Ecological engineering on rocky shores: Grazing, predation, nutrient availability and their influence on epifaunal communities

By

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A thesis submitted in fulfilment of the requirements for the degree MSc in the
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December 2015

ABSTRACT

“Ecosystem engineers modify, create/destroy habitat and directly/indirectly modulate availability of resources to other species by causing physical state changes to biotic and abiotic materials” (Jones *et al*, 1994, page 1). Previous studies have analysed top-down and bottom-up relationships to determine which form of regulation is key in controlling community composition. This study assessed the direct and indirect effects of top down and bottom up factors on the epifaunal communities of macro-algae. Epifauna are subject to the direct top-down effects of predation and bottom up effects of habitat availability. Habitat availability in turn experiences the direct top down effects of grazing and bottom up effects of nutrient availability due to upwelling. Grazing and upwelling may therefore have indirect effects on macro-algal epifauna. Four treatments (Procedural controls, Controls, Predator or Grazer exclusion) set out in a block design (n = 5) were monitored monthly for algal cover of the substratum for 12 months with the surface area of algal plants and epifaunal species composition and abundances assessed at the end of the experiment. The red alga *Gelidium pristoides* was selected as the ecosystem engineer as it is common, supports a diverse community of epiphytic animals and acts as a nursery for small epifaunal organisms. The experiment was run at two upwelling sites interspersed with two non-upwelling sites. Sites were separated on scales of 100km along approximately 500km of coastline. Dipping whole algae in dish washing liquid provided a strong relationship between their surface area and the weight of the film of dish washing liquid covering them. Surface area was strongly correlated to dry weight but neither surface area nor dry weight was correlated to algal cover of the substratum. Algal cover was influenced by the interactions of treatment with site (nested in upwelling) and upwelling. At all sites, treatments that allowed access to grazers, Grazer + and Control treatments, showed no significant differences and these two treatments had lower algal cover than Predator + and Closed treatments which did not differ from one another

[Grazer + = Control < Predator + = Closed]. A total of 44 epifaunal species were identified, with the predominant orders being Amphipoda and Isopoda. Primer results showed that only site had a significant effect on species composition, with sites that were further apart being more different. Site (nested in upwelling) had an effect on total epifaunal abundances when data were non-normalised. When total epifaunal abundances were normalised for algal cover of the substratum or algal surface area to provide density data, predation had no significant effect. Grazing did have a significant effect, but only when data were normalised to algal surface area, not cover, leading to the conclusion that indirect top-down factors through grazing of the sea weed are important in structuring epifaunal communities depending on how habitat availability is measured.

Key words: Ecosystem engineering, top-down, bottom-up, *Gelidium pristoides*

ACKNOWLEDGEMENTS

I am sincerely grateful to my supervisor, Professor Christopher McQuaid for affording me the opportunity to work on this project. I thank you for the academic brilliance that contributed significantly to all aspects of this study. Thank you for your abundant support, guidance and patience throughout the course of this thesis, as well as for your assistance in editing and help with statistical analysis of the data.

Thank you to my co-supervisor, Dr Justin Lathlean, for providing assistance with the methods and setting up of the experiments.

A very big thank you must go to my parents, Albert and Siphathisiwe Ndlovu, for their continuous support, assistance and faith in me.

Thank you to the South African Weather Services for providing me with wind data.

Thank you to my friends (Zolile Maseko, Olwethu Duna and Current Masunungure………you guys are the best), Coastal Research Group and everyone for your constant support and encouragement and to those who helped out on field trips, a big thank you to you.

Financial support was provided by the National Research Foundation (NRF).

Last but not least I thank the Almighty for giving me the opportunity to pursue this MSc and getting me through all the challenges and tribulations that I faced moulding me become the man I am today.

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Chapter 1 : General Introduction

Large-scale processes regulating ecosystems

Ecosystem functioning incorporates both the biological and physical processes within ecosystems, which include the flow of materials and energy within an ecosystem. Two dominant theories have been proposed to try and explain how ecosystems function: through bottom-up and top-down control. Top-down and bottom-up control relationships have been analysed in many previous studies of marine benthic systems to determine which form of regulation is most influential in controlling community composition (e.g. Menge, 2000; Blanchette *et al*, 2009) and Menge (2000) concluded that both top-down and bottom-up controls play a role in community structuring. Rocky shore communities offer an ideal environment to study bottom-up vs top down relationships as these communities are diverse and manipulation of organisms in these communities to understand such relationships is relatively easy because these habitats show a very steep environmental gradient (from sea to land) across scales of metres.

Bottom-up control states that resource supply to primary producers is the ultimate control of ecosystems by controlling the nature and strength of species interactions and this control includes food supply to primary consumers. For example, if nutrient availability increases there will be an increase in the production of autotrophs and this will be propagated throughout all the trophic levels. All trophic levels will respond by increasing/ booming in abundance or biomass due to an increase in nutrients within the ecosystem (Worm *et al*, 2002). Bottom-up controls involve the amount of primary production in an ecosystem, primary production determines the amount of energy available for the higher trophic levels thus high primary production will result in increased production at the higher trophic levels. Bottom-up control implies that primary productivity is the main driver of species distribution in ecosystems but its influences can be modified directly or indirectly by temperature (Cole and McQuaid, 2010).

Theories of top-down control state that grazing and predation on lower trophic levels ultimately control ecosystem functioning. This theory states that an increase in predators will lead to a decrease in grazers and consequently less pressure on primary producers (Burkepile and Hay, 2006). Top-down control refers to how higher trophic levels control lower ones. For example, top-down effects can result in trophic cascades (Frank *et al,* 2005) e.g. the collapse of the top predator cod that resulted in high abundances of the planktivorous Sprat which then also hindered the recovery of cod by preying on their larvae (Casini *et al*, 2009).

Trophic cascades are drastic changes in the abundances of one or multiple species within a community or changes in the relative abundances of multiple species in a community due to changes in the abundance of one key species (Heithaus *et al*, 2008). It is more likely that secondary extinctions may occur especially in the case of threatened species which depend on very few specific food sources that are in turn dependent on a keystone species. A top-down cascade occurs when there is removal of a top predator leading to the disruption of food chains and food webs at lower trophic levels. A bottom up cascade occurs when the whole system is affected by the removal of a primary producer or consumer resulting in population reduction of all species in the whole community that are dependent on that primary producer (Frank *et al*, 2005). In marine ecosystems, evidence has suggested that there are indirect links showing that extinctions of large top level predators changes how communities function by changing relationships of organism in communities, thus changing species community composition as a whole (Dayton *et al,* 1989; Hewitt *et al,* 2006).

The principal cause of top-down cascading effects in communities is the loss of key top predators resulting in an increase in the abundances of their prey species through predator release. The prey species will then be able to overexploit its food resources such that their food resources will be decreased and at times to the extent that their food sources will start disappearing. When food sources are diminishing, consumers will starve and they may even go extinct. For herbivorous species, their release and subsequent overexploitation of plants may lead to loss of plant biodiversity in that area (Heithaus *et al*, 2008). Other herbivorous organisms in the community that depend upon these same plants for their survival either as food or as habitat may go extinct as well.

Removal of top predators in communities leads to the restructuring of communities and food webs (Emond *et al*, 2015). Trophic cascades are responsible for changes in species composition, abundance and the structure of communities and as such they can be described as domino effects as a removal of a top predator has a big impact by affecting many components species in a community (Coleman and Williams, 2002).

Declines in marine top predators can initiate trophic cascades e.g. abrupt decline of sea otters in North America due to predation from killer whales (Estes *et al*, 1998). Understanding how marine predators affect the dynamics of communities by preying (direct predation) on certain species or changing prey behaviour (anti-predator mechanisms) of some species can help scientists to predict the ecological consequences of losing a predator in that community (Heithaus *et al*, 2008). Top-down control of ecosystems due to trophic cascades brings about opportunities for studying, understanding, manipulation and setting up of management plans for affected ecosystems (Frank *et al*, 2005).

Population numbers and productivity cascades from the top trophic levels of the food chain to the bottom levels can produce drastic effects on the whole ecosystem. With top-down processes known for having the ability of structuring communities and ecosystems, it is important to differentiate the processes of both top-down and bottom-up controls and how their relative strengths may vary in space and time. In the study of top-down vs bottom-up controls it is also important to note that these controls occur simultaneously and also to note other factors affecting communities directly or indirectly.

Temperature has a strong influence on the biological processes taking place in communities, direct effects of temperature are debatable (Rohde, 1992; Cole and McQuaid, 2010) but biological factors such as competition and predation are considered to be directly or indirectly affected by temperature. Productivity is a bottom-up driver of species distribution in ecosystems and it is also directly or indirectly influenced by temperature e.g. Cole and McQuaid (2010) found that temperature and primary production influence species diversity and abundances at a larger scale.

Importance of biodiversity in communities

Biodiversity is thought to give rise to community stability as communities with many species are thought to bring about stability and those with few species are deemed unstable and can be subject to collapse if they are faced with a major disaster (McCann, 2000). Communities with many species are characterised by complex relationships of grazing, competition and predation. Increases in biodiversity (number of species present) and having many trophic levels help in bringing about community stability and these two factors have a strong influence on community processes and on how species interact (Duffy *et al*, 2005). Having complex interactions in a community means that species are able to self-regulate themselves to optimum populations that can survive due to the prey-predator relations e.g. increase in prey will mean more food for predators who will feed on the prey reducing their numbers and few prey species will also mean fewer predators as they will be less food to support high predator population numbers. Some ecologists have argued that the strength with which species interact, is important in determining stability, some have come to the conclusion that diversity is positively correlated to stability (McCann, 2000) and others have concluded that biodiversity can be used as a critical indicator of the status of the ecosystem (Palumbi *et al*, 2008).

Increases in species richness have been said to increase functional diversity and habitat complexity with involving a variety of biological processes which lead to an increase in the stability of the whole community (Tilman *et al*, 1997). Habitat complexity is important in influencing the patterns of abundance, size and frequency distributions of species whilst the regulation of population numbers is often determined by predation (Smith, 1993).

Previous experiments in small systems have demonstrated that over short periods of time, increased species richness has the ability to increase stability and make some ecosystems function more efficiently (Tilman *et al*, 1996; Peterson *et al*, 1998). Processes that affect species abundance and richness have been linked to habitat complexity (Smith, 1993) as they are important in bringing stability to communities.

Ecosystem engineering

Rocky shores are considered to be highly productive (Crowe *et al*, 2011) and are significant in underpinning coastal food webs as they are characterised by strongly interacting species. Since rocky shores are rich productive communities, they provide a platform to study biological processes as they are easily accessible and are home to a range of seaweeds which support a lot of benthic fauna. In this study, the sea weed (*Gelidium pristoides*) was considered as an ecosystem engineer due to the high association of this seaweed with epifauna.

“Ecosystem engineers are organisms that modify, create or destroy habitat and directly or indirectly modulate the availability of resources to other species, causing physical state changes to biotic and abiotic materials” (Jones *et al*, 1994; page 1) and they tend to influence the success of other species (Erwin, 2008). Ecosystem engineers perform diverse functions in ecological communities. These functions include the regulation of biogeochemical cycles, altering disturbance regimes, modifying the physical state of the environment, and regulating ecological processes such as grazing and predation (Peterson *et al*, 1998) and regulating interactions such as pollination (Fleming and Sosa, 1994; Peterson *et al*, 1998). Physical resources that tend to be influenced by ecosystem engineering vary from habitat/living space to light, humidity, sediments, heat, water and physical materials (Crooks, 2002). Ecosystem engineers can be viewed as keystone species; they can be described as organisms that have a disproportionately large effect towards their own environment in relation to their abundance. Ecosystem engineers or keystone species are of great importance in communities compared to other species as they are involved in structuring and maintaining ecological communities by affecting many other organisms and processes in the whole community. Basically they are important in determining the types of species living within a community and population numbers of the various species in these communities (Jones *et al*, 1994). Without keystone species, communities would be totally different or cease to function altogether as other species in the community rely heavily on them and this shows how a very few individual species, which are ecological engineers or keystone species can have a huge impact on the whole community.

When the sea weed is grazed there is modification of the physical environment for other species and this process is termed physical ecosystem engineering (Erwin, 2008). Physical ecosystem modification involves the creating or destroying of new habitats, this alters the distribution of resources, which can lead to enhanced biodiversity (Erwin, 2008; Lewis and

Anderson, 2012). Physical changes in the state of the environment can directly influence the nature of the species and the species overall composition of communities. These physical changes have a direct influence on non-food resources such as living space and an indirect influence of regulating abiotic forces that affect how resources are used by other organisms in the community (Jones *et al*, 1997).

It has been argued that, at small scales, the consequences of ecological engineering can be either positive or negative to species richness and abundance, but the net positive results are seen more often at larger scales (Jones *et al*, 1997). Ecosystem engineers are said to bring about physical changes to the environment in two ways (Jones *et al*, 1997). **1.** Autogenic physical engineers that occur due to the growth or development of the engineer, with the engineer being part of the engineered environment. **2.** Allogenic engineers alter the physical state of the environment but the engineer is not part of the engineered environment.

It has been noted that ecosystem engineering has positive impacts on biodiversity by creating habitats that can be occupied by other species through increased structural heterogeneity and patchiness as well as by directly providing increased resources. Environmental heterogeneity due to ecosystem engineering is likely to increase biodiversity thus diversity begets diversity (Erwin, 2008).

Ecosystem engineering and epifauna on rocky shores

Biological communities show continuous trends along environmental gradients (Bustamante *et al*, 1997), with rocky shores representing a change in environment from land to sea. Rocky shores are characterised by harsh conditions for organisms to live in, they experience continuously changing physical conditions such as temperature, salinity, air and wave exposure as well as regular emersion/immersion. Ecosystem engineers found in rocky shores play an important role in ensuring survival of fauna during these stressful conditions by offering protection to small invertebrates. At low tide when organisms are exposed to heat, they can find shelter within the fronds of sea weeds and avoid desiccation and also these invertebrates can get protection from the sea weed when they are exposed to strong wave force. Engineers in rocky shore communities include organisms such as mussels, barnacles and algae (Jones *et al*, 1997; Gutierrez *et al*, 2003).

Intertidal ecologists have recognized that there are two important local physical forces that are responsible for shaping intertidal rocky shore communities. Gradients of desiccation from low in the shore to high up in the shore influence vertical zonation and the effects caused by wave force tend to shape the general horizontal zonation of rocky shores (Stephenson and Stephenson, 1949; Bustamante *et al*, 1997).

Three broad zones are recognised on rocky shores based on their characteristic biological communities, these zones extend from above the spring high tide mark down to the spring low tide mark beyond which the sea bed is covered by sea water at all times (Bustamante *et al*, 1997). The supralittoral zone, or splash zone is never submerged, but is regularly splashed by water and almost resembles the terrestrial habitat in that it is dry for prolonged periods with organisms such as some barnacles, semi-terrestrial isopods and littorinids well adapted to living in the harsh dry conditions experienced in this region. The eulittoral zone or true intertidal zone extends from the spring high tide mark to the spring low tide mark. This zone is exposed to wave action with organisms found in this zone adapted to clinging onto the rocks to withstand the pounding of waves. The sublittoral zone or subtidal zone is directly below the eulittoral zone, is permanently covered by seawater and is dominated by marine algae with high rates of primary productivity (Stephenson and Stephenson, 1949).

The theory in rocky intertidal communities is that physiological stress sets upper limits for species whilst lower limits are set up by biological interactions (Blamey and Branch, 2008).

Desiccation and wave action are recognised as the most dominant forces in the determination of zonation and the upper limits of a species' (Bustamante *et al*, 1997). Desiccation is the main limiter in the spray zones and high tide zones, where organisms are wetted occasionally by splashes from waves. High up in these zones, organisms such as littorinid snails and limpets are found since they are mobile, can hide in rock crevices and are adapted to this zone as they can seal their shells to avoid water loss. Temperature, wind and humidity are three environmental variables that contribute to desiccation, and all can change rapidly in the intertidal.

Competition and predation become limiting factors as we move lower in the intertidal zone, organisms compete for resources such as space, food, light and shelter especially when resources are limited. Predation has a strong influence on the populations of many benthic invertebrates such that many benthic organisms have developed strategies to avoid predators (Lefcheck *et al*, 2014). Predators, both carnivores and herbivores affect the distribution and abundance of species with carnivores affecting the survival of their prey while herbivores tend to affect the size and distribution of algae (Steneck and Watling, 1982).

In rocky intertidal and epifaunal communities attachment space is a potential limiting resource for both plants and animals (Paterson, 1979) and predation can function to open up new space, which is then available for colonization by other new species.

Upwelling and how it influences marine ecosystems

Upwelling is important in marine intertidal communities as it leads to increased productivity of marine intertidal communities (Bosman *et al*, 1987; Broitman *et al*, 2001) and can be viewed as a bottom-up factor. Upwelling increases resource supply by adding nutrients to the community leading to high primary productivity rates. Primary production in the sea occurs in the euphotic zone near the surface of the sea, whilst most remineralization of organic matter occurs on the ocean floor (Bosman *et al*, 1987) thus upwelling is important as it conveys nutrients from deep waters to the surface where they are utilized. Upwelling brings nutrients such as nitrates and phosphates to the surface thus increasing the growth of primary producers such as macro-algae and phytoplankton, which are then consumed by other organisms either directly or as detritus. Upwelling is important in intertidal communities as it influences biological processes such as competition, predation, larval transport and settlement (Morgan *et al*, 2009). Upwelling has been shown to influence the biomass and distribution of primary producers which include macro-algae in intertidal communities and has been found to influence algal cover, growth rates and biomass (Bosman *et al*, 1987).

Primary productivity is strongly influenced by nutrient availability (Houston and Wolverton, 2009) and this is shown by rapid productivity of phytoplankton in nutrient rich areas. Coastal areas, especially those that experience upwelling, have high primary productivity rates (Cole and McQuaid, 2010) and an increase in primary productivity leads to direct effects on associated fauna, increasing population densities, carrying capacities and diversity of species in communities.

It is hypothesized that rocky shores within upwelling regions will have higher diversity and species abundances due to enhanced primary production (Bosman *et al*, 1987). Relationships at all trophic levels are influenced by primary productivity, factors that directly influence primary productivity have an influence on the productivity of the whole ecosystem thus these factors influence the relationships of all organisms in all trophic levels. According to Bosman *et al* (1987), areas that are influenced by upwelling support greater biomass per unit area not only of algae, but also of herbivorous limpets.

Wind driven coastal upwelling occurs when the wind blows parallel to the coastline with the coastline producing a surface Ekman layer transport directed 90° to the right or left of the wind direction depending on the hemisphere. This process results in the rising of deep ocean waters near the coast supplied from the offshore region (Tomczak and Godfrey, 1994). Winds will drive the warm sea surface waters offshore and by doing this the colder underneath sea waters will rise to the surface, upwelling in the inshore zone bringing with it nutrients from deeper in the ocean.

Another process driving upwelling is current dynamic uplift and tidal pumping of the ocean water below the thermocline and this process is independent of wind (Tomczak and Godfrey, 1994). The depth of the thermocline in the water column is proportional to the speed at which the current is moving, thus a change of current will result in a change in the depth of the thermocline in the water column. Different thermocline depths lead to changes towards the inshore side of the current, and this leads to the speed of the current increasing resulting in a change in the depth of the thermocline. On certain occasions the thermocline can be driven towards a coastal area bringing cold nutrient rich waters from the ocean. This process is called dynamic uplift of the thermocline and it is responsible for the frequent upwelling instances within the Agulhas Bank (Walker, 1986; Tomczak and Godfrey, 1994). Dynamic uplift normally happens in short events of only a few days duration due to changes in thermocline depth experienced within the water column. This type of upwelling has been observed close to Port Alfred (Lutjeharms *et al*, 2000) with recorded sea surface temperatures revealing upwelling activity. Factors that determine the occurrence of upwelling include topography, wind direction and the conditions of the deep ocean. Upwelling types usually occur simultaneously, they rarely occur in isolation.

Importance of herbivores in intertidal communities

Intertidal macro-algae exhibit seasonal changes in abundance and diversity due to both environmental factors and biological effects including herbivory. Grazers such as gastropods and limpets play an important role in determining the distribution and abundance of algae by exerting top-down control, giving them an important role in structuring rocky intertidal communities (Forrest *et al*, 2001) and thus herbivores have indirect effects on other processes that are carried out by the algae (Lewis and Anderson, 2012). Herbivores affect the size and structure of algae, hence by doing this they alter living space for epifauna which rely on the size and structure of algae to hide from predators and to get protection from wave force. This herbivory indirectly affects the number of epifauna that will be supported by the sea weed thus it is an important determining factor in epifauna communities.

Marine ecologists measure grazing behaviour by using density of grazers in communities (Forrest *et al*, 2001) as a proxy for grazing pressure. In the case of benthic species, organisms counted during low tide can be used to estimate the number of herbivores for that particular area.

Importance of seaweeds to epifaunal communities

Macro-algae are important habitat forming organisms in intertidal ecosystems as they act as primary producers and also provide habitat for associated fauna. *Gelidium pristoides* is known to be important to epifauna in South Africa (Beckley, 1981), surfaces colonised by *G. pristoides* are diverse, and include rocks, tubeworms, encrusting coralline algae and especially on limpets within the lower intertidal zones were limpets are abundant and on barnacles in much higher zones (Steyn, 2009).

Seaweeds play a very important role in epifaunal communities. Their primary importance is being the major food of herbivorous grazing animals, through which they contribute to higher trophic levels in the food-web (Murphy *et al*, 2006). They also provide shelter and provide substrata on which invertebrates can attach and act as nurseries for many marine organisms (Steyn, 2009).

Epifaunal communities are controlled by top-down factors such as predation and grazing, where by predators prey direct on the epifauna living within the sea weed and with grazers determining the amount of sea weed present in the community for epifauna to utilise. Bottom-up factors include direct factors such habitat availability offered by the sea weed to epifauna and indirect factors such as nutrient availability which influences the growth of the sea weed leading to more habitat for epifauna.

There is a positive correlation between biodiversity and habitat forming or modifying organisms (Stachowicz, 2001; Bates and DeWreede, 2007). Provision or modification of habitat for other species is called biogenic habitat provision (Bates and DeWreede, 2007), however there are situations in which habitat forming species are assemblages of taxa that may collectively act as habitat for other organisms. Crustaceans, polychaetes and gastropods are found in abundance on the surfaces of seaweeds (Taylor, 1997) and they play an important role as grazers and as food for other organisms such as fish. Abundances of epifauna increases with an increase in size of a seaweed (Gunnill, 1982), thus the bigger the seaweed, the more epifauna will be present on that seaweed.

More emphasis from species-level diversity to functional diversity (Crowe *et al*, 2011) is important. Functional diversity takes into account how species interact in communities (Duffy *et al*, 2005) and an emphasis on functional diversity is important to make sure that feeding modes and habitat provision of certain species are taken into account so that the loss of key species (keystone species) in a community can be easily predicted. This will help to predict the impacts on the community resulting from the loss of keystone species and studies on ecological engineers can help marine ecologists to determine how community-level ecological processes may be affected and the consequences for the whole community. Extinctions at a global scale are usually rare in marine environments but local extinctions and changes in species abundance and richness are widespread (Stachowicz *et al*, 2007; Crowe *et al*, 2011) thus it is important to understand the role of keystone species to be able to manage marine communities.

Importance of epifauna in marine ecosystems

Epifauna includes all benthic animals that live on marine vegetation of the sea floor. These benthic organisms may attach to surfaces or range freely by crawling and swimming. Some of these species use macro-algae at certain times (i.e. during low tide amphipods avoid desiccation by taking refuge in algae), while others inhabit algae permanently. Benthic invertebrate fauna play a vital role in nutrient cycling, detritus decomposition and act as food for higher trophic levels. Invertebrate epifauna are lower order prey items that are important for larger higher order invertebrates and fishes (Smith, 1993). Epifaunal animals are attracted to sea weed as it affords physical refuge from predators or for associated food resources (Gibbons, 1988; Smith, 1993).

Previous studies have shown that high epifaunal abundances are seen during times when there is high algal biomass (Smith, 1993). Habitat complexity and predation (Edgar, 1991; Smith, 1993) have been viewed as major processes driving the abundance of organisms and it has been demonstrated that habitat complexity is important in influencing and underpinning patterns of epifaunal abundance and their distribution. Habitat complexity is the extent, number and diversity of habitat types (Smith, 1993). Habitat complexity moderates predation through reduced foraging success by predators or by shaping the relationship between predation and competition (Smith, 1993), while predation directly affects epifauna living within algae so that epifaunal communities associated with macro-algae tend to be affected by both habitat complexity and predation (Edgar, 1991).

Study system: *Gelidium pristoides* and its epifauna on South African rocky shores

Gelidium pristoides is a seaweed found in the littoral zone and its distribution ranges from Sea Point on the west coast to all of South Africa's east coast (Beckley, 1981) (**Fig 1.1**). Previous investigations have shown that *G. pristoides* is home to diverse and abundant epifaunal communities (Gibbons, 1988).

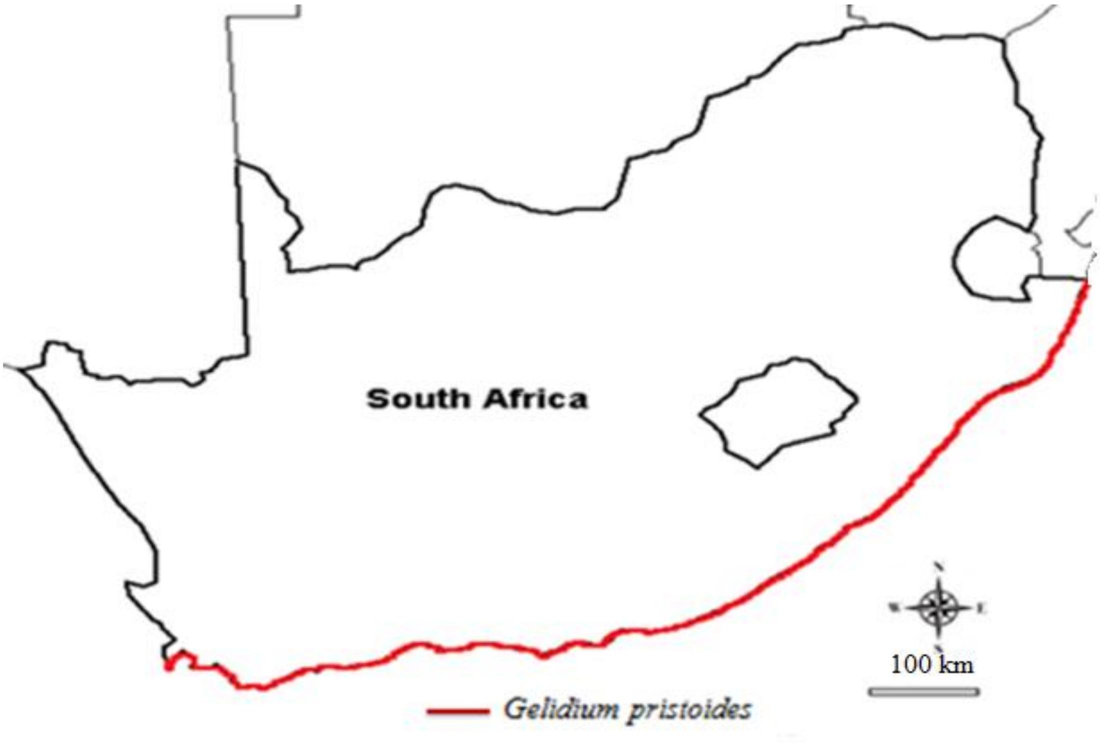

Figure 1.1: Distribution of *G. pristoides* in South Africa.

Gelidium pristoides is common on the mid- to lower-eulittoral zones of the south coast of South Africa. This seaweed is harvested commercially in seaweed concession areas (Steyn, 2009) so that it can be exported and used for the production of agar.

Epifauna are organisms that live on surfaces such as rock or aquatic plant surfaces (Beckley, 1981), for this study epifauna were considered as organisms living on sea weed surfaces. Many biological processes such as grazing and predation influence epifaunal communities, acting directly on them and also modifying their environment. Limpets are the predominant grazers of *G. pristoides* (Branch, 1981). Grazers include limpets such as *Siphonaria serrata, Siphonaria concinna*, herbivorous snails, *Tricolia capensis*, winkles, *Gibbula spp* and *Oxystele* spp. Predators will include organisms like starfish, shorebirds, black oystercatchers, whelks, octopuses and omnivorous crabs. Limpets are key grazers in rocky shores and they graze on algae and in the process they make food available to other smaller organisms such as nematodes, annelids, harpacticoid copepods and dipteral larvae. Limpets graze on algae in the early stages thus regulating their recruitment and in some instances directly consume mature algae (Davies *et al*, 1997; Crowe *et al*, 2011), while predators will directly prey on the epifauna living within the sea weed.

Physical factors such as wave exposure, desiccation, temperature and light intensity experienced on different rocky shores exert a number of both harmful and beneficial effects to the communities they support (Bustamante and Branch, 1996, Bakker *et al*, 2015). During high tide, algae are immersed under water, experiencing wave action, taking up nutrients from the water and experiencing low light intensities, during low tide, they are exposed to air and subject to water loss, high light intensities and sometimes fresh water (Steyn, 2009, Bakker *et al*, 2015). These exposed conditions are considered stressful, especially due to desiccation through evaporative water loss and tolerance of desiccation influences seaweed zonation (Abe *et al*, 2001).

According to Davison and Pearson (1996), two types of stress occur in seaweeds. First, limitation stress which is due to the lack or inadequate supply of nutrients or resources to the sea weed thus leading to reductions in growth rate. Second, disruptive stress is due to the adverse effects that the sea weed is exposed to such as grazing which result in physical damage or loss of productive tissues so that a lot of resources will be channelled to preventing/ reducing grazing or repairing damaged tissues. To deter grazers, some sea weeds release secondary metabolites and this can also benefit organisms such as amphipods that tend to occupy chemically defended sea weeds. These sea weeds will be able to grow, providing habitat to epifauna hence more hiding space for epifauna from predators due to reduced/less grazing as secondary metabolites will provide chemical protection from grazers (Duffy and Hay, 1994).

Davison and Pearson thus consider stress to have negative consequences, but Lichtenthaler (1996) suggest that stress can have positive effects on plants while Renaud *et al,* (1990) suggested that stress may increase or decrease a plants susceptibility to herbivory. They suggested that mild stress can trigger beneficiary metabolic activities which can result in an increase in physiological activity and this type of stress is called eu-stress. Stress resulting in damage to the plant, reducing the production and success of the plant is dis-stress. Stress dose and the organism’s tolerance limits will determine the results of the stress experienced by the organism and how the plant grows thus indirectly affecting other organisms which depend on that plant for their survival (Steyn, 2009).

Aims of the study

For ecologists, understanding and predicting factors that determine community composition is important. Understanding factors that influence distribution, abundances and relationships of species in epifaunal communities is important. Direct factors such as competition, predation and indirect factors such nutrient availability greatly influence what happens in epifaunal communities. In this study, the aims were to test the direct effects of predation and upwelling on epifaunal communities and as well as to test the indirect effects of grazing and algal cover and how they influence epifaunal communities. Because the effects of grazing are balanced against those of nutrient availability, the study also focussed on categorising sites in terms of whether they experience upwelling or not. The objective here was to measure intensity, frequency and duration of upwelling so that the sites can be evaluated in terms of nutrients brought up by the process of upwelling and also to quantify grazing pressure by counting the number of grazers per $2m^2$ plots to test for possible differences between upwelling and non-upwelling sites.

Chapter 2 : Study region/area

Oceanic conditions

Two major currents dominate the oceanography of South Africa namely the Benguela current along the west coast and the Agulhas current (**Fig 2.1**) along the east and south coasts (Lutjeharms, 2006). The Agulhas current is strongest between 25°-30° S latitude along the east coast of South Africa moving predominantly from north-east to south-west and remains in close proximity to the continental shelf. Between 34°-35° the Agulhas current deflects away from the coast following the triangular continental shelf known as the Agulhas Bank (Beckley and van Ballegooyen, 1991). This process creates contrasting levels of upwelling and down-welling along the south and east coasts of South Africa. On the east coast, warm waters of the Agulhas current flow towards the southwest at speeds of >1m/s (Lutjeharms, 2006) and closer to Port Elizabeth the current starts to meander forming eddies and attendant warm water plumes. For example, organic content along the eastern Agulhas Bank lies between 0.0 and 3.9% per unit mass whereas matter content from the western Agulhas is between 4.9% and 11% (Lutjeharms, 2006) showing the influence of the Benguela current on the western side of the Agulhas Bank. Winds that drive upwelling along the south coast are parallel to the coast, but upwelling is not always related to wind (Lutjeharms, 2006)

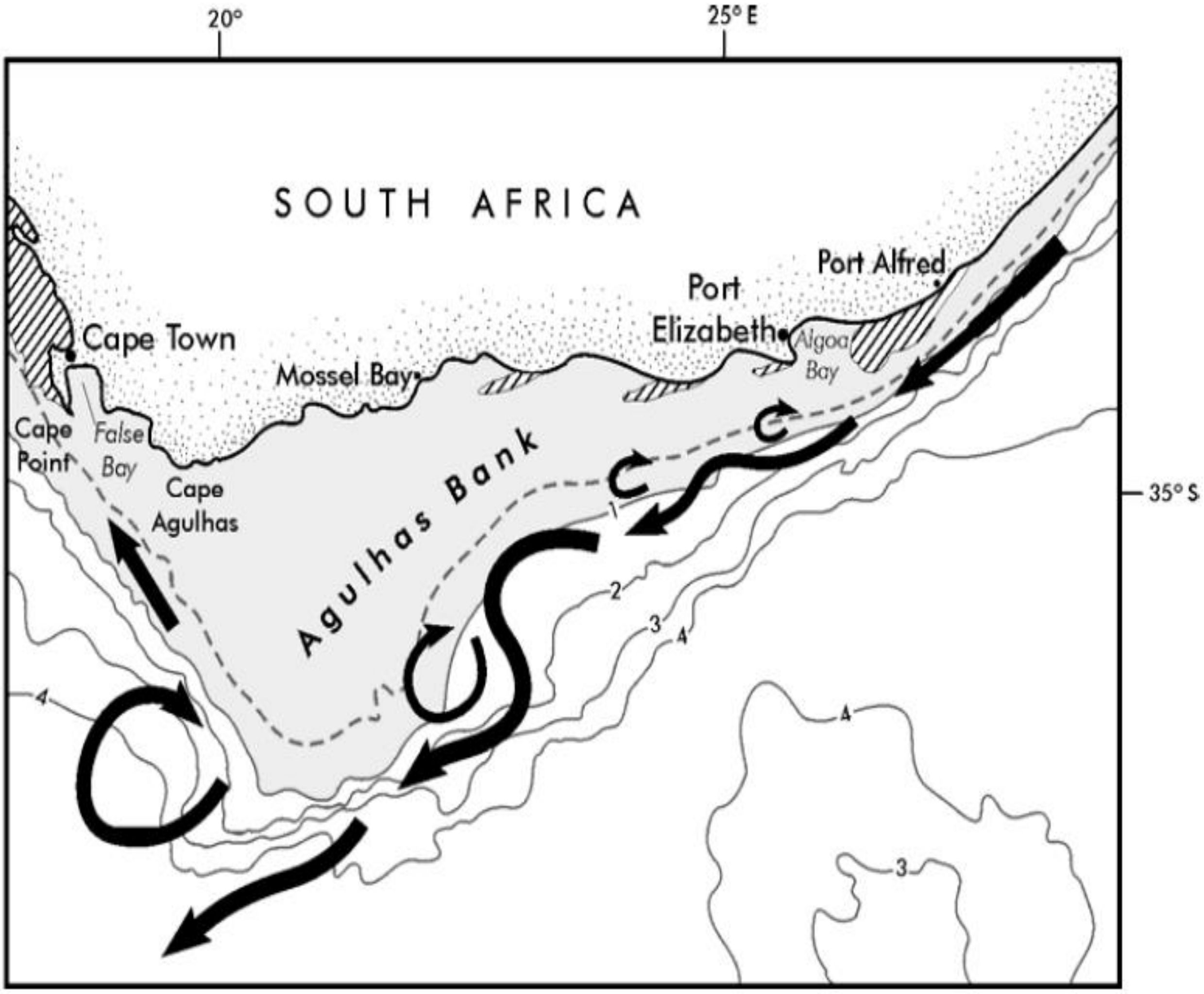

Figure 2.1: Bathymetry of the continental shelf off the south coast of South Africa, showing the major circulatory elements. This covers the southern Agulhas Current regime and upwelling is shown by hatching (Lutjeharms, 2006).

The oceanography of the south coast of South Africa is dominated by the Agulhas current and upwelling is found in two instances **1.** The shoreward edge of the Agulhas current and the continental slope along its full length and at locations where the width of the shelf increases along the path of the current as it moves towards Port Elizabeth (Lutjeharms, 2007). **2.** Wind induced upwelling which happens along the coastline when persistent strong easterly winds bring cold waters up in the form of eddies along the south coast of South Africa (Lutjeharms, 2006).

Sea surface temperatures (SST) can be used as a measure of upwelling as processes that happen during upwelling induce rapid fluctuations of coastal sea-surface temperatures. Changes in sea surface temperatures allow scientists to establish the occurrence of upwelling in an area. Sea surface temperatures have been used to identify upwelling areas before (Lutjeharms *et al*, 2000; Xavier *et al*, 2007) and satellite images showing sea surface temperatures have been used to locate upwelling regions. Sea temperatures recorded *in situ* can help provide insight into upwelling events, since upwelling is responsible for bringing cold nutrient waters from the deep sea, thus temperature changes are important indicators of when upwelling occurs.

Study sites

This study was undertaken within the mid-shore region at four exposed rocky shores along the south east coast of South Africa (**Fig 2.2**). The study sites included two sites thought to be characterised by upwelling (Port Alfred 58˚ 36' 85.8''S, 26˚ 53' 55.8'' E and Brenton on Sea 34˚ 04' 31.7''S, 23˚ 01' 29.5''E) interspersed with two sites believed to be characterised by non-upwelling sites (Kidd's Beach 32º 55' 14.2'' S, 27º 29' 18.0'' E and Kini Bay 34˚ 01' 17.2''S, 25˚ 22' 58.3'' E).

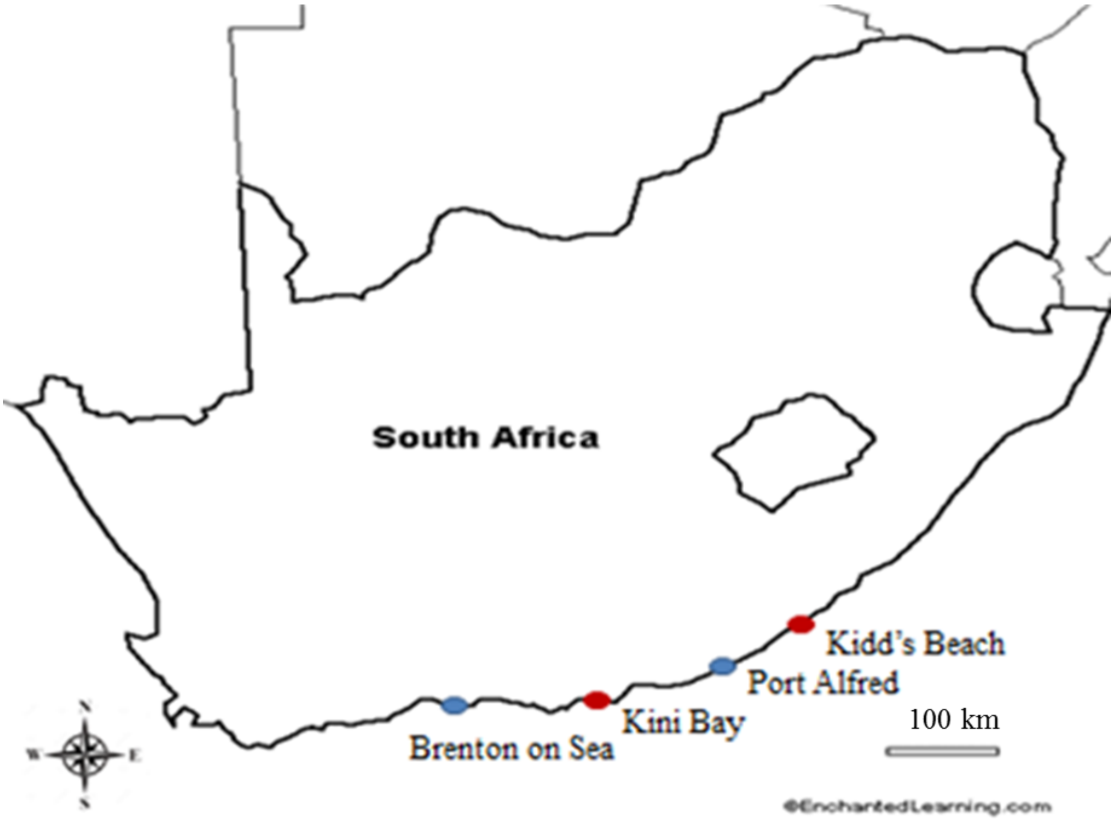

Figure 2.2: Map showing all the four study sites in the south east coast of South Africa and the distribution of *Gelidium pristoides*.

🔴 Non upwelling (Kidd's Beach and Kini Bay)

🔵 Upwelling (Port Alfred and Brenton on Sea)

All four sites are made of different rock formations and structure (**Fig 2.2**). Kidd's Beach comprises dolerite dykes and sills (Lubke and De Moor, 1998) from the Karoo super group and Port Alfred is made of quartzite rock formations with gullies from the Witteberg group. Kini Bay consists of angular sedimentary rocks which are quite quartzite-like sandstone with dark colouration while Brenton on Sea consists of sandstone rocks which are pale grey to white in colouration. The intertidal communities of all four sites were similar in nature with clear zonation and these sites were separated from each other by 10s to 100s of kilometres.

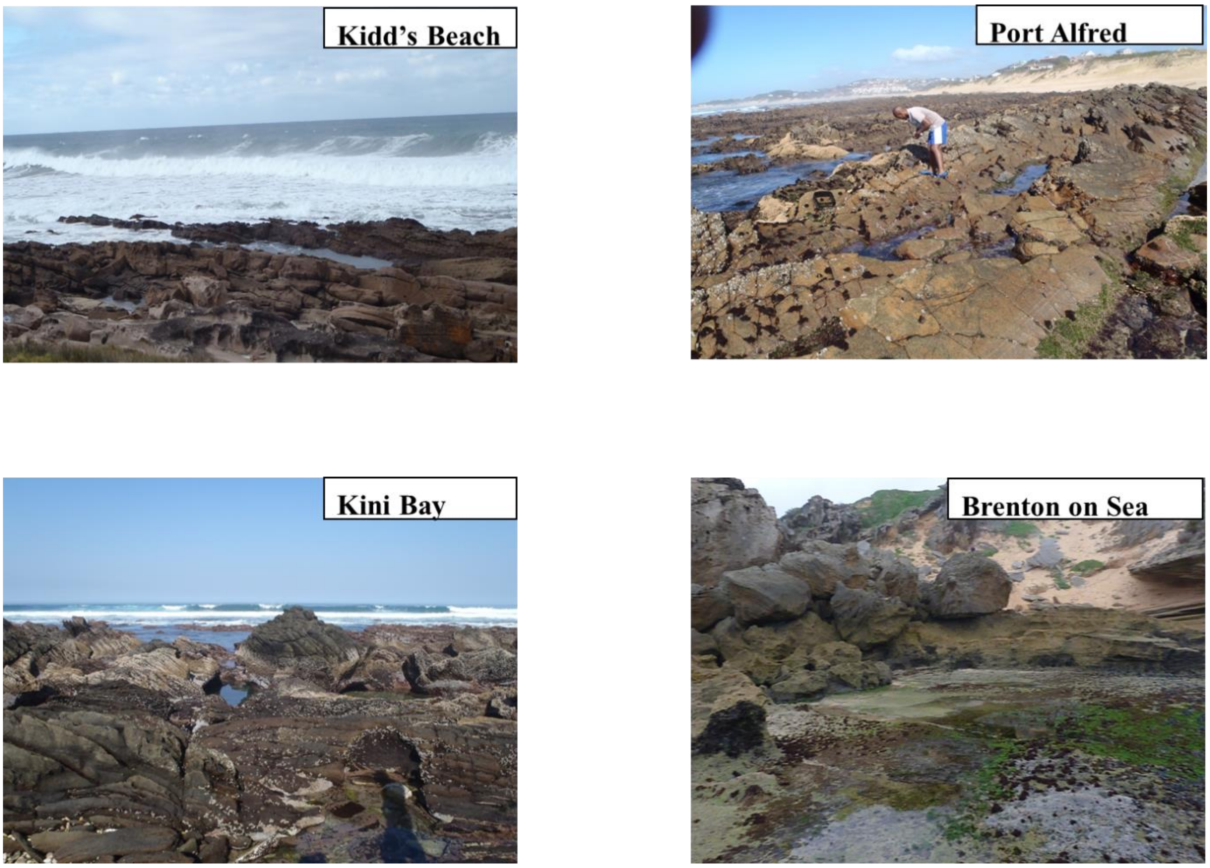

Figure 2.3: Site characteristics of all four sites (Kidd's Beach, Port Alfred, Kini Bay, Brenton on Sea).

Rocky shores of similar elevation in the lower eulittoral zone that were characterised by high cover of *G. pristoides* and many herbivorous organisms were selected for the study. Shores with moderate wave exposure and gentle slopes (<30˚) were selected. Treatments were set up in the mid shore level at each site and consisted of exclusion cages, artificial wire mesh structures, used to manipulate the presence of mobile predators and grazers, with the goal of evaluating biological interactions (Miller and Gaylord, 2007).

Study species

G. pristoides is a common rhodophyte alga on the south-east coast of South Africa normaly found in the mid-shore of intertidal communities extending from Seapoint on the west coast to Port Edward on the east coast (Gibbons, 1988). It is often confined to rock surfaces, shells of limpets, barnacles or reef-worm tubes.

Treatments were used to control access of benthic grazers and pelagic predators to the experimental plots. Pelagic predators of epifauna are likely to have been various species of fish and the main benthic grazers at the sites were the limpets *Cymbula oculus, Scutellastra granularis*, *Siphonaria concinna* and the winkle *Oxystele variegata.*

C. oculus is a true limpet with flat dull brown shell, a marine gastropod mollusk in the family Patellidae normaly found in the midshore and feeds on a wide range of algae. *S. granularis* is a true limpet in the family Patellidae, abundant on the mid to high-shore, again feeding on a range of algae i.e. known to feed on *Gelidium pristoides* (Branch, 1971) and it is distributed throughtout the whole South African coastline. *S. concinna* is in the family Siphonariidae, the pulmonate false limpets, and occurs in the mid-shore zone and its distribution extends from Cape Point to Zululand. *O. variegata* is a species of sea snail, the variegated topshell, feeding on a wide range of algae and occurs on the west and southern coasts of South Africa, from Namibia to North Transkei.

Chapter 3 : Oceanographic patterns and intertidal community structure.

Introduction

Previous experiments have shown that both nutrients (bottom-up) and the abundance of herbivores (top-down) have a strong influence on the structure of macro-algal assemblages (Nielsen, 2001; Worm *et al*, 2002; Nielsen and Navarrete, 2004). Bottom-up effects of resource/nutrients supply tend to propagate up the food web, first by being absorbed and utilised by plants to indirectly control patterns of abundance and distribution at high trophic levels (Nielsen, 2001). In particular the rate of resource supply has a profound impact on the abundance and diversity of primary producers in both terrestrial and marine environments (Nielsen, 2001).

Previous studies have shown that algal abundance can be modified by the proximity to upwelling centres (Nielsen, 2001), while other studies have also shown that macro-algal abundance has a strong influence on the abundance of herbivores and also on algal-herbivore interactions (Bustamante *et al*, 1995; Nielsen and Navarrete, 2004). Intertidal communities in coastal upwelling areas are expected to have enhanced algal production and phytoplankton growth because they receive more nutrients which in turn will lead to an increase in the representation or abundance of sessile filter feeders (Menge *et al,* 1997) and productivity of the intertidal community as a whole (Bosman *et al*, 1987). Variation in nutrient supply (e.g. through upwelling) is an important source of variation in plant-herbivore interactions in rocky shores (Nielsen and Navarrete, 2004).

Aims

After subjectively selecting the study sites, this experiment focussed on confirming if these sites experience upwelling or not. The focus was to measure intensity, frequency and duration of upwelling so that the sites can be assessed in terms of nutrients brought up by the process of upwelling and also to quantify grazing pressure by counting the number of grazers per $2m^2$ plots to compare differences between upwelling and non-upwelling sites.

Methods

Quantifying duration, intensity and frequency of upwelling events.

This was achieved using two complimentary approaches

1. In situ temperature data

Temperature iButtons DS1921L model (Dallas Semiconductor), embedded in a waterproof resin (3M Scotchcast 2130 Flame Retardant Compound), and placed inside an empty mussel shell were used to record ambient temperatures with a precision of 0.5˚C every 30 minutes at each of the four study sites from September 2014- June 2015. Three iButtons were used to record temperature at each site and the average was used in all calculations. These temperature measurements were used to estimate the number and duration of upwelling events by identifying periods when sea temperatures dropped by 5˚C within 24 hours (Xavier *et al*, 2007). Since iButtons recorded a mixture of air and sea temperatures as they were placed in intertidal zones, tide timetables which allow tidal predictions by showing the daily high and low tide predictions for a particular location were used to identify periods or sections of data associated with submergence of the iButtons. Upwelling frequency at each of the four sites was calculated by counting the number of upwelling events, which were days when temperature dropped by 5˚C or more. The duration of upwelling events was calculated by counting the number of days it took for temperature to return to its previous temperature before the drop, whilst the frequency of upwelling events was calculated as the total number of upwelling events.

2. Wind data

Wind speed and direction have previously been used to estimate the intensity and frequency of upwelling along the coast (Bakun, 1973; Weidberg *et al*, 2015). Wind data were collected from four meteorological stations in close proximity to each of the four study sites from 01 June 2014 to 06 June 2015 (South African Weather Service, 2015). These were: East London, Port Alfred, Port Elizabeth and Knysna. Following methods developed by Bakun, (1973), hourly wind speed and direction for each day were used to calculate an ‘upwelling index’ using the equation: $UPW=P_a*C_D*V_{9m}*V_{9m-x}*f^{-1}*P_w^{-1}$ (Bakun, 1973)

Where P_a = air density

C_D = drag coefficient approximated as 0.0014

V_{9m} = mean height-corrected wind speed

V_{9m-x} = alongshore vectorial component (estimated as zonal winds for this coast)

f^{-1} = Coriolis parameter ($9.9*10^{-5}$ at middle latitudes) and

P_w = water density (1025 kg m^{-3})

Positive values represent periods of upwelling and negative values represent periods of down-welling. Monthly upwelling duration at each of the four sites was categorised as long, medium or short based on the number of consecutive days within the month that experienced upwelling events (i.e. long $\geq$ 6 days; medium between 3-6 days; short $\leq$ 3 days).

To test if upwelling sites had more upwelling events than non-upwelling sites, a one way ANOVA with upwelling (fixed, two levels) and total number of upwelling events as the dependent factor was performed in Statistica 12.

Quantifying grazing pressure

To assess differences in the amount of grazing pressure potentially experienced by *Gelidium pristoides* at each of the four sites, abundances of the limpets *Cymbula oculus, Scutellastra granularis*, *Siphonaria concinna* and the grazing top shell *Oxystele variagata* where estimated using two randomly placed 2m × 1m quadrats in each site (24- 27 September 2014). This was done to show the number of grazers per square meter at each site and to estimate the grazing pressure exerted by grazers. Grazers inside the 2m x 1m plots were identified using Branch *et al*, (2007).

Results

Temperature

Port Alfred and Brenton on Sea (**Fig 3.5**), identified *a priori* as the upwelling sites had many more upwelling days, 44 and 39 respectively than the two non-upwelling sites with Kidd's Beach having 27 upwelling days and Kini Bay recording 13 days of upwelling. As expected many of these upwelling days occurred during the summer months. Port Alfred had many days of clear upwelling while upwelling at Brenton on Sea was weaker, with temperature drops less drastic than those of Port Alfred but Kidd's Beach and Kini Bay were more or less similar to each other in terms of temperature drops.

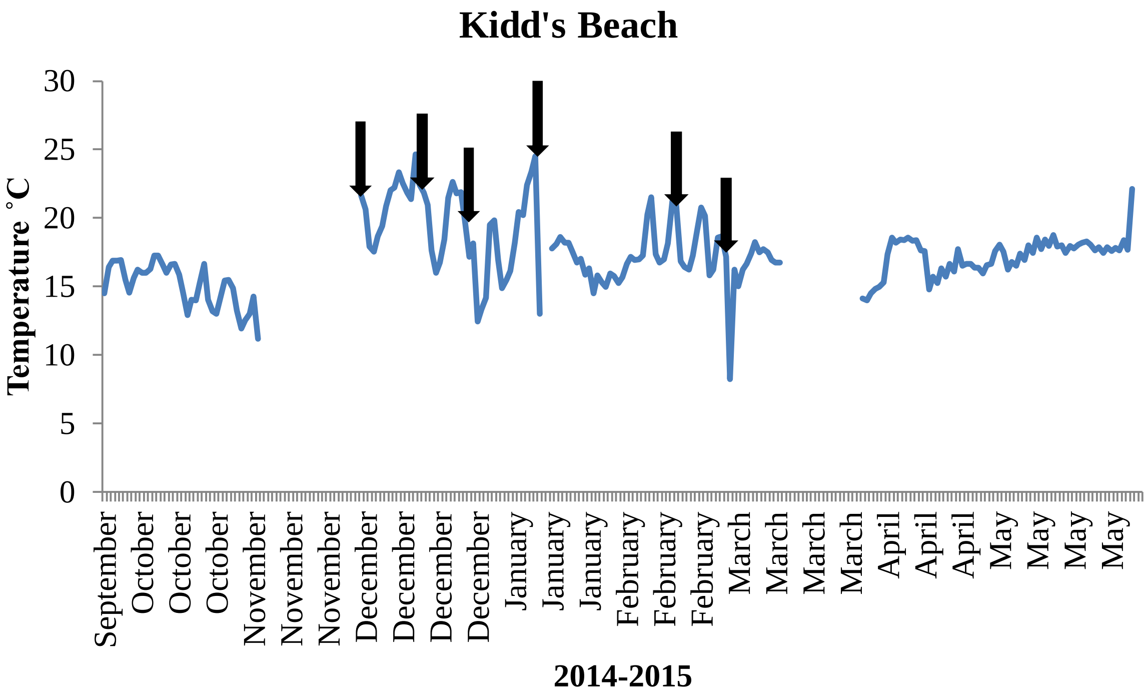

Figure 3.1: Sea surface temperature at Kidd's Beach with upwelling events represented by black arrows and there are gaps when temperature loggers were faulty.

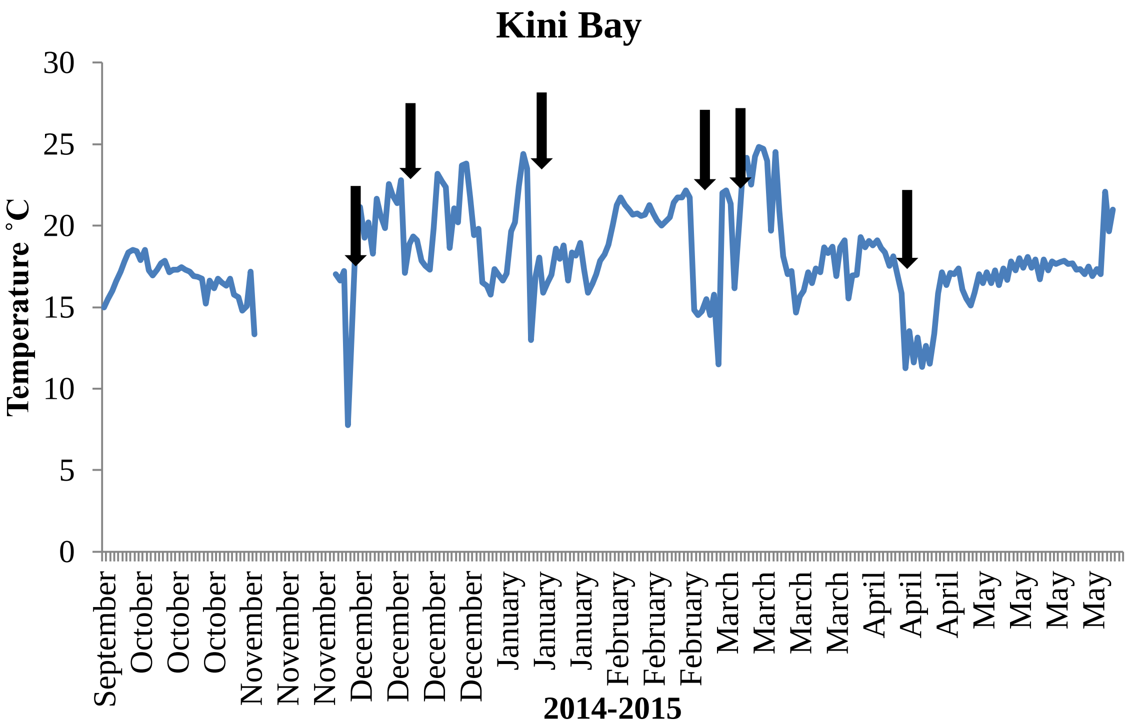

Figure 3.2: Sea surface temperature at Kini Bay with upwelling events represented by black arrows and there are gaps when temperature loggers were faulty.

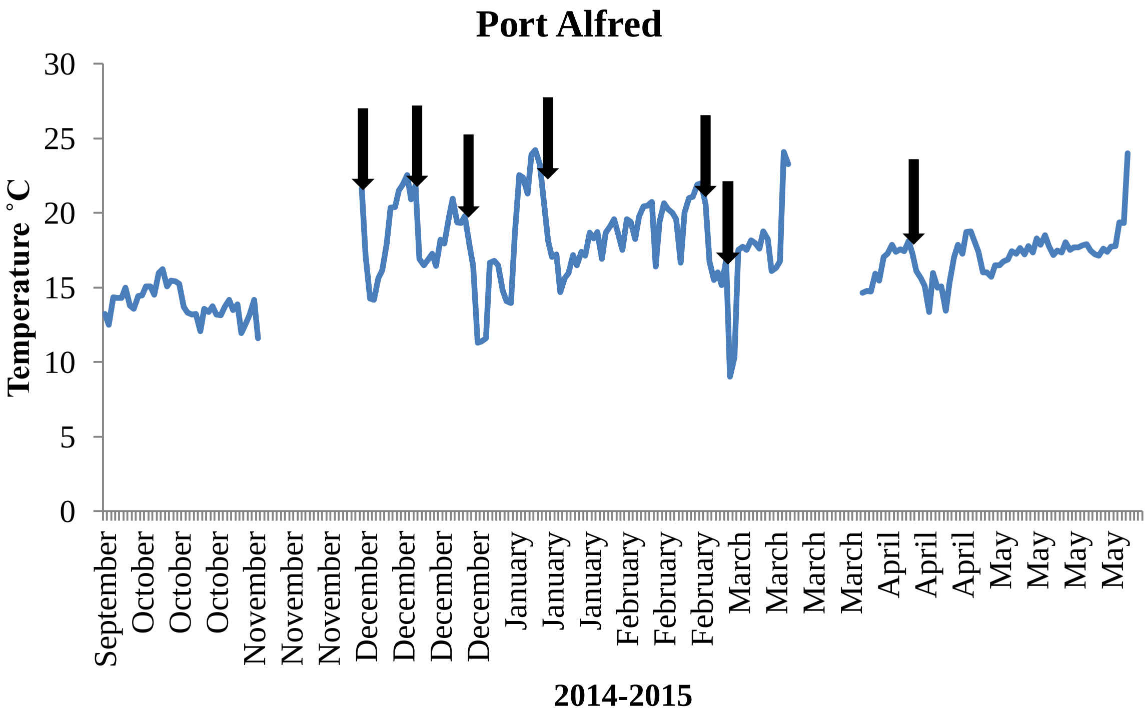

Figure 3.3: Sea surface temperature at Port Alfred with upwelling events represented by black arrows and there are gaps when temperature loggers were faulty.

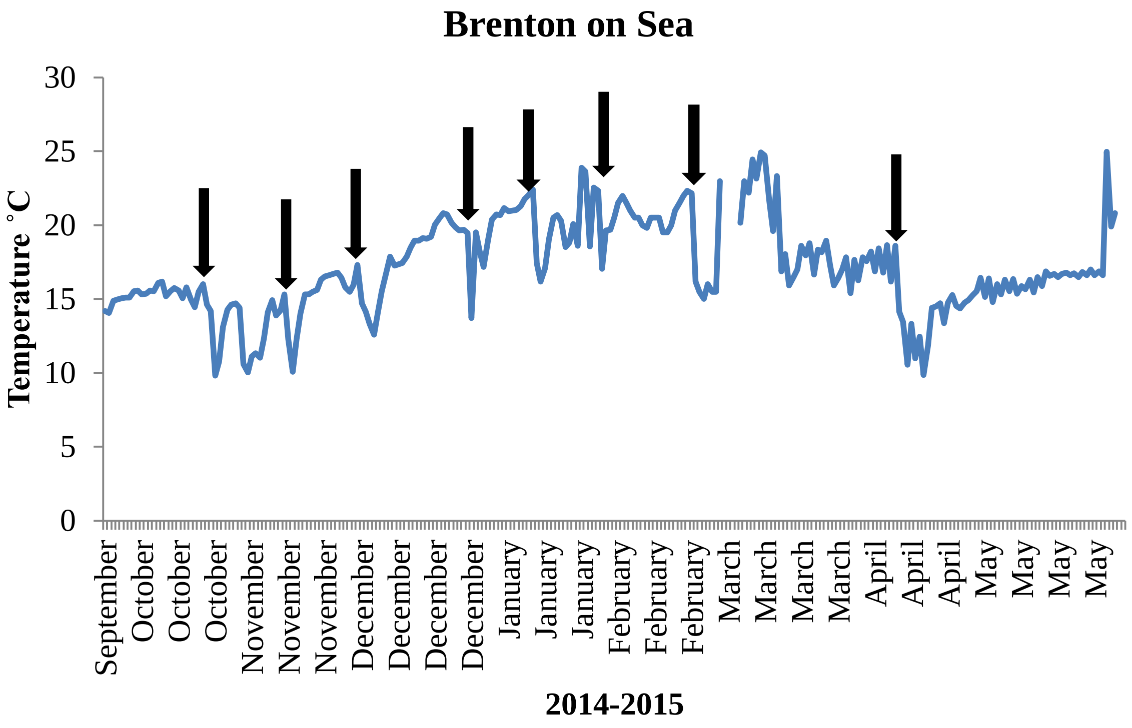

Figure 3.4: Sea surface temperature at Brenton on Sea with upwelling events represented by black arrows.

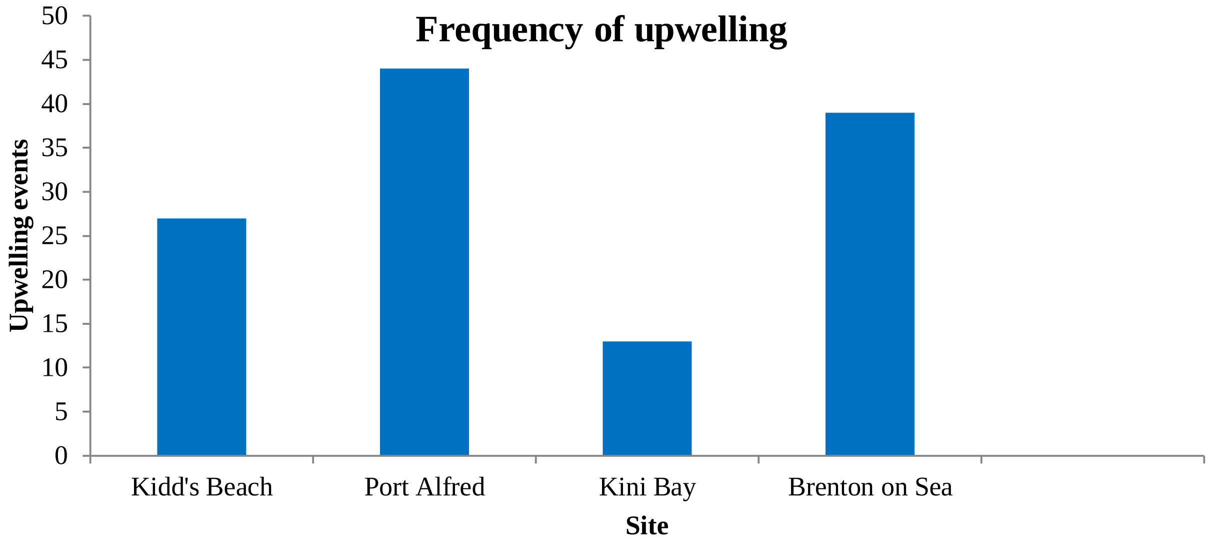

Figure 3.5: Total number of upwelling events at all four sites (Kidd’s Beach, Port Alfred, Kini Bay and Brenton on Sea).

To test if upwelling sites had more upwelling events than non-upwelling sites, a factorial 2-way ANOVA with upwelling (fixed, two levels) and month (fixed, ten levels) was performed in Statistica 12. Temperature recorded within the same time frame in all four sites was used as in some instances temperature loggers were faulty and could not record. Upwelling sites had significantly more upwelling events than non-upwelling sites (p<0.05, **Table 3.1**).

Table 3.1: Factorial ANOVA summary of results comparing upwelling vs non-upwelling sites using temperature data.

Effect	SS	df	MS	F	p
Intercept	372.100	1	372.100	33.982	0.000
Upwelling	57.600	1	57.600	5.260	**0.0328**
Month	505.400	9	56.156	5.128	**0.001**
Upwelling*Month	131.900	9	14.656	1.338	0.279
Error	219.000	20	10.950		

Wind data

Upwelling indices derived from wind data demonstrated that upwelling was less persistent at Kini Bay and Kidds Beach (**Figs 3.6 and 3.7**). The average upwelling index (based on values above zero) for these two non-upwelling sites were113.14 and 405.16 respectively (**Figs 3.6 and 3.7**).

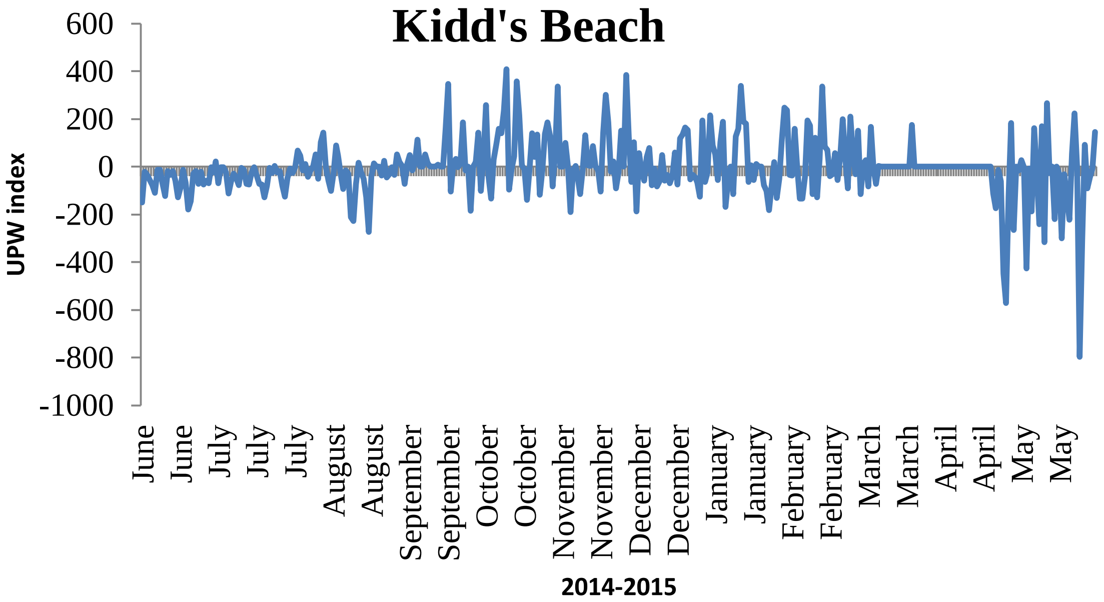

Figure 3.6: Upwelling index of Kidd's Beach.

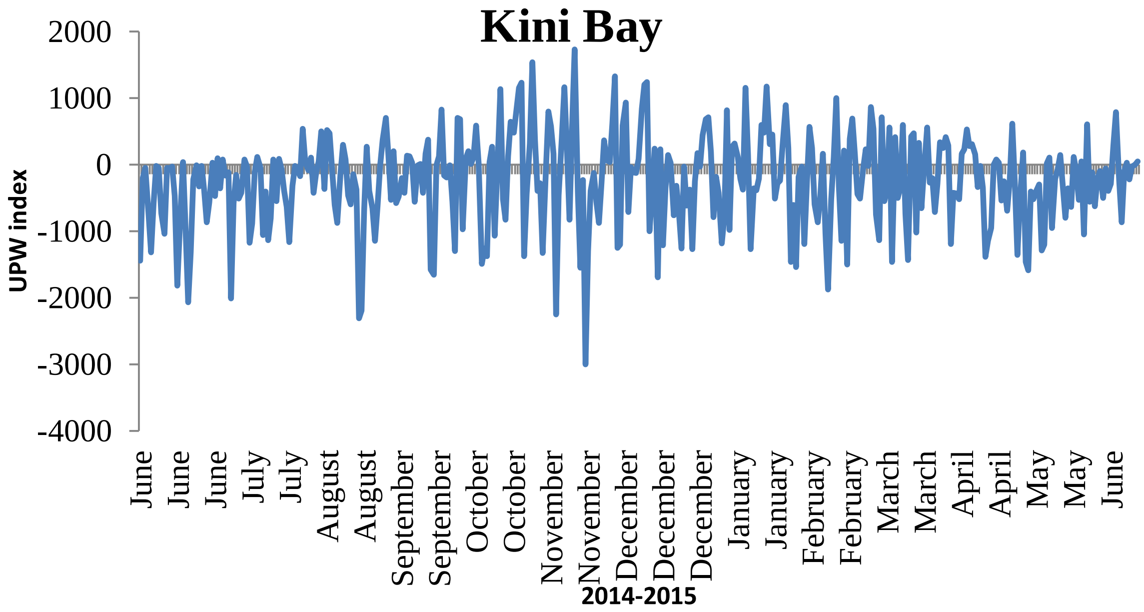

Figure 3.7: Upwelling index of Kini Bay.

Upwelling indices (**Figs 3.8 and 3.9**) show that of Port Alfred and Brenton on Sea, the two upwelling sites had more upwelling events than the two non-upwelling sites even though the mean upwelling index value was very low for Brenton on Sea . Port Alfred had an average of 334.75 and Brenton on Sea had an average 37.15 in terms of the mean upwelling index values (based on values above zero) but it had upwelling events of longer duration.

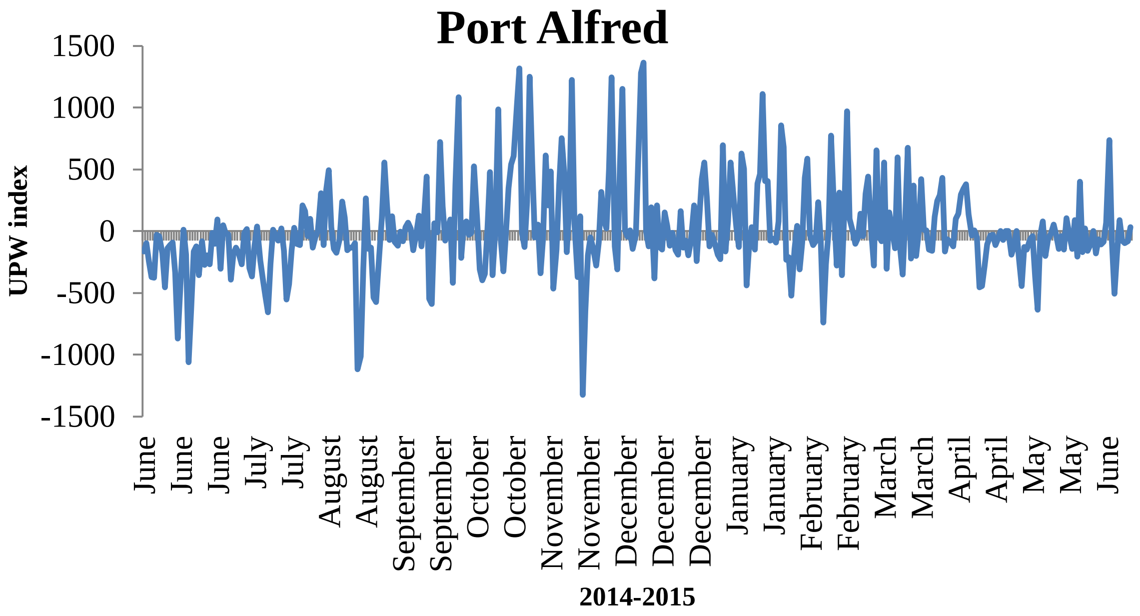

Figure 3.8: Upwelling index of Port Alfred.

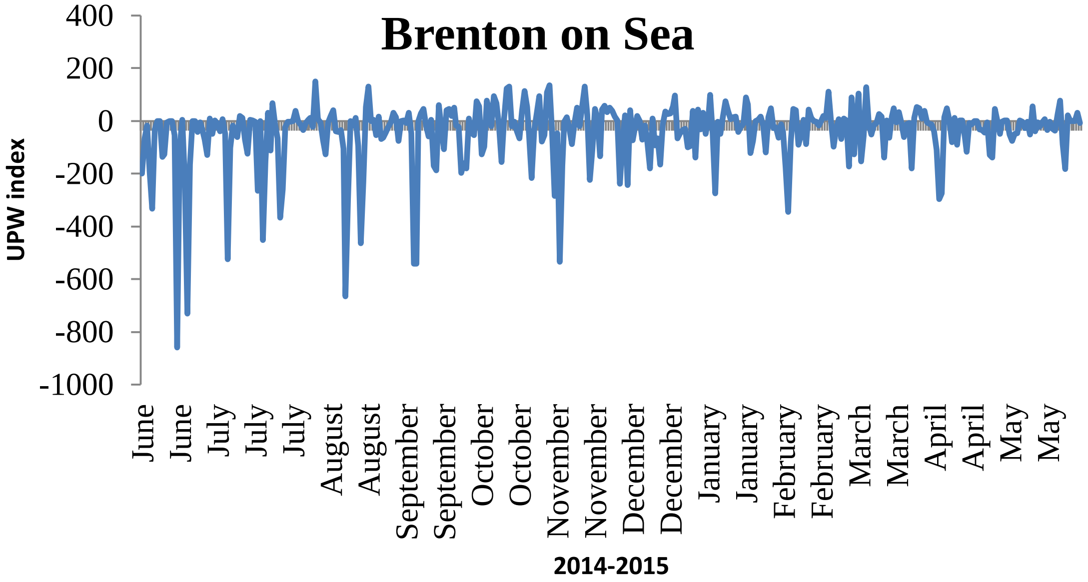

Figure 3.9: Upwelling index of Brenton on Sea.

As with temperature data, all four sites showed a similar trend in terms of seasonality of the upwelling index. Between the months of June and July they had many values that were below zero, indicating less upwelling during winter months than summer months. From the months August to September positive values can be seen, illustrating the beginning of upwelling towards summer with the months from October till February experiencing a lot of upwelling events. The seasonal trends observed show that there were more upwelling events during summer months than during the winter months as seen in all four sites.

The number of upwelling events in each month for Kidd’s Beach and Kini Bay the two non-upwelling sites are shown in **Figs 3.11** and **3.12.** At the two non-upwelling sites there were very short periods of upwelling between June and September with a few medium periods of upwelling from October to around April. It is apparent that upwelling is related to season, with many upwelling events during summer as observed by the many medium and short periods upwelling events in summer compared to the fewer, shorter upwelling events in winter.

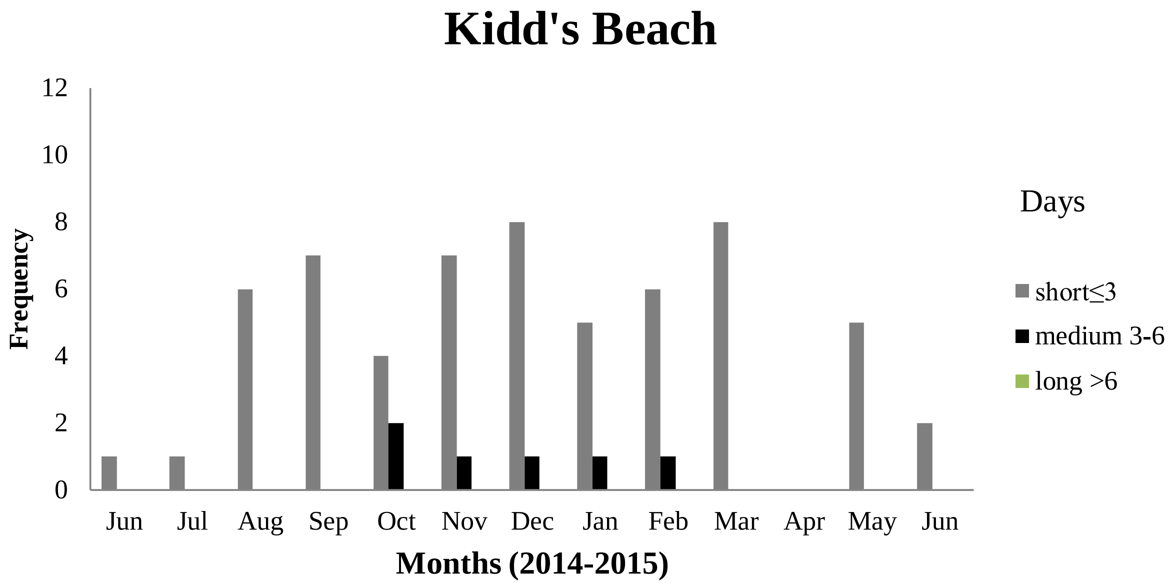

Figure 3.10: Number of upwelling events in Kidd’s Beach, upwelling events categorised by duration as long, short or medium.

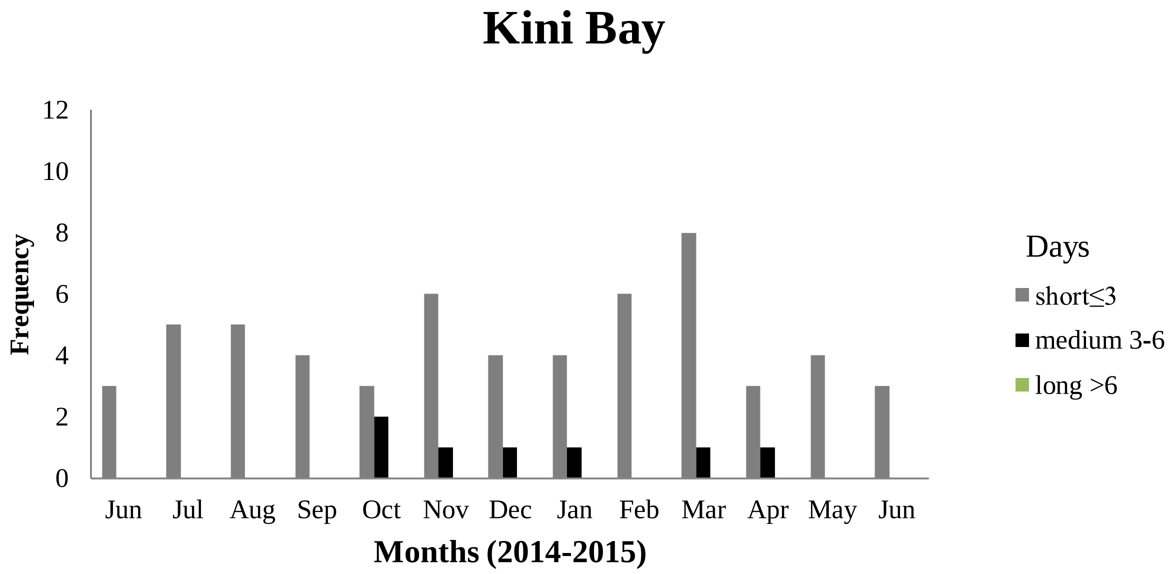

Figure 3.11: Number of upwelling events in Kini Bay, upwelling events categorised by duration as long, short or medium.

Upwelling events for each month for Port Alfred and Brenton on Sea are shown in **Fig 3.13** and **3.14**. As expected these two sites had more upwelling events compared to the two non-upwelling sites. At non-upwelling sites (Kidd's Beach and Kini Bay) the frequency of upwelling events averaged between 4 and 6 upwelling events per month whereas the upwelling sites (Port Alfred and Brenton on Sea) averaged between 6 and 8 events a month. Brenton on Sea had more prolonged upwelling with a few occasions when upwelling events lasted for longer than 6 days (long upwelling) during the months of December and January. Seasonality was also apparent with the two upwelling sites showing the same trend of having more upwelling events during summer than winter.

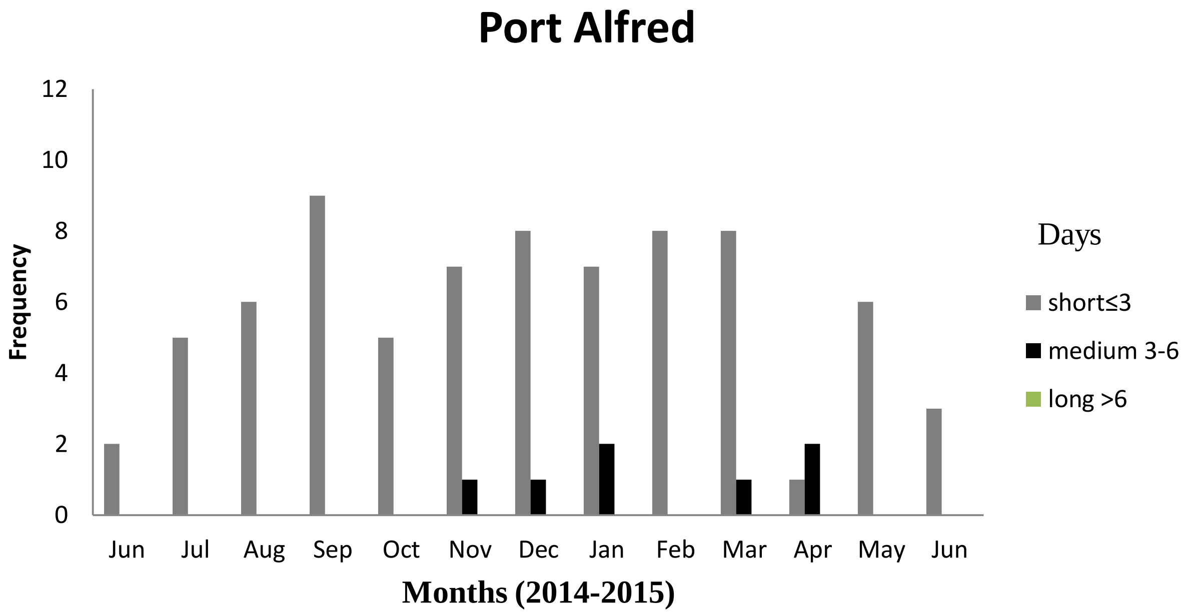

Figure 3.12: Number of upwelling events in Port Alfred, upwelling events categorised by duration as long, short or medium.

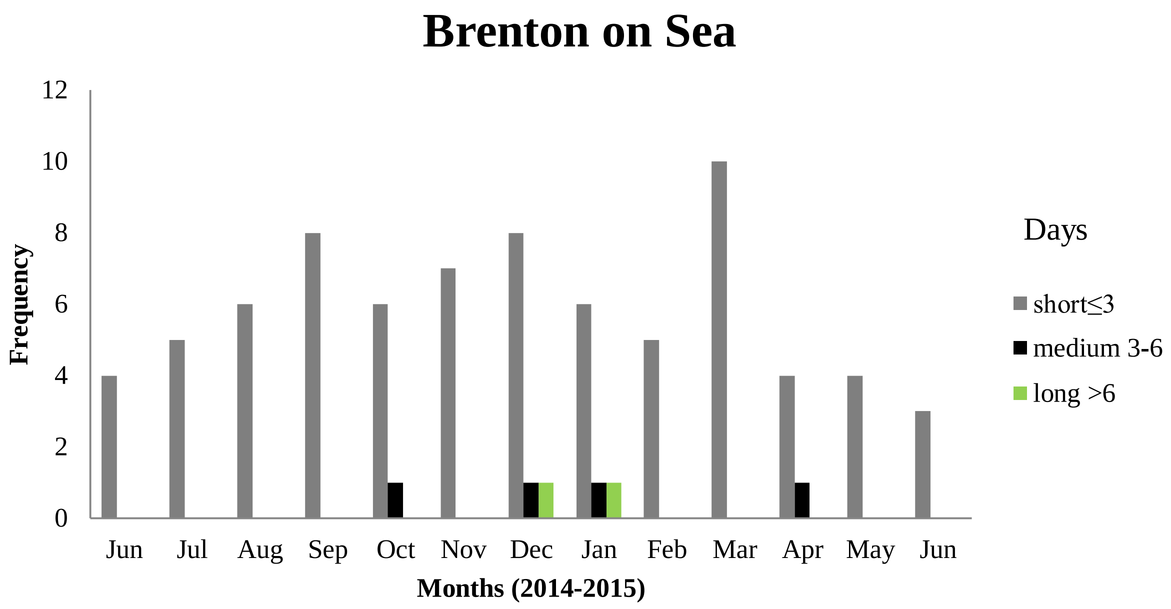

Figure 3.13: Number of upwelling events in Brenton on Sea, upwelling events categorised by duration as long, short or medium.

In total Kidd's Beach had 122 upwelling days recorded and Kini Bay had 137 upwelling days recorded during the whole study period. Port Alfred and Brenton on Sea had 146 and 141 days of upwelling respectively (days that recorded positive values) which was high compared to the two non-upwelling sites. Upwelling lasted for longer in the upwelling sites with a duration of short or medium upwelling events experienced many times and Brenton on Sea received two long upwelling events that lasted for longer than 6 consecutive days.

To test if upwelling sites had more days of upwelling than non-upwelling sites, a one way ANOVA with upwelling (fixed, two levels) and total number of upwelling days as the dependent factor was performed in Statistica 12. Upwelling sites had more upwelling days than non-upwelling sites, $p<0.05$ (**Table 3.2**) and there was a great difference in terms of the duration of upwelling events (short, medium and long). This supports the findings from wind data which also indicated that upwelling sites experienced more upwelling than the sites that were categorised *a priori* as non-upwelling in this study.

Table 3.2: One way ANOVA summary of results comparing upwelling vs non-upwelling sites using wind data.

Effect	SS	df	Ms	F	P
Upwelling	272.3	1	272.3	1089	**0.001**

Grazing pressure

Four common grazers which appeared at all four sites the lmpets *Scutellastra granularis, Cymbula oculus, Siphonaria concinna and* the winkle *Oxystele variegata* were quantified. The most abundant species were *Scutellastra granularis* and *Siphonaria concinna* with *C. oculus* and *O. variegata* being relatively rare. The two upwelling sites had higher species densities of these browsers compared to the non-upwelling sites except for one species (*C. oculus)* as there was only one individual at Brenton on Sea. Port Alfred had more individuals whilst Kidd's Beach had the least number of individuals counted. *Scutellastra granularis,* with 187 individuals was the most abundant species at all four sites followed by *Siphonaria concinna* which had 119 individuals. Upwelling sites are expected to experience more grazing pressure due to the higher density of grazers in these sites although it is worth noting that the real difference here was in numbers of *Scutellastra granularis* with the other species showing some differences between upwelling and non-upwelling, but *S. granularis* showed a really strong effect.

Table 3.3: Mean number of each species counted at each site.

Species	*Scutellastra granularis*	*Cymbula oculus*	*Siphonaria concinna*	*Oxystele variegata*
Kidd's Beach	22	5	17	3
Kini Bay	11	10	26	4
Port Alfred	97	15	32	7
Brenton on Sea	57	1	44	6

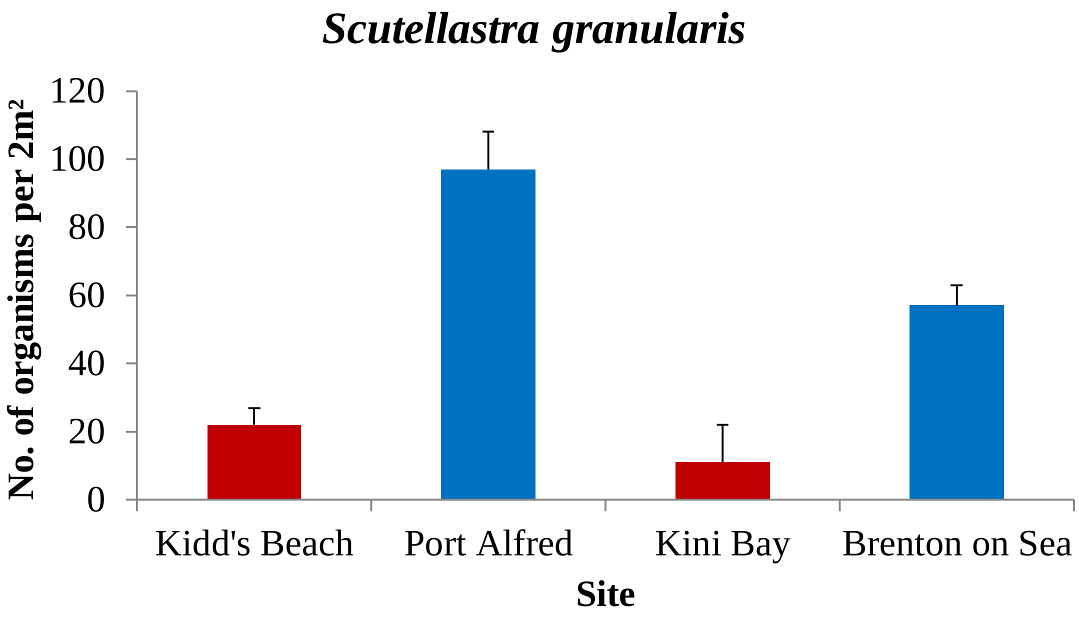

Figure 3.14: Number of *Scutellastra granularis*

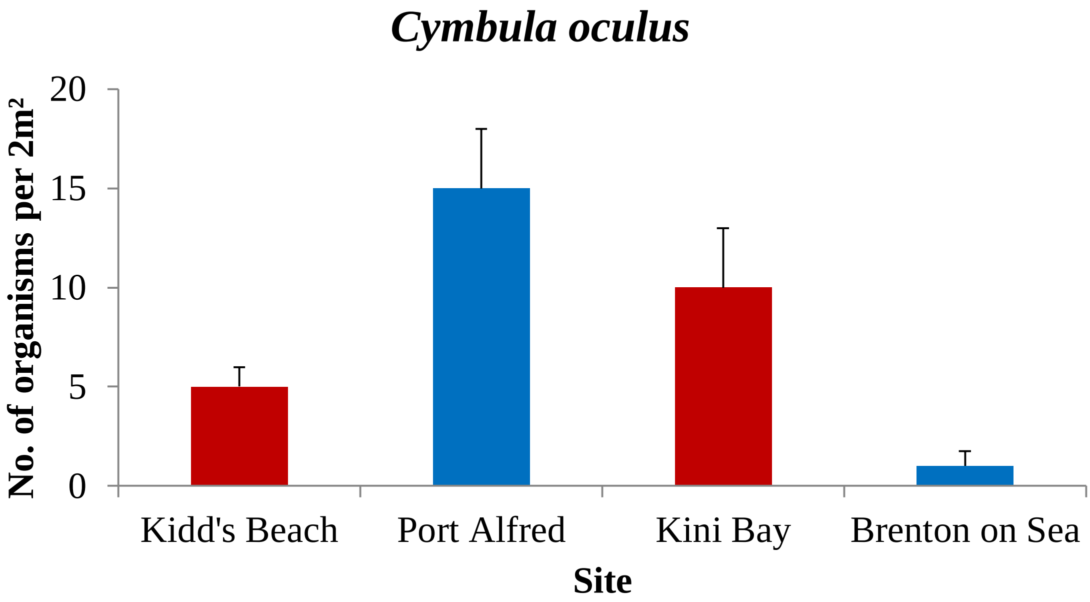

Figure 3.15: Number of *Cymbula oculus*.

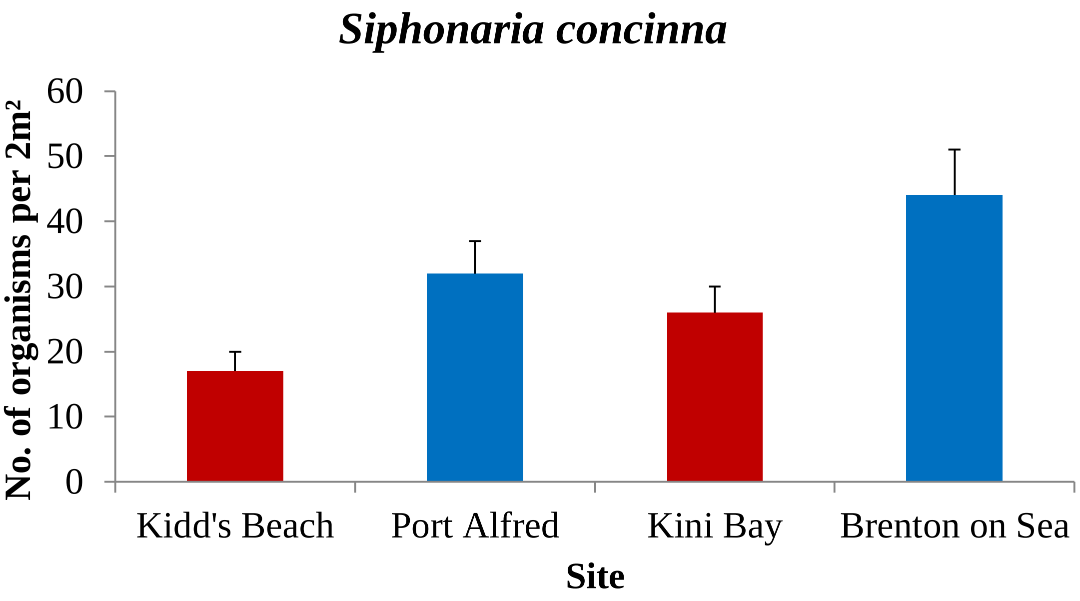

Figure 3.16: Number of *Siphonaria concinna*.

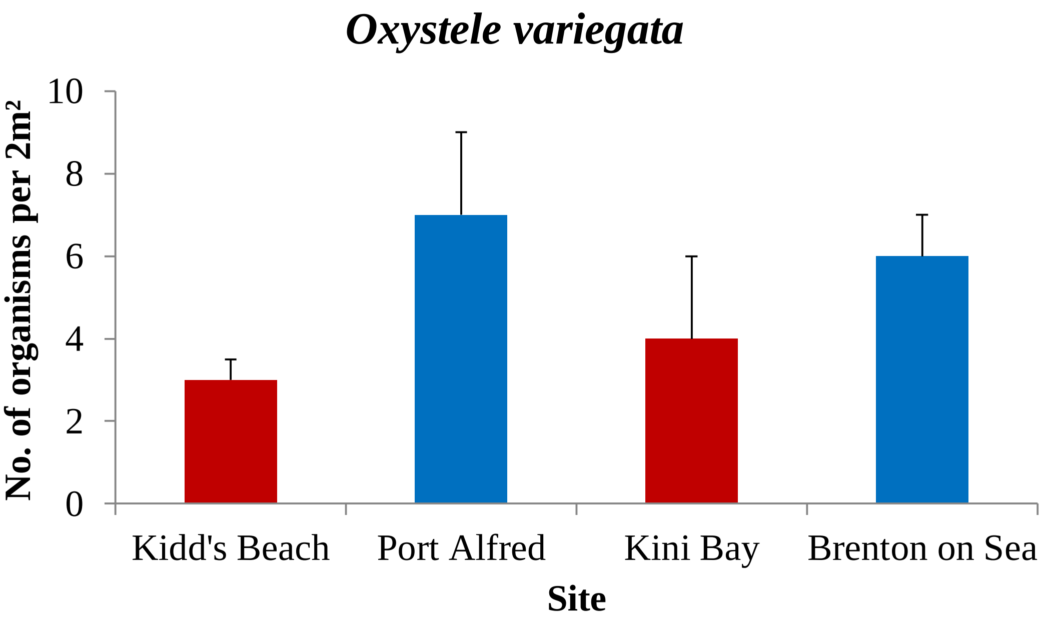

Figure 3.17: Number of *Oxystele variegata*.

Discussion

This study confirmed the *a priori* classification of shores by upwelling (e.g. Port Alfred and Brenton on Sea show more upwelling though Brenton on Sea had low intensity shown by the upwelling index for wind data) than the other two sites. Many studies have successfully used wind data and sea surface temperatures as measures of upwelling in upwelling regions around the world (e.g. Walker, 1986; Tomczak and Godfrey, 1994; Lutjeharms *et al*, 2000; Xavier *et al*, 2007). Intensity, persistence and frequency of coastal upwelling have been calculated from wind speed and direction as well as from measurements of sea surface temperatures (SST). In a study by Xavier *et al*, (2007), sea surface temperature was used to characterise the physical environment and onshore upwelling intensity at several sites. Rapid drops in sea surface temperature can be viewed as upwelling events as this is associated with rising of deep cold ocean waters bringing nutrients closer to the surface.

Hourly wind speed and direction have been used to calculate an upwelling index by Bakun, (1973) and Weidberg *et al*, (2015). The use of wind data to quantify upwelling is important as it allows scientists to count the number of upwelling events and the frequency of upwelling in an area through time. This study made use of both wind data (wind speed and direction) and sea surface temperature (SST) to quantify upwelling. Numbers of upwelling events calculated from sea surface temperatures and wind data were useful to clearly distinguish between frequencies at the two types of sites and to distinguish clearly short, medium and long upwelling events.

The use of sea surface temperature measurements and wind data can be coupled with the use of other measures of upwelling like satellite imagery of temperature or chlorophyll and measurements of phytoplankton to get more supporting information about upwelling. Combining all these measurements would enable a more detailed measure of upwelling in coastal areas. It is useful to use more measures to get more reliable information on how upwelling happens in a particular area.

The study also managed to assess the influence of upwelling on the number of herbivores at each site. Upwelling had a strong influence on the number of herbivores (particularly *Scutellastra granularis*) as the upwelling sites (Port Alfred and Brenton on Sea) had more herbivores per two square meter than the non-upwelling sites (Kidd's Beach and Kini Bay) (**Table 3.3**). These results are in line with those of Bosman *et al*, (1987) that upwelling regions support higher abundances of herbivorous organisms that non-upwelling regions. A study conducted by Bosman *et al*, (1987) showed that algal cover and the biomass of herbivorous limpets supported per unit area on rocky shores were significantly greater in upwelling regions than in regions without coastal upwelling; however they also discovered that cover of sessile filter-feeding organisms was significantly greater in non-upwelling shores compared to upwelling shores. McQuaid and Branch, (1985) suggested that competition for space between algae and filter feeders, which might be a partial explanation for this observation with algae outcompeting filter feeders where there are lots of nutrients. Intertidal algae have been observed to respond to nutrient enrichment (Bosman *et al*, 1987) and increased algal production leads to enhanced biomass of herbivorous limpets supported within that community. Nutrient enrichment as a result of upwelling has also been linked with an increase in the abundance of sessile organisms (Menge *et al*, 1997) and in the functioning of the whole intertidal community, although research by Broitman *et al*, (2001) was contradictory to predictions of bottom-up community regulation models as there were no significant differences in herbivores and predators due to upwelling.

Conclusions

Sea surface temperatures and wind data can both be used to quantify upwelling, to calculate the number of upwelling events and make it possible to differentiate brief from long-lasting upwelling events. From the wind and temperature data, sites that were considered to be upwelling (Port Alfred and Brenton on Sea) had many upwelling events that lasted longer in the case of Brenton on Sea than sites that were considered to be non-upwelling (Kidd's Beach and Kini Bay). From counting the herbivores in 2m x 1m plots it can be concluded that these upwelling sites support more herbivorous organisms per two square meters than non-upwelling sites, although the difference was mainly due to *Scutellastra granularis* and to a lesser degree *Siphonaria concinna,* while *Cymbula oculus* and *Oxystele variegata* showed little/no effect of upwelling.

Chapter 4 : Grazing, predation and the influence of sea weed surface area on epifaunal communities

Introduction

Ecosystem engineers add the physical structure and alter the abiotic environment of epifaunal communities (Jones *et al*, 1997; Hastings *et al*, 2007; Wright *et al*, 2014) and knowing more about them can help in their management. Macro-algae are often important ecosystem engineers as they responsible for modifying habitats and providing habitat for epifauna (Beckley, 1981). While predation can affect epifauna directly, nutrient variability and grazing can affect epifaunal communities indirectly by influencing the ecosystem engineers on which they depend.

Top-down and bottom up factors have been implicated as factors determining community assemblages. Many previous studies have tried to analyse relationships between top-down and bottom-up factors (Menge, 2000) and epifaunal communities on rocky shores are ideal for such studies. Explaining the distribution, abundances and relationships of species in aquatic environments is important as it can improve our understanding of processes influencing the distributions and abundances of species.

Upwelling is responsible for bringing in nutrients from deep sea waters and it can be considered as a bottom-up factor, affecting macro-algae directly and thus affecting epifauna indirectly. Predation and grazing which influence trophic levels from above are considered to be top-down factors in this study, predation affecting the epifauna directly and grazing indirectly. Upwelling indirectly affects epifauna, as nutrients brought up by upwelling can affect algal abundance, with an increase in nutrient availability resulting in more algal growth and thus affecting habitat availability for epifaunal organisms that depend on algae for their survival. An increase in algal growth will mean more surfaces for periphyton to attach to and an increase in periphyton will attract a lot of epifaunal grazing species (Klumpp *et al*, 1992) thus providing a potential indirect effect of upwelling on epifauna. Bosman *et al*, (1987) found that upwelling regions supported significantly more algal cover, ground cover of sessile organisms and biomass of herbivorous limpets per unit area on rocky shores than regions where there was no coastal upwelling.

Grazing and predation are top-down controlling factors. Grazers affect the distribution and abundance of algae (Forrest *et al*, 2001) and thus they have indirect effects on other processes that are carried out by the algae, such as providing epifaunal habitat, whereas predation has a direct effect on epifauna. Grazers will alter living space for epifauna by changing the physical structure of algae and the change in state of algae may influence predation as this will be determined by the amount and quality of space available for epifauna to hide from predators.

Importance of sea weed surface area to epifaunal communities

Algal surface area is an important ecological parameter because of the ecological functions it brings to communities (Dahl, 1973). Quantifying surface area allows scientist to know more about the structure and form of sea weeds and this helps in understanding the relationship between organisms living within the sea weed and how they interact with each other. Surfaces are boundaries at which transfers take place (Dahl, 1973), thus in algae, they are determinants of the uptake of nutrients. In the case of epifaunal communities the surface area of sea weeds provides a point of attachment and can provide protection. Thus the quantification and analysis of surface area is important in understanding and interpreting the functioning of communities. Sea weeds provide protection for benthic fauna as they serve as a refuge from predation during high tide (Wright *et al*, 2014) and provide enhanced survivorship during low tide.

This chapter aimed at assessing factors influencing epifaunal community composition, establishing a relationship between surface area and the number of epifauna living within an ecological engineer. For organisms living in epifaunal communities, greater surface area may mean greater attachment space for protection from wave force and protection from potential predators. Increased surface area of the ecological engineer is of great importance to benthic fauna that depend on it for their survival. Reduced surface area of the engineer means that benthic fauna are vulnerable to wave forces and predation thus less surface area might lead to fewer or different epifauna. Surface area has been described as an “essential resource” (Dayton, 1975a) as it can be a limiting resource in communities. For example, efficient production of surface area of many coral reef organisms and the utilisation of those surfaces by secondary occupants results in competitive forces that are a major determinant of coral reef communities (Dayton, 1975a). In this study I am concerned with the influence of the common rhodophyte, *Gelidium pristoides* on the epifauna that it supports. *Gelidium pristoides* is a dominant mid-shore alga often confined to the shells of limpets, barnacles and rock surfaces. Fronds of *G. pristoides* are narrow and flat with a mid-rib; the fronds have serrated margins and branch into irregular small leaflets. *G. pristoides* is a sea weed that supports an abundant and diverse epifauna (Beckley, 1981) and it has great commercial use as it is harvested to make agar (Steyn, 2009).

Aims and objectives

The aim of the study was to assess the influence of a biological engineer (*Gelidium pristoides*) and predation on epifaunal communities at upwelling and non-upwelling sites on rocky shores of the south east coast of South Africa. As algal cover is likely to be important, the study also considered the indirect effects of grazing on epifauna through its influence on algal cover. Further objectives of the study include assessing the influence of upwelling and grazing on epifaunal communities. The study aimed at testing if upwelling can lead to greater algal cover and whether this will lead to greater epifaunal abundances. Another objective was to assess if more algal cover will increase habitat complexity and if this will lead to greater densities of epifauna (e.g. more epifauna per square cm of alga).

The study focused on the following

- Does grazing have an effect on algal cover and the community structure of epifauna?
- Does upwelling have an influence on algal cover and community structure of epifauna?
- Does surface area of sea weed (*G. pristoides*) influence community structure of epifaunal communities?

Hypotheses

- Predation will directly affect epifaunal abundances.
- Algal cover will directly affect epifaunal abundances and community structure.
- Effects of grazers will reduce algal cover and indirectly affect community structure of epifauna.
- Upwelling will increase algal cover when grazers are excluded.
- As surface area of sea weed increases so does epifaunal density (number of epifauna per cm^2 of sea weed).

Methods

The experimental set up used stainless steel cages of 20cm x 20cm x 15cm height and with mesh size of 20 mm to exclude/include combinations of benthic grazers and swimming predators (**Fig 4.1**). Five blocks separated by at least 5 meters from each other in each site were haphazardly selected to set up the experiment. The experiment was started in June 2014 and left to run till June 2015. In each block, the following 4 treatments were applied to the experimental plots: **1.** Total exclusion cages (TE or closed), these were closed cages that excluded both grazers and predators. **2.** Grazer + (G+), which allowed access to grazers, but not predators. These were roofed cages with sides that did not reach the substratum, allowing access to benthic grazers. **3.** Controls (Co), which had screws marking the four corners of the plot, with the plot being otherwise undisturbed **4.** Predators + (P+), plots which had closed sides and an open roof to allow access to pelagic predators, while not allowing benthic grazers to come inside the cage. All plots included patches with initially similar amounts of the alga, *G. pristoides* with a total of 20 plots per site. Sites were separated by 10s - 100s of kilometres.

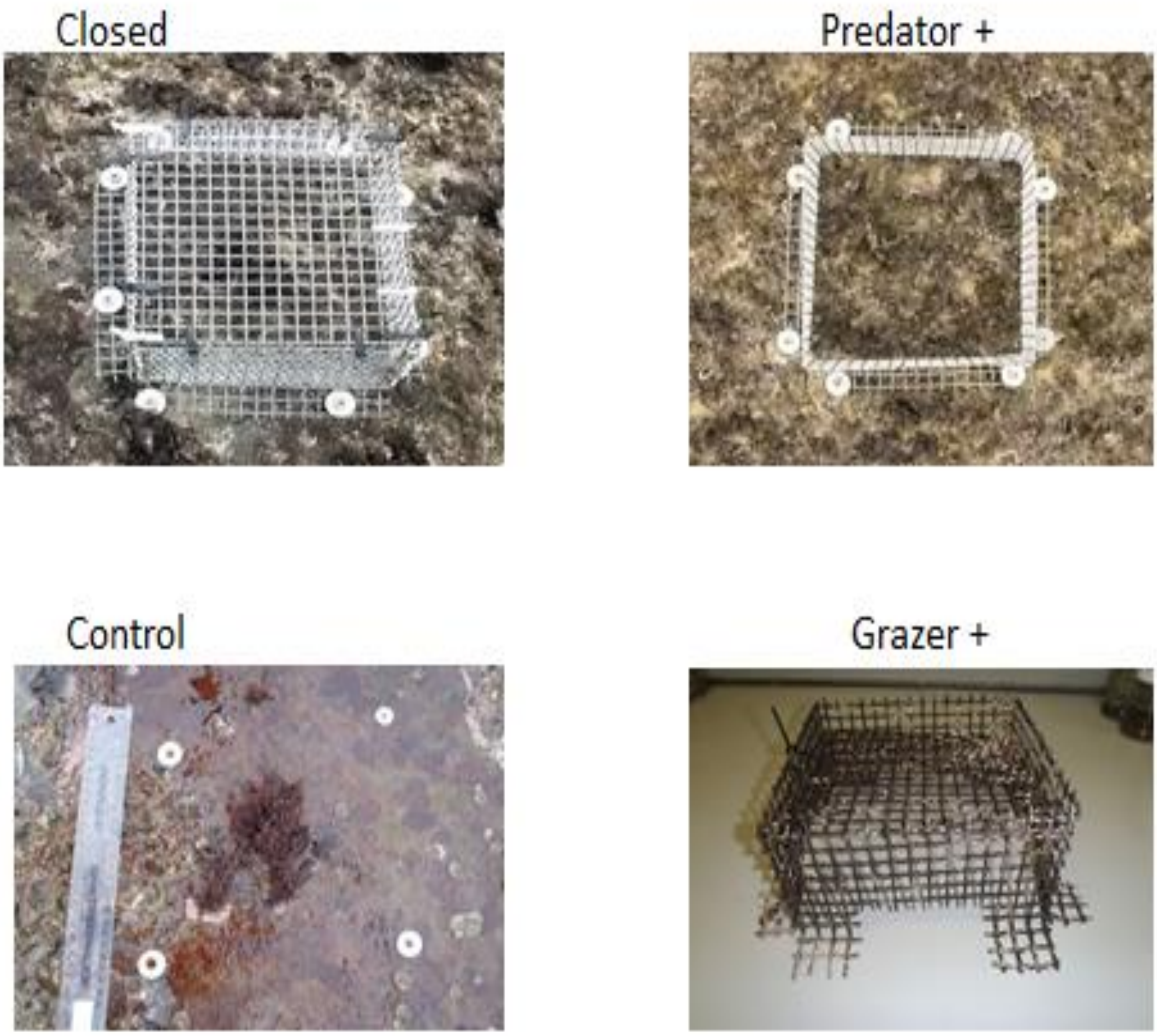

Figure 4.1: Different treatments that were set up at all four sites (Closed, Control, Grazer + and Predator +).

Cages were attached to the substratum using rawl plugs and a battery operated drill. Monitoring of the cages was done on a monthly basis during spring low tides for the first 6 months and once every two months for the last 6 months. Loose and old screws were replaced with stainless steel screws and eye bolts on every visit. During every field visit photographs of algal cover in each experimental plot were taken and a wire brush was used to remove any algae growing on the cages.

To convert algal biomass to surface area, an experiment was carried out using dish washing liquid (Harold and Hall, 1978). Small fronds of algae (*G. pristoides*) were weighed to get the initial wet weight then dipped into commercial dish washing liquid and then re-weighed after excess liquid was allowed to drip off. The weight of the surface film remaining on the fronds was obtained by subtracting the initial weight of the sea weed from the weight of the sea weed after being immersed in dish wash. The same algal fronds were then flattened under glass and photographed using a light microscope. Using the computer program Image J, the surface area of each frond was calculated. The weight of the surface film was regressed against the calculated surface area to obtain a relationship between weight of the surface film and surface area. This provided an equation allowing the surface area to be calculated from the weight of surface film. This equation was used to calculate the surface area of sea weed from each plot after the completion of the whole experiment.

After 12 months, at the end of the experiment, exclusion cages were removed and all living material that was inside was removed, placed into plastic jars, and stored in 10% formalin for not less than 48 hours while waiting to be sorted. In the lab, the alga was washed of all organisms before the blotted and the dry weight were measured. Blotted weight was taken immediately after washing with the algae rolled in tissue paper to remove water before weighing.

Weight of algae immersed in dish washing liquid was measured soon after measuring the blotted weight, the algae from each treatment were immersed into dish washing liquid, removed and allowed to drip for 30 seconds before being re-weighed. Surface area was calculated from the weight of surface film using the equation $y = 5.2281x + 0.0607$ (y = surface area, x = weight of surface film) derived from the initial surface area experiment.

For dry weight, the algae were placed into brown paper bags, which were placed inside an oven (60˚C) for 48 hours. In the lab, all the organisms washed from the algae were stored in 70% ethanol. Identification keys for isopods (Kensley, 1978), amphipods (Griffiths, 1976) and polychaetes (Day, 1967) were used to identify all the epifauna collected to species level under a light microscope. Molluscs were identified using Branch *et al*, (2007).

Percentage algal cover within plots was calculated from photographs taken at the start of the experiment and during each visit to the sites. Algal cover was calculated for each plot (20cm X 20cm), using Coral Point Count (CPCe) and the point intercept method. A total of 49 points were randomly superimposed on each photograph, the ones placed over alga were used to calculate percentage algal cover out of the total 49 points.

Data analysis

1. a. Algal cover

Change in algal cover was predicted to result in a change in the community structure of epifauna, as more algal cover will offer protection and hiding places for epifauna and a decrease in algal cover was expected to result in fewer individuals and possibly fewer species. As a first step to test this model, a three way nested analysis of variance (ANOVA) was run using Statistica 12, this was used to assess the influence of treatment (fixed factor, 4 levels), upwelling (fixed, 2 levels) and site (nested in upwelling, random, four levels) on algal cover.

b. Surface area

It was predicted that upwelling, treatment and surface area (more surface area = more habitat) would have an influence on epifaunal communities. Algal surface area was expected to have an influence on the abundance of individual epifaunal species per cm^2 of sea weed. Density of epifauna (total number of epifaunal individuals per cm^2 of sea weed) was calculated by normalising the data for each plot using the calculated surface area of alga and analysed the same way as algal cover using three-way nested ANOVA.

2. Epifaunal community structure

a. Non-normalised data

Upwelling, treatment and site were expected to have an effect on community structure of epifauna. To test the hypotheses on the epifaunal community, a multivariate analysis was done using a permutational analysis of variance (PERMANOVA) based on the Bray Curtis similarity measures in PRIMER 6. Using the Bray Curtis similarity matrix to check the similarity of species within each plot in terms of treatment, site and upwelling, a two way, type III PERMANOVA with 9999 permutations in PRIMER 6 was used. To visualise differences in terms of upwelling or non-upwelling, influence of treatments and site, non-metric multidimensional scaling (nMDS) ordinations based on the Bray Curtis similarity matrix measures with untransformed data were plotted in PRIMER 6. A SIMPER analysis in PRIMER 6 was used to assess the percentage contributions to differences of each species among all sites (Kidd's Beach, Port Alfred, Kini Bay and Brenton on Sea).

b. Normalised data

Epifaunal abundances were normalised to values per square centimetre of sea weed (surface area) and also normalised for algal cover. Abundances of each species of epifauna per cm^2 of sea weed (surface area) and per cm^2 algal cover were calculated by dividing epifaunal numbers by surface area or algal cover of *G. pristoides* in each plot. Normalised data were analysed in the same way as the original data.

c. Total abundances

Upwelling, treatment and site were expected to have affected the abundance epifauna. To test this, a three way nested analyses of variance (ANOVA) was run using Statistica 12, to assess the influence of treatment (fixed factor, 4 levels), upwelling (fixed, 2 levels) and site (nested in upwelling, random, four levels). Separate analyses were run for: the total number of epifaunal individuals (i.e. epifaunal abundance) in each plot; density of epifauna (number of epifauna per cm^2 of sea weed surface area) in each plot, and density of epifauna per unit algal cover (number of epifauna per cm^2 of algal cover) in each plot.

Results

Each site supported between 13 to 19 species, the most abundant taxa being crustaceans (amphipods and isopods), with some polychaetes and gastropods. A total of 44 species (**Table 4.1**) were recorded.

Table 4.1: Species identified in this study

Amphipods	**Isopods**	**Gastropods**	**Polychaetes**
Afrochiltonia capensis	*Cymodecella sublevis*	*Burnupena lagenaria*	*Boccardia polybranchia*
Amaryllis macrophthalma	*Dynamenella australis*	*Burnupena pubescens*	*Eunice aphroditois*
Ampelisca palmata	*Dynamenella huttoni*	*Helcion dunkeri*	*Lepidonotus semitectus clava*
Atylus swammerdamei	*Exosphaeroma pallidum*	*Gibbula multicolor*	*Lumbrineris tetrauna*
Hyale grandicornis	*Tylos capensis*	*Oxystele variegata*	*Scololepis squamata*
Leucothoe spinicarpa	*Jaeropsis paulensis*	*Siphonaria concinna*	*Naineris laevigata*
Lysianassa ceratina	*Synidotea variegata*	*Tricolia capensis*	*Notomastus latericeus*
Metaleptamphopus membrisetata	*Exosphaeroma porrectum*	*Tricolia neritina*	*Pseudonereis variegata*
Paramoera capensis	*Isopoda species A*	*Gastropoda species A*	*Lysidice natalensis*
Parandania boecki	*Isopoda species B*		*Arabella iricolor*
Phistica marina		**Bivalves**	*Polychaeta species A*
Nicippe tumida	**Chitons**	*Mytilus galloprovincialis*	*Polychaeta species B*
Amphipoda species A	*Onithochiton literatus*	*Perna perna*	
	Acanthochiton garnoti	*Choromytilus meridionalis*	
	Chitonidae species A		

Surfarce area

A significant positive correlation (p = 0.000003) was found between surface area and weight of surface film (r-exp = 0.576) and r-calc = 0.94562 (r-calculated > r- expected). A regression equation (y = 5.2281x + 0.0607) (**Fig 4.2**) was obtained for the relationship between surface of algae and weight of surface film and this equation was used to calculate the surface area of the algae at the end of the experiment.

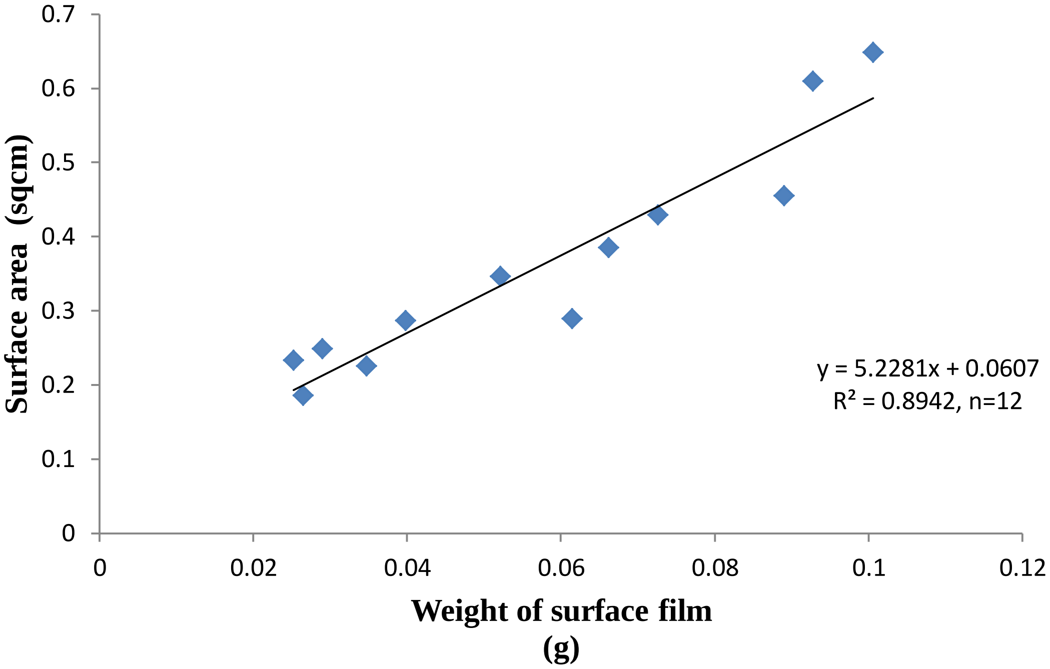

Figure 4.2: Relationship between surface area and weight of surface film.

A three-way nested ANOVA (**Table 4.2**) showed that upwelling, site, treatment and their interactions had no significant effects ($p>0.05$) on sea weed surface area.

Table 4.2: Factorial ANOVA summary of results for surface area at the end of the experiment.

Effect	Effect	df	MS	F	p
Intercept	Fixed	1	7684.57	35.28	0.15
Upwelling	Fixed	1	1094.71	4.51	0.28
Site(Upwelling)	Random	1	242.95	3.84	0.06
Treatment	Fixed	3	9.33	0.25	0.86
Upwelling*Treatment	Fixed	3	96.12	1.52	0.22
Site*Treatment	Random	3	38.03	0.60	0.62
Error		51	63.19		

Correlation (Surface area, dry weight and algal cover)

A significant positive correlation ($p = 0.0001$, $r = 0.9289$) was found between surface area and dry weight. A regression equation ($y = 5.5002x + 3152.8$) (**Fig 4.3**) was obtained for the relationship between surface area of algae and dry weight. Surface area was significantly correlated to dry weight but neither surface area nor dry weight was correlated to algal cover ($p>0.05$ in both cases).

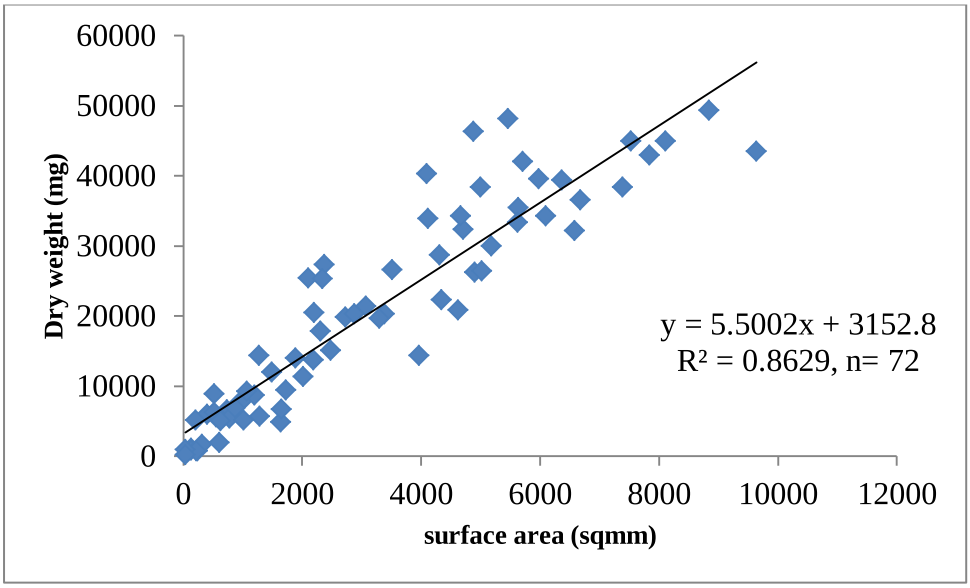

Figure 4.3: Relationship between algal surface area and dry weight.

Algal cover

Beginning of experiment

Algal cover calculated from photographs taken at the beginning of the experiment showed no significant differences among treatments at all four sites (**Table 4.3** and **Fig 4.4**). This confirms that all the treatments had equivalent algal cover at the onset of the experiment (p>0.05).

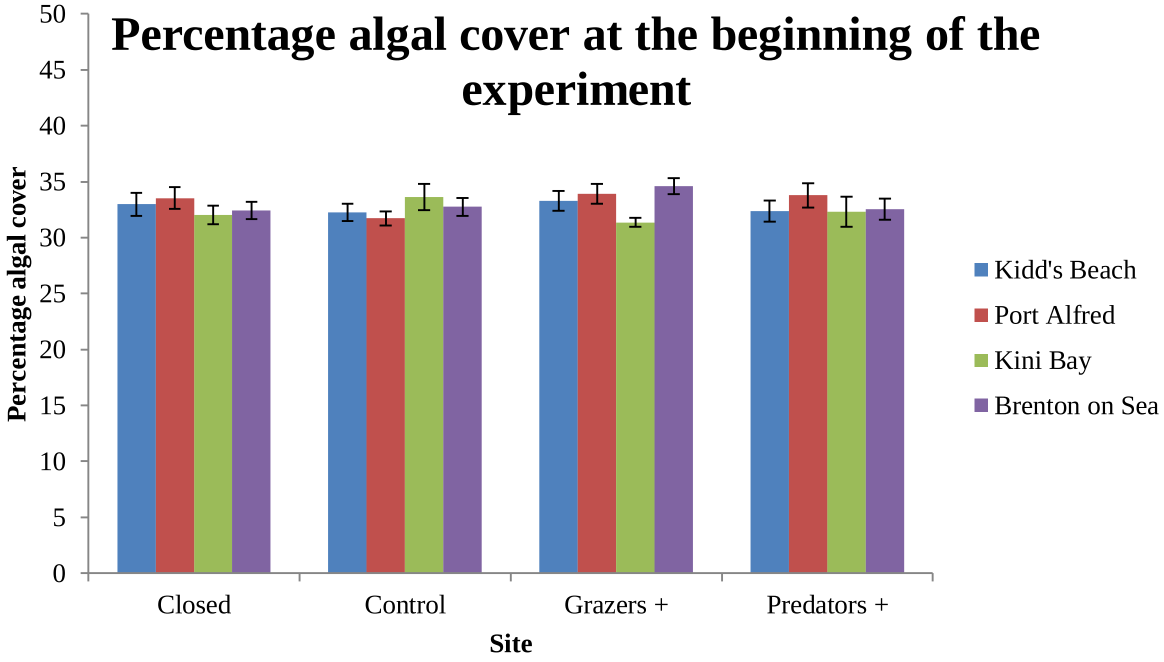

Figure 4.4: Algal cover of different treatments at all four sites (Kidd's Beach, Port Alfred, Kini Bay and Brenton on Sea) at the start of the experiment. Values are means plus/minus standard deviation.

Table 4.3: Factorial ANOVA, summary of results for algal cover at the beginning of the experiment.

Effect	Effect	d.f	MS	F	p
Intercept	Fixed	1	86310.1	38087.8	0.07
Upwelling	Fixed	1	8.13	29.44	0.12
Site(Upwelling)	Random	1	0.28	0.07	0.79
Treatment	Fixed	3	0.89	0.15	0.92
Upwelling*Treatment	Fixed	3	7.94	1.97	0.13
Site*Treatment	Random	3	6.02	1.49	0.22
Error		67	4.03		

Changes in algal cover throughout the course of the experiment in the Closed, Control, Grazer + and Predator + treatments are shown in (**Figs 4.5, 4.6, 4.7 and 4.8** respectively). These changes may have been partly due to seasonal effects as plots that were protected from grazing (i.e. Closed treatments) had reduced algal cover from July till September, with increasing algal cover in the months of November up until January. Algal cover in the other plots will reflect a combination of seasonality with grazing or other effects.

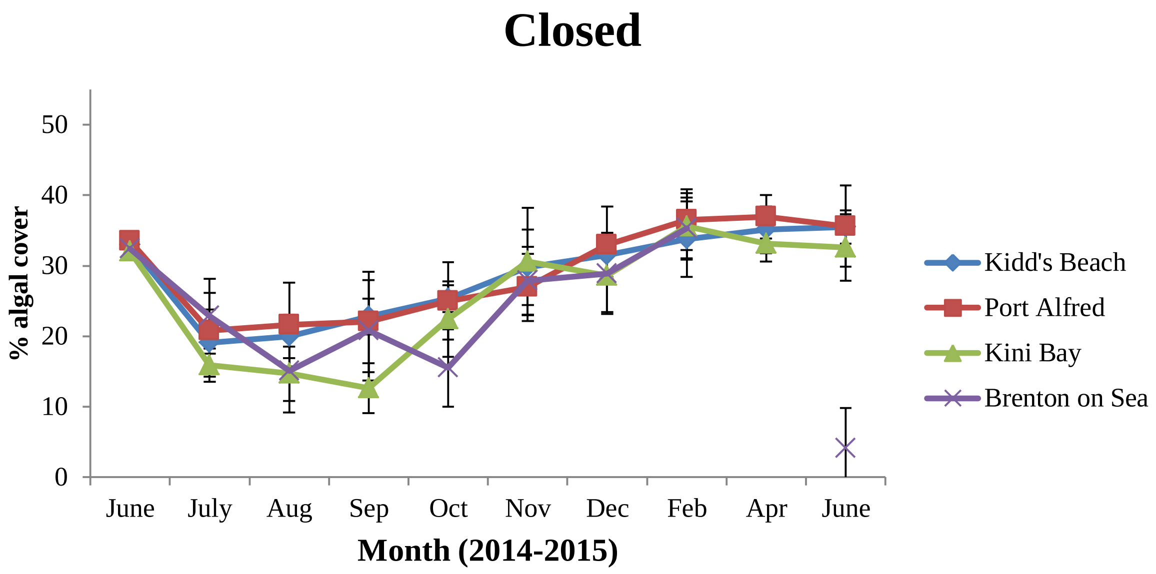

Figure 4.5: Mean percentages of algal cover in the Closed plots. Values are means plus/minus standard deviation.

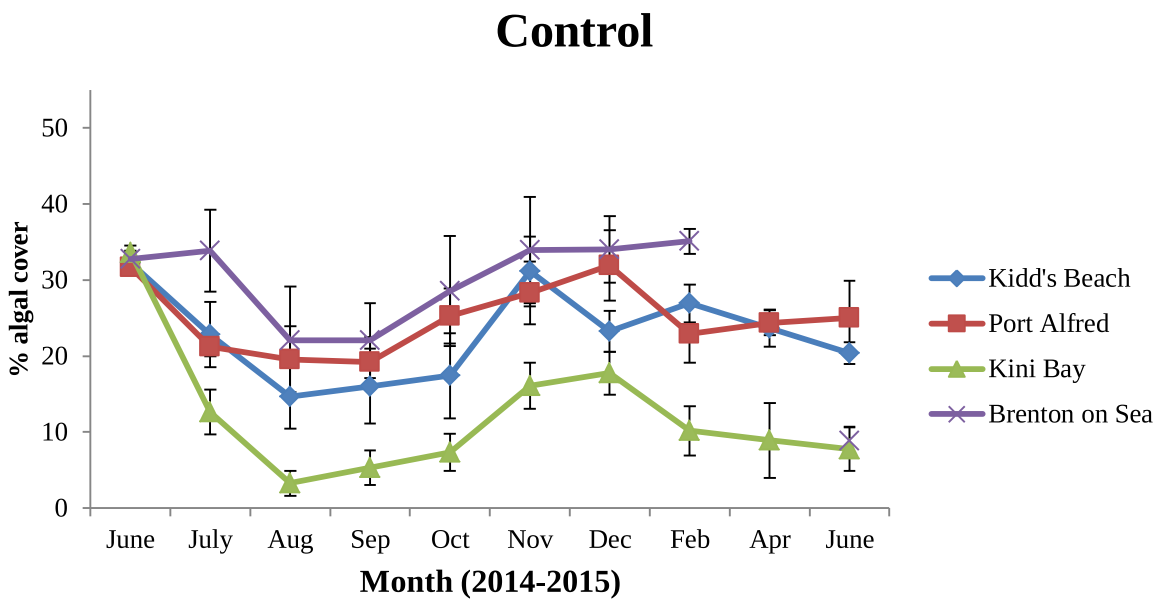

Figure 4.6: Mean percentages of algal cover in the Control plots. Values are means plus/minus standard deviation.

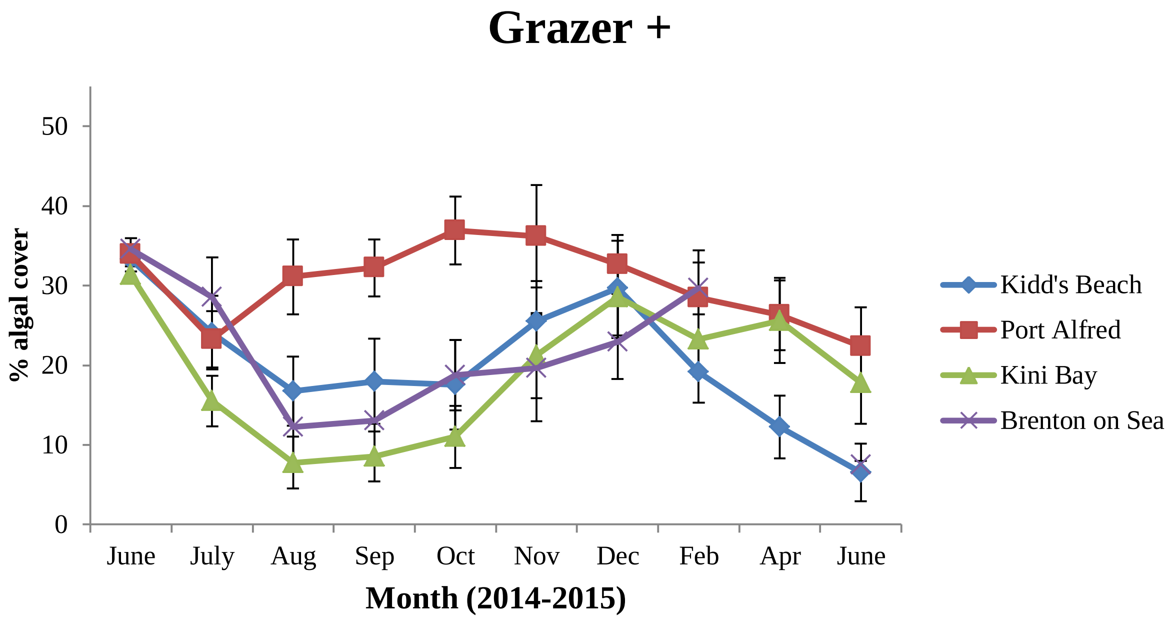

Figure 4.7: Mean percentages of algal cover in the Grazer + plots. Values are means plus/minus standard deviation.

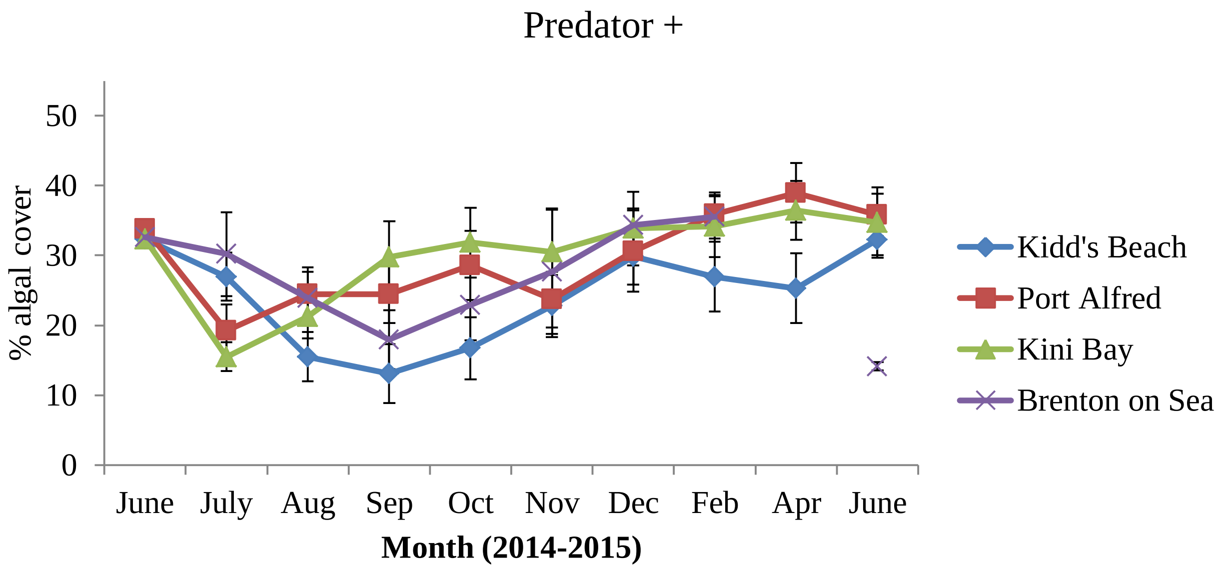

Figure 4.8: Mean percentages of algal cover in the Predator + plots. Values are means plus/minus standard deviation.

From the trend of the change in algae cover, no clear cut differences were observed between upwelling and non-upwelling sites. An influence of treatment can be seen as plots that excluded grazers had more algal cover than the plots that allowed gazers to come in. The site at Brenton on Sea was inundated with sand between February and March (data missing for April), so for the analysis, algal cover for the month of February was used in a three-way nested ANOVA (**Table 4.4**). Upwelling, site nested in upwelling and treatment had no significant effect (p>0.05) but the interaction of treatment with upwelling and site had significant effects on algal cover (p<0.05).

Table 4.4: Factorial ANOVA summary of results for algal cover for the month of February 2015.

Effect	Effect	df	MS	F	p
Intercept	Fixed	1	66815.5	330.54	0.00
Upwelling	Fixed	1	50.75	0.65	0.57
Site(Upwelling)	Random	1	78.61	2.27	0.14
Treatment	Fixed	3	618.7	3.91	0.15
Upwelling*Treatment	Fixed	3	197.2	5.68	**0.00**
Site*Treatment	Random	3	158.23	4.56	**0.01**
Error		67	34.7		

Post hoc (Tukey HSD) tests indicated that there were significant differences among treatments ($p<0.05$) within each site. Percentage algal cover was significantly different among sites (post hoc, $p < 0.05$) and in terms of treatment but upwelling had less influence on algal cover with no significant effect. At all sites, the Grazer + and Control treatments showed no significant differences indicating that there was no artefact due to the treatment. These two treatments had lower algal cover than Predator + and Closed (post hoc, $p < 0.05$), which did not differ from one another (post hoc $p > 0.05$, **Fig 4.9**) i.e. Grazer + = Control < Predator+ = Closed. This trend was observed at all four sites. The interaction of upwelling and treatment resulted from a minor difference in the effect of treatment. At upwelling sites, the Closed treatment differed significantly from Control and Grazer +, while at non-upwelling sites, the difference was non-significant (**Fig 4.9**, post hoc), algal cover in the Grazer + and Control plots was similar in the upwelling and non-upwelling sites and this might be due to the fact that upwelling sites had significantly higher densities of grazers (chapter 3, **Table 3.3)**, which might have exerted pressure on the algae. Site had a significant effect on algal cover (post hoc, $p < 0.05$, **Fig 4.10**) with Kidd's Beach similar to Port Alfred and Kini Bay but Brenton on Sea having significantly higher cover than the first two.

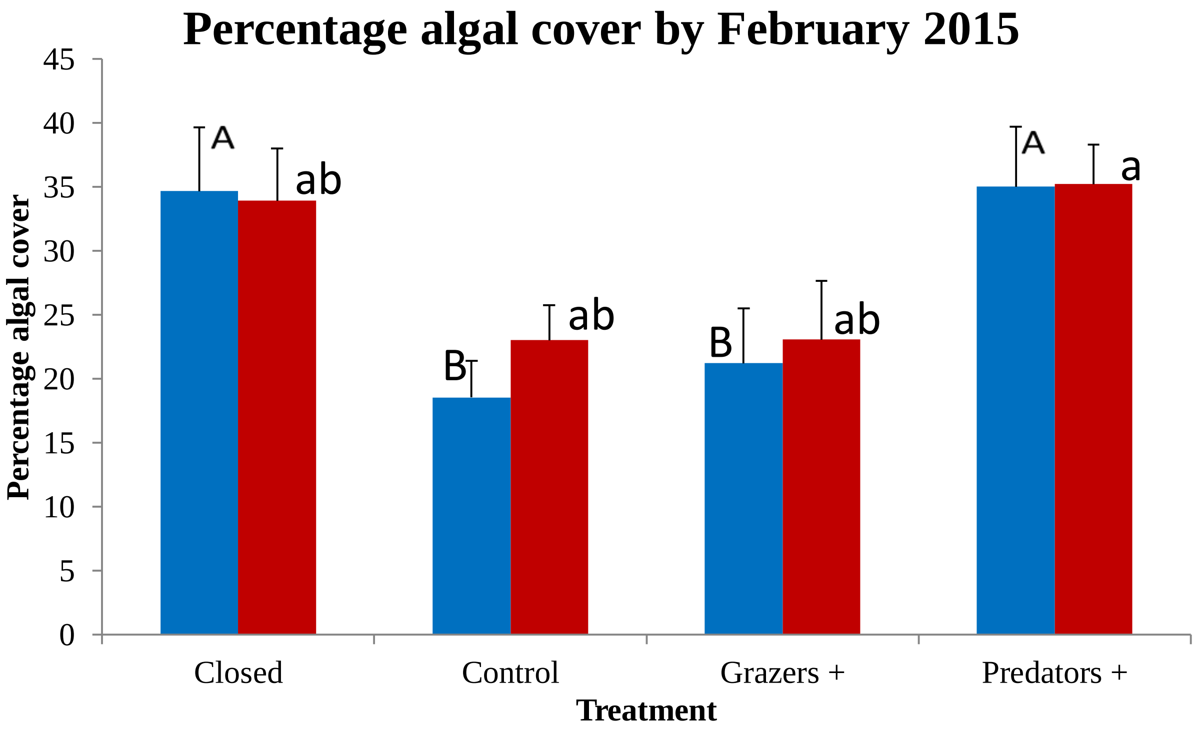

Figure 4.9: Mean algal cover of different treatments for upwelling sites in blue (Port Alfred and Brenton on Sea) and non-upwelling, sites in red (Kidd's Beach and Kini Bay). Homogenous groups are indicated by uppercase letters for upwelling and lower case letters for non-upwelling sites.

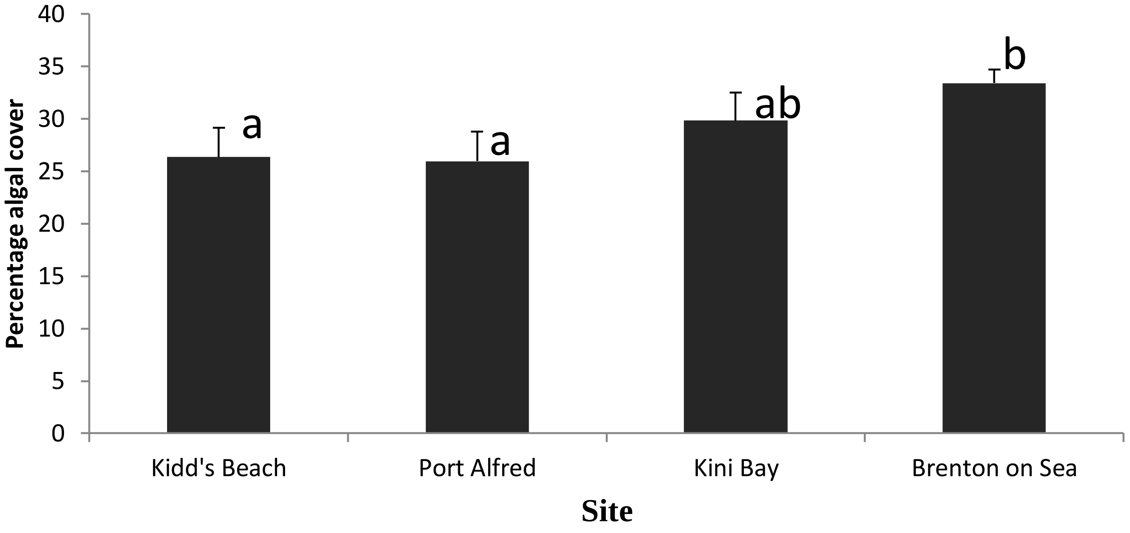

Figure 4.10: Mean algal cover of different sites (Kidd's Beach and Kini Bay, Port Alfred and Brenton on Sea) for the month of February, treatments pooled. Letters indicate homogenous groups ($p < 0.05$).

Epifaunal community structure

Unlike algal cover, epifaunal data are from samples collected at the end of the experiment in June 2015.

(i) Non-normalised data

The dendrogram in **Fig 4.11**, based on the original data for epifaunal abundances suggests that site had an influence on epifaunal community structure with a clear frequent grouping in terms of site. There was no grouping in terms of upwelling or treatment, suggesting that treatment and upwelling had no influence on community structure of epifaunal communities.

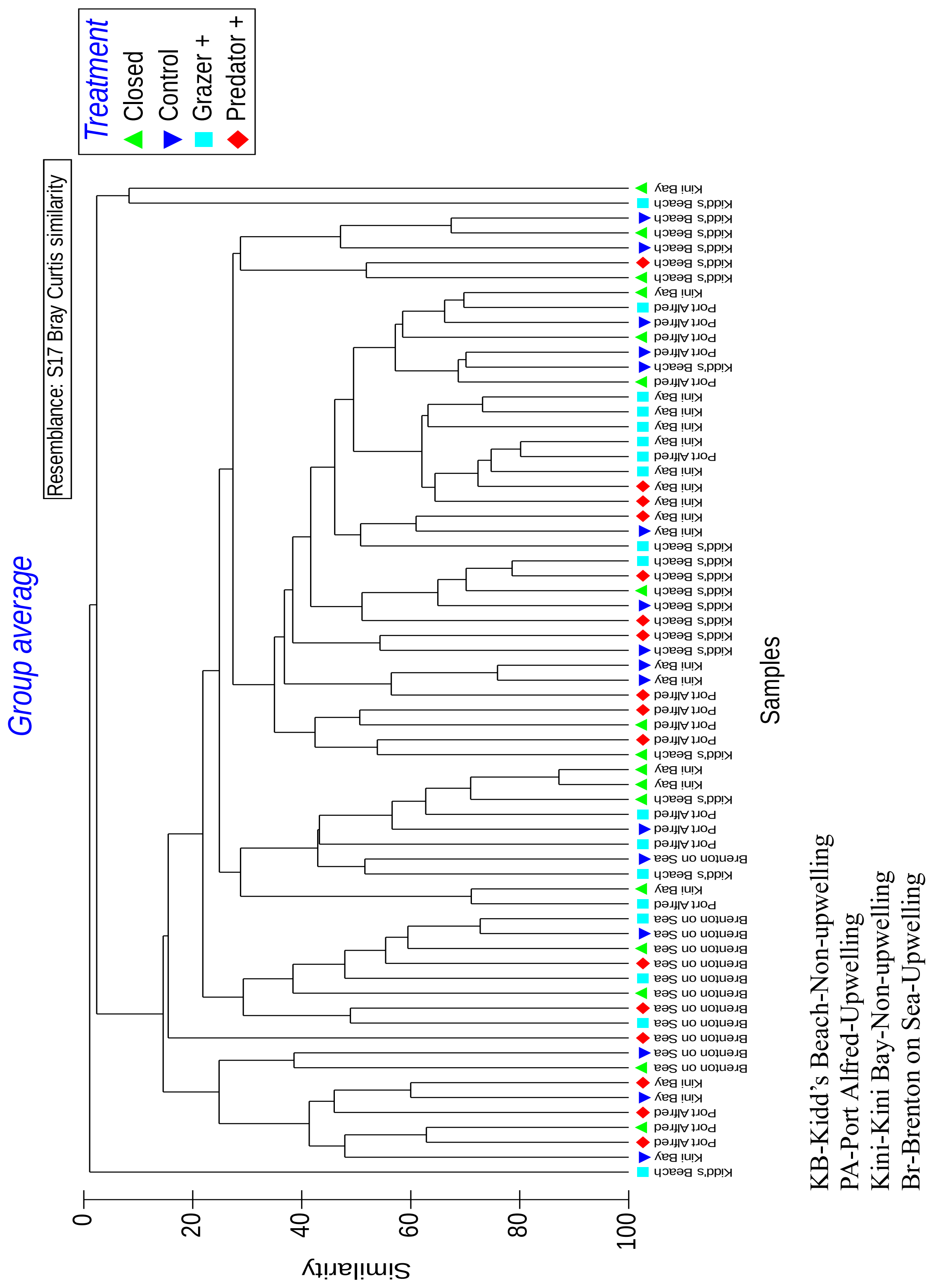

Figure 4.11: Results of classification analysis of epifaunal communities based on Bray Curtis matrix. Site names are given and symbols indicate treatments.

PERMANOVA based on the Bray Curtis matrix indicated a significant difference among sites (p = **0.0001**, **Table 4.5**). This showed that site had a strong influence on the community structure of epifaunal communities.

Table 4.5: PERMANOVA table of results; influence of upwelling, site and treatment and interactions on community structure of epifaunal communities.

Source	df	SS	MS	Pseudo-F	P(perm)	Unique perms	P(MC)
Up	1	15356	15356	1.0356	0.5039	6	0.4361
Tr	3	7473.8	2491.3	0.94436	0.5687	9885	0.5728
Si(Up)	2	30172	15086	6.2262	**0.0001**	9900	**0.0001**
UpxTr	3	8478.3	2826.1	1.0713	0.3957	9901	0.385
Si(Up)xTr	6	15855	2642.5	1.0906	0.2632	9823	0.2836
Res	56	1.36E+05	2423				
Total	71	2.10E+05					

Upwelling

The lack of effect of upwelling is brought out in an nMDS plot, which has an acceptable stress level (stress= 0.18). There is an overlap between upwelling and non-upwelling sites, showing lack of grouping. The nMDS plot (**Fig 4.12**) shows that there was no difference between upwelling and non-upwelling shores in terms of epifaunal composition.

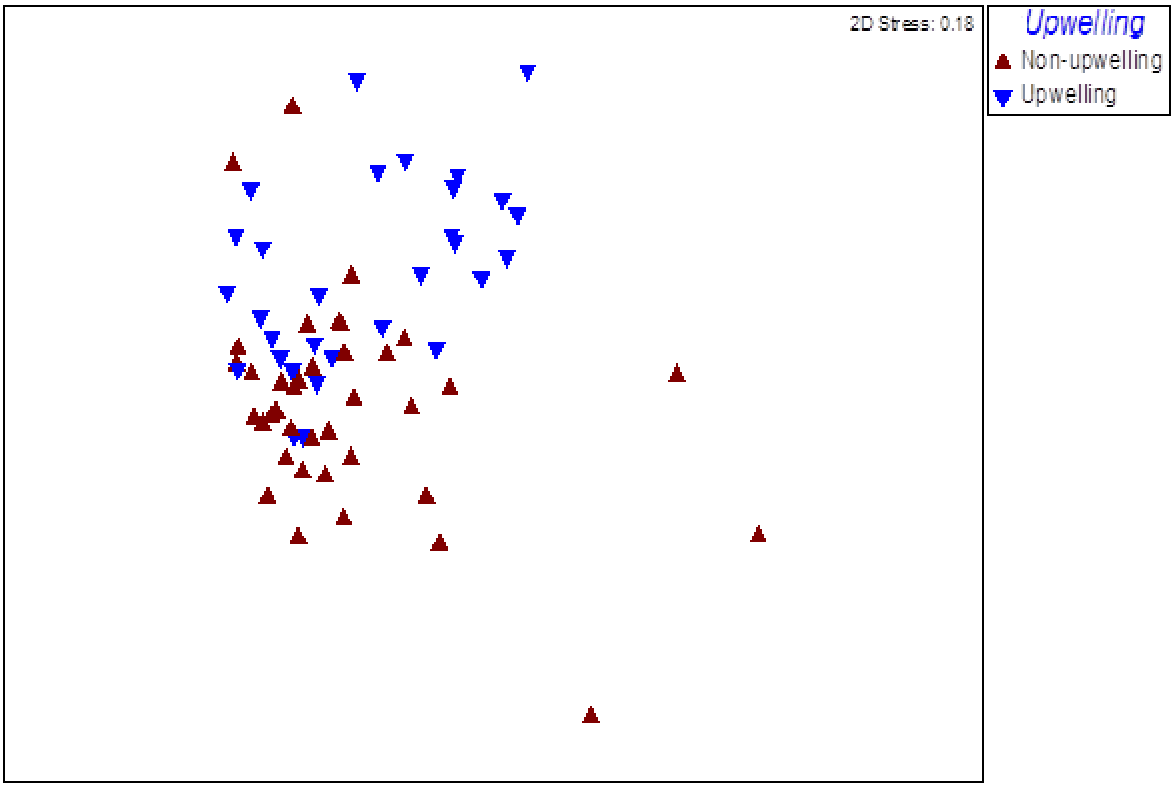

Figure 4.12: Non-metric Multi-Dimensional Scaling plot showing lack of difference between upwelling and non-upwelling sites in terms of epifaunal composition.

Site

The influence of site (nested in upwelling) on community structure (**Table 4.5**) is visualised in **Fig 4.13**, which shows clearly the grouping of sites, thus showing that there is more similarity in terms of location, with samples collected from the same location being similar. Kidd's Beach, a non-upwelling site is represented by the green dots starting from below with a slight overlap with Kini Bay, the other non-upwelling site, which also overlaps with Port Alfred in the middle, while Brenton is virtually on its own, represented by red dots. There is more or less an arc from Kidd's Beach (the most northerly site) to Brenton on Sea (the most southerly site) with an upwelling/non-upwelling overlap being between Port Alfred and Kini Bay, which are the two central sites. This appears to be an effect of geography, rather than proximity, as the two sites that physically are closest together are Port Alfred and Kidd's Beach.

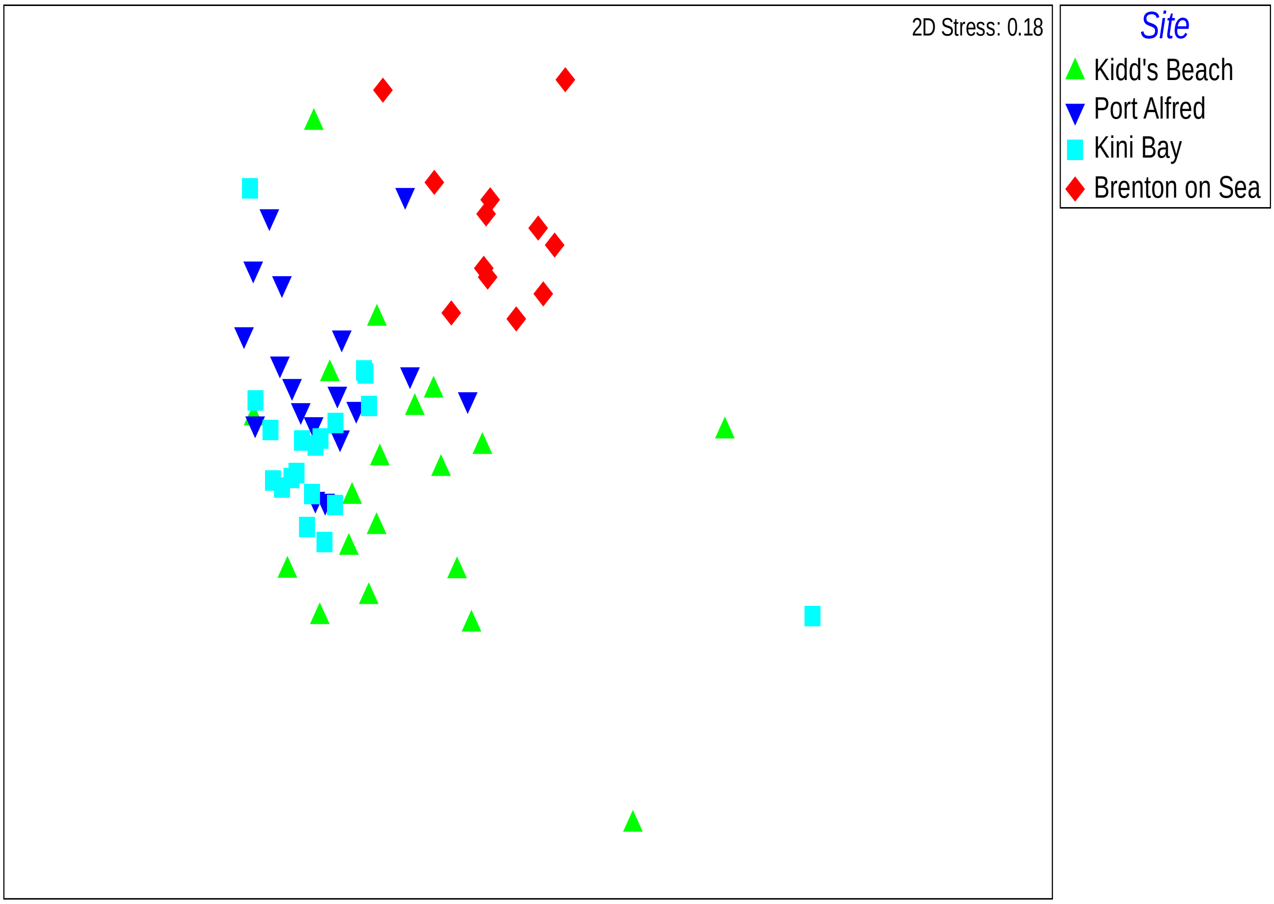

Figure 4.13: Non-metric Multidimensional Scaling (MDS) showing the influence of site on community structure of epifaunal communities.

Treatment

Treatment had no influence on community structure (**Table 4.5**) with no grouping in terms of treatment in the nMDS plot (**Fig 4.14**). There appeared to be mixed grouping with no clear separation/grouping of similar treatments as shown also by the dendrogram (**Fig 4.11**).

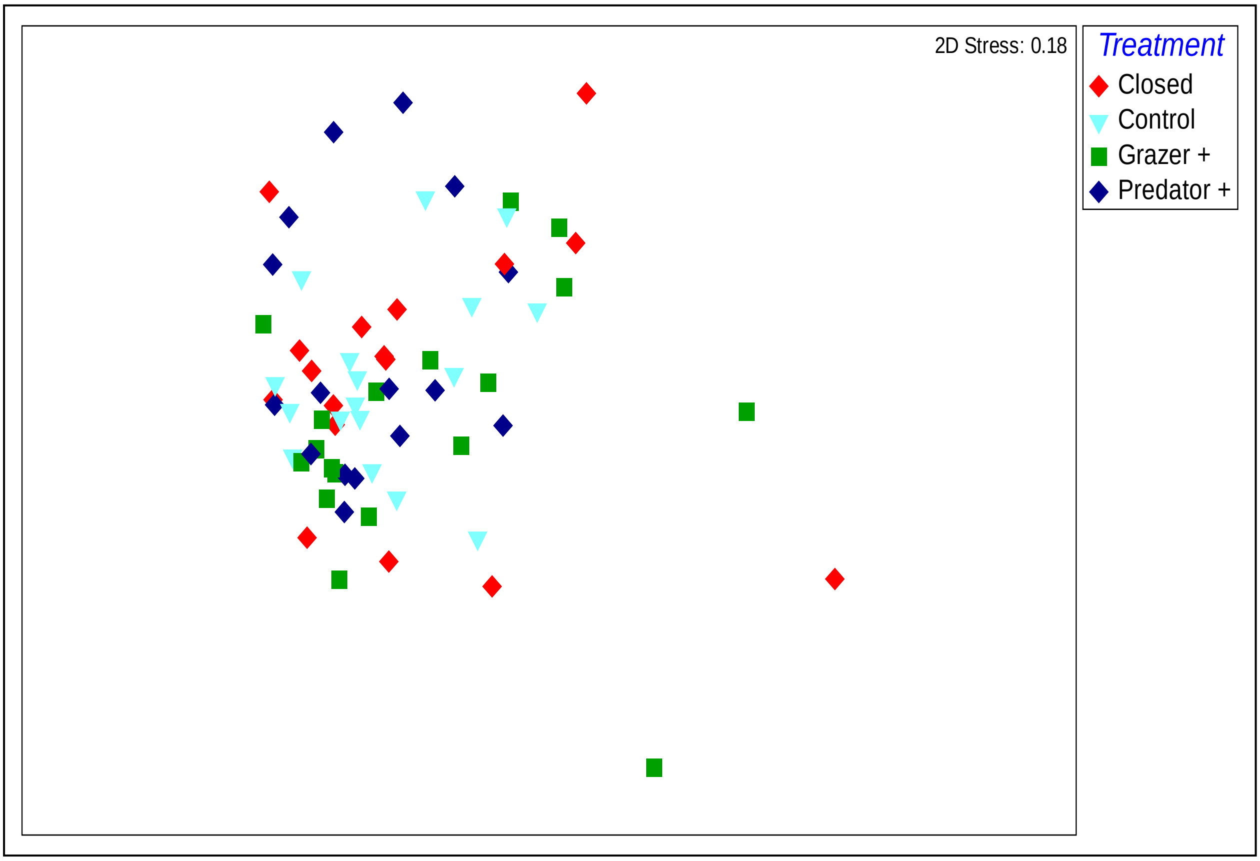

Figure 4.14: nMDS illustrating the lack of differences in the structure of epifaunal communities subject to different treatments.

SIMPER Analysis

A SIMPER analysis in PRIMER 6 was used to assess the differences among sites. Based on the Bray-Curtis similarity measures a breakdown of differences in percentage among sites was observed. All four study sites were different from each other in terms of species composition (p= **0.0001**); **Table 4.6** shows percentage dissimilarities among sites in terms of species composition. More than 60% dissimilarity in species composition was seen for all sites, with Kini Bay and Port Alfred being least (66.32%) and Brenton on Sea and Kidd's Beach most (85.73%) dissimilar. These high dissimilarities clearly show that all study sites were different from each other in terms of epifaunal community structure. .

Table 4.6: Percentage dissimilarities in species composition among sites.

	Kidd's Beach	Port Alfred	Kini Bay	Brenton on Sea
Kidd's Beach				
Port Alfred	75.47			
Kini Bay	74.03	66.32		
Brenton on Sea	85.73	83.41	84.82	

(ii) Normalised to surface area

The dendrogram in **Fig 4.15** suggests that upwelling and treatment had no influence on epifaunal community structure when normalised for surface area of sea weed. There was no clear cut grouping of upwelling vs non-upwelling but there was some grouping by site as indicated by the Permanova analysis (**Table 4.7**).

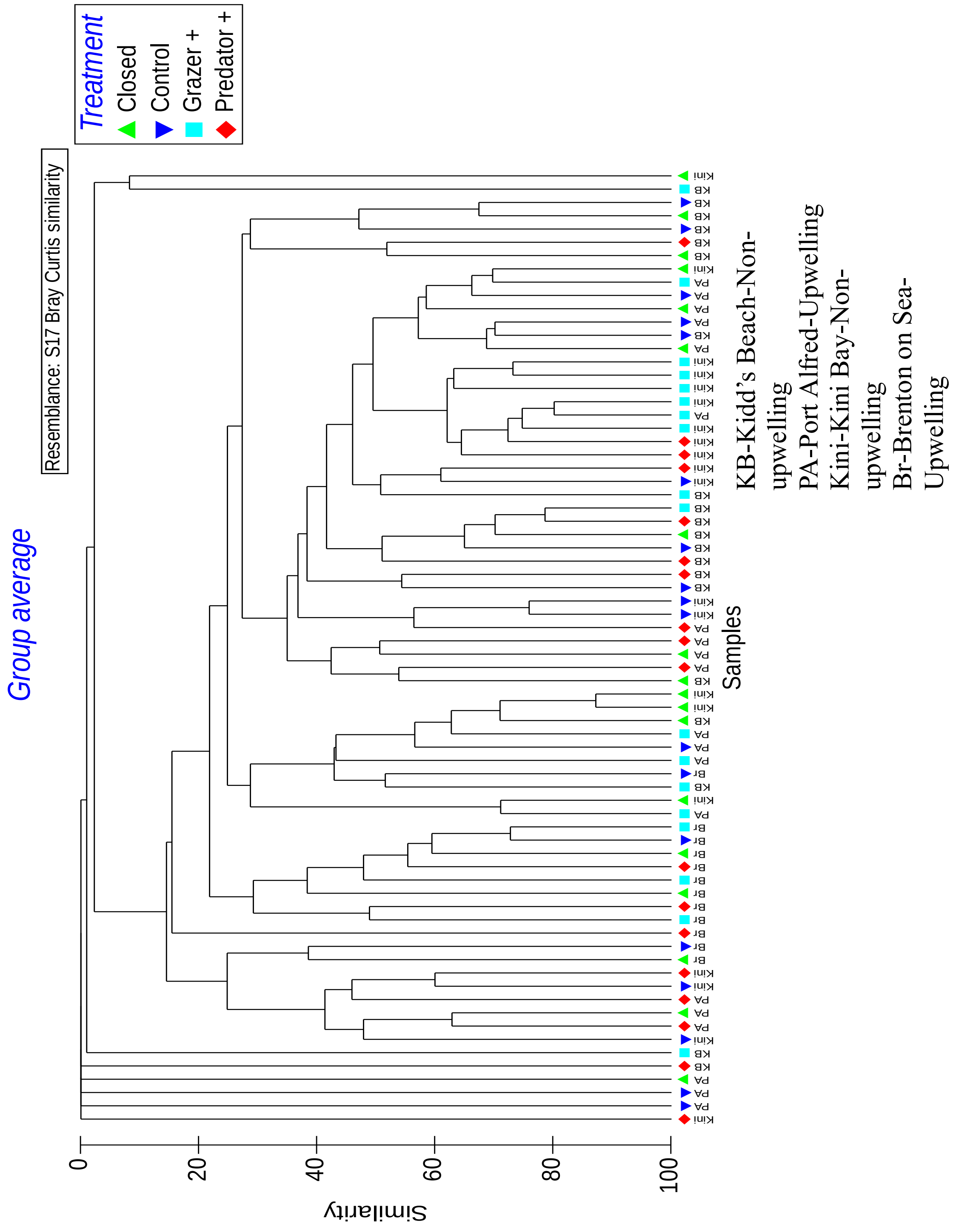

Figure 4.15: Results of classification analysis of epifaunal communities based on Bray Curtis matrix showing the influence of upwelling, site (names given) and treatment (symbols) on the abundance of individual species per cm² in epifaunal communities.

Data on the surface area of algae in each plot were used to normalise the abundances of each epifaunal species to surface area (cm²) of sea weed and this was used to derive a normalised Bray Curtis similarity matrix. This matrix was used to test the effects of treatment, upwelling and site using a type III PERMANOVA with 9999 permutations in PRIMER 6.The results were the same as for the non-normalised data (**Table 4.5**), there was no effect of upwelling and treatment though again there was a significant effect of treatment (p=**0.0001**, **Table 4.7**).

Table 4.7: PERMANOVA table of results; influence of upwelling, site and treatment and interactions on community composition when this was normalised to individual epifaunal species per cm² of sea weed.

Source	df	SS	MS	Pseudo-F	P(perm)	Unique perms	P(MC)
Up	1	10178	10178	0.94186	0.5017	6	0.5225
Tr	3	9332.3	3110.8	0.9588	0.5292	9911	0.5373
Si(Up)	2	21952	10976	4.1322	**0.0001**	9873	**0.0001**
UpxTr	3	8951.7	2983.9	0.9197	0.5593	9927	0.6022
Si(Up)xTr	6	19540	3256.7	1.2261	0.0831	9817	0.0988
Res	56	1.49E+05	2656.2				
Total	71	2.17E+05					

Upwelling had no influence on the epifaunal community when the data were normalised to surface area; the dendrogram (**Fig 4.15**) and the nMDS plot (**Fig 4. 16**) show little grouping of upwelling vs non upwelling and considerable overlap, showing that there is no significant difference between upwelling and non-upwelling sites.

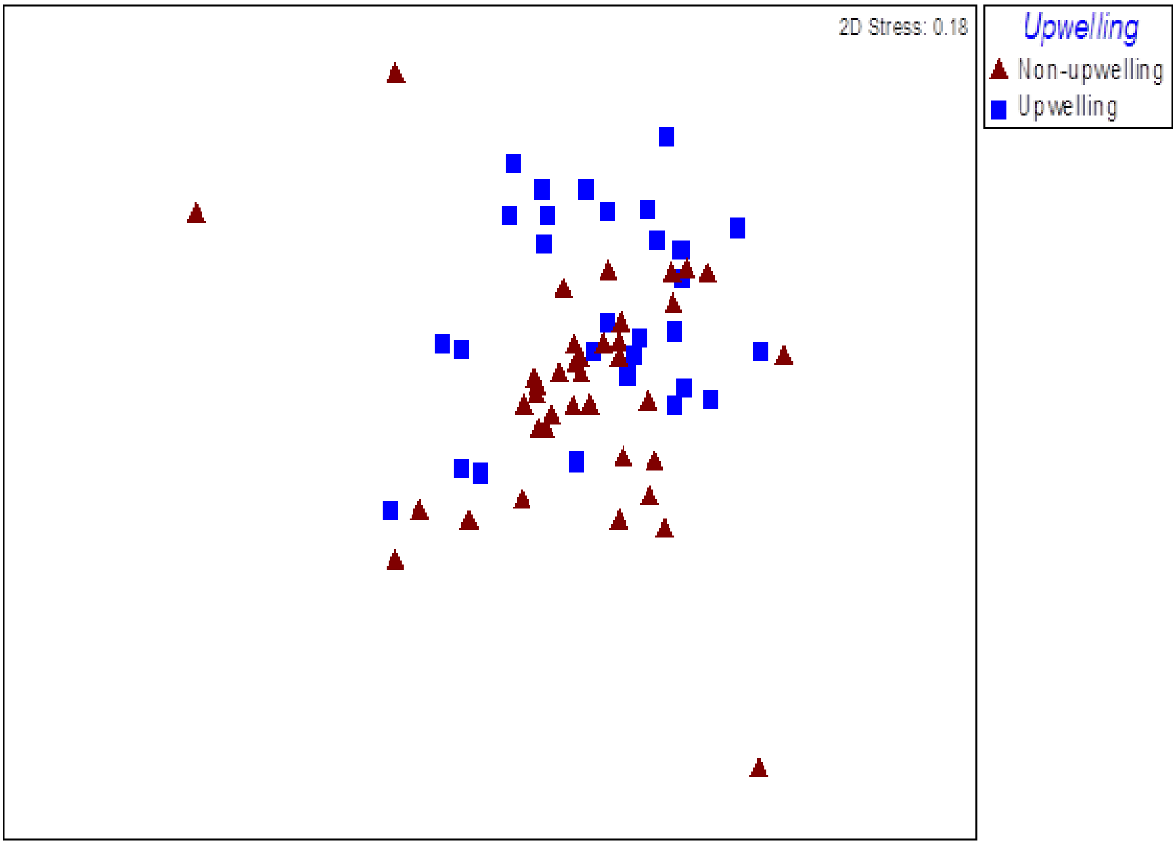

Figure 4.16: Non-metric Multidimensional Scaling plot showing lack of difference in epifaunal community structure with respect to upwelling when data are normalised to surface area of sea weed.

Treatment had no influence on the abundance of each individual epifaunal species per cm² of sea weed, the nMDS plot clearly shows no grouping in terms of treatment (**Fig 4.17**).

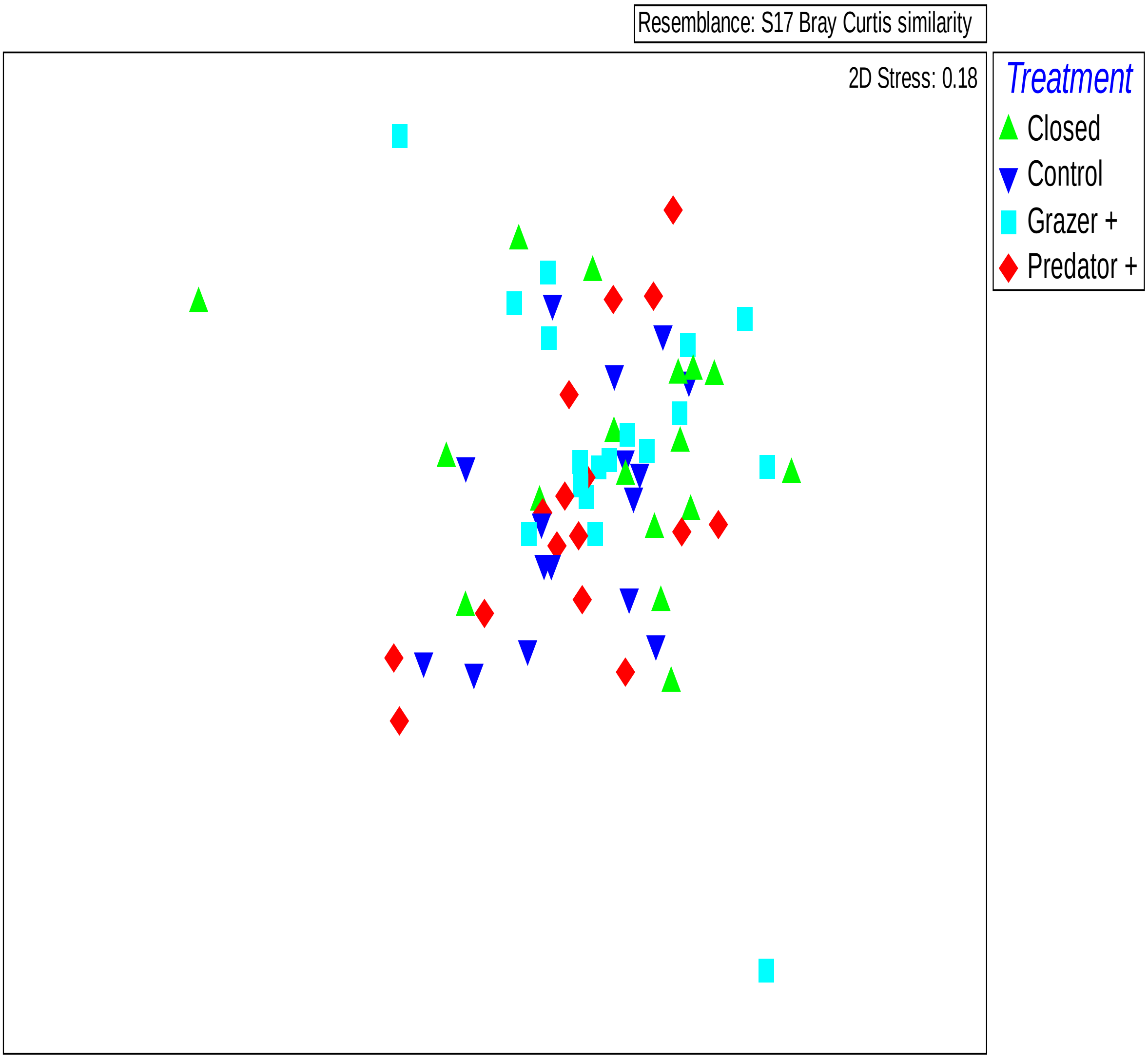

Figure 4.17: Non-metric Multidimensional Scaling plot showing lack of difference in epifaunal community structure with respect to treatment when data are normalised to surface area of sea weed.

Site had a significant influence on the epifaunal community when normalised to cm² of sea weed. The nMDS plot (**Fig 4.18**) shows the degree of grouping of samples by sites, thus showing that samples collected from the same location tend to be similar although this effect is less clear than for the non-normalised data (**Fig 4.11**). Kidd's Beach, a non-upwelling site is represented by the green dots starting from below with a slight overlap with Kini Bay the other non-upwelling site which also overlaps with Port Alfred in the middle and Brenton again on its own represented by red dots.

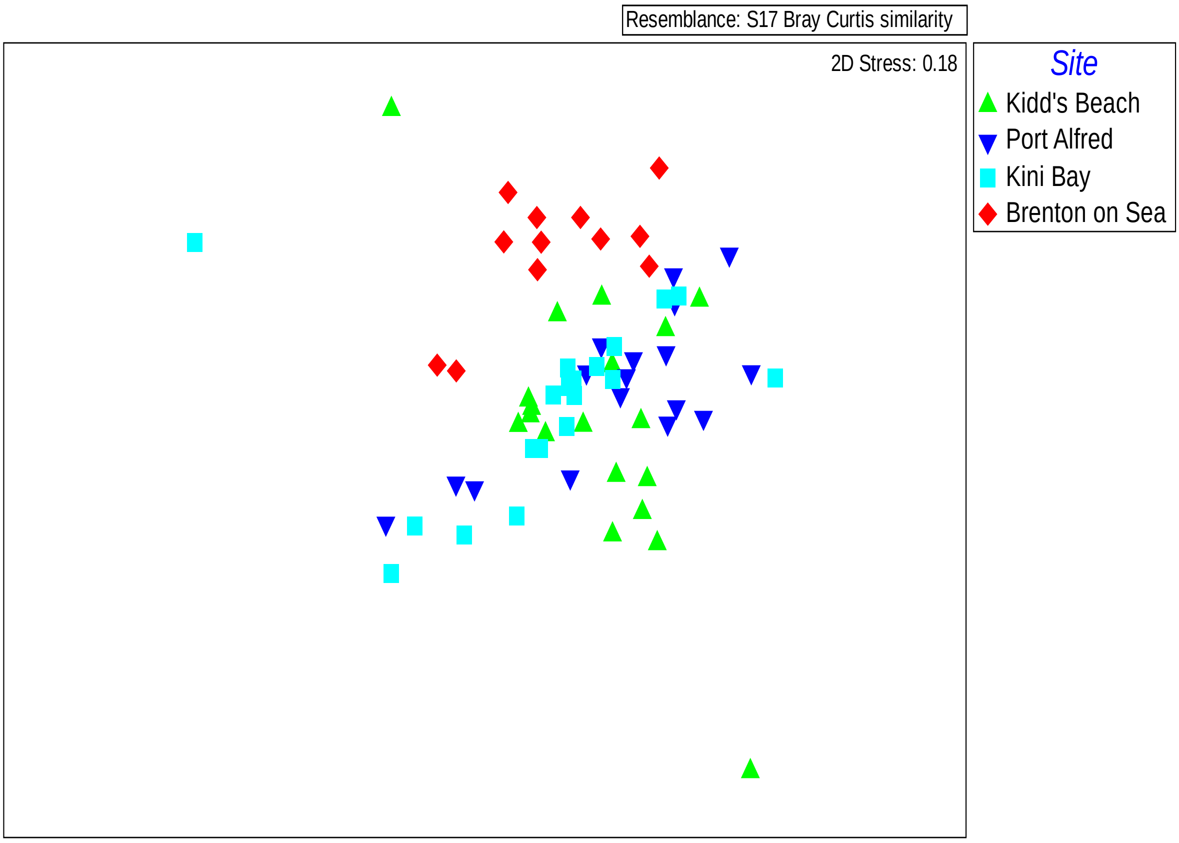

Figure 4.18: non-metric Multidimensional Scaling plot showing differences among sites due to the abundance of each individual epifaunal species per cm² of sea weed.

A SIMPER analysis in PRIMER 6 was used to assess the percentage differences among sites based on the abundances of species of epifauna per cm² of sea weed (**Table 4.8).** In all cases, sites differed by >70%, clearly showing that all study sites were different from each other in terms of the abundance of individual species of epifauna per cm² of sea weed and the pattern was the same as for the non-normalised data. As for the non-normalised data (Table 4.7), the separation of Brenton on Sea from the other sites visible in Fig 4.18 comes out clearly in this analysis.

Table 4.8: Dissimilarity percentages of sites due to abundance of individual species of epifauna per cm² of sea weed (Kidd’s Beach, Port Alfred, Kini Bay and Brenton on Sea).

	Kidd's Beach	Port Alfred	Kini Bay	Brenton on Sea
Kidd's Beach				
Port Alfred	79.71			
Kini Bay	77.57	76.04		
Brenton on Sea	83.08	83.93	81.03	

(iii) Normalised to cover

When epifaunal abundances were normalised to algal cover, the results were the same as when normalised to surface area, with site having the only significant effect (p=**0.0001**, **Table 4.9**).

Table 4.9: PERMANOVA table of results; influence of upwelling, site and treatment and interactions on community structure when this was normalised to algal cover

Source	df	SS	MS	Pseudo-F	P(perm)	Unique perms	P(MC)
Up	1	6271.5	6271.5	0.63056	0.8351	6	0.7766
Tr	3	8185.8	2728.6	1.0055	0.4826	9903	0.4693
Si(Up)	2	20183	10091	3.4027	**0.0001**	9904	**0.0001**
UpxTr	3	9818.7	3272.9	1.2061	0.2759	9916	0.2615
Si(Up)xTr	6	16250	2708.3	0.91324	0.6631	9839	0.6468
Res	56	1.66E+05	2965.6				
Total	71	2.24E+05					

Total abundances

(i) Total number of epifauna

Upwelling and treatment had no influence on the total epifaunal numbers in each plot but site had a significant influence (p=**0.03322, Table 4.10**). All sites were different from each other (post hoc, $p < 0.05$ in all cases).

Table 4.10: Factorial ANOVA summary of results for the total number of epifauna in each plot.

Effect	Effect	df	MS	F	p
Intercept	Fixed	1	519541	30.39	0.11
Upwelling	Fixed	1	67448.4	3.99	0.3
Site(Upwelling)	Random	1	16889.2	4.79	**0.03**
Treatment	Fixed	3	3487.3	0.93	0.52
Upwelling*Treatment	Fixed	3	9418.7	2.67	0.06
Site*Treatment	Random	3	3729.7	1.06	0.38
Error		51	3525.6		

(ii) Normalised to cover

Upwelling and site had no significant influence but treatment had a significant influence (p=**0.0206**, **Table 4.11**) when total epifaunal abundance was normalised to algal cover. Closed and Predator + plots were not significantly different from each other and nor were the Control and the Grazer + plots, but the Control and Grazer + plots were different from the Predator + and Closed plots (**Fig 4.19**, Control = Grazer + ≠ Predator + = Closed, post hoc).

Table 4.11: Factorial ANOVA summary of results for data normalised per algal cover in each plot.

Effect	Effect	df	MS	F	p

Intercept	Fixed	1	336.32	22.47	0.08
Upwelling	Fixed	1	6.8128	11.54	0.18
Site(Upwelling)	Random	1	0.5903	0.15	0.7
Treatment	Fixed	3	38.5508	17.71	**0.02**
Upwelling*Treatment	Fixed	3	1.8634	0.47	0.7
Site*Treatment	Random	3	2.1767	0.55	0.65
Error		51	3.9302		

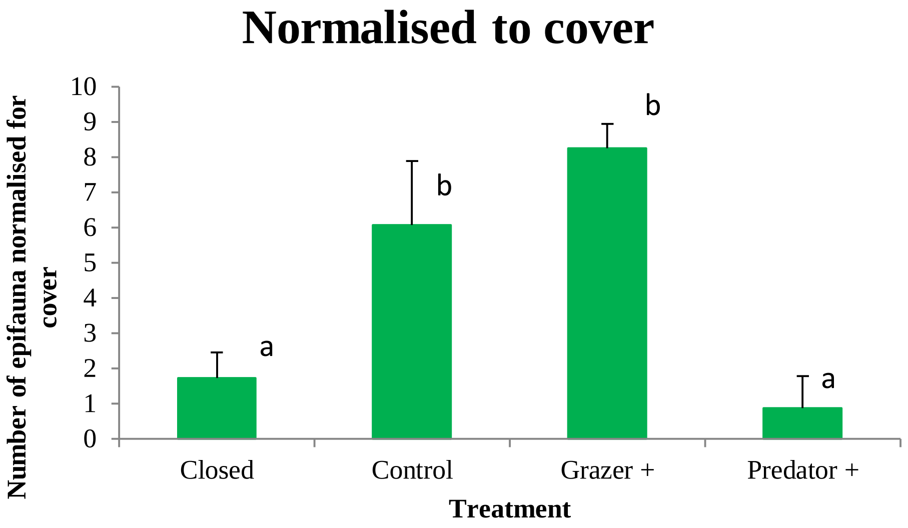

Figure 4.19: Mean number of epifauna normalised to algal cover among treatments, treatments pooled. Letters indicate homogenous groups ($p < 0.05$).

(iii) Normalised to area

Upwelling and site had no significant influence but treatment had a significant influence (p=**0.0213**, **Table 4.12**) when data were normalised for surface area. Closed, Control and Predator + plots were not significantly different from each other, but Closed and Predator + were significantly different from the Grazer + plots except that the Control and Grazer + plots were not different from each other (**Fig 4.20**, Control = Grazer +, Control = Predator + = Closed, Grazer + ≠ Closed = Predator +, post hoc).

Table 4.12: Factorial ANOVA summary of results for data normalised for algal surface area of each plot.

Effect	Effect	df	MS	F	p
Intercept	Fixed	1	4958.37	28.19	0
Upwelling	Fixed	1	257.798	1.47	0.23
Site(Upwelling)	Random	1	2.8	0.02	0.9
Treatment	Fixed	3	612.672	3.48	**0.02**
Upwelling*Treatment	Fixed	3	366.281	2.08	0.11
Site*Treatment	Random	3	110.726	0.63	0.6
Error		51	175.887		

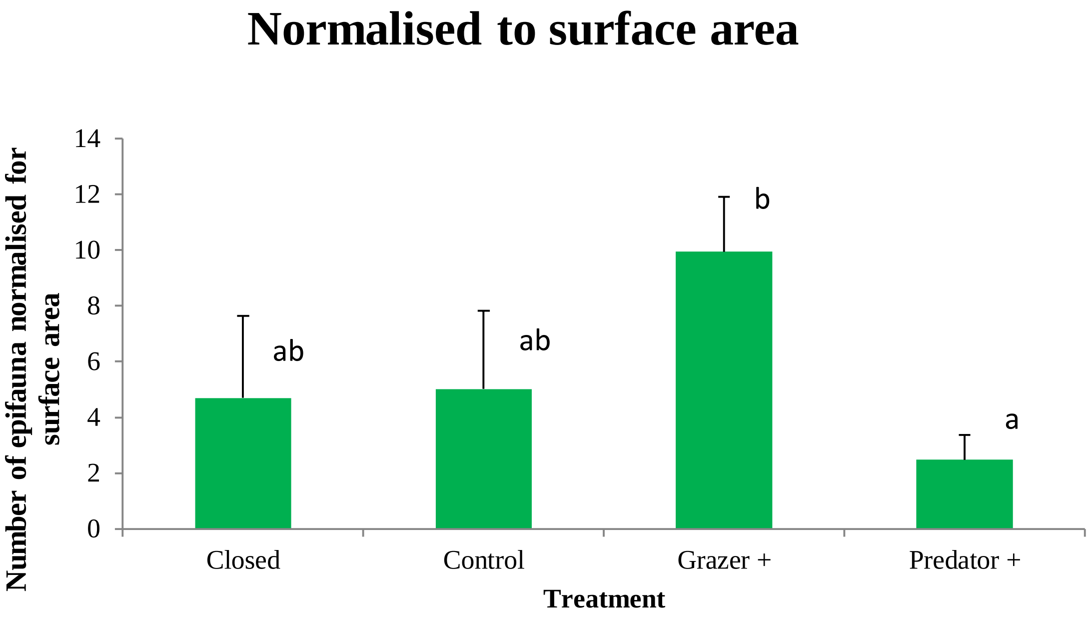

Figure 4.20: Mean number of epifauna normalised to surface area among treatments, treatments pooled. Letters indicate homogenous groups ($p < 0.05$).

Summary of epifaunal effects

Generally comparisons of treatments produced similar results when data were normalised for algal surface area or algal cover, with one important exception (**Table 4.15**). The critical tests for the effects of predation were the comparison of the Control vs Grazer + plots and Closed vs Predator + plots (**Table 4.13**), with both comparisons being non-significant regardless of how data were normalised. The real tests for the effects of grazing were the comparisons of

Grazer + vs Closed and Predator + vs Control both of which were non-significant when data were normalised for surface area but significant when data were normalised for algal cover (**Table 4.15**). Thus, whether grazing significantly affected the epifaunal community depended on whether epifaunal data were normalised for algal cover or surface area.

Table 4.13: Summary of results between Grazer + vs Closed and Predator + vs Control when data were normalised for algal cover and surface area.

	Normalised to area	Normalised to cover
Grazer+ vs Closed	NS	$P<0.05$
Predator+ vs Control	NS	$P<0.05$

Table 4.14: Treatments differentiated by the absence or presence of grazing or predation.

Closed	No grazing, No predation
Control	Grazing, Predation
Grazer +	Grazing, No predation
Predator +	No grazing, Predation

Table 4.15: Tukey HSD summary of results for the combined data normalised for algal cover and surface area. Red for surface area, black for algal cover. NS = Non-significant, S = significant.

	Closed	Control	Grazer +	Predator +
Closed				
Control	**NS, S**			
Grazer +	**NS, S**	**NS, NS**		
Predator +	**NS, NS**	**NS, S**	**S, S**	

DISCUSSION

Intertidal communities are ideal for examining interactions of organisms between trophic levels. *Gelidium pristoides* is an important sea weed because of the influence it has on the structure and functioning of epifaunal communities, and it can be viewed as a keystone species, foundation species or ecosystem engineer. As an ecosystem engineer, it is responsible for influencing the composition and abundance of other species in a community (Jones *et al*, 1997; Shelton, 2010) or having a role in structuring communities by modifying environmental conditions, relationships between species and the availability of resources through its presence. Ecosystem engineers can be used to assess the likelihood of successful restoration (Byers *et al*, 2006) as they can be manipulated to facilitate the change of a community to a desired state. Studying factors affecting keystone species and their influence on the environment can provide knowledge on the type of changes necessary for successful restoration and how restoration efforts can be most effective through natural ecosystem engineering. The significance of a given keystone/foundation species in a community depends on the extent or magnitude of the effect that it has on the whole community (Shelton, 2010) and also on the number of available species that can perform the same function in that community.

Understanding the processes or factors that determine the abundance, distribution and persistence of keystone species and their effects on the environment is of paramount importance as it enables the management of diverse ecological communities. It is not only the effect of keystone species on their environment that is important, but the factors (in this case nutrient availability and grazing) affecting their population dynamics are also important as their influence can have cascading effects on the whole community. Heithuas *et al*, (2008) suggested management of marine predators should be for the maintenance of both density and risk driven ecological processes and this will help marine ecologists to gain insights into the influence of top predators in an inquiry on top-down processes. This study has effectively shown the influence of nutrient availability (upwelling), grazing/browsing, predation, algal cover and algal surface area on epifaunal communities.

Jones *et al*, (1997) argued that ecosystem engineering has both negative and positive net effects on species richness and abundances at small scales, however the consensus is that net effects are more likely to be positive at larger scales. The raging debate (Menge, 2000; Burkepile and Hay, 2006) about the relative importance of top-down and bottom-up control in marine ecosystems will continue but direct knowledge of how ecosystem engineers interact with other species is paramount towards management of epifaunal communities. This study addressed direct and indirect bottom-up effects, direct effects of upwelling on algae and indirect effects of upwelling on epifauna through its effects on algae as well as direct and indirect top-down effects, direct effects on epifauna through predation and indirect effects on epifauna through grazing of algae.

Percentage algal cover

Increased nutrient supply due to upwelling is usually associated with enhanced local primary production (Xavier *et al*, 2007), but this was not the case in the present experiment, with upwelling sites having more or less the same percentage algal cover as non-upwelling sites at both the end and the start of the experiment. Plots that allowed access to grazers, Grazer + and Control plots had similar amounts of algal cover at both upwelling and non-upwelling sites and this may be attributed to the fact that there were higher grazer densities (chapter 3) at upwelling sites, presumably leading to greater grazing pressure on the algae. Plots that denied access to grazers, Predator + and Closed plots had more or less the same amount of algal cover at both upwelling and non-upwelling sites and it is unclear as to why they had the same algal cover ($P > 0.05$).

Grazing had a strong influence on percentage cover, as algal cover varied with treatment (**Fig 4.9**), with plots that excluded grazers (Closed and Predator +) having significantly greater cover than the plots that allowed access to grazers (Grazer + and Controls). The interaction of upwelling and treatment had a significant effect on algal cover ($p < 0.05$), but this reflected a difference in the intensity of the pattern, not a difference in the pattern. The patterns were identical at the two types of site; grazed plots had less algal cover, but the predator+ vs grazer+ and closed vs control comparisons were significant only at upwelling sites (**Fig 4.9**).

Percentage algal cover in closed treatments varied with season at all sites (**Figs 4.5 - 4.8**), with winter months having low cover compared to the summer months presumably due to the combination of seasonal effects combined with higher rates of upwelling during summer (**Fig 3.14** and **3.5 - 3.8**) as shown by both temperature data from loggers and the upwelling index (**Figs 3.5 -3.8**) calculated from wind data. The seasonal pattern was, however, modified where grazers had access (**Figs 4.6** and **4.7**).

Surface area

There was a strong positive correlation between algal surface area and dry weight (**Fig 4.3**), but there was no correlation between either surface area or dry weight and algal cover, showing that the form or structure of the sea weed from which algal cover was calculated was not related to its dry weight or surface area. Interestingly surface area and dry weight gave different results from cover, neither showing significant influences of either upwelling or treatment. In contrast algal cover was influenced by the interaction of treatment with both upwelling and site while surface area was only influenced by site (**Table 4.4**). Grazers reduced percentage algal cover but surface area and dry weight were not affected by grazing. This shows that the alga must grow differently in the presence of grazers. As cover is reduced by grazing, but biomass and area are not reduced, the plants must grow longer or more densely to compensate for the reduction in cover.

Epifaunal community structure

Non-normalised data, data normalised for algal cover and for surface area

Upwelling (top-down) and treatment had no significant influence on the community structure of epifaunal communities, but site had a significant effect (**Table 4.5**). The influence of site was due to geography with sites that were furthest from each other being more different than sites that were closer to each other (**Table 4.6**). Emond *et al*, (2015) suggested that bottom-up and density-dependent processes have a stronger influence on the regulation of communities than top-down controls on early recruitment patterns of snow crabs. In contrast top-down mechanisms were found to have a strong influence in a study of cod, *Gadus morhua*. Casini *et al*, (2008) found out that reductions of cod populations directly affected its main prey, the zooplanktivorous sprat (*Sprattus sprattus*), and indirectly the summer biomass of zooplankton and phytoplankton through cascading top-down processes.

When normalised for cover the results were the same as when normalised for surface area and also the same as for the non-normalised data, with only site having a significant influence. This implies that epifauna may react to algal surface area or biomass, but not to cover. Cover changed with treatment, but, like algal surface area and dry weight, overall epifaunal community structure did not respond to treatment.

Total epifaunal abundances

Original data

Upwelling and treatment had no influence on the total epifaunal numbers in each plot but site had a significant influence (p=**0.0332, Table 4.10**). All sites were different from each other (post hoc, p<0.05, all cases), with the implication that the differences might have been due to geography.

Data normalised for algal cover and for surface area

Upwelling and site had no significant influence but treatment had a significant influence when data were normalised for algal cover and for surface area (**Tables 4.11** and **4.12**). They were both affected by site and treatment, but with noticeable differences in how treatments differed when normalised for algal cover (**Fig 4.19**, Control = Grazer + > Predator + = Closed, post hoc) and when normalised for surface area (**Fig 4.20**, Control = Grazer +, Control = Predator + = Closed, Grazer + ≠ Closed = Predator +, post hoc). The key test for the effects of predation was in the comparison of the Control vs the Grazer + and Closed vs Predator + plots (**Table 4.15**) neither of which was significant when the data were normalised for either algal cover or for surface area. This indicates that predation did not have a strong influence on total epifaunal abundances. The key test for the indirect effects of grazing on epifaunal abundances was in the Grazer + vs Closed and Predator + vs Control plots (**Table 4.13)**. These comparisons were both non-significant when epifaunal data were normalised for surface area but, they were both significant when normalised for cover, indicating that whether we think grazing is important to epifaunal abundances depends on how we measure habitat availability. Expressing the abundance of organisms per unit of surface area or of cover may lead to different conclusions with the results indicating that algae reactor grow differently after being grazed.

Conclusion

There was a strong relationship between surface area and weight of surface film, this strong relationship showed that it was possible to estimate algal surface area. Surface area had a strong correlation with dry weight but neither surface area nor dry weight was correlated to algal cover and this might be attributed to the fact that alga grows differently in the presence of grazers as surface area and dry weight were not affected by grazing treatment. Algal cover was affected differently by upwelling and treatment from surface area and dry weight. Algal cover was influenced by interactions of treatment with site and upwelling but algal surface area and dry weight were only influenced by site. Epifaunal community structure, analysed using Primer, did not respond to treatment, even when normalised to algal surface area, but epifaunal abundances did. When total epifaunal abundances were normalised for algal cover and surface area, predation had no significant effect, but grazing had a significant effect on the abundances of epifauna. Indirect top-down factors through grazing of sea weed are important to epifaunal communities when looking at their total abundances as the influence of treatment with plots that were subjected to grazing had a significant effect.

Chapter 5 : General discussion

The understanding and identification of forces that drive the structuring of communities is important as it enables marine ecologists to predict what may happen to communities in the future and allows ecologists to draft proper management plans for marine communities (Forrest *et al*, 2001). Chapter 3 focussed on classifying sites in terms of upwelling, the focus was on how sites differed in terms of nutrients brought up by the process of upwelling. This involved the use of temperature loggers coupled with wind data to confirm the classification of upwelling sites and sites that were considered as non-upwelling. The study also focussed on top-down vs bottom-up factors with emphasis on the direct and indirect influence of upwelling, predation and grazing on epifaunal communities (Chapter 4). The main aim was to assess how the ecological engineer (*Gelidium pristoides*) affects species composition in epifaunal communities when exposed to different nutrient levels (upwelling vs non-upwelling), how grazing of *G. pristoides* can have indirect effects and how predation can directly influence species composition in epifaunal communities.

The methods used to confirm the identification of upwelling sites (SST and wind data) were complementary to each other, showing a similar trend. These methods have been used in the past for other studies (Bakun, 1973; Xavier, 2007; Weidberg *et al*, 2015) but for this study they were used concurrently and both identified significant differences between upwelling and non-upwelling sites in terms of the number of upwelling days and upwelling events recorded for the whole study period, although Brenton on Sea had on average a low intensity of the upwelling index (**Fig 3.9**). The results obtained also showed that temperature data and wind data can be used together to classify sites in terms of upwelling or non-upwelling and to determine the strength of upwelling. In this study sites were also different from each other in terms of the density of grazers (**Figs 3.14 - 3.17**), with upwelling sites having higher densities of grazers per m^2. This might be due to the fact that in upwelling regions there are more nutrients and there is high primary production, increased algal cover to support quite a number of organisms as opposed to regions where there is low nutrient availability, leading to less algal cover (Nielsen and Navarrete, 2004; Steyn, 2009).

The interactions of treatment with upwelling and site had a significant impact on algal cover (**Table 4.4**), but upwelling, site and treatment were not significant showing that the effects of treatment differ among sites and between upwelling and non-upwelling sites i.e. treatment interacted with site and upwelling. This was in contrast with the findings of Bosman *et al*, (1987) that upwelling has a strong influence by supplying nutrients needed for the growth of alga and the findings of (Forrest *et al*, 2001) that herbivores play an important role in limiting the growth of algae in epifaunal communities.

Algal surface area was strongly correlated to dry weight but neither surface area nor dry weight was correlated to algal cover (**Fig 4.3**). The results for surface area and dry weight were the same but different from those for algal cover. This prompts the idea that grazing had an effect on algal morphology as the presence of grazers reduced cover while biomass and area were unaffected.

Using raw abundance data, PRIMER results showed that epifaunal community structure was significantly influenced by site (**Fig 4.4**), but upwelling and treatment had no significant influence. When the data were normalised for both algal surface area and algal cover the results were the same with only site having a significant effect, with all sites being different from each other. The differences among sites might have been a geographic effect with sites that were furthest from each other being more different compared to the ones that were relatively closer to each other (**Tables 4.6** and **4.8**).

Similarly, Anova results for the total epifaunal abundances showed that site (**Table 4.10**) had a significant effect but not upwelling or treatment. When data were normalised for algal cover and surface area, however, only treatment had a significant effect (**Table 4.11** and **4.12**) with tests for the effects of predation being the comparison of the Control vs Grazer + plots and Closed vs Predator + plots and both comparisons were non-significant regardless of how the data were normalised. The tests for the effects of grazing were the comparisons of Grazer + vs Closed and Predator + vs Control, with both non-significant when data were normalised for surface area but significant when data were normalised for algal cover and this indicates that grazing is a strong influencing factor in epifaunal communities, but only when the data are considered in the context of algal cover, not surface area. Grazing, which indirectly affects epifauna through removal of sea weed and thus living space/habitat is an important factor in epifaunal communities when looking at the total abundances when data were normalised for cover. When total epifaunal abundances were normalised for algal cover and surface area, predation had no significant effect but grazing had a significant effect on epifanaul abundances indirectly through the effect of grazers consuming algae leading to the conclusion that indirect top-down factors through grazing of the sea weed are important in structuring these epifaunal communities. Although in this study top-down processes had a strong influence on epifaunal communities, continuous research for longer periods might be necessary to assess whether these or bottom-up processes dominate and also to clearly understand the importance of ecological engineers to epifaunal communities.

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