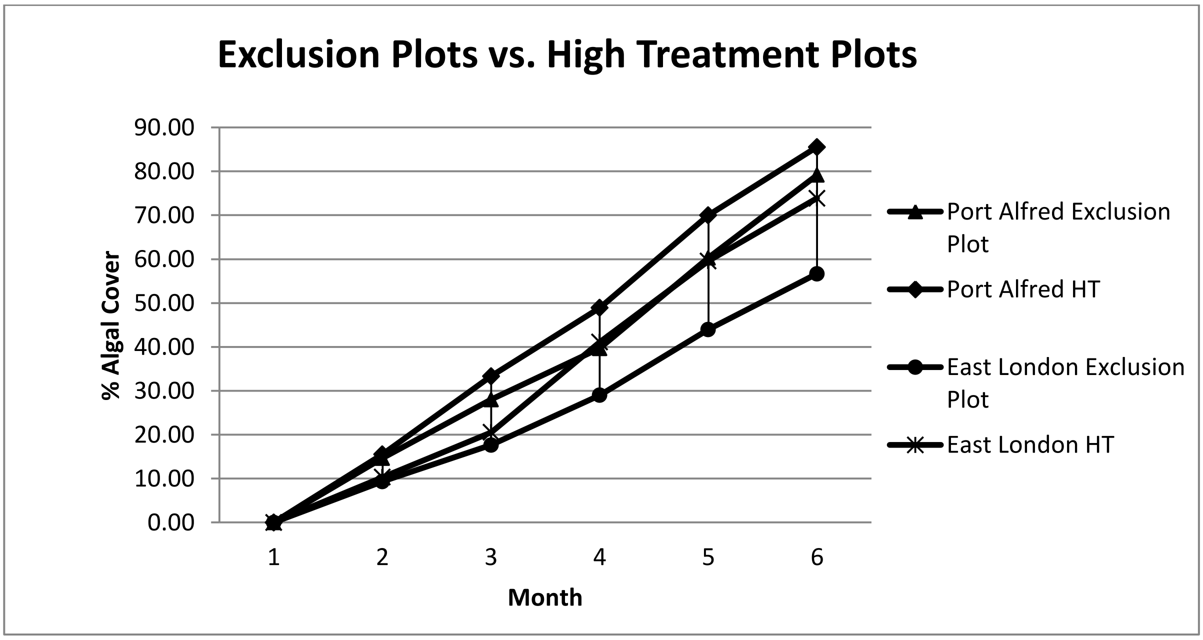

Figure 3.4: Percentage of algal cover compared between the grazer exclusion plots from experiment 1 and high nutrient enrichment plots from experiment 2.

3.3.2 ALGAL RECOVERY AND BIOMASS

Recovery patterns in the treatment plots were similar at both sites with a thin biofilm appearing within two weeks after torching the plots. The initial algal species to colonise thereafter was *Ulva rigida.* The brown alga *Ralfsia verrucosa* began to establish after four months at the Port Alfred site and in small patches after five months at the East London site. These recovery patterns are similar to the findings is a study conducted by Kraufvelin *et al.* (2006a) where the green algae initially responded to nutrient enrichment and the brown algae responded after a delay.

The rate of algal recovery in the HT plots differed between the two sites, with the Port Alfred upwelling site having slightly faster recovery rates than the non-upwelling site at East London. Port Alfred had reached just over 80% recovery by six months while East London had only reached 70% recovery within the same time in the HT plots. The LT plots however experienced very similar recovery rates with both sites only reaching approximately 60% recovery within the six months. The effects of treatment and site on final biomass were tested using two-way ANOVA which showed significant effects of both factors, but no significant interaction.

Table 3.3: Two-way ANOVA conducted on effects of nutrients on algal growth. Significant values shown in bold ($p<0.05$).

	DF	MS	F	p
Site	1	0.00095	3401.71	**<0.001**
Treatment	3	3524.50	126.22	**<0.01**
Site*Treatment	3	0.11385	25.29	0.06
Error	16	8.42		

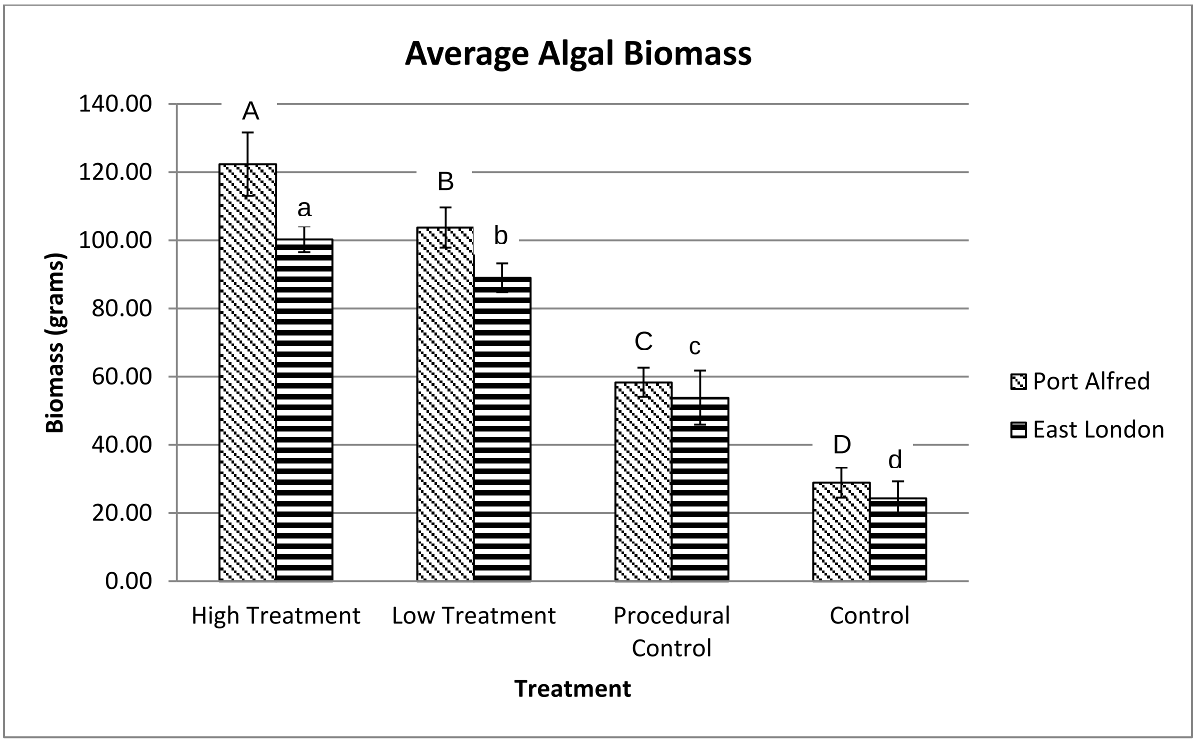

Figure 3.5: Average algal biomass at last sampling date for the four treatments at the two sites.

The Tukey tests indicated significant differences among all treatments within each site (i.e. HT > LT > PC > C, Figure 3.4, P < 0.01 in all cases). Comparing treatments between sites, there were no significant differences for either C or PC treatments (P > 0.05 in both cases), while both LT and HT treatments showed significantly (P < 0.01) higher biomass at Port Alfred.

3.3.3 OCEANOGRAPHIC CONDITIONS

Records of Sea Surface Temperature (SST) show that on average water temperature was colder in spring and summer months (Figure 3.6), with Port Alfred (mean 18.08°C ± 1.62) experiencing slightly cooler conditions than East London (19.24°C ± 1.60) on the whole. Water temperature was warmer and varied slightly less in winter months, with Port Alfred experiencing water temperatures of 19.03°C ± 0.07 and East London 20.33°C ± 0.080.

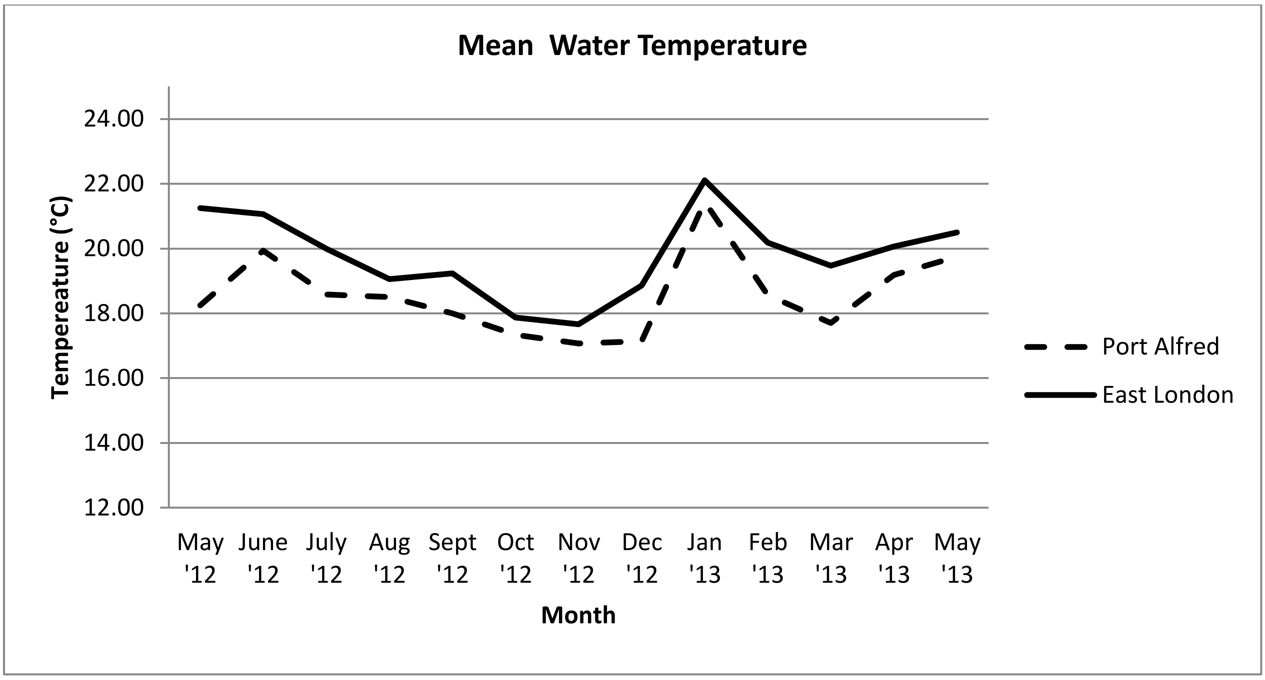

Figure 3.6: Mean Sea Surface Temperature for the four sites for the experimental year from May 2012- May 2013.

3.4 DISCUSSION

The results of the nutrient enrichment study above have shown that nutrient enriched plots are strongly associated with increased growth rates of the fast growing *Ulva* species, as expected in Hypothesis 1. These results are comparable with results found in a number of studies (Hillebrand *et al.* 2000; Nielsen and Navarrete 2004; Burkepile and Hay 2006) that have shown that increased nutrients lead to positive effects on the growth of fast growing algae. The comparison of the algal cover between the grazer exclusion plots of the first experiment and the high nutrient enrichment plots of this experiment further confirms the association between increased nutrients and increased *Ulva* growth rates, without the influence of grazers, although obviously this was confounded with temporal effects. The similarity in algal cover between the LT treatment at the upwelling site, Port Alfred, and the HT treatment at the non-upwelling site, East London, indicates that a high enrichment of nutrients at the non-upwelling site results in an algal growth rate similar to that found with low nutrient input at the upwelling site.

Conversely, studies have found that the negative effects of grazers on algal cover are stronger than the positive effects of increased nutrients in low nutrient environments (Masterson *et al*. 2008; Kraufvelin *et al.* 2010), such as the East London site. This implies that, although the increased nutrients in this study initially increased the algal cover, the impact of grazers may supersede the effects of the nutrients and ultimately determine the community composition, indicating that the bottom-up effects of nutrients may be impeded by top-down effects of grazers (Nielsen 2003).

3.4.1 EFFECT OF ENHANCED NUTRIENTS ON BIOMASS

The significantly higher algal biomass found in both the HT and the LT plots compared to the PC and C plots at the upwelling and non-upwelling site indicate that the enhanced nutrients may have had a positive effect on the algal growth rate. In this comparison, the effects of enhanced nutrients were confounded with the absence of grazers, but the increase in both cover and biomass in HT compared to LT plots (Anova followed by Tukey tests, $P < 0.01$ in both cases) confirms the effectiveness of nutrient enhancement. A study conducted by Burkepile and Hay (2006) found similar results where nutrient enrichment resulted in an increased abundance of primary producers in their study. This effect was even greater at the non-upwelling site where natural nutrient conditions are low, as shown by the greater increase in both cover and biomass between the LT and HT treatments (Figures 3.1, 3.4). However when looking at the nutrient enriched plots at the upwelling site, the algal biomass was only significantly higher in the HT plots compared to the grazer exclusion plots in experiment 1, while there was no significant difference in algal cover between the LT plots and grazer exclusion plots, suggesting that the level of nutrient enrichment needs to be notably higher than the natural level of nutrients in upwelling environments in order for any influence in algal growth or biomass to be noted.

Increased nutrients have also been found to influence animal biomass such that herbivore biomass is often higher at lower nutrient concentrations as there is a higher diversity of palatable algal species on the rocky shores, whereas at higher nutrient sites such as those at high upwelling intensity, the grazer biomass is lower due to the low species diversity of fast-growing resilient algal species (Nielsen 2003; Nielsen and Navarrete 2004), but see also Kraufvelin *et al.* (2006b) and Diaz *et al.* (2012) for a contrasting situation. It can further be stated that grazers play a minor role at high upwelling sites but become increasingly more important in controlling the algal community at low nutrient sites (Hillebrand *et al.* 2000; Nielsen and Navarrete 2004), as they can actively choose food sources that are structurally more palatable and contain higher nutrient concentrations than other algal species, thereby changing the composition and competitive structure of the algal community (Hillebrand *et al.* 2000).

The enhanced nutrients at the East London site would potentially have resulted in greater abundances of *Ulva rigida* being preferentially grazed due to its increased cover, nutrient value and dominance over corticated algae species. This corresponds to studies conducted by Russell and Connell (2007) where they compared the food preference of herbivores subject to either low or high nutrient conditions. They found that herbivores in low nutrient systems, such as those found at East London, will consume larger quantities of low nutrient food in naturally low nutrient conditions to gain the required nutrients, but will preferentially consume larger quantities of nutrient rich food when available.

3.4.2 FACTORS AFFECTING NUTRIENT CONCENTRATION

Anthropogenic impacts are often the leading causes of nutrient enrichment of rivers, estuaries and the coastal environment, due to activities such as agriculture (including the use of artificial fertilizers), industry, and sewage disposal through both river-runoff and direct addition, often resulting in eutrophication of these environments (De Jonge *et al*. 2002; Chislock *et al.* 2013).

Another factor affecting the nutrient concentrations on rocky shores is the local-scale autochthonous supply of nutrients in the form of ammonium from filter feeders, such as mussels (Aquilino *et al.* 2009). Ammonium is known to be a readily usable form of nitrate to many algal species, with *Ulva* spp. having the highest ammonium uptake rates (Bracken and Stachowicz 2006). The level of ammonium available to the algae may also have an influence on the algal community structure and coverage on the rocks as it will facilitate fast growing species which can inhibit later successional and perennial species (Bracken and Stachowicz 2006; Kraufvelin *et al.* 2006a). The change in algal community can also have secondary consequences for the macrofaunal species which are dependent on the perennial algal species and may result in their relocation and changes in their feeding patterns as their habitat changes (Benedetti-Cecchi *et al.* 2001; Kraufvelin *et al.* 2006a).

However, these additions in nutrient level should be analysed on a gradient scale, as nutrient poor systems will benefit from increased nutrients and an increase in algal diversity will be seen, whereas in a nutrient rich system any increases in nutrients may tip the nutrients over the critical level and a decline in algal diversity will be seen (Bracken and Nielsen 2004). It has been suggested that macrofaunal community changes are similar to those of the algal patterns. As the nutrient gradient is increased, a decrease in the animal community is observed as the nutrient enrichment favours a few dominant species (Bracken and Nielsen 2004).

3.4.3 TOP-DOWN AND BOTTOM-UP CONTROL

The increased algal growth rate and decreased diversity associated with the enhanced nutrients in this experiment demonstrate the importance of bottom-up control on rocky shore algae. Although top-down control from grazing is important in structuring the algal community in low nutrient systems, as seen in the grazer exclusion experiment, bottom-up control from the enhanced nutrients can have a greater effect on the ecosystem by altering the food preferences and feeding behaviour of the herbivores due to the higher abundance of fast-growing high nutrient algal species (Russell and Connell 2007).

However, a change in feeding behaviour of the grazers ultimately has a greater effect on the algal abundance as the herbivores will consume greater quantities of the nutrient rich algae. Thus to answer the question, do top-down, bottom-up or a combination of both factors direct the dynamics of these systems, we need to consider the state of the environment. Nutrient poor systems are in general likely to be controlled by top-down factors whereas nutrient rich systems, such as upwelling regions, may initially be controlled by bottom-up factors but will ultimately be controlled by a combination of both bottom-up and top-down factors.

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CHAPTER 4 – General Conclusion and General References

4.1 GENERAL DISCUSSION

This study on South African rocky shores provides insight on spatial variability of grazing and the role of limpets on determining the algal species composition. The findings of these studies have shown significant differences between treatments and sites, with significant differences not only occurring in algal cover but also algal growth rates and recruitment patterns between treatments. The small scale local processes acting within a few centimetres (plots) or tens of meters (blocks) can also be reflected over larger scales such as sites (upwelling/non-upwelling shores).

The methods used in these studies have proven to be effective in meeting the aims and objectives set out at the beginning of the study. The fact that generally no significant differences between exclusion plots and the two types of control plots suggests that anti-fouling paint is effective in excluding molluscan herbivores, without introducing major experimental artifacts. The results of these studies have indicated that grazers affect the diversity and growth of the algal assemblages at both upwelling and non-upwelling shores, but have a stronger influence at high nutrient sites such as the upwelling shores at St Francis and Port Alfred, where the rate of algal growth is higher and the diversity of algae is lower. The results have shown that grazing is an important regulator of algal recruitment patterns and can largely change the species composition of the rocky shores.

However there are gaps in these studies as they mainly looked at new growth on bare rocks after a disturbance and have not considered the effects of grazing and nutrients on existing algal communities. These gaps can be overcome by performing further studies such as that by Kraufvelin *et al. (*2006a) to look at the effects of nutrient enrichment on existing rocky shore algal communities in South Africa in order to determine if the enhanced nutrients influence changes in the algal and faunal community composition. More work can look at the role of other grazers in controlling algae assemblages as well as different algae-algae interactions to determine the role of competition on rocky shores (Johnson *et al*. 1997).

Existing encrusting red algae have been known to inhibit the settlement and recruitment of perennial macroalgae as they can remove the algae spores that settle on the coralline algae's surfaces by losing the surface cell layer (Keats *et al*. 1996). This will affect the rate of algal growth in natural undisturbed habitats and could possibly have an influence in both grazer limited and nutrient enriched habitats. In order to understand the possible effects of a natural disturbance, further research is needed on encrusting algae-perennial algae interactions to better understand the dynamics of the ecosystem function and services.

The physical changes of environments, such as increased temperatures, change in light intensity, rising sea levels and changes in physio-chemical properties of the sea water due to the increasing effects of climate change present multiple stressors on the ecosystem and further influence the rocky shore communities (Mieszkowska *et al.* 2006; Hawkins *et al*. 2009). By understanding the present changes and using previous studies as models to simulate disturbances on rocky shores, it may be possible to forecast future changes and responses of the community assemblages and biodiversity due the impacts of climate change (Thompson *et al*. 2002). By continuously monitoring the shores, ecologists will be able to observe patterns of change either from biological disturbance or changes in the environment (Thompson *et al*. 2002).

One of the major challenges for ecologists is predicting how small scale processes translate to larger scales and to determine if small scale changes will affect the patterns and processes occurring on larger scales. Previous studies (Benedetti-Cecchi *et al.* 1996; Steinbeck *et al.* 2005) have shown the difficulty with predicting the correct spatial extent of impacts on ecosystem patterns and processes as impacts can be felt from a few meters, such as local grazing effects, to a few hundred kilometres, such as upwelling events. Another challenge faced is the design of the sampling programme and methodology as this can vary between ecologists and possibly lead to different results according to the questions being asked (Benedetti-Cecchi *et al.* 1996) which can alter the predictions of scale variations.

Conclusions:

Studies (Worm *et al.* 2002; Aronson *et al.* 2005; Burkepile and Hay 2006) with similar results to those found in my experiments have shown that by looking at the combined effects of reduced herbivore pressure and increased nutrient enrichment in a broader context such as the effects on coral reefs, increased algal growth rates can cause detrimental impacts on the ecosystem such as promoting the shift from coral dominated reefs to algal dominated reefs. By understanding the drivers of change and how these changes affect the ecosystem function and services, extrapolations can be made as to how the relationship between biodiversity and ecosystem function will be affected and possibly be conserved (Williams *et al.* 2013).

In general, these studies have demonstrated that various factors such as the effects from increased nutrients at upwelling cells and the change in herbivore pressure due to enhanced nutrients can determine the abundance and diversity within the community. However, when considering the whole ecosystem, one cannot look at the effects of a single grazing species in isolation, as many factors not considered in this thesis can affect the grazing pressure, such as predation pressure from higher trophic levels (Menge and Sutherland 1987), additional grazer species influencing the primary producers (Menge 1995), the productivity of the environment (Lotze *et al.* 2001) and through direct or indirect effects of environmental changes (Menge 1995).

By comparing results from this study with results from a study conducted on the West Coast of South Africa, where upwelling occurs frequently along the Benguela Current, we can determine the large scale geographical variations in community structures. These findings can contribute to a better understanding of ecosystem dynamics, with insight into questions surrounding ecosystem recovery from disturbance and potential threats from alien invasive species (Sousa 1979).

4.2 REFERENCES

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