The roles of intertidal marine gastropod shells as secondary substrate for macroalgae.

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A thesis submitted in fulfillment of the requirements for the degree of MSc in the Department of Biodiversity and Conservation Biology, University of the Western Cape.

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August 2014

I declare that

"The roles of intertidal marine gastropod shells as secondary substrate for macroalgae"

is my own work, that it has not been submitted for any degree or examination at any other university, and that all the sources I have used or quoted have been indicated and acknowledged by complete references.

9 May 2014

This thesis is dedicated to my husband, Yonnick Puckree and my sisters Andrea and Nicole Padua for their continued patience and support, and especially to my late mother Loretta Padua, for always encouraging my studies and for being my pillar of strength.

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Abstract

Primary space within the marine benthos is by far the most limited resource for which all sessile organisms must compete. It only ever becomes available when the organisms occupying it dies or are forced to leave the area. It has long been established that herbivorous molluscs play an important role in freeing up space on rocky intertidal shores. However, their grazing activities, although freeing up space, often result in diminished species diversity because most intertidal algae and invertebrates are either consumed or displaced. The exploitation of microhabitats (secondary space) therefore becomes important under such scenarios and is known to increase the biodiversity of a particular area. Ironically, mollusc shells are known to provide such microhabitats as they increase the available surface area for the settlement of a variety of epizoic organisms. While the international literature abounds with examples of the importance of mollusc shells as secondary substrata, virtually nothing is known of these associations within a South African context.

Surveys were conducted on five more or less equidistant intertidal rocky shore communities (Kalk Bay, Rooiels, Sandbaai, Pearly Beach, Stinkbaai) within the South African western biogeographic transition zone. At all sites, invertebrate densities and biomass, and algal and lichen percent cover abundance were sampled along transect lines running more or less parallel to the shoreline from mean high water spring (MHWS) tide mark to mean low water spring (MLWS) tide mark. Along each transect line, 10 quadrats (0.5 m x 0.5 m) were placed at regular 1 m intervals. For biomass determinations twenty (20) representative individuals of each invertebrate species were brought back to the laboratory. In addition, molluscs which are less affected by changes in environmental factors associated with desiccation stress, and that are known to have profound effects on the distributions of other intertidal organisms, here referred to as 'resident' species (*Cymbula oculus*, *Scutellastra longicosta*, *S. cochlear*, *S. argenvillei*), were also selectively sampled. For these species, twenty (20) photographs of each were taken to determine algal and lichen percent cover abundance on their shells. Similarly, twenty (20) *O. sinensis* individuals encountered along a transect line were also collected to determine the comparative importance of winkles.

Total density and biomass (for all invertebrates and 'resident' species) data were subjected to cluster analyses using the Bray-Curtis similarity index. Thereafter a one-way ANOVA using a Bonferroni Post hoc test was performed to determine the comparative density and biomass distributions across each shore studied. Based on presence/absence data, a Mann-Whitney U test was conducted to determine differences between individual epizoic species occurring on the primary rock substratum and on shells of 'resident' molluscs. Epizoics, on their respective substrata, were compared using a Kruskal-Wallis pairwise comparison to establish differences in their percent cover. To determine diversity, the Shannon index and the Inverse Simpson's index were used. In order to determine differences in diversity between substrata, a Friedmans two-way ANOVA (for resident limpets) and a Kruskal-Wallis pairwise comparison (for *O. sinensis*) was used. For all tests performed a 95 % confidence limit was applied and so differences amongst treatments were considered statistically significant at $p < 0.05$.

With a few notable exceptions (presence of the invasive mussel *Mytilus galloprovincialis* along the mid to low shore at most sites, general absence of barnacles at most Mid-eulittoral zone sites, and the absence of dense beds of foliose and turfy algae in the Mid-eulittoral zone at all sites), the zonation patterns within the western biogeographic transition zone are consistent with that published for the South African south coast. Density and biomass patterns across the shore show similarities from west to east with distal sites displaying patterns more similar to their nearest neighbouring sites. When all invertebrate data are pooled, for both density and biomass, sites group strongly according to the geographic profile. However, when data from only the 'resident' species are examined, the data show a stronger correlation to site exposure. An examination of algal and lichen percent cover abundance showed that diversity generally increased down the shore, but were much reduced in the Mid-eulittoral zone. This zone coincided with high densities of the limpet *C. oculus*. Although all limpets examined bore a number of epizoic algae and lichens, overall, limpet shells (particularly from the western sites) from the Mid-eulittoral zone are comparatively more important than those occurring in the Lower eulittoral zone. Despite the limpets *S. cochlear* and *S. argenvillei* bearing comparatively higher numbers of epizoics than either *C. oculus* or *S. longicosta* from the Mid-eulittoral zone, and despite the winkle *O. sinensis* providing an important settlement substrata for a number of encrusting algae and lichens, the former two limpets and the winkle do not appear to be more important than the surrounding primary substrata that they inhabit.

The results of the study show that notably within the mid-shore environment, mollusc shells provide important spatial refuges for a host of grazer susceptible algae and lichens that are otherwise grazed when they recruit there. On the low shore, mollusc shells appear to act largely as extensions of the primary substratum by providing increased settlement surface area. On rocky intertidal environments within the western biogeographic transition zone, mollusc shells provide important microhabitats as well as increased surface area for the settlement of a variety of epizoic organisms.

Keywords: South African biogeography, western biogeographic transition zone, mollusc shells as secondary substrata, algal and lichen diversity.

1.1 Zonation on rocky shores

The vertical distribution of animals and plants throughout the rocky intertidal zone is termed zonation (Stephenson and Stephenson 1949, 1972, Lubchenco 1980). The first attempt to standardize global zonation patterns was by Stephenson and Stephenson (1949). Their preliminary work spoke of a "universal zonation pattern" that comprised three zones namely, the Supralittoral fringe, the Midlittoral zone and the Infralittoral fringe. The uppermost zone, the Supralittoral fringe is characteristically dry, forming the boundary between land and sea. This zone is only exposed to oceanic waters via spray suspension or when its lower parts are wet or submerged by exceptionally high tides during extreme weather conditions. The Midlittoral zone (situated between the Supralittoral and the Infralittoral fringe) experiences periods of immersion and emersion daily. This zone has a high species abundance and diversity compared to the Supralittoral fringe. The Infralittoral fringe is the zone lowest on the shore and is exposed during spring low tide events and covered during neap tides. The species composition in this zone is highly variable, but has the highest species abundance and diversity compared to other intertidal zones.

Later, Stephenson and Stephenson (1972) changed their definition of "universal" to "widespread" as the former statement lead to some misinterpretation. Even though Stephenson and Stephenson's (1949) revised zonation pattern received much criticism (Womersley and Edmonds 1952) many agreed with the general terminology (Batham 1956, Guiler 1953, Lewis 1955) so that it became even more acceptable after the publication of Stephenson and Stephenson's (1979) *Life between tide-marks on rocky shores* (Raffaelli and Hawkins 1996). The terminology proposed by Stephenson and Stephenson (1972) is based on the relative positions of the major community organisations. Consequently, zones were named according to locally distributed organisms, which may be specific to various coastlines. One such example may be seen along the South African coastline, where the *Littorina* zone is so named due to the high densities of *Afrolittorina knysnaensis* (Krauss). In the international terminology, this zone is equivalent to the Supralittoral fringe.

1.2 Causes of zonation

Over a spatial gradient, established intertidal organisms need to adapt to increasing physiological and biological stresses resulting in organisms being rarely found above their critical level (Colman 1933, Doty 1946, Wolcott 1973, Dethier 1982, Williams and Morritt 1995, Tomaneck and Helmuth 2002). For many years scientists considered it was the physical stresses experienced higher along the shore that solely determined the settlement of various organisms (Engelmann 1884, Oltman 1892, Colman 1933, Doty 1946, Evans 1947). However, it is now widely accepted that the causes for zonation may be divided into two categories, physical and biological factors (Connell 1972, Schonbeck and Norton 1978, Lubchenco 1980, Carter and Anderson 1991, Boaventura *et al.* 2002). In general, it was considered that physical factors determine the upper limits of species distributions (e.g. Connell 1972, Lubchenco 1980, Underwood 1980, Graham 1997, Sanford 2002) while biological factors determine the lower limits of species distributions (e.g. Chapman 1957, 1974, Kitching and Ebling 1961, Jones and Kain 1967, Connell 1972, Branch 1975, Menge *et al.* 1997).

1.2.1 Physical factors affecting zonation

Investigations into the physical factors affecting zonation began as far back as the late 1800's and were mainly based on single physical factors affecting zonation patterns. Marine botanists concluded that it was largely the light quality and quantity that resulted in green seaweeds settling towards the top of the shore, brown seaweeds in the middle and red seaweeds lowest along the shore (Engelmann 1884, Oltman 1892). Colman (1933) developed the first theory of critical tide levels, which is based on the fact that marine organisms occur at specific heights along the shore where rapid changes in immersion and emersion occurred. However, herbivore removal experiments on rocky intertidal shores of the British Isles (e.g. Burrows and Lodge 1951, Hawkins and Hartnoll 1982, Raffaelli and Hawkins 1996) soon discredited this theory as significant increases in green algal percent cover occurred across all zones when herbivores were excluded.

Once algal spores and invertebrate larvae have settled on an appropriate substratum, any number of physical factors mainly associated with desiccation stress may come into play. The height along the shore has particularly been considered the most important factor as it contributes to the length of time an organism is immersed and emersed (Roberts *et al.* 1997, Tomanek and Somero 2000, Stillman and Somero 2000) as well as the degree of desiccation and associated osmotic stress (Lent 1968, Dayton 1971). Species that are vulnerable to desiccation stress would be found lower along the shore where they would experience longer immersion times and vice versa.

Another important physical factor is the degree of wave exposure (Dayton 1971, Little and Kitching 1996, Bustamante *et al.* 1997). Along the rocky shore intertidal environment, waves prevent the desiccation of organisms and also assist in the transportation and distribution of nutrients and larvae (Bertocci *et al.* 2007). Wave exposure influences the structure of the intertidal community by removing or limiting vulnerable predators (e.g. whelks in the mussel-canopy interaction) (McCook and Chapman 1991), restricting certain organisms from colonizing (e.g. growth of ephemeral algae) (Valdivia and Thiel 2006), and the removal of sessile organisms by the turning over of boulders that contribute to an increase in species diversity (Sousa 1979, Garcia and Diaz-Pulido 2006).

1.2.2 Biological factors affecting zonation

The lower limits of zonation patterns along rocky intertidal shores have traditionally been seen as being determined by biological factors (Connell 1972, Lubchenco 1980). Such factors include predation (Connell 1961, Paine 1974), herbivory (Dayton 1971, Connell 1972, Lubchenco and Menge 1978, Sousa 1979, Underwood 1980, Underwood and Jernakoff 1984, Janke 1990, Anderson and Underwood 1997), competition (Dayton 1975, Schonbeck and Norton 1980, Norton 1985), larval settlement (Denley and Underwood 1979, Little and Kitching 1996) and bulldozing (Petraitis 1983, Underwood *et al.* 1983, Blinn *et al.* 1989, Hunt and Scheibling 1997, Chan and Williams 2003, Chan *et al.* 2006, Aguilera and Navarrete 2007).

It has been well established that intertidal predators on rocky shores have the ability to affect the distribution and densities of intertidal invertebrates (Paine 1966, 1974, Dayton 1971, Menge 1976, Menge and Sutherland 1987, Navarrete and Menge 1996, Bertness 1999, Maneveldt *et al.*

2009). A famous predator-prey example is that of the sea star *Pisaster ochraceus* (Brandt) and the mussel *Mytilus californianus* Conrad. In the absence of predation, the mussel has the ability to competitively exclude all other sessile invertebrates, rendering all primary space unavailable (Paine 1966). *Pisaster ochraceus* has evolved to selectively prey on *M. californianus* and in doing so renews the vital limiting resource of space. This freed space allows the area to be colonised by an array of intertidal species, greatly increasing the species diversity (Paine 1966).

Herbivory has similarly been documented as an important biological factor influencing intertidal species distribution and diversity (Sousa 1979, Underwood 1980, Lubchenco and Gaines 1981, Underwood and Jernakoff 1984, Kaehler and Williams 1996, Anderson and Underwood 1997, Williams *et al.* 2000, Boaventura *et al.* 2002, Maneveldt *et al.* 2009). One of the most common examples exists between sea urchins and their surrounding benthic communities. Sea urchin removal often results in an almost immediate increase in algal diversity (Paine and Vadas 1969, Paine 1980). The presence of this ferocious generalist grazer has been shown to reduce algal cover abundance and algal diversity, and prevents algal succession (Paine and Vadas 1969, Lubchenco 1978, Paine 1980).

Competition has been proven to be another important biological factor capable of structuring marine benthic communities (Lubchenco 1980, Branch 1985, Wootton 1993, 1998, Yakovis *et al.* 2008, Holomuzki *et al.* 2010). There are different modes of competition: real competition, which occurs directly through interference; and apparent competition, which occurs indirectly through exploitation (Holt 1977, Branch 1985, Holomuzki *et al.* 2010). Interference competition on its own usually leads to competitive exclusion while exploitation competition usually results in coexistence so that seemingly weaker competitors can also inhabit an area (Thorp 1976, Branch 1985). The research of Underwood (e.g. 1976, 1978) are good examples of the role of exploitation competition in allowing for coexistence among competing species.

After the publications of Matthews (1917) and Wilson (1932), larval settlement was seen as an equally important biological factor controlling intertidal species distributions. For larval settlement, three factors mainly determine success in recruitment and a species' subsequent vertical distribution. First, mobile adults may migrate to suitable substrata (Grosberg 1982). Second, larvae actively select the appropriate substratum according to intertidal height above the shore or where adults have already settled (Paine 1974, Grosberg 1982, Keough and Downes 1982, Raimondi 1991, Abelson and Denny 1997, Jenkins 2005, Matson *et al.* 2010). Third, larvae and spores are found in different layers of stratified waters so that they land at different heights along the shore (Grosberg 1982, Shanks 1983, 1986). Over the years, support for each of these models has been variably presented.

More recently bulldozing has been shown to be an important biological factor controlling the intertidal distribution of species. Bulldozing occurs when the leading edge of a species lays so close to the substratum that its movements cause damage to the substratum and to any species it encounters (Blinn *et al.* 1989). Bulldozing by limpets (Dayton 1971, Blinn *et al.* 1989, Berlow and Navarrette 1997, Chan and Williams 2003, Chan *et al.* 2006, Aguilera and Navarrette 2007, Denny *et al.* 2009), littorinids (Jennings and Hunt 2011) and sea urchins (Sammarco 1980, Maldonado and Uriz 1998) have been reported to cause early post-settlement mortality of barnacles, other limpets and ascidians. Consequently, bulldozing often greatly impacts communities by controlling adult species' vertical zonation patterns (Dayton 1971, Berlow and Navarrette 1997, Chan and Williams 2003, Chan *et al.* 2006).

From these examples above, it is clear that the vertical distribution of organisms on rocky shores is a result of both physical factors associated with desiccation stress, and due to the complex interactions between organisms (Dayton 1971, Grosberg 1982, Menge and Sutherland 1987, Wootton 1993, 1998, Little and Kitching 1996, Holomuzki *et al.* 2010). It is now widely accepted that physical factors are generally responsible for setting the upper limits of zonation whereas biological factors are generally responsible for setting the lower limits. It should, however, be noted that increasingly, biological factors are being shown to be equally important in setting the upper limits of species' intertidal distributions (Lubchenco 1980, Underwood 1980, Underwood and Jernakoff 1981, Boaventura *et al.* 2002, Maneveldt *et al.* 2009).

1.3 The role of molluscs in controlling intertidal distribution patterns

The behaviour of herbivorous gastropods has various impacts on their surrounding environments. It has long been shown that molluscan herbivores play an integral role in structuring the abundance, distribution and diversity of algal communities along rocky shores (Paine and Vadas 1969, Lubchenco 1978, Sousa 1979, Underwood 1980, Underwood and Jernakoff 1984, Kaehler and Williams 1996, Anderson and Underwood 1997, Williams *et al.* 2000, Maneveldt *et al.* 2009). Lubchenco (1978), for example, showed that within tidal pools, the removal of *Littorina littorea* (Linnaeus) under *Chondrus crispus* Stackhouse dominated conditions, resulted in *Entermorpha* sp. outcompeting *C. crispus.* When *L. littorea* was added to an *Entermorpha* sp.

dominated pool, the *Entermorpha* sp. was consumed by the winkle and *C. crispus* re-emerged as the dominant alga. However, when *L. littorea* were present in intermediate densities, ephemeral and perennial algae were found to coexist in the same vicinity. More recently, Maneveldt *et al.* (2009) showed that herbivory from the generalist grazer *Cymbula oculus* (Born) not only controls algal abundance and diversity, but through indiscriminate predation of larvae, the limpet also affects the distribution and densities of other intertidal invertebrates.

Not all herbivore-algal interactions are negative though. Mucous trails left behind by molluscs have been shown to act as an organic enrichment for the establishment of algal areas along which they move, as well as fertiliser for their own gardens (Stimson 1970, Connor 1986, Evans and Williams 1991). The territorial, gardening limpet *Lottia gigantea* (Sowerby), for example, actively excludes sessile invertebrates as well as lays down a mucous trail (Stimson 1970). It has even been suggested that limpets have the ability to manipulate the primary productivity of the areas they inhabit by renewing mucus trails; renewed mucus trails have been argued to trap algal spores thus creating opportunities for algal colonization, which combined with regular grazing of more common species of algae, assists in regulating coexistence among algal species capable of surviving (Stimson 1970, Connor 1986, Evans and Williams 1991).

Probably the most important direct benefit from grazing by molluscs is the advantages associated with algal gardening. For example, the South African territorial gardening limpet *Scutellastra cochlear* (Born) forms an association with the turfy algae *Herposiphonia heringii* (Harvey) Falkenberg and *Gelidium micropterum* Kützing. The limpets form dense aggregations, often of several hundred per meter square, on the low shore with juvenile limpets often restricted to the shells of mature ones (Branch 1975a, Branch 1975b). Through this behaviour, most other fleshy and turfy algae are effectively excluded from the limpets' territories, barring the two fringing garden algae and occasionally the coralline alga *Spongites yendoi* (Foslie) Y.M.Chamberlain (Branch 1975a, 1975b, Branch *et al.* 1992, Plaganyi and Branch 2000). The association also benefits the limpet. The gardening algae have been shown to have a high organic content that provide the limpets with an excellent food source; in return, the limpets excrete high levels of ammonium that serve as nutrients for the algae (Branch *et al.* 1992, Plaganyi and Branch 2000). This mutualistic association allows the gardens to maintain a high percent cover on the primary substratum on the low shore along South African west and southern west coast sites.

1.4 The importance of space in the marine benthos

Primary space within the marine benthos is by far the most limited resource for which all sessile organisms must compete (Connell 1961, Pequegnat 1964, Dayton 1971, Paine 1971, Branch 1975b, 1985, Jackson 1977, Dudgeon *et al.* 1999, Rossi and Snyder 2001, Bell 2005). In the marine environment, space is an absolute resource because it is not easily renewable (Dayton 1971, Underwood 1978, Branch 1985, Dudgeon *et al.* 1999). Space only ever becomes available when the organism occupying it dies, or is forced to leave the area (by factors such as disturbance, predation/herbivory or competition) (Connell 1961, Pequegnat 1964, Dayton 1971, Paine 1971, Jackson 1977, Branch 1985, Chadwick 1987, Rossi and Snyder 2001, Bell 2005).

Most often, physical disturbance has been shown to be essential in renewing primary space. Factors such as wave exposure, battering and desiccation stress not only result in the provision of space, but they also aid in the distribution and abundance of sessile species (Connell 1961, Paine 1966, Dayton 1971, Osman 1977, Underwood 1980, Grosberg 1982, McCook and Chapman 1991, Blanchette 1996, Boström and Bonsdorff 2000, Garcia and Diaz-Pulido 2006, Valdivia and Thiel 2006, Bertocci *et al.* 2007). In the absence of disturbance, species diversity has been shown to decline rather than remain high largely because communities often reach a stage in which they are dominated by later successional stages that outcompete other successional stages (Dayton 1971, Sousa 1979). Similarly, if the disturbance is too frequent species diversity is also low because only opportunistic, early successional species can colonise (Sousa 1979). At intermediate disturbance frequencies, species diversity is generally highest because the community is comprised of a mixture of early, middle and late successional stages (Dayton 1971, Sousa 1979, Fraschetti *et al.* 2001).

Herbivores and predators also play important roles in structuring the abundance and diversity along rocky intertidal shores (Underwood *et al.* 1983, Anderson and Underwood 1997). In general, herbivores reduce species diversity by completely denuding intertidal zones of all algae (Petraitis 1987, Anderson *et al.* 1991, Dye 1993, Berlow and Navarrete 1997, Maneveldt *et al.* 2006, 2009). In addition, herbivores have the ability to enhance or inhibit the recruitment of various species by either altering the rates of succession (speeding or slowing it down) (Dayton 1971, Sousa 1979, Lubchenco 1983, Breitburg 1985, Farrell 1991, Maneveldt *et al.* 2009) or causing completely different communities to emerge (Anderson and Underwood 1997). Herbivore-defended algal species, that are competitively subordinate to faster growing, more palatable algal species, for example, rely heavily on grazers for their co-existence (Steneck 1983, Paine 1984, Dethier *et al.* 1991, Steneck *et al.* 1991, Keats and Maneveldt 1994, Keats *et al.*

1994, Kaelheler and Williams 1996, Stachowicz and Hay 1996, Nagarkar and Williams 1999, Bulleri 2005, Maneveldt *et al.* 2006). Although less important than herbivory on rocky intertidal shores, predation plays a similarly important role in controlling the densities of many dominant invertebrate species and often results in the freeing up of primary space (Paine 1966, Paine 1974, Menge and Sutherland 1976, Underwood 1978, Johnston *et al.* 2002). In the absence of the predatory starfish for example, mussels tend to dominate the primary substratum by outcompeting all other organisms (Paine 1966, 1974, Menge and Sutherland 1976).

Since space is an absolute resource that often limits an organisms range, competition between organisms arise (Connell 1961, Dayton 1971, Paine 1974). This results in a hierarchy of dominance so that in the absence of physical disturbance, one or a very few organisms dominate over and out-competes other organisms (Dayton 1971, Seapy and Littler 1982). A diverse community structure is therefore more likely to be present under intermediate disturbance regimes that regularly free up space (Dayton 1971, Sousa 1979, Menge *et al.* 1985, Dial and Roughgarden 1998, Roxburgh *et al.* 2004).

1.5 The role of mollusc shells as secondary substrata in benthic communities

The exploitation of microhabitats (secondary space) is known to increase the biodiversity of a particular area (Bell 2005). In marine ecosystems, mollusc shells often provide such microhabitats as they increase the available surface area for the settlement of a variety of epizoic organisms (Bell 2005, Nakin and Somers 2007). Such secondary substrata become particularly important in rocky intertidal benthic environments where primary space is the most limiting resource, largely because it is often not quickly and easily renewed (Dayton 1971, Branch 1985, Bell 2005). Mollusc shells, even empty or fragmented ones, affect the heterogeneity and structure of benthic communities because they alter the availability of resources (including space) to other organisms (Vance 1978, Black and Peterson 1987, Kidwell and Gyllenhall 1998, Gutierrez *et al.* 2003, Bell 2005). Such alterations may occur directly by creating microhabitats and secondary habitats for otherwise epilithic organisms (Karlson and Shenk 1983, Gutierrez *et al.* 2003) and/or indirectly by affecting the biotic and abiotic factors surrounding the shell (Vance 1978, Gutierrez *et al.* 2003). The degree of these changes is ultimately dependent on the physico-chemical structure and spatial arrangement of the shells (Gutierrez *et al.* 2003). In either case (whether directly or indirectly), diversity of sessile organisms is greatly increased by the presence of mollusc shells as secondary substrata (Lohse 1992, Creed 2000, Barnes 2001, Bell 2005, Zeeman *et al.* 2013).

Non-geniculate coralline red algae in particular are known to benefit directly from such epizoic interactions with a wide variety of molluscan shells, whether these shells have occupants or not (Steneck 1986, McKinney 1996, Bell 2005). *Lithothamnion tophiforme* (Esper) Unger, for example, is found to mostly recruit to the shells of scallops; the alga continues to grow on the scallop shells even once the animal has died (Adey *et al.* 2005). In contrast, *Phymatolithon* sp. from the North Atlantic rarely recruit to living mollusc shells and are found to occur epizoically only on empty mussel shells (Adey 1966).

1.6 The coastal and nearshore biogeography of South Africa

Division of the South African coastline into various marine biogeographic provinces has historically been achieved using two criteria. The first and most popular criterion was formulated by Eckman (1953) and is based on the presence of endemic species. If more than 10 % of the total number of species in a particular area is endemic, then the area is delineated as a separate province (Eckman 1953, Briggs 1974, 1995, Vermeiji 1978, Boschi 2000, Bolton *et al.* 2004, Fox and Beckely 2005, Floeter *et al.* 2008, Briggs and Bowen 2012). The second criterion, which is more generally followed by seaweed biologists, is based on how homogenous a coastline is, so that a biogeographic province may be defined as an area that contains homogenous biota which is separated from other areas of the coastline by discontinuities in the inhabiting flora and/or fauna (van den Hoek and Donze 1967, Awad *et al.* 2002, Bolton *et al.* 2004, Anderson *et al.* 2009).

Documentation of the coastal biogeography of southern Africa dates back to the mid 1800s' where initially only one coastal province ("South African Province") was recognised (Harvey 1847, Forbes 1856, Woodward 1856, Ortman 1896). However, regional delimitations differed markedly according to taxonomic groups. For example, based on decapod Crustacea, the South African Province began in Angola and extended around Cape Point to a location between East London and Port Elizabeth (Ortman 1986). Based on molluscs (Forbes 1856, Woodward 1856) though, the South African Province extended from Bogenfels (Namibia) around Cape Point to just north of Durban. The one-province notion thus proved problematic for most marine scientists.

Following the extensive research by Stephenson and Stephenson (1948), three major faunal regions (or provinces) were identified for the South African coastline. These were the cool-temperate west coast (located between Port Nolloth and Cape Point), the warm-temperate south coast (located within the region of False Bay and Port St. Johns), and the subtropical east coast (located between Port St. Johns and northern KwaZulu-Natal) (Penrith and Kensley 1970, Stephenson and Stephenson 1972, Bolton 1986). Having been widely accepted, these regions are now more commonly termed the Benguela Marine Province, the Agulhas Marine Province and the Indo-West Pacific Province respectively (Figure 1) (Anderson *et al.* 2009, Fakoya *et al.* 2011, Bolton *et al.* 2012, Briggs and Bowen 2012).

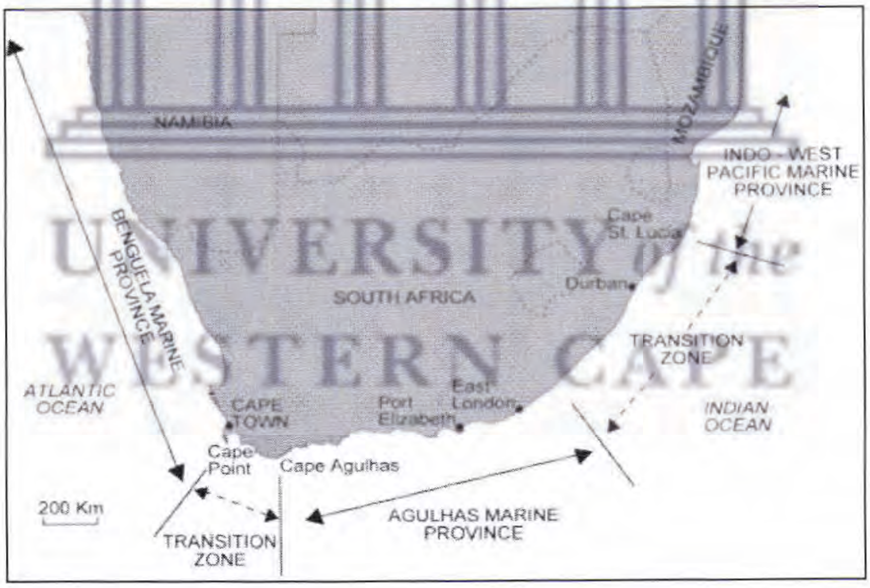

Figure 1: Map of the South African coastline showing the seaweed biogeographical regions including the two transition zones (Anderson *et al.* 2009).

The west coast, which falls within the Benguela Marine Province, experiences annual average sea surface temperatures of 12-13 °C as it is affected by cool upwelled water resulting in the habitation of flora classified as cool-temperate (Bolton 1986, Stegenga *et al.* 1997, Anderson *et al.* 2009). The Agulhas Marine Province experiences annual average sea surface temperatures of 17.2-18.2 °C with warm-temperate algal species inhabiting this region, many of which are classified as endemic (Bolton 1986, Bolton and Anderson 1997, Bolton and Stegenga 2002, Bolton *et al.* 2004, Maneveldt *et al.* 2008, Maneveldt and van der Merwe 2012). The Indo-West Pacific Province experiences annual average sea surface temperatures of approximately 22 °C, resulting in the habitation of a tropical algal flora (Bolton *et al.* 2004, Anderson *et al.* 2005, DeClerk *et al.* 2005).

Due to the relatively high number of endemic species located in the transition zones between the three marine provinces, two transition zones were identified. The western biogeographic transition zone is located within the Cape Peninsula and experiences rapid changes in temperature; this region comprises species representative of both its bordering provinces (Bolton and Anderson 1997, Leliaert *et al.* 2000). The eastern biogeographic transition zone is considered to be located between Hlluleka and St. Lucia Bay and is thought to extend as far north as Isipingo/Durban (Farrell *et al.* 1993, Bolton *et al.* 2004). According to seaweed data, there is a more gradual overlap between the south coast flora and the sub-tropical East African flora (Bolton *et al.* 2004). Only 2 % of this mixture of tropical and temperate flora is considered to be endemic as the region comprises equal numbers of seaweed biota representative of both the Agulhas and Indo-West Pacific Marine Provinces.

1.7 Zonation patterns on South African rocky shores

On a more localised scale, the rocky intertidal shores of South Africa can be divided into roughly five zones (Stephenson and Stephenson 1949). The first of these zones, situated highest along the shore, is the Infratidal zone (or Supralittoral fringe). The next zone, known as the eulittoral (or intertidal) zone is sub-divided into: the Upper eulittoral zone (plus an oyster belt on the east coast); the Mid-eulittoral zone; and the Lower eulittoral zone. Lowest on the shore is the Sublittoral fringe.

The South African intertidal zone is variously dominated by different assemblages of organisms and subsequently given different local names (Branch and Branch 1981). The Littorina zone (Supralittoral fringe) along the entire coastline is variously dominated by three species of Littorinid snails. *Porphyra* spp. are one of the few algal species capable of surviving in this zone. Along all three coasts the upper Balanoid (Upper eulittoral) zone is dominated by barnacles, but this zone is also home to a wide variety of winkles, limpets and a few algal species. On the east coast, the upper Balanoid zone is bordered by an oyster belt at its upper limits. On the west and south coasts the lower Balanoid (Mid-eulittoral) zone is generally dominated by dense beds of fleshy macroalgae while on the east coast it is dominated by zoanthids, sponges, mussels and coralline algae (Branch and Branch 1981, Bolton and Stegenga 1987). On the west coast the Lower eulittoral zone is called the Cochlear/Argenvillei zone due to more or less equal densities of the limpets *S. cochlear* and *Scutellastra argenvillei* (Krauss) (Branch and Branch 1981, Maneveldt *et al.* 2009). On the south coast the Lower eulittoral zone is called the Cochlear zone while on the east coast the zone dominated by zoanthids and sponges (lower Balanoid) extends into this zone. The Infratidal (sublittoral fringe) zone is lowest on the shore and is dominated by kelp species (Branch and Branch 1981).

1.8 Observations

Within the intertidal zone of Kalk Bay (False Bay) for example, the dense beds of macroalgae, which are characteristic of the lower Balanoid zone along the south and west coasts (Branch and Branch 1981), are absent. Instead the zone is dominated by the generalist herbivorous limpet *C. oculus*, which has been shown to prevent and inhibit the recruitment and colonization of algae and other invertebrates in the Mid-eulittoral zone (Maneveldt *et al.* 2009). As a consequence, a number of epilithic algal species are found only epizoically on the shells of a variety of molluscan herbivores (*pers. obs.*). Since the study by Maneveldt *et al.* (2009) we have made similar observations across the Cape Peninsula.

1.9 Aims of study

The associations between algae and molluscan herbivores have been widely documented. How algae survive within the rocky intertidal zones is integral to understanding their ecology as they are the main primary producers. Under intense herbivore pressure, epilithic algae are often found to occur solely as epizoics (Steneck 1986, McKinney 1996, Bell 2005). While such knowledge is fairly well documented elsewhere (e.g. Steneck 1986, Warner 1997, Bell 2005, Ayres-Peres and Mantelatto 2010), within a South African context the importance of mollusc shells as secondary substrata is a fairly recent phenomenon (see e.g. Zeeman *et al.* 2013). Following on from the findings of Maneveldt *et al.* (2009), the aim of this research was to determine the relative importance of intertidal mollusc shells as secondary substrata for otherwise epilithic algae. Furthermore, it is the intention of this research to provide data of this nature along a geographic gradient from west to east within the western biogeographic transition zone[1] of South Africa. . In order to adequately determine the relative importance of intertidal mollusc shells as secondary substrata, an understanding of the distributions, densities and biomass of the dominant visible intertidal molluscs is also required. Following previous observations (e.g. Maneveldt *et al.* 2009) we predict that algal percent cover abundance and diversity will be greater on intertidal mollusc shells than on the adjacent rocky primary substratum.

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[1] Within South Africa, False Bay (and the surrounding Peninsula) has the greatest number of range-restricted endemics (Awad *et al.* 2002). The western edge (Cape Peninsula) of the Western overlap region coincides with centres of high sampling activity. This suggests high sampling bias and probably accounts for the finding. The Western overlap region was chosen as a study area to address some of this sampling bias.

2.1 Introduction

South Africa's coastline has been divided into three distinct biogeographic regions (Stephenson and Stephenson 1949, 1972, Penrith and Kensley 1970, Bolton 1986, Bolton and Anderson 1997, Anderson *et al.* 2009). From east to west these biogeographic regions are known as: 1) the Indo-West Pacific Marine Province (a subtropical east coast region); 2) the Agulhas Marine Province (a warm temperate south coast region); and 3) the Benguela Marine Province (a cool temperate west coast region) (Bolton 1986, Bolton and Anderson 1997, Anderson *et al.* 2009). Bordering these regions is what is known as an overlap or biogeographic transition zone in which there is a mingling of the biota of both neighbouring regions. South Africa has two such zones. Although there is a general consensus on the geographic locations of South Africas' coastal biogeographic regions, there is still debate as to the precise boundaries of the transition zones (Bolton 1986, Farrell *et al.* 1993, Bolton *et al.* 2004, Anderson *et al.* 2009). Generally speaking, the eastern transition zone lies between Hlluleka and St. Lucia Bay and is thought to extend as far north as Isipingo/Durban in KwaZulu-Natal (Farrell *et al.* 1993, Bolton *et al.* 2004), while the western transition zone is located roughly between the Cape Peninsula and that area just east of Cape Agulhas (Bolton and Anderson 1997, Leliaert *et al.* 2000).

The western biogeographic transition zone falls between the Benguela Marine Province and the Agulhas Marine Province (Bolton and Anderson 1997, Leliaert *et al.* 2000). This region experiences rapid changes in both temperature and species composition indicative of both provinces (Bolton and Anderson 1997), and is characterized by dense beds of kelp (*Ecklonia maxima* (Osbeck) Papenfuss and *Laminaria pallida* Greville ex J.Agardh (Leliaert *et al.* 2000). Unlike winter months where the sea surface temperatures along the Cape Peninsula are fairly constant (McQuaid and Branch 1984, 1985, Dufois and Rouault 2012), during summer months, the eastern coasts of the Cape Peninsula (falling within False Bay) are generally influenced by warm water from the Agulhas Current whereas the western coast is influenced by upwelled, cold, nutrient-rich water from the Benguela Current (Lucas *et al.* 2014). The water bodies with their different summer sea surface temperatures are separated by very little land (77.15 km; Google Earth) and have inevitably resulted in the high species endemism reported for the area (Stephenson and Stephenson 1972, Emanual *et al.* 1992, Harrison 2002, Bolton *et al.* 2004, Sink *et al.* 2004, Hanekom 2011). Research within the western transition zone has, however, largely been focused around the western extent of the zone, notably as a consequence of the high sampling activity and thus strong sampling bias associated with the closer proximity of the research institutions within the area (Awad *et al.* 2002). With this in mind, the aim of the current project was to devote research effort to intertidal areas east of the Cape Peninsula. Here we compare the benthic intertidal invertebrate density and biomass patterns along the biogeographic gradient from west to east within the western biogeographic transition zone.

2.2 Materials and Methods

2.2.1 Study sites

Surveys of intertidal rocky shore communities were conducted, on a spring tide, during the cooler months of 2011 (July – September), and during forecasted overcast days in the warmer months of October 2011 – February 2012 so as to adequately sample those invertebrates that are more susceptible to high light intensities and high temperatures. Sampling was done at five, more or less equidistant localities (see below) from west to east within the western biogeographic transition zone.

- Kalk Bay (34°7'54.24"S, 18°26'52.56"E), located along the north western shore of False Bay, is moderately exposed to on-shore south-easterly winds and to wave action (Maneveldt *et al.* 2009).
- Rooiels (34°18'3.69"S, 18°48'49.36"E), an exposed coastline located along the south eastern shore of False Bay, experiences prevailing off-shore south-easterly winds that sand blast the eastern facing rock surfaces (Malherbe 2011).
- Sandbaai (34°25'42.85"S, 19°12'2.11"E), located south east of False Bay, is situated within a slight embayment, is moderately protected from south-westerly winds, and is moderately exposed to wave action (Bownes and McQuaid 2006).
- Pearly Beach (34°40'19.06"S, 19°30'29.42"E), located still further south east of False Bay, is exposed to south-westerly winds and to wave action (Engelsman 2009).
- Stinkbaai (34°48'25.17"S, 20° 3'32.39"E), located at Cape Agulhas, is a wave exposed site experiencing strong south-easterly winds in summer and north-easterly winds in winter (Kraaij *et al.* 2008).

2.2.2 Invertebrate densities and biomass

Based on initial observations of species distributions and assemblages across the intertidal zone at all sites, five zones were identified: Supralittoral; upper, Upper eulittoral; lower, Upper eulittoral; Mid-eulittoral; and Lower eulittoral. Sampling was done within each of these zones at all sites along transect lines running more or less perpendicular to the shoreline from mean high water spring (MHWS) tide mark to mean low water spring (MLWS) tide mark, taking care to avoid rock pools. Along each transect line (within each zone), 10 quadrats (0.5 m x 0.5 m) were placed at regular 1 m intervals, so that each zone had 10 replicate samples. Within each quadrat the densities of observed invertebrate species were recorded. Twenty (20) representative individuals of each species were randomly collected and brought back to the laboratory for biomass estimations. Biomass was determined using drained wet weight, with the shell on. An average biomass of the twenty individuals (per species) was calculated and then extrapolated for each quadrat and then per metre squared.

For the purpose of this study, molluscs which are less affected by changes in environmental factors associated with desiccation stress, and that are known to have profound effects on the distributions of other intertidal organisms, are referred to as 'resident' species. Such species included the limpets *Cymbula oculus* (Born), *Scutellastra longicosta* (Lamark), *Scutellastra cochlear* (Born) and *Scutellastra argenvillei* (Krauss). Irrespective of the changing short-term (hours to days), more localised environmental conditions, these species would be readily available for sampling and collection and could thus be used as a proxy for the way the different shores and their communities sampled, might respond over time to different (geographic) environmental conditions.

2.2.3 Data analysis

Invertebrate density and biomass data are presented as means ± standard errors (SE) and graphically represented on a log scale. Using Primer 5, the total density and biomass (for observed invertebrates and 'resident' species) data were subjected to cluster analyses using the Bray-Curtis similarity index by applying the group average linkage. Thereafter, using SPSS (Student Package for Social Sciences), a one-way ANOVA using a Bonferroni Post hoc test was performed on the log transformed data to determine the comparative density and biomass distributions across each shore studied. Analysis was firstly based on the total density and biomass of observed invertebrate species and then on the total density and biomass of 'resident' species. Mean values were sorted in descending order and the *p*-values for the Bonferroni Post hoc test used to assign significance letters (a, b, etc.). The analyses were conducted on both sets of invertebrates (observed invertebrates; 'resident' species) in order to determine which would provide a better geographical pattern. For all tests performed a 95 % confidence limit was applied and so differences amongst treatments were considered statistically significant at $p < 0.05$.

2.3 Results

2.3.1 Localised invertebrate patterns

Based on invertebrate species distributions and assemblages across all sites, five intertidal zones (Supralittoral fringe, upper, Upper eulittoral zone, lower, Upper eulittoral zone, Mid-eulittoral zone, Lower eulittoral zone) were identified (Figures 2.1-2.5). In general, the number of invertebrate species increases down the shore, but is abruptly reduced in the Lower eulittoral zone again.

2.3.1.1 Supralittoral Except at Stinkbaai (Cape Agulhas) where *Helcion pectunculus* (Gmelin) was also sampled, *A. knysnaensis* was the sole invertebrate recorded (Figures 2.1-2.5). Although not recorded in the quadrats (largely due to their comparatively low densities), the limpet was present at all sites (*pers. obs.*) However, even at Stinkbaai, *A. knysnaensis* was the dominant invertebrate.

2.3.1.2 upper, Upper eulittoral

Across the geographic gradient of sites, *Siphonaria capensis* Quoy and Gaimard and *Oxystele variegata* (Anton) were the most noticeable invertebrates in this zone (Figures 2.1-2.5). These species' relative dominance of the zone, however, decreased from west to east as the zone became increasingly co-dominated by a variety of other invertebrates.

2.3.1.3 lower, Upper eulittoral

Of all the zones, this zone had the greatest number of invertebrate species for all study sites (Figs 2.1-2.5). Barnacles (*Tetraclita serrata* Darwin, *Chthamalus dentatus* Krauss) consistently dominated this zone with *C. dentatus* being the most noticeable of the species across the entire geographic range. The invasive Mediterranean mussel *Mytilus galloprovincialis* Lamark was a noticeable feature of the western-most shores (Kalk Bay and more so at Rooiels and Sandbaai), but were absent from the two eastern-most shores (Pearly Beach, Stinkbaai). *Siphonaria capensis* was still a commonly recorded species.

2.3.1.4 Mid-eulittoral

Species richness varied substantially between sites. While not necessarily reflected in the density values, in terms of biomass *C. oculus* was the most characteristic feature of this zone at all sites (Figures 2.1-2.5). The invasive Mediterranean mussel *M. galloprovincialis* again featured at the two western-most shores (Kalk Bay, Rooiels) and was particularly prominent at Rooiels.

2.3.1.5 Lower eulittoral

Of the lower zones, this zone generally had the lowest species richness, largely being dominated by the territorial, gardening limpet *S. cochlear* (Figures 2.1-2.5). Species richness in this zone generally increased from west to east along the geographic gradient. Interestingly, the invasive Mediterranean mussel *M. galloprovincialis* also featured at Sandbaai and Pearly Beach. This latter observation is interesting because the mussel was not observed in the Mid-eulittoral zone at Sandbaai nor in any of the upper zones at Pearly Beach. Also interesting was the general absence of the larger *S. argenvillei* from the distal study sites (Kalk Bay and Sandbaai) although a few scattered individuals were observed that were too infrequent to be recorded (*pers. obs.*).

Table 2.1: List of invertebrate species collected throughout the study.

Taxa	Key to generic names	Main feature
Afrolittorina knysnaensis (Krauss)	*A. knysnaensis*	sea snail/periwinkle
Helcion pectunculus (Gmelin)	*H. pectunculus*	true limpet
Cymbula oculus (Born)	*C. oculus*	true limpet
Siphonaria capensis Quoy and Gaimard	*S. capensis*	sea snail/false limpet
Scutellastra granularis (Linnaeus)	*S. granularis*	true limpet
Scutellastra cochlear (Born)	*S. cochlear*	territorial true limpet
Scutellastra argenvillei (Krauss)	*S. argenvillei*	true limpet
Scutellastra longicosta (Lamark)	*S. longicosta*	true limpet
Oxystele sinensis (Gmelin)	*O. sinensis*	sea snail
Oxystele tigrina (Anton)	*O. tigrina*	sea snail
Oxtstele variegata (Anton)	*O. variegata*	sea snail
Acanthochitona garnoti (Blainville)	*A. garnoti*	chiton
Burnupena sp.	*Burnupena* sp.	whelk
Parvulastra exigua (Lamark)	*P. exigua*	star fish
Tetraclita serrata Darwin	*T. serrata*	barnacle
Octomeris angulosa (Sowerby)	*O. angulosa*	barnacle
Chthamalus dentatus Krauss	*C.dentatus*	barnacle
Actinia equina (Linnaeus)	*A. equina*	anemone
Mytilus galloprovincialis Lamark	*M. galloprovincialis*	mussel
Helcion pectunculus (Gmelin)	*H. pectunculus*	true limpet

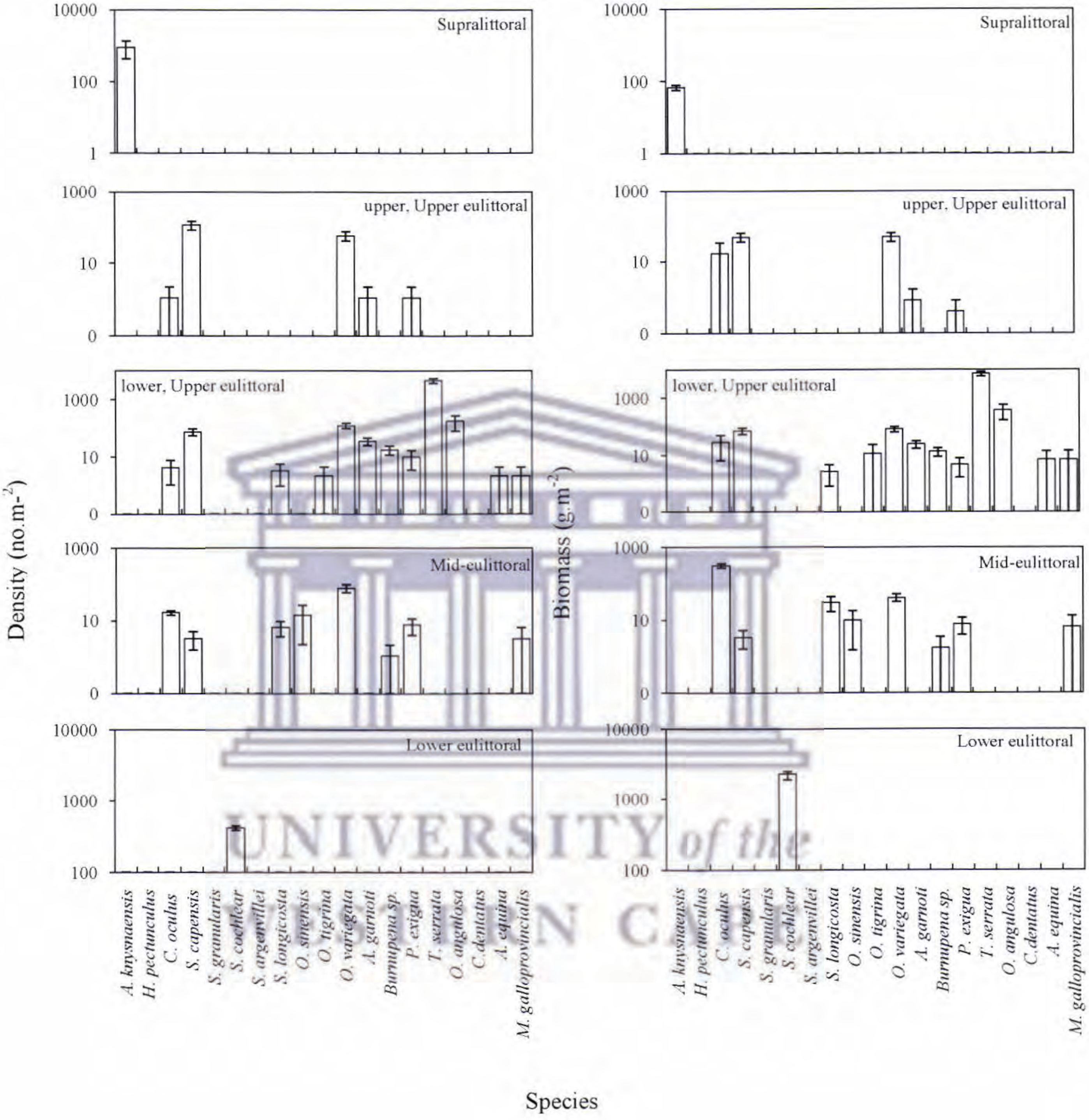

Figure 2.1: Densities and biomass estimations (mean ± SE) of observed invertebrate species at Kalk Bay (Key to generic names are presented in Table 2.1).

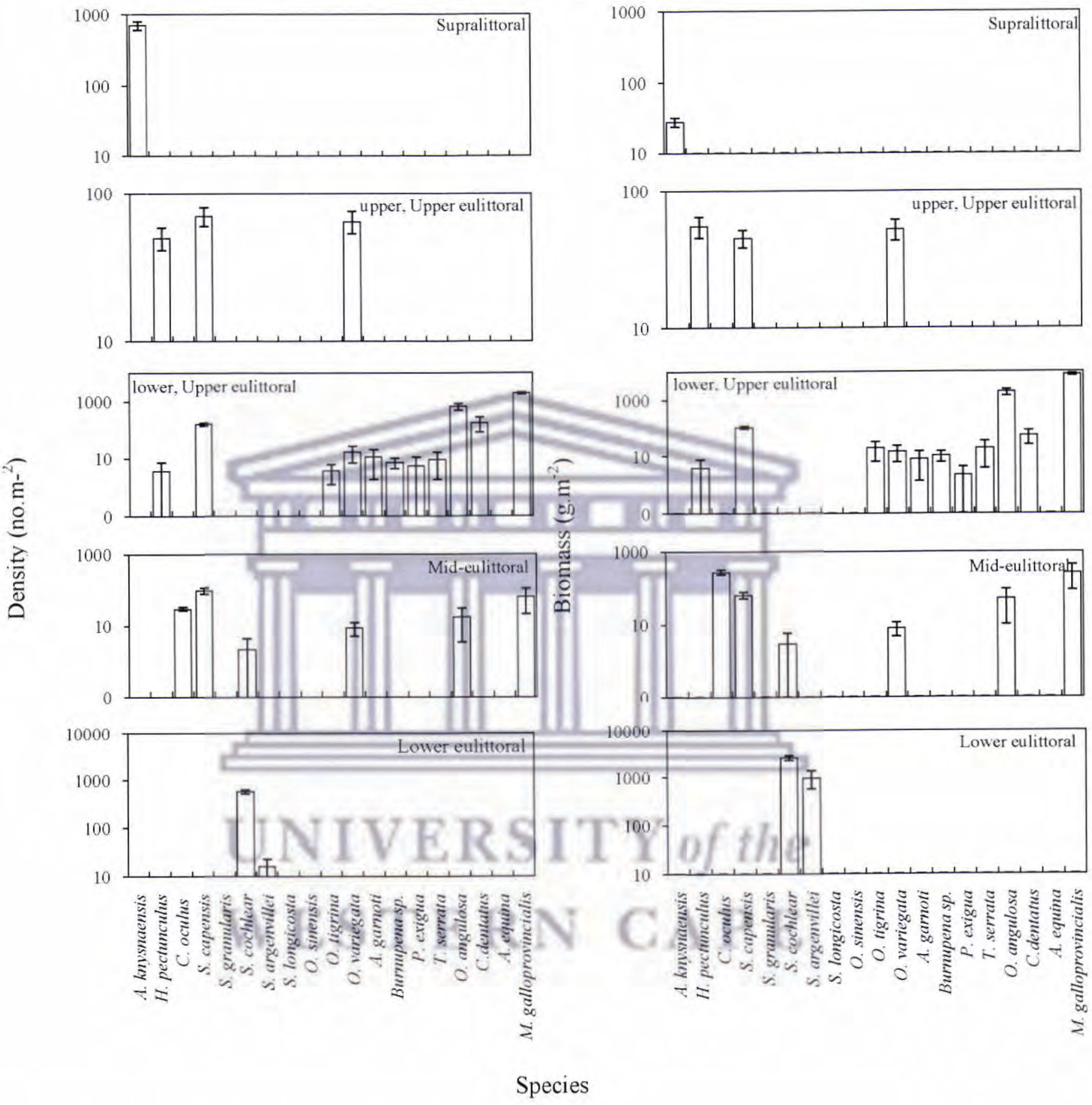

Figure 2.2: Densities and biomass estimations (mean ± SE) of observed invertebrates at Rooiels (Key to generic names are presented in Table 2.1).

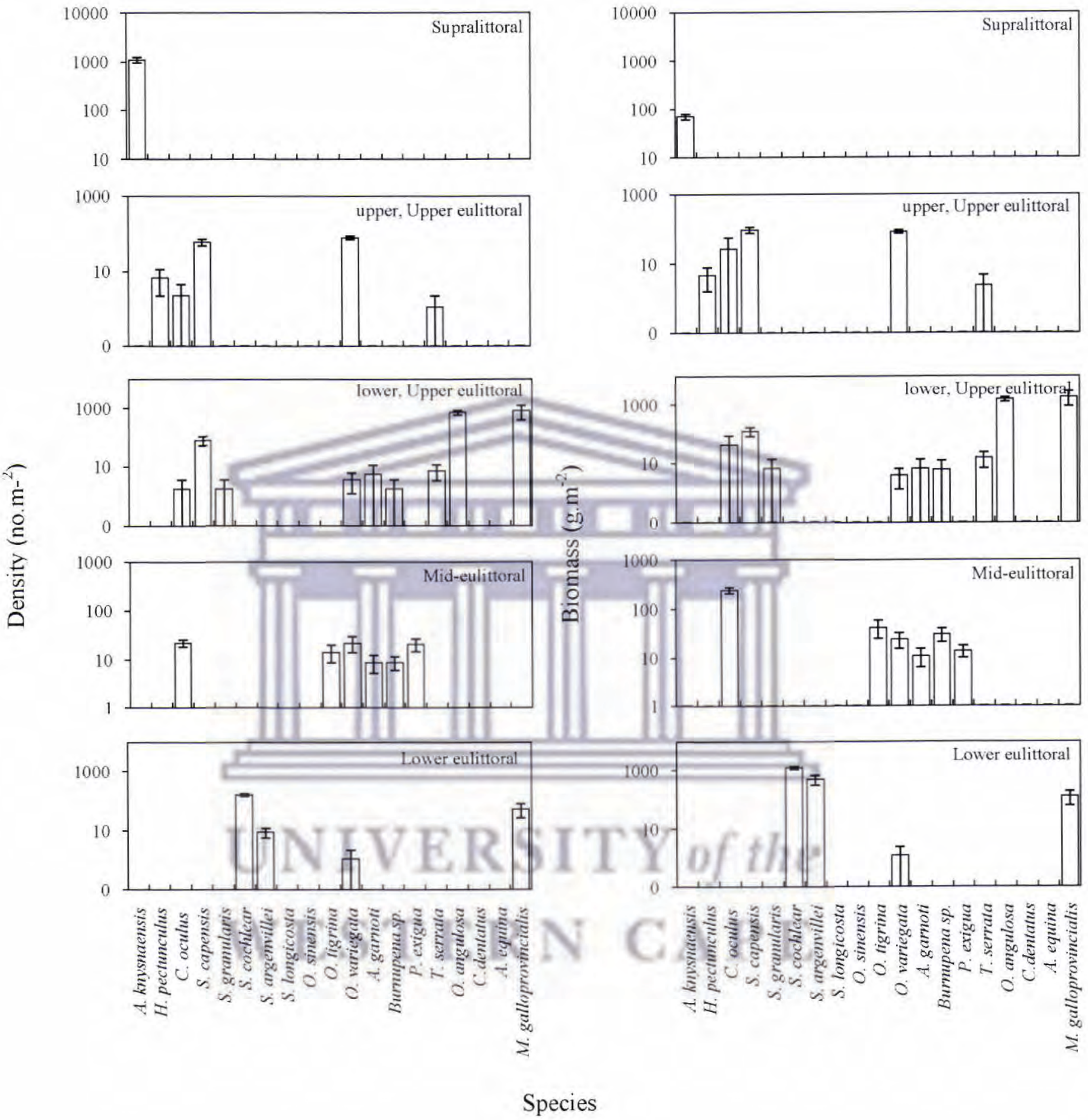

Figure 2.3: Densities and biomass estimations (mean ± SE) of observed invertebrates at Sandbaai (Key to generic names are presented in Table 2.1).

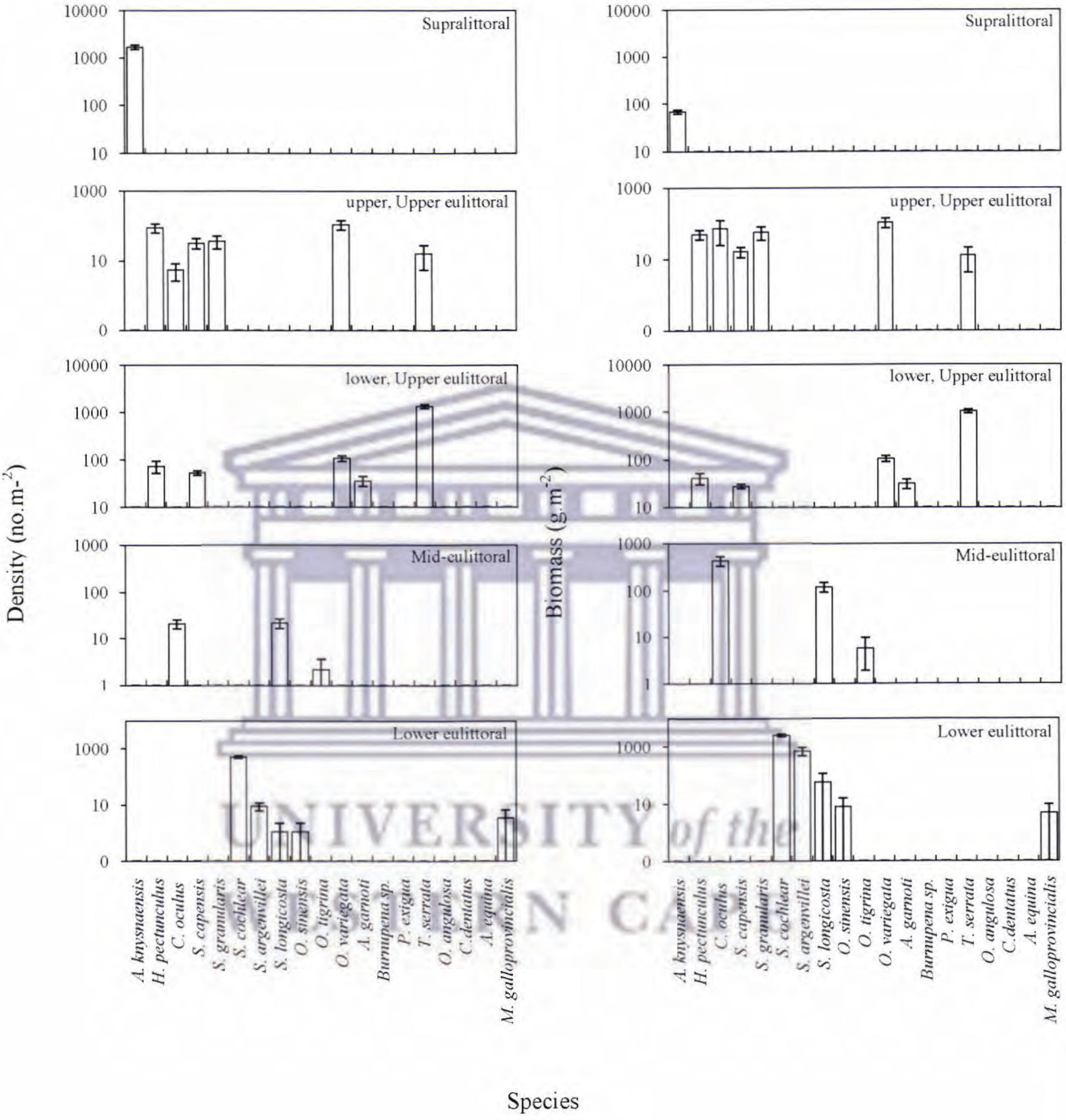

Figure 2.4: Densities and biomass estimations (mean ± SE) of observed invertebrates at Pearly Beach (Key to generic names are presented in Table 2.1).

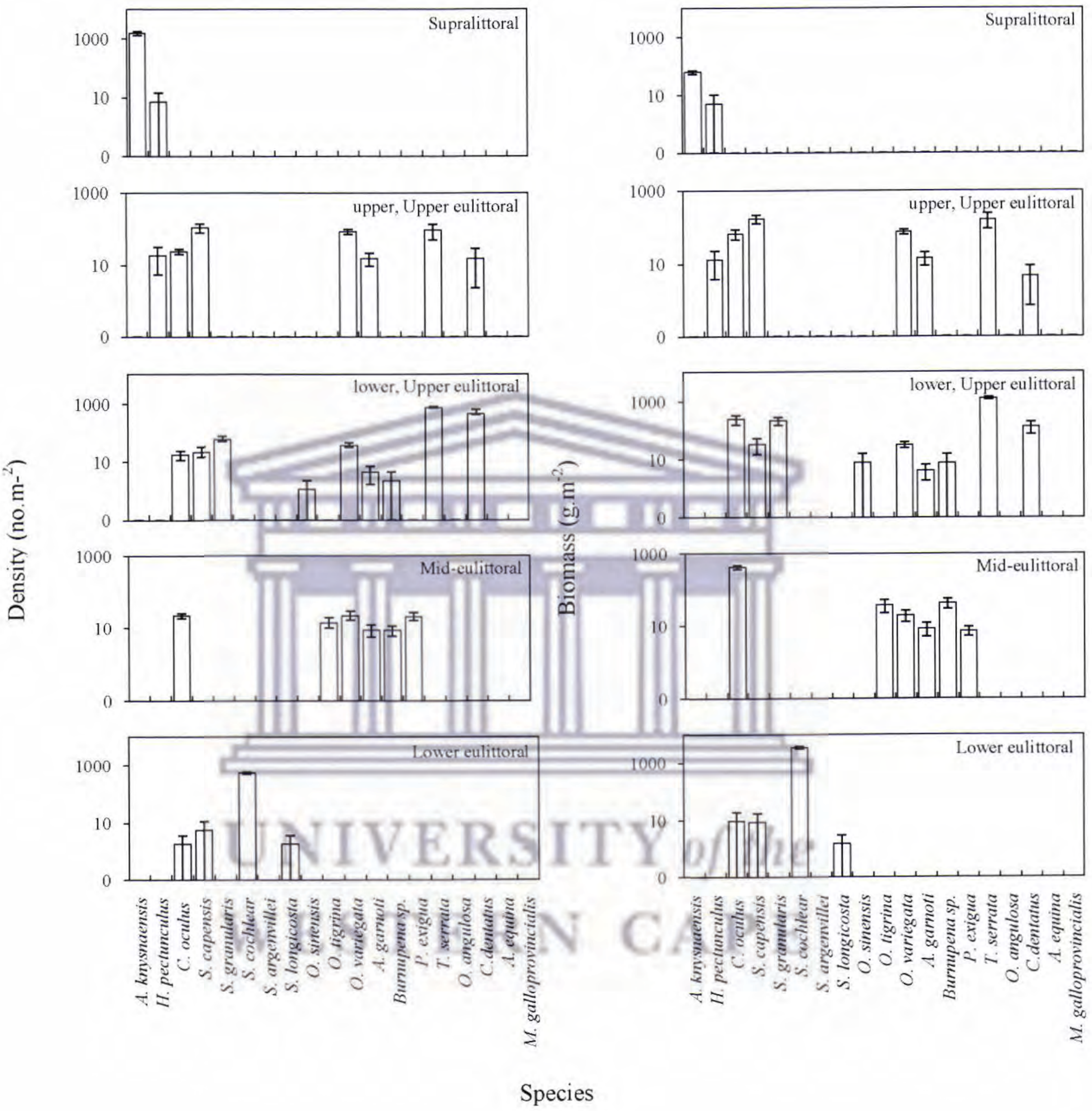

Figure 2.5: Density and biomass estimations (mean ± SE) of observed invertebrates at Stinkbaai (Key to generic names are presented in Table 2.1).

2.3.2 Distribution of density and biomass across shores

An examination of the density and biomass patterns across the shore show similarities from west to east with extreme (distal) sites (Kalk Bay and Sandbaai) displaying patterns more similar to their nearest neighbour sites (Figure: 2.6). Kalk Bay, Rooiels and Sandbaai have their greatest density and biomass within the Mid-eulittoral zone. At Pearly Beach and Stinkbaai, the greatest density was recorded in the Supralittoral fringe and Mid-eulittoral zone, while the greatest biomass was recorded in the Lower eulittoral zone. Sandbaai appears to represent the transitional patterns (for both density and biomass) between that evident from the western (Kalk Bay, Rooiels) and eastern (Pearly Beach, Stinkbaai) sites.

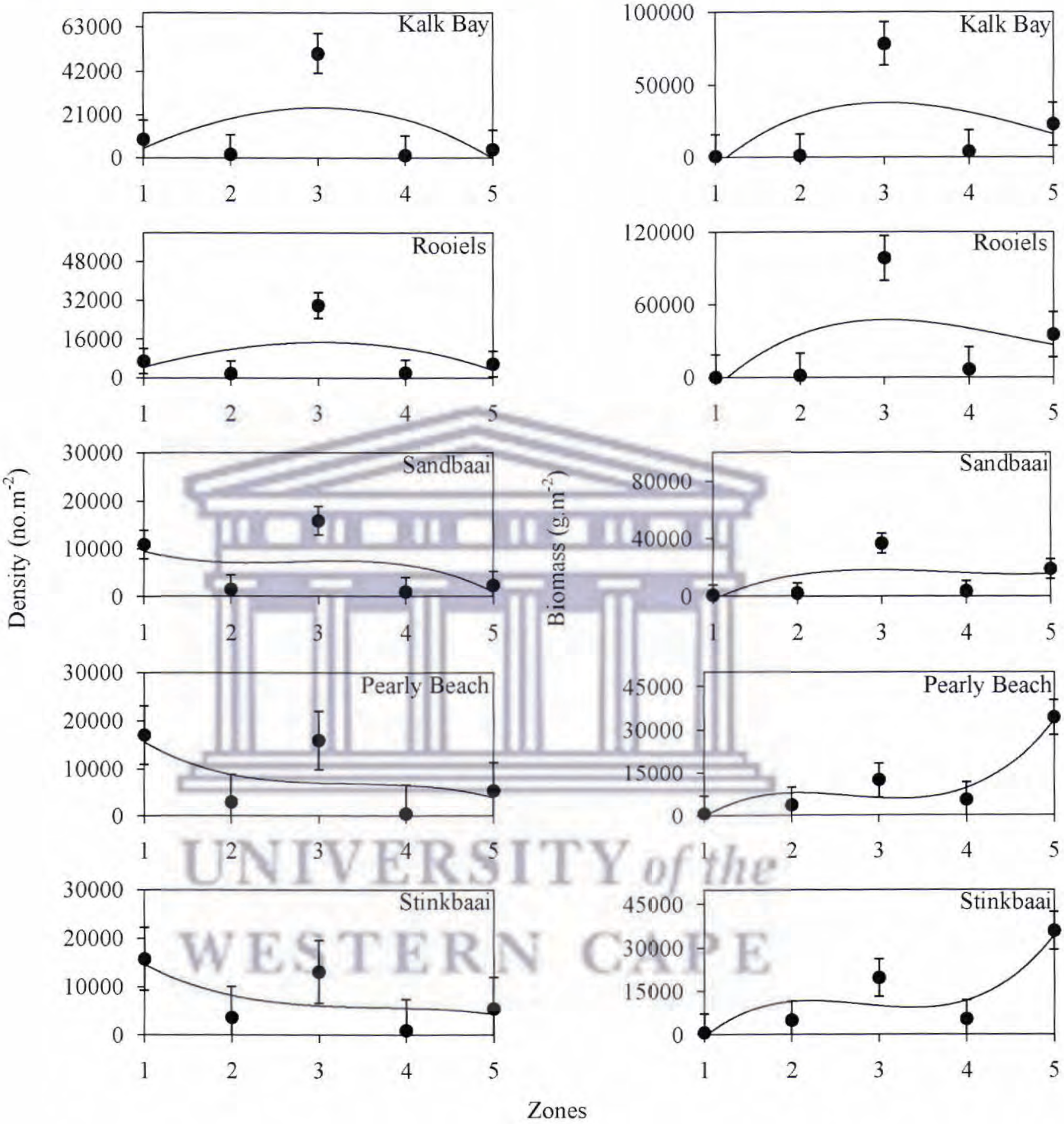

Figure 2.6: Distribution of total invertebrate densities and biomass across the intertidal zone at all sites (Numbers on the X-axis represent zones: 1-Supralittoral, 2 - upper, Upper eulittoral, 3 - lower, Upper eulittoral, 4-Mid-eulittoral, 5-Lower eulittoral). Sites are presented from west (top) to east (bottom).

2.3.3 Geographic patterns

When all invertebrate data are pooled, for both density and biomass, sites group strongly according to the geographic profile (from west to east) (Figures 2.7-2.10). The western-most sites Kalk Bay and Rooiels always cluster closest together (density 92.5 % similarity, p = 0.060; biomass 78 % similarity, p = 0.060) and similarly do the eastern-most sites Pearly Beach and Stinkbaai (density 94 % similarity, p = 1.000; biomass 92 % similarity, p = 1.000) (Figures 2.8 and Figure 2.10). Sandbaai clusters more closely to the eastern-most sites (density 90.5 % similarity, p = 1.000; biomass 86.5 % similarity, p = 1.000) and appears to represent a transition site. The two clusters (Kalk Bay + Rooiels; Sandbaai + Pearly Beach + Stinkbaai) differ in densities by approximately 9.5 % ($p < 0.001$) and in biomass by approximately 35 % ($p < 0.001$).

When data from only the 'resident' species are examined, different patterns emerge (Figures 2.11-2.14). For density, the same geographic pattern is observed (Figures 2.11-2.12). The western-most sites Kalk Bay and Rooiels again cluster closest together (79 % similarity, p = 0.058) and similarly do the eastern-most sites Pearly Beach and Stinkbaai (density 90 % similarity, p = 1.000). This time, however, Sandbaai clusters more closely to the western-most sites (55% similarity), even though it remains statistically different to them ($p < 0.001$). The two clusters (Kalk Bay + Rooiels + Sandbaai; Pearly Beach + Stinkbaai) differ by 82 % ($p < 0.001$) (Figure 2.12). In contrast to when all invertebrates are pooled, when only 'resident' species biomass is analysed (Figures 2.13-2.14), the eastern sites Pearly Beach and Stinkbaai pool together (92.5 % similarity, p = 1.000) and cluster with Rooiels (82.5 %, p = 1.000). In contrast to the density data, for biomass Kalk Bay and Sandbaai cluster as a unit (82.5 % Similarity, p = 0.940). The two groups (Kalk Bay + Sandbaai; Rooiels + Pearly Beach + Stinkbaai) differ by 27.5 % ($p < 0.001$). 'Resident' species biomass data cluster according to exposure. The exposed sites (Kalk Bay, Sandbaai) have greater biomass of 'resident' species than the semi-exposed sites (Rooiels, Pearly Beach, Stinkbaai) ($p < 0.001$).

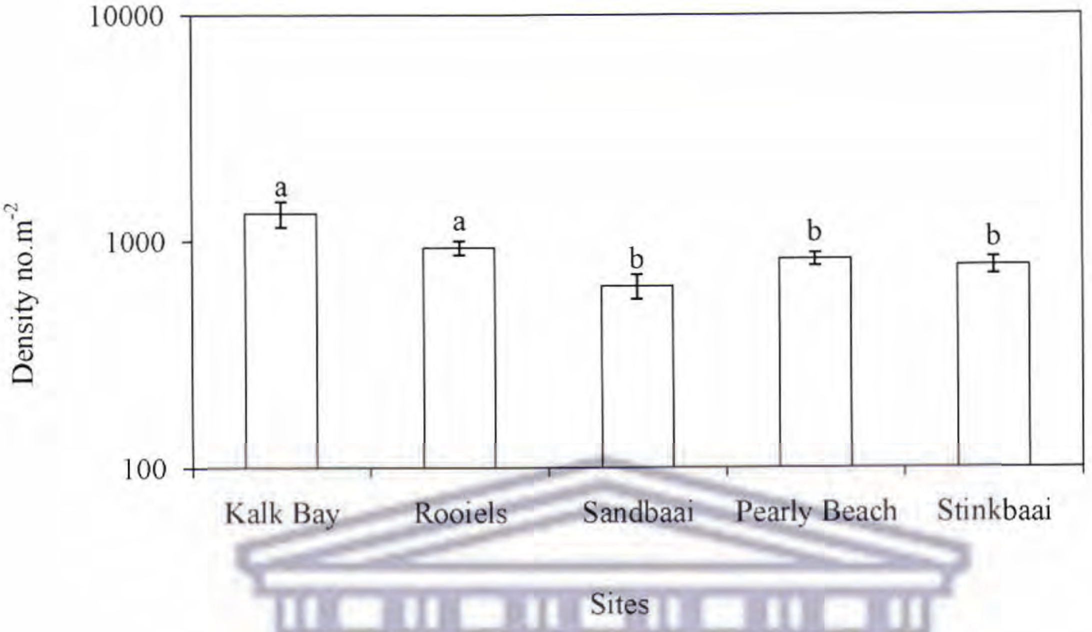

Figure 2.7: Density (mean ± SE) of observed invertebrate species reordered for each site. Data are presented according to the geographical location of the study sites from west to east. Bars with the same letters are not statistically different.

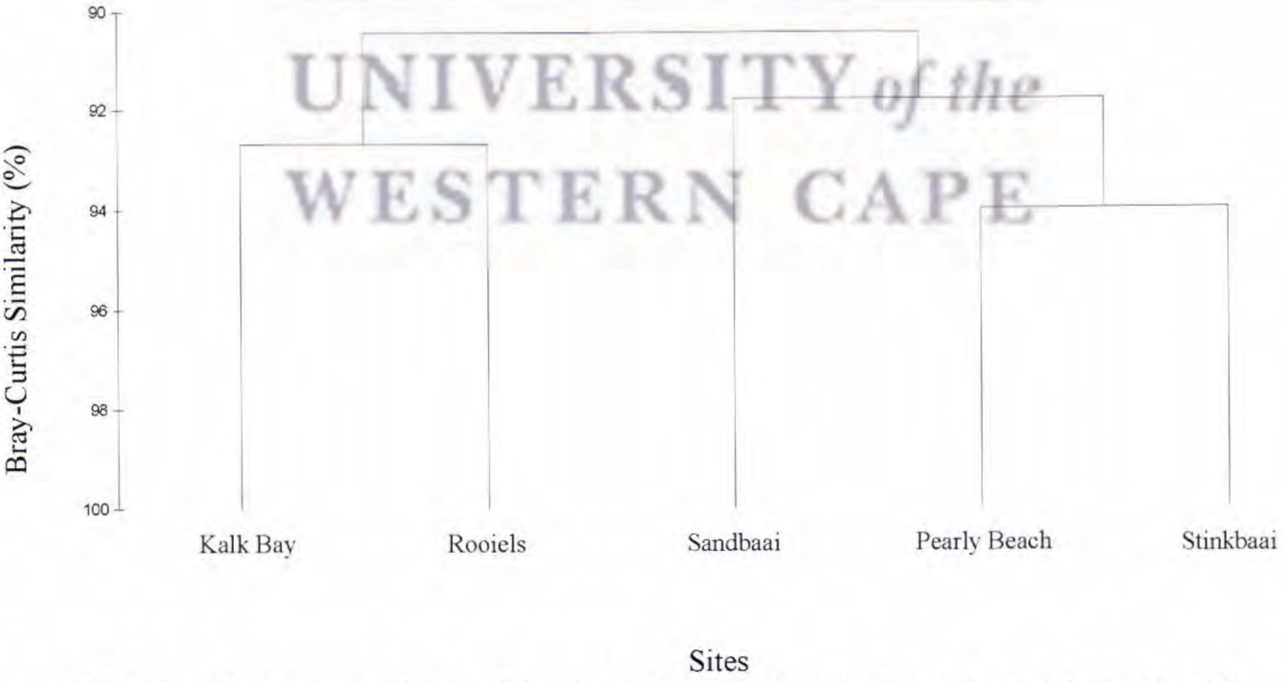

Figure 2.8: Dendrogram of the five localities (Bray-Curtis index) based on total densities of observed invertebrate species.

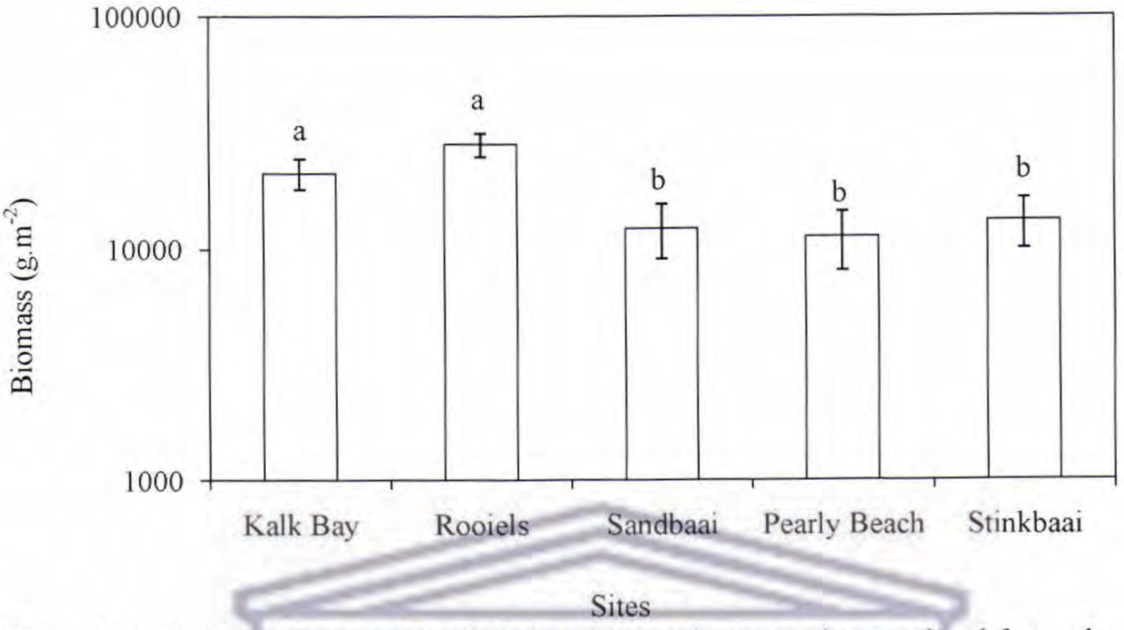

Figure 2.9: Biomass (mean ± SE) of observed invertebrate species reordered for each site. Data are presented according to the geographical location of the study sites from west to east. Bars with the same letters are not statistically different.

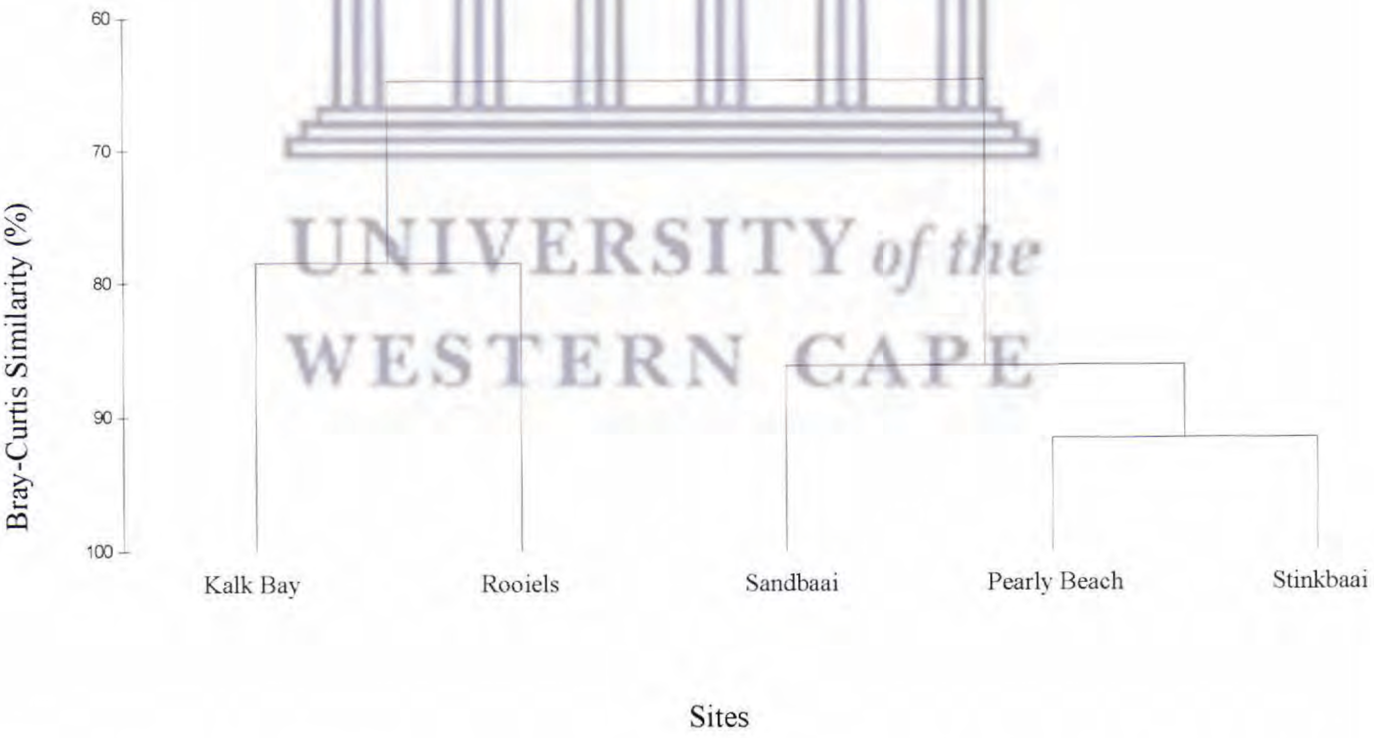

Figure 2.10: Dendrogram of the five localities (Bray-Curtis index) based on observed biomass of all invertebrate species.

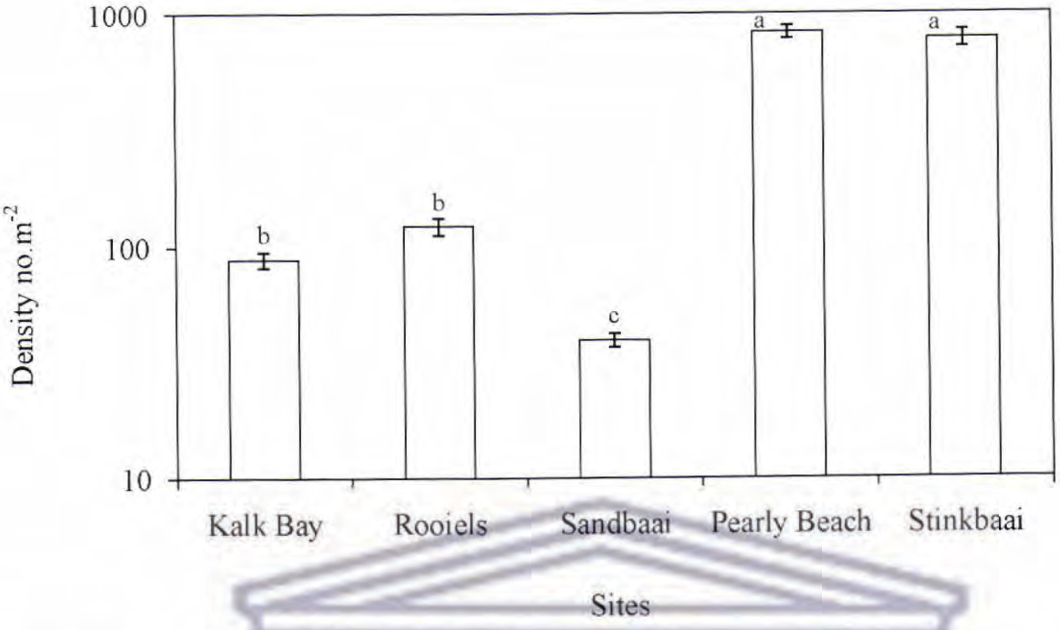

Figure 2.11: Density (mean ± SE) of all 'resident' species recorded for each site. Data are presented according to the geographical location of the study sites from west to east. Bars with the same letters are not statistically different.

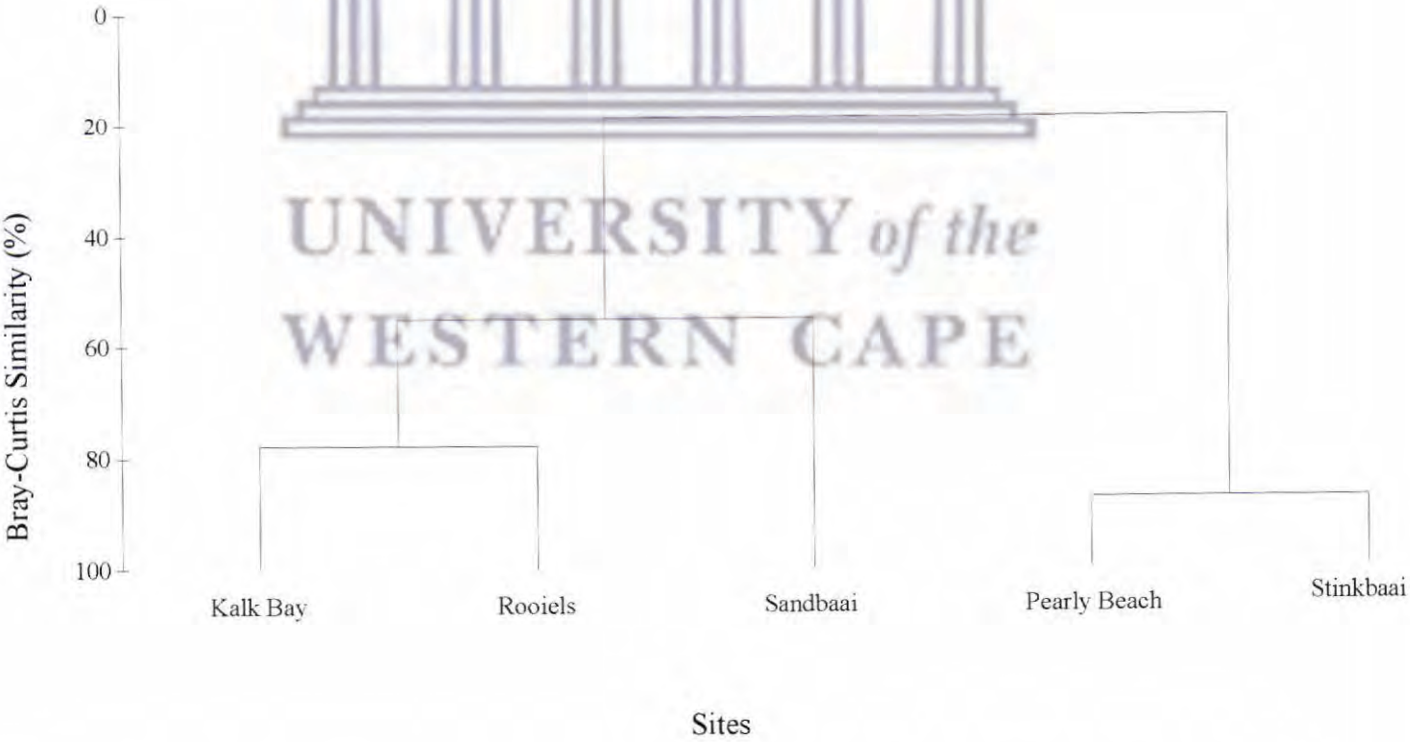

Figure2.12: Dendrogram of the five localities (Bray-Curtis index) based on total density of all 'resident' species

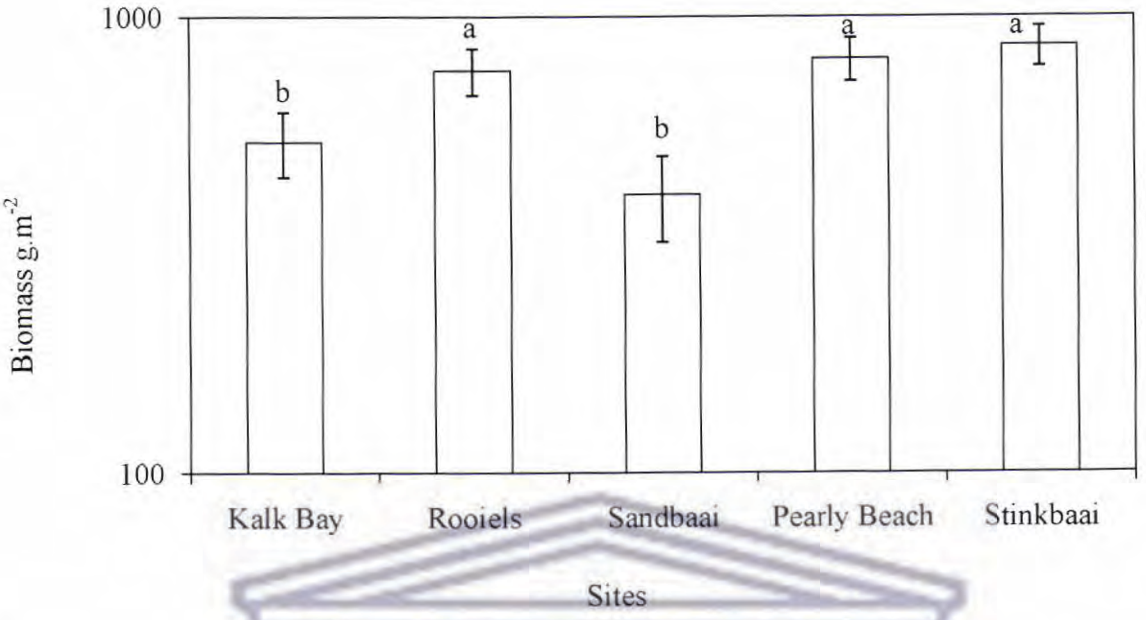

Figure 2.13: Biomass (mean ± SE) of all 'resident' species recorded for each site. Data are presented according to the geographical location of the study sites from west to east. Bars with the same letters are not statistically different.

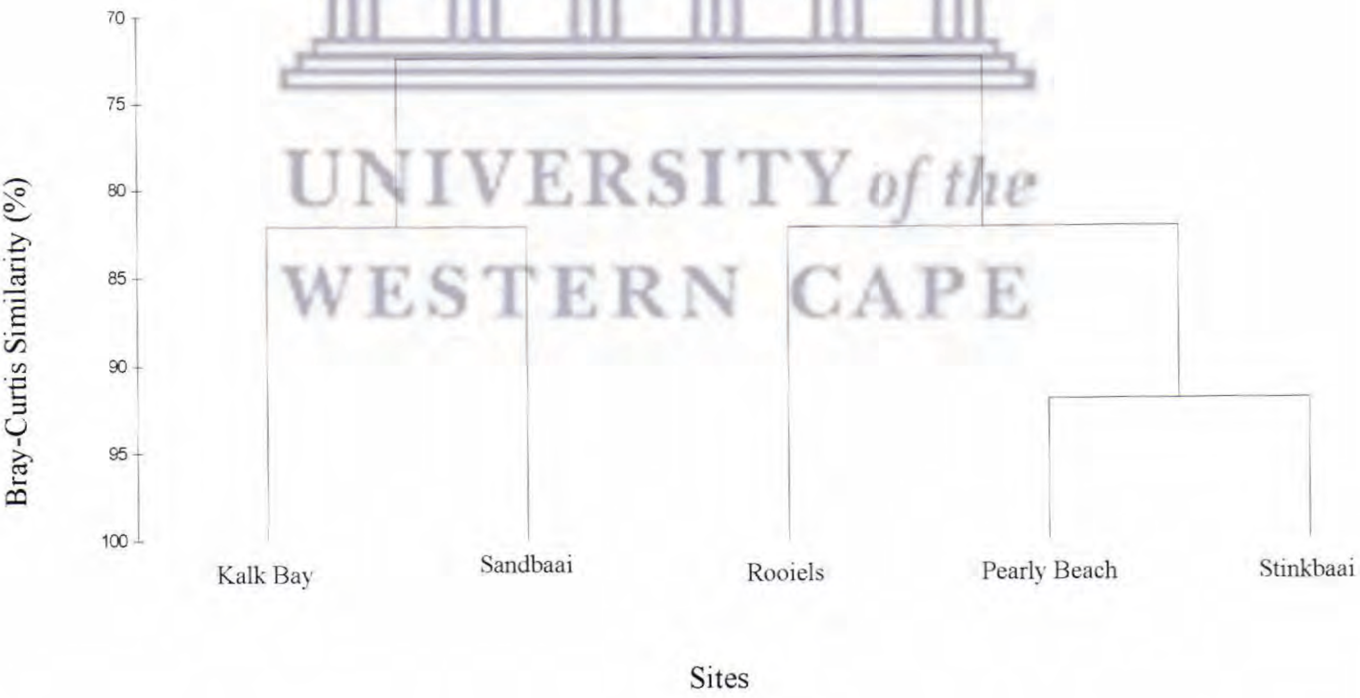

Figure2.14: Dendrogram of the five localities (Bray-Curtis index) based on total biomass of all 'resident' species.

2.4 Discussion

With a few notable exceptions (presence of the invasive mussel *Mytilus galloprovincialis* and the general absence of barnacles at most Mid-eulittoral zones sites), the distribution patterns of invertebrates within all zones at all sites studied are consistent with that published for the South African south coast (Branch and Branch 1981). The invasive marine mussel *Mytilus galloprovincialis*, which was found to varying degrees at all sites except the eastern-most Stinkbaai, is the most successful marine invasive species in South Africa. This is largely due to the species' high fecundity, high larval survival rate, high colonisation rate and tolerance to desiccation stress (McQuaid and Phillips 2000, Branch and Steffani 2004, Robinson *et al.* 2004, Robinson *et al.* 2005, Robinson *et al.* 2007, Nicastro *et al.* 2008). First recorded in 1979 in Saldanha Bay (west coast, South Africa), the species has extended its range as far east as East London (Steffani and Branch 2003, Robinson *et al.* 2005). The mussel has the ability to completely change the structure of rocky intertidal shores by displacing key species (Robinson *et al.* 2004, Bownes and McQuaid 2006, Robinson *et al.* 2007) and so it was perhaps not surprising to encounter it in this study. It is strange though that we did not record the species at Stinkbaai.

The absence of barnacles from the Mid-eulittoral zone at most sites (except at Rooiels) was another notable exception to the published literature. The reason for this absence was most likely the presence of high densities of the limpet *C. oculus* (see Maneveldt *et al.* 2009). It is well known that limpets have a great effect on barnacle colonization (Blinn *et al.* 1989, Dye 1995, Hunt and Scheibling 1997, Chan and Williams 2003, Chan *et al.* 2006, Aguilera and Navarrete 2007, Maneveldt *et al.* 2009). *Cymbula oculus*, through indiscriminate predation of invertebrate larvae (Maneveldt *et al.* 2009) and also by exerting a bulldozing effect on especially new recruits, more than likely limits the distribution and densities of barnacles along shores where the limpet has achieved moderately high densities (see also Blinn *et al.* 1989, Chan and Williams 2003).

Similarly as with the zonation patterns, the peaks in density and biomass along the mid-shore, at least for the western-most sites, are consistent with the published literature (e.g. Menge and Farrell 1989, Bustamante *et al.* 1997). This pattern is reported to result from the inability of most grazers to effectively control the recruitment and colonisation of sessile organisms along the mid-shore (Lewis 1964, Newell 1979, Bustamante *et al.* 1997). The eastern-most sites, however, bear a different pattern with similarly high invertebrate densities in the high shore and comparatively greater biomass on the low shore. It should be stressed though that the comparable densities in the high shore and greater biomass on the low shore at these eastern sites is rather a consequence of: 1) the much reduced invertebrate densities and biomass within the mid-shore environments at these eastern sites; and 2) the comparatively greater densities of the territorial gardening limpet *Scutellastra cochlear* at Stinkbaai. It may well also be that the few invertebrate grazers along the mid-shore at the more exposed eastern sites are more effective on these shores than they typically are at the western-most shores.

Much research has been conducted on the distinguishing characteristics of rocky shores and their varying degrees of exposure (to wave and wind) (Ballantine 1961, Stephenson and Stephenson 1974, Seapy and Littler 1978, McQuaid and Branch 1984, 1985, Bustamante *et al.* 1997, Johnson *et al.* 1997). It has been widely publicised that invertebrate biomass increases with an increasing degree of exposure (McQuaid and Branch 1985, Bustamante *et al.* 1997, Ricciardi and Bourget 1999). While this has proven true for the 'resident' species observed in this study, it did not prove to be so when the biomass of all invertebrates were pooled. At least within the western biogeographic transition zone, there is a strong geographic pattern in invertebrate biomass that is largely independent of the degree of exposure. Having said this, it may well be that the differences in the degrees of exposure (exposed vs semi-exposed) between the sites from this study may indeed be only minor and thus no clear differences based on exposure might be evident. Transition zones represent the most extreme limit of a species' distribution and as a result many species are present, but occur in low densities and biomass (McQuaid and Branch 1984, Awad *et al.* 2002).Overall, Sandbaai displayed the lowest invertebrate densities and biomass suggesting that within the western biogeographic transition zone this location may represent the internal transitioning area for the larger majority of both west coast and south coast invertebrate species found in the biogeographic transition zone.

Logically, a more holistic view of the relationships between the five locations should be evident when one considers the total density and biomass of all invertebrate species. The data shows a consistent geographical relationship from west to east for invertebrate density and biomass and so it seems that the degree of exposure is of lesser importance than the physical location within the western biogeographic transition zone.

In conclusion, with a few notable exceptions, the zonation patterns within the western biogeographic transition zone follow that which has previously been reported for South African southwest coast rocky shores. Observing only 'resident' species are probably less reliable because different outcomes are presented when comparing density and biomass data. Furthermore, examination of only 'resident' species does not show any clear geographic trends. This therefore suggests that the host of other invertebrate species add huge value to our understanding of community structure and ecosystem dynamics on rocky shores.

3.1 Introduction

The exploitation of microhabitats tends to increase the biodiversity of a particular area (Bell 2005). In marine ecosystems, mollusc shells often provide microhabitats as well as increased surface area for the settlement of a variety of epizoic organisms (Bell 2005, Nakin and Somers 2007, Wernber *et al.* 2010). Such secondary substrata become particularly important in rocky intertidal benthic environments where primary space is the most limiting resource, largely because it is often non-renewable (Dayton 1971, Branch 1985, Bell 2005). Mollusc shells, even empty or fragmented ones (Vance 1978, Kidwell and Gyllenhall 1998), affect the heterogeneity and structure of benthic communities because they alter the availability of resources to other organisms (Black and Peterson 1987, Gutierrez *et al.* 2003, Bell 2005). These alterations may occur directly by creating microhabitats and secondary habitats for otherwise epilithic organisms (Karlson and Shenk 1983, Gutierrez *et al.* 2003), or indirectly by affecting the biotic and abiotic factors surrounding the shell (Vance 1978, Gutierrez *et al.* 2003). In either case, diversity of sessile organisms is greatly increased by the presence of such secondary substrata (Lohse 1992, Creed 2000, Barnes 2001, Bell 2005).

The majority of published research on marine epizoic interactions (e.g. Lohse 1992, Barnes 2001, Schejter and Bremec 2007) have shown that epizoic organisms do not display settlement preferences, but that the resultant associations are simply as a consequence of the limitation of primary space. While research on the relative importance of secondary space is gaining momentum in the international literature, such evidence (e.g. Zeeman *et al.* 2013) is limited for South African shores and has largely only been hypothesised (e.g. Eager 2010). Even more limited are data comparing the importance of secondary space along geographic gradients. The aim of this study was to document the importance of limpet and winkle shells as secondary space on South African rocky shores within the western biogeographic transition zone.

3.2 Methods and Materials

3.2.1 Study sites and sampling procedures

Sampling was done across the entire intertidal zone at: Kalk Bay (34° 7'54.24"S, 18°26'52.56"E); Rooiels (34°18'3.69"S, 18°48'49.36"E); Sandbaai (34°25'42.85"S, 19°12'2.11"E); Pearly Beach (34°40'19.06"S, 19°30'29.42"E); and Stinkbaai (34°48'25.17"S, 20° 3'32.39"E) (see chapter 2 for a description of these sites). Based on initial observations of species distributions and assemblages across the intertidal zone at all sites, five zones were identified: Supralittoral; upper, Upper eulittoral; lower, Upper eulittoral; Mid-eulittoral; and Lower eulittoral. Sampling was done within each of these zones at all sites along transect lines running more or less perpendicular to the shoreline from mean high water spring (MHWS) tide mark to mean low water spring (MLWS) tide mark, taking care to avoid rock pools. Along each transect line (within each zone), 10 quadrats (0.5 m x 0.5 m) were placed at regular 1 m intervals, so that each zone had 10 replicate samples. Within quadrats, algal and lichen percent cover on the primary substratum was recorded.

In addition, twenty (20) photographs of the first encountered, mature 'resident' limpets[1] within quadrats from the Mid- (*S. longicosta*, *C. oculus*) and Lower eulittoral (*S. cochlear*, *S. argenvillei*) zones were taken. These molluscs are less affected by changes in environmental factors associated with desiccation stress, and are known to have profound effects on the distributions of other intertidal organisms. Irrespective of the changing short-term (hours to days), more localised environmental conditions, these species would be readily available for sampling and collection and could thus be used as a proxy for the way the different shores and their communities sampled, might respond over time to different (geographic)

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[1] See chapter 2 for a definition of a 'resident' limpet.

environmental conditions. Only these two zones were sampled as they presented the greatest density of possible secondary substrates (see chapter 2). Photographs were processed using digital imaging software (see below) to determine epizoic percent cover on the limpet shells.

Even though *Oxystele sinensis* winkles were not classified as 'resident' molluscs, virtually all mature winkles encountered bore epizoics. Other species of winkles encountered were not found to bear any epizoics. Consequently individuals of *O. sinensis* were collected to determine the potential contribution of winkle shells to the secondary substrata. Similarly as with other molluscs, the first twenty (20) *O. sinensis* individuals encountered along a transect line were also collected. Due to their largely shallow subtidal and tide pool distributions (Branch and Branch 1981, Griffiths 1981, Branch *et al.* 1994, Pulfrich and Branch 2002), *O. sinensis* individuals were not readily encountered in the intertidal zone at all sites. At such sites deliberate collections of winkles were made from low shore rock pools. Under such conditions, the first 20 winkles encountered where collected.

3.2.2 Data analysis

To determine cover of epizoics (as a percentage of the total limpet shell surface) on 'resident' limpets, the image analysis programme ImageJ (Rasband W.S., Maryland, USA) was used (n = 16 representative limpets per species). For the winkles, three dimensional images were taken using the 3dMD acquisition system(3dMDface^{TM}System, 3dMD Ltd., Atlanta, GA, USA) to accommodate their spherical shape (Figure: 3.2.2.1). This system allowed for a single 270° 3D image capture as well as a 2D rendering of the images for direct comparison and analysis. Winkles were rotated a full 180° to compensate for the remaining un-captured portion and the two 3D images merged to render a full 360° capture. The 2D rendered images were then analysed using the ImageJ image analysis programme (n = 20 winkle shells).

Similarly as with the limpets, epizoic cover was determined as a percentage of the total winkle shell surface.

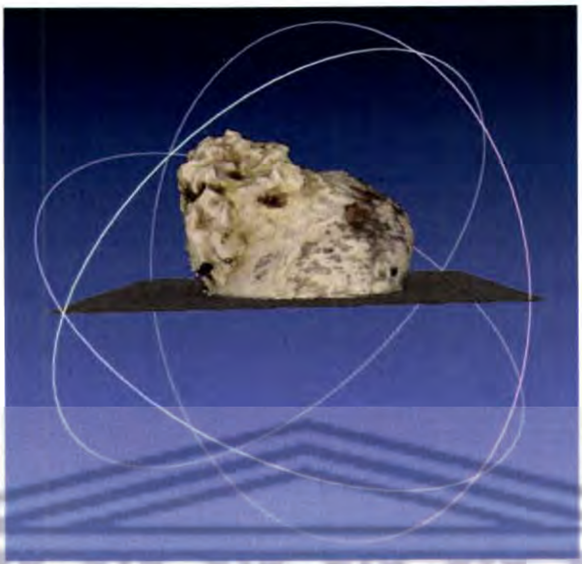

Figure 3.2.2.1: A 2D rendering of the 3D image capture of a single *O. sinensis* winkle bearing a coralline epizoic.

3.2.3 Statistical analysis

Using presence (value = 1) / absence (value = 0) analysis, a Mann-Whitney U test was conducted to determine differences between individual epizoic species occurring on the primary rock substratum and on (secondary substrata) shells of 'resident' molluscs. Epizoics, on their respective substrata, were compared using a Kruskal-Wallis pairwise, unequal variance comparison to establish differences in their percent cover. Data were then presented as percentages while the statistical letters assigned to them were based on the ranking of the Kruskal-Wallis values, resulting in standard error bars not always corresponding. A 95 % confidence limit was applied and so data were considered statistically significant at $p < 0.05$. All data are presented as means ± standard error (SE). All statistical analysis was conducted using SPSS (Student Package for Social Science).

To determine diversity, the Shannon index (eq. 1) and the Inverse Simpson's index (eq. 2) were used (Magurran 2004).The Inverse Simpson's index is more robust than the Shannon index as it is less dependent on rare species (Magurran 2004). The latter index was therefore used to rank the diversity between substrata. Data were also jack-knifed to generate an overall index of diversity (with associated 95% confidence limit) for each sample following the protocols outlined by Magurran (2004). In order to determine differences in diversity between substrata, a Friedmans two-way ANOVA was used (Juan and Hewitt 2011). Species occurring in less than 5 % of the samples were excluded from the diversity statistics as rare species reflect stochastic sampling effects and therefore add noise rather than information to the statistical solution (Gauch 1982, Clarke and Green 1988, Clark and Gorly 2001, Bailey *et al*. 2004).

$$H' = -\Sigma\, p_i \ln p_i \qquad \text{eq. 1}$$

Where:

H' = Shannon index

$\Sigma$is the sum of

pi = the proportion of individuals found in the ith species

ln= natural log

$$\check{D}=1-\Sigma((ni(ni-1))/(N(N-1))) \qquad \text{eq. 2}$$

Where:

$\check{D}$= Inverse Simpson's index

$\Sigma$is the sum of

ni=number of individuals in the ith species

N= total number of individuals

In addition to these diversity indices, the Simpson's measure of evenness (eq. 3) (Magurran 2004) was calculated to help explain the resulting diversity values.

$$E = \frac{1/\check{D}}{S} \qquad \text{eq. 3}$$

Where:

E= Simpson's measure of evenness

$\check{D}$=Inverse Simpson's index

S= number of species in the sample

Epizoics on the shells of *O. sinensis* were compared against those on the primary rocky substratum using a Kruskal-Wallis pairwise comparison to establish differences in percent cover within sites. Data were then presented as percentages while the statistical letters assigned to them were based on the ranking of the Kruskal-Wallis values, resulting in standard error bars not always corresponding. A 95 % confidence limit was applied and so data were considered statistically significant at $p < 0.05$. All data are represented as means ± standard error (SE).

3.3 Results

3.3.1 Primary substratum algal percent cover

At all sites within the Supralittoral zone, algal cover was completely absent (Figures 3.3.1-3.3.5). Within the upper, Upper eulittoral zone at all sites, the primary substratum was similarly comprised of predominantly bare rock. Algal and lichen diversity generally increased down the shore, but were some what reduced in the Mid-eulittoral zone.

3.3.2 Importance of resident limpets as secondary substrata

Although all limpets examined bore a number of epizoic algae and lichens, overall, of the two zones sampled, secondary substratata are only comparatively important in the Mid-eulittoral zone (Table 3.3.1). This trend is also evident at Kalk Bay (Table: 3.3.2). Overall, the 'resident' limpets *C. oculus* and *S. longicosta* are far more important as secondary substrates at these latter two sites than at the other sites sampled (Figure 3.3.6). Despite the limpets *S. cochlear* and *S. argenvillei* (Figure 3.3.7) bearing comparatively higher numbers of epizoic species than either *C. oculus* or *S. longicosta*, the former two limpets do not appear to be more important than the surrounding primary substrata that they inhabit (Tables 3.3.1 – 3.3.6). When taxa were grouped into functional groups, no statistical difference can be observed between either primary or secondary substrata within either the Mid-eulittoral or the Lower eulittoral zones (Table: 3.3.7). This is so despite foliose and filamentous algae being absent from the primary substratum within the Mid-eulittoral zone at all sites. Overall, intertidal mollusc shells are important secondary substratea along the western shores (Kalk Bay and Rooiels), but are less so along the eastern shores (Pearly Beach and Stinkbaai).

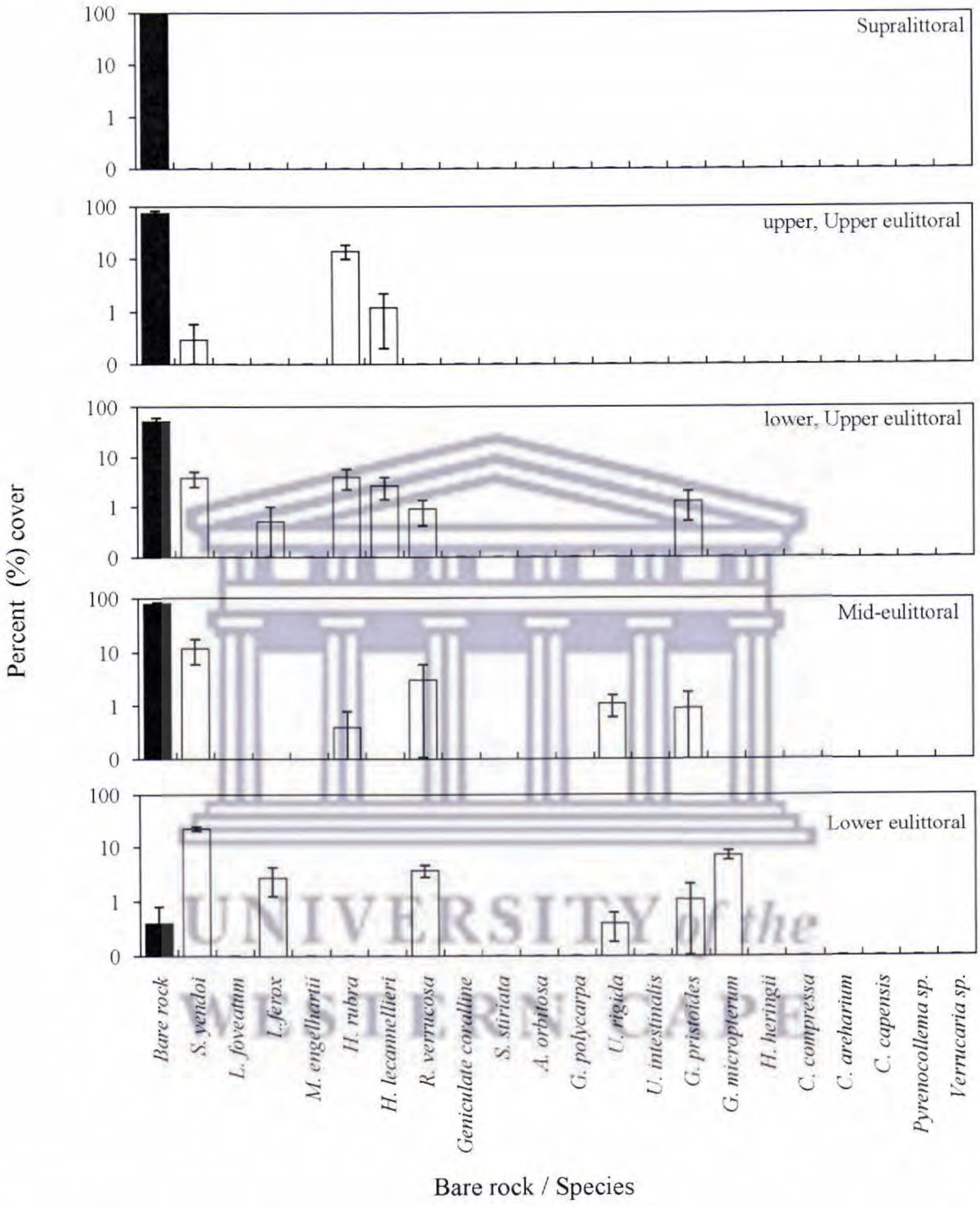

Figure 3.3.1: Algal and lichen percent cover (mean ± SE) abundance on the primary rocky substratum at Kalk Bay. Note that all species encountered for the study are presented on the X-axis (Key to generic names presented in Table 3.3.1).

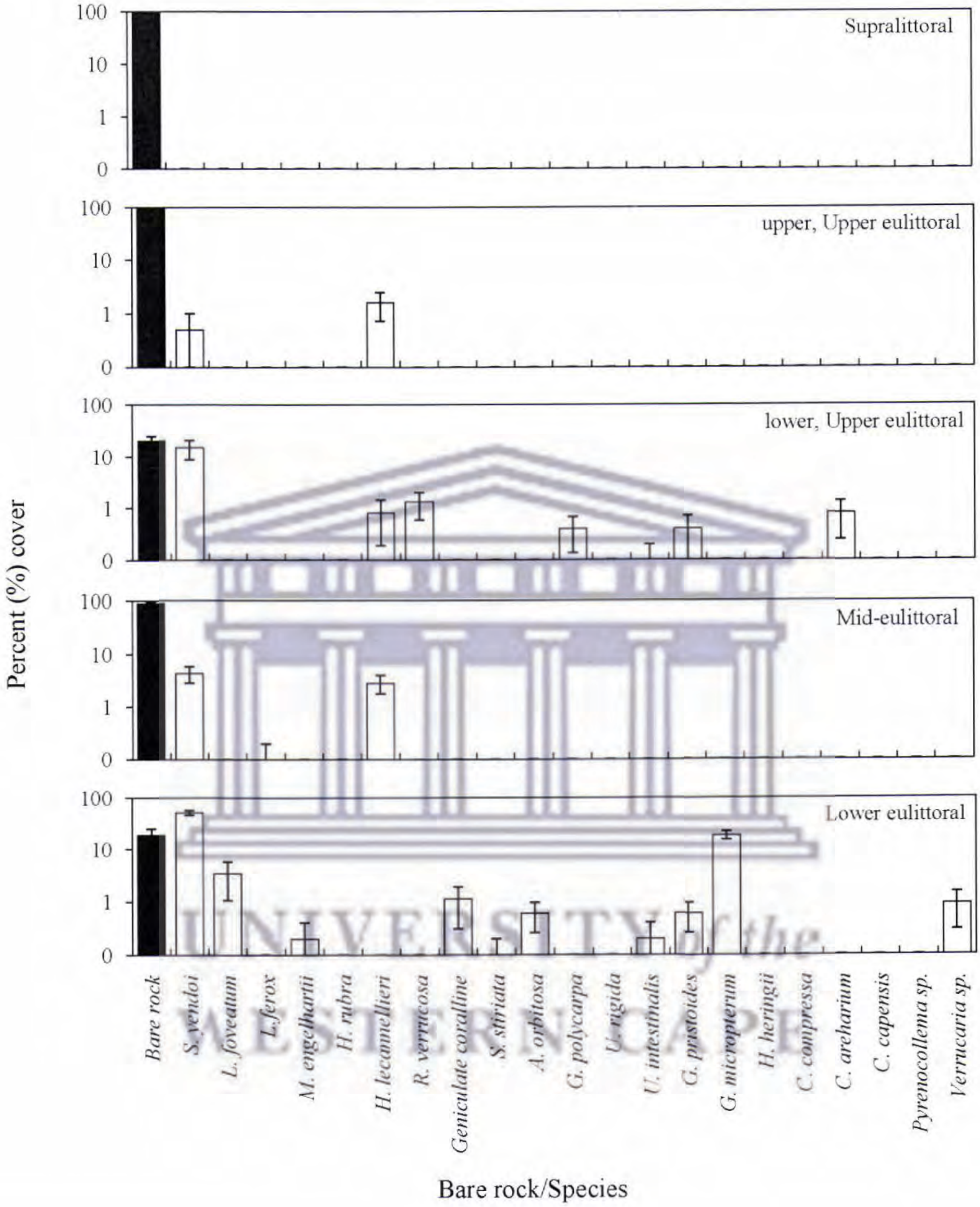

Figure 3.3.2: Algal and lichen percent cover (mean ± SE) abunance on the primary rocky substratum at Rooiels. Note that all species encountered for the study are presented on the X-axis (Key to generic names presented in Table 3.3.1).

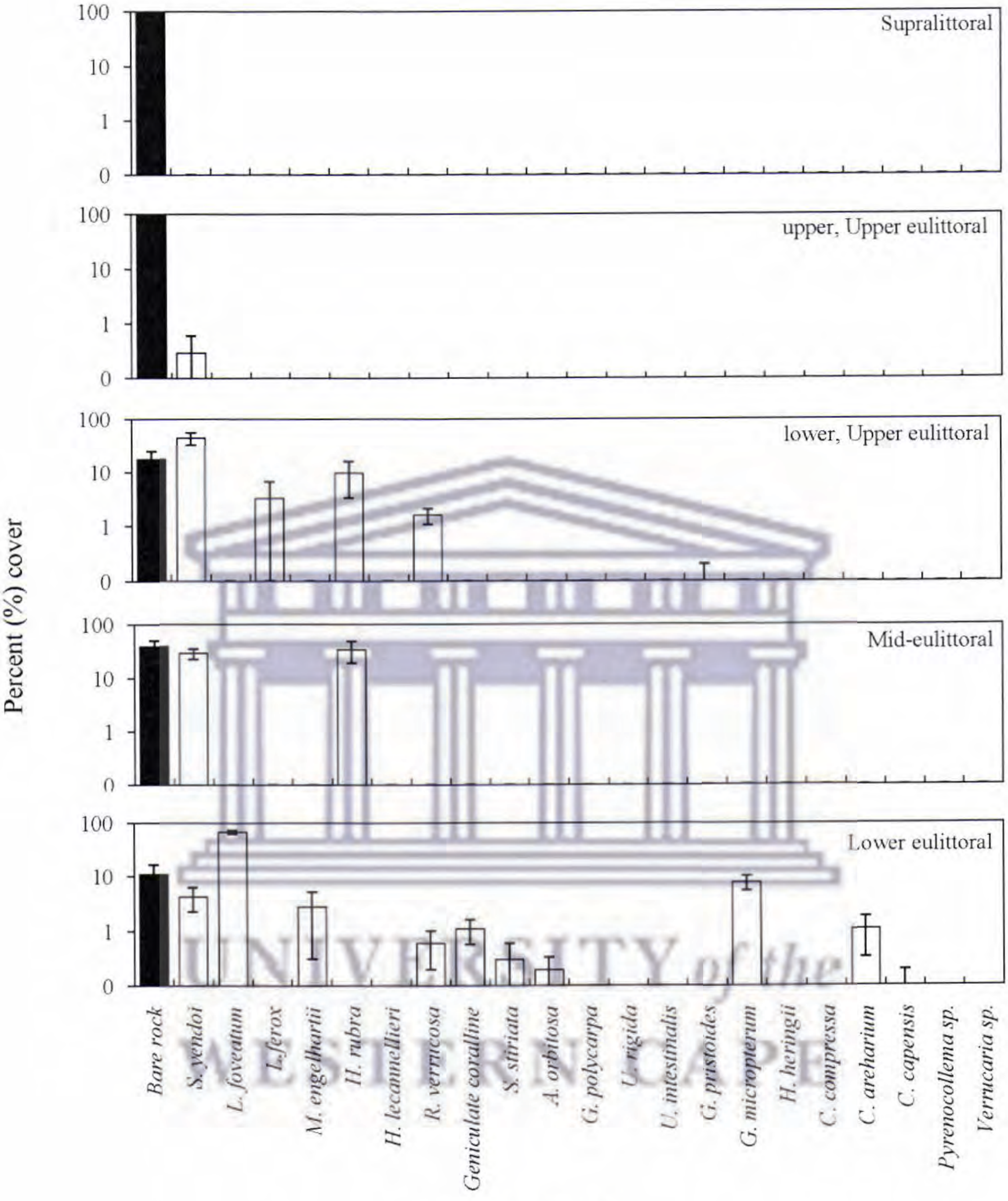

Figure 3.3.3: Algal and lichen percent cover (mean ± SE) abunance on the primary rocky substratum at Sandbaai. Note that all species encountered for the study are presented on the X-axis (Key to generic names presented in Table 3.3.1).

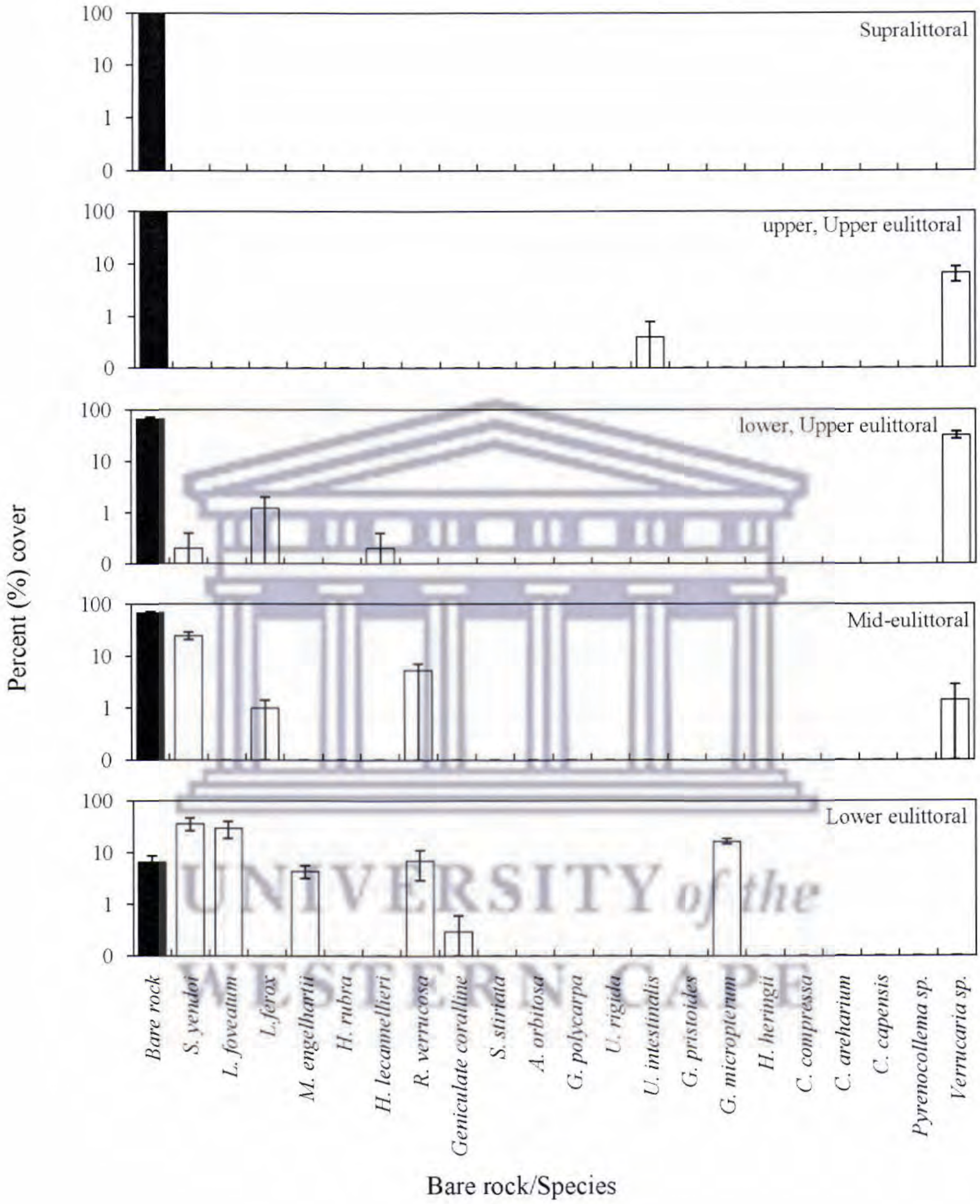

Figure 3.3.4: Algal and lichen percent cover (mean ± SE) abunance on the primary rocky substratum at Pearly Beach. Note that all species encountered for the study are presented on the X-axis (Key to generic names presented in Table 3.3.1).

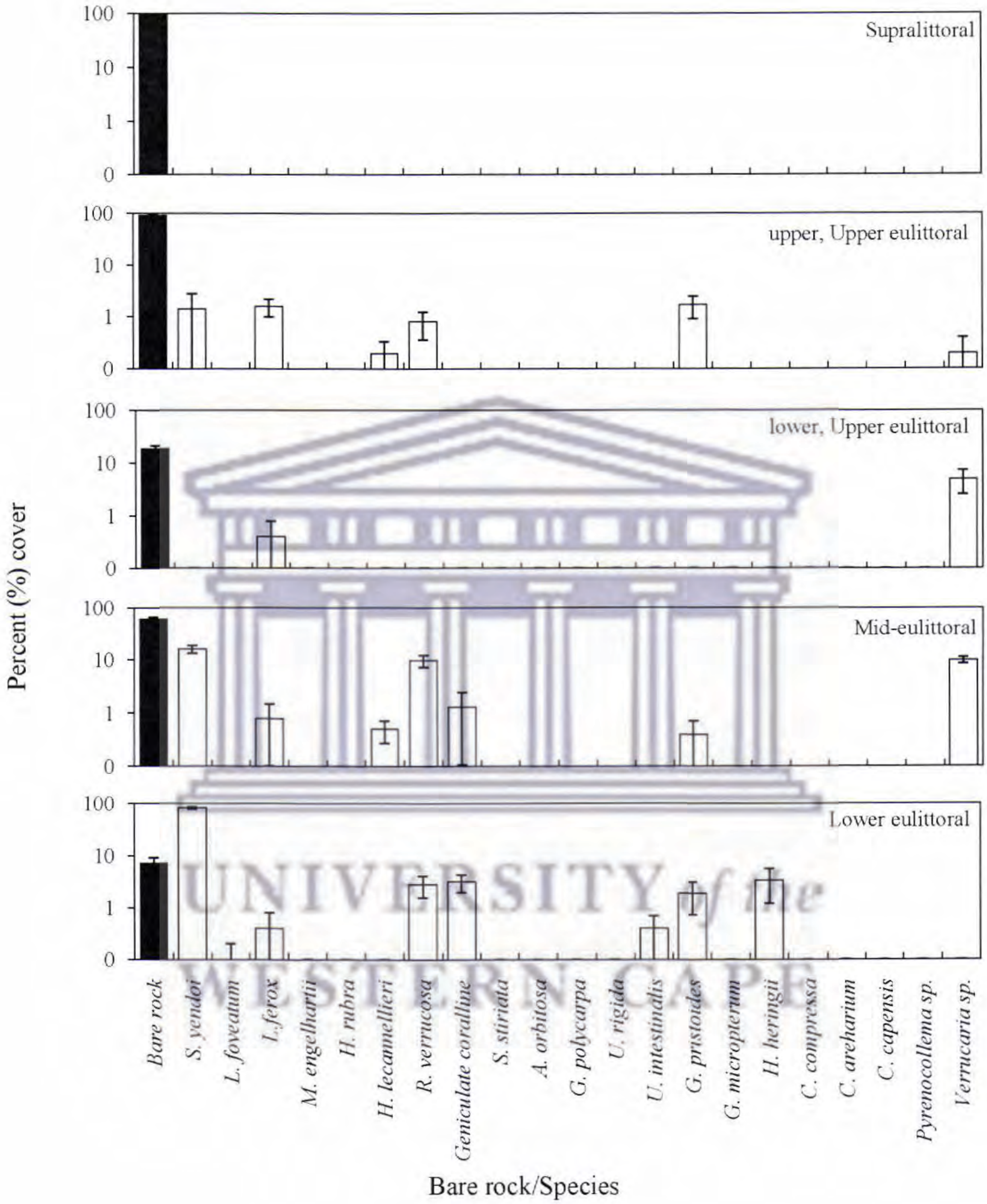

Figure 3.3.5: Algal and lichen percent cover (mean ± SE) abunance on the primary rocky substratum at Stinkbaai. Note that all species encountered for the study are presented on the X-axis (Key to generic names are presented in Table 3.3.1).

Table 3.3.1: Macroalgae and lichens surveyed from all sites, their main features and their presence (+) and/or absence (-) on the primary (bedrock) and secondary (shells of 'resident' molluscs) substrata.

Taxa	Key to generic names	Main feature	Mid-eulittoral		Lower eulittoral	
			Primary	Secondary	Primary	Secondary
Spongites yendoi (Foslie) Chamberlain	*S. yendoi*	Encrusting coralline red	+	+	+	+
Leptophytum foveatum (Foslie) D. Penrose & Woelkerling	*L. foveatum*	Encrusting coralline red	-	-	+	+
Leptophytum ferox (Foslie) Y.M.Chamberlain & D.W. Keats	*L. ferox*	Encrusting coralline red	+	+	+	+
Mesophyllum engelhartii (Foslie) W.H. Adey	*M. engelhartii*	Encrusting coralline red	-	-	+	+
Hildenbrandia rubra (Sommerfelt) Meneghini	*H. rubra*	Encrusting fleshy red alga	+	+	-	-
Hildenbrandia lecannellieri Hariot	*H. lecannellieri*	Encrusting fleshy red alga	+	+	-	-
Ralfsia verrucosa (Areschoug) J. Agardh	*R. verrucosa*	Encrusting fleshy brown	+	+	+	+
Geniculate coralline	Geniculate coralline	Geniculate coralline red	+	+	+	+
Sarcothalia stiriata (Turner) Leister	*S. stiriata*	Foliose red alga	-	-	+	-
Aeodes orbitosa (Suhr) F. Schmitz	*A. orbitosa*	Foliose red alga	-	-	+	-
Gigartina polycarpa (Kützing) Setchell & N.L. Gardner	*G. polycarpa*	Foliose red alga	-	+	-	+
Ulva rigida C. Agardh	*U. rigida*	Foliose green alga	-	+	-	+
Ulva intestinalis Linnaeus	*U. intestinalis*	Foliose green alga	-	+	+	+
Gelidium pristoides (Turner) Kützing	*G. pristoides*	Turfy red alga	+	+	+	+
Gelidium micropterum Kützing	*G. micropterum*	Turfy red alga	-	+	+	+
Herposiphonia heringii (Harvey) Falkenberg	*H. heringii*	Turfy red alga	-	-	+	-
Champia compressa Harvey	*C. compressa*	Filamentous red alga	-	+	-	-
Ceramium arenarium Simmons	*C. arenarium*	Filamentous red alga	-	-	+	+
Cladophora capensis (C. Agardh) De Toni	*C. capensis*	Filamentous green alga	-	+	+	-
Pyrenocollema sp.	*Pyrenocollema* sp.	Marine lichen	-	+	-	+
Verrucaria sp.	*Verrucaria* sp.	Marine lichen	+	+	+	+
Number of taxa			8	15	15	14
			U-value: 60; p = 0.003		U-value: 153; p = 0.695	

Table 3.3.2: Macroalgae and lichens surveyed from Kalk Bay, their main features and their presence (+) and/or absence (-) on the primary (bedrock) and secondary (shells of 'resident' molluscs) substrata.

Taxa	Main feature	Mid-eulittoral		Lower eulittoral	
		Primary	Secondary	Primary	Secondary
Spongite yendoi (Foslie) Chamberlain	Encrusting coralline red alga	+	+	+	+
Leptophytum ferox (Foslie) Y.M. Chamberlain & D.W. Keats	Encrusting coralline red alga	-	-	+	+
Hildenbrandia rubra (Sommerfelt) Meneghini	Encrusting fleshy red alga	+	+	-	-
Ralfsia verrucosa (Areschoug) J. Agardh	Encrusting fleshy brown alga	+	+	+	+
Geniculate coralline	Geniculate coralline red alga	-	+	-	+
Gigartina polycarpa (Kützing) Setchell & N.L. Gardner	Foliose red alga	-	+	-	-
Ulva rigida C. Agardh	Foliose green alga	+	-	+	-
Ulva intestinalis Linnaeus	Foliose green alga	-	+	-	-
Gelidium pristoides (Turner) Kützing	Turfy red alga	+	+	+	+
Gelidium micropterum Kützing	Turfy red alga	-	+	+	+
Champia compressa Harvey	Filamentous red alga	-	+	-	-
Cladophora capensis (C. Agardh) De Toni	Filamentous green alga	-	+	-	-
Pyrenocollema sp.	Marine lichen	-	+	-	+
Verrucaria sp.	Marine lichen	-	+	-	-
Number of taxa		5	12	6	7
		U-value: 39; p = 0.005		U-value: 28; p = 0.587	

Table 3.3.3: Macroalgae and lichens surveyed from Rooiels, their main features and their presence (+) and/or absence (-) on the primary (bedrock) and secondary (shells of 'resident' molluscs) substrata.

Taxa	Main feature	Mid-eulittoral		Lower eulittoral	
		Primary	Secondary	Primary	Secondary
Spongite syendoi (Foslie) Chamberlain	Encrusting coralline red alga	+	+	+	+
Leptophytum foveatum (Foslie) D. Penrose & Woelkerling	Encrusting coralline red alga	-	-	+	+
Leptophytum ferox (Foslie) Y.M. Chamberlain & D.W. Keats	Encrusting coralline red alga	+	-	-	+
Mesophyllum engelhartii (Foslie) W.H. Adey	Encrusting coralline red alga	-	-	+	+
Hildenbrandia lecannellieri Hariot	Encrusting fleshy red alga	+	-	-	-
Ralfsia verrucosa (Areschoug) J. Agardh	Encrusting fleshy brown alga	-	+	-	+
Geniculate coralline	Geniculate coralline red alga	-	+	+	+
Sarcothalia stiriata (Turner) Leister	Foliose red alga	-	-	+	-
Aeodes orbitosa (Suhr) F. Schmitz	Foliose red alga	-	-	+	-
Gigartina polycarpa (Kützing) Setchell & N.L. Gardner	Foliose red alga	-	+	-	-
Ulva rigida C. Agardh	Foliose green alga	-	-	+	-
Ulva intestinalis Linnaeus	Foliose green alga	-	-	-	-
Gelidium pristoides (Turner) Kützing	Turfy red alga	-	+	+	+
Gelidium micropterum Kützing	Turfy red alga	-	-	+	+
Pyrenocollema sp.	Marine lichen	-	+	-	+
Verrucaria sp.	Marine lichen	-	+	+	+
Number of taxa		3	7	10	10
		U-value: 22; p = 0.073		U-value: 84; p = 0.972	

Table 3.3.4: Macroalgae and lichens surveyed from Sandbaai, their main features and their presence (+) and/or absence (-) on the primary (bedrock) and secondary (shells of 'resident' molluscs) substrata.

Taxa	Main feature	Mid-eulittoral		Lower eulittoral	
		Primary	Secondary	Primar	Secondary
Spongites yendoi (Foslie) Y.M. Chamberlain	Encrusting coralline red alga	+	+	+	+
Leptophytum foveatum (Foslie) D. Penrose & Woelkerling	Encrusting coralline red alga	-	-	+	+
Leptophytum ferox (Foslie) Y.M.Chamberlain & D.W. Keats	Encrusting coralline red alga	-	-	-	+
Mesophyllum engelhartii (Foslie) W.H. Adey	Encrusting coralline red alga	-	-	+	-
Hildenbrandia rubra (Sommerfelt) Meneghini	Encrusting fleshy red alga	+	+	-	-
Ralfsia verrucosa (Areschoug) J. Agardh	Encrusting fleshy brown alga	-	-	+	+
Geniculate coralline	Geniculate coralline red alga	-	-	+	+
Sarcothalia stiriata (Turner) Leister	Foliose red alga	-	-	+	-
Aeodes orbitosa (Suhr) F. Schmitz	Foliose red alga	-	-	+	-
Gigartina polycarpa (Kützing) Setchell & N.L. Gardner	Foliose red alga	-	-	-	+
Ulva rigida C. Agardh	Foliose green alga	-	-	-	+
Ulva intestinalis Linnaeus	Foliose green alga	-	-	-	+
Gelidium pristoides (Turner) Kützing	Turfy red alga	-	-	-	+
Gelidium micropterum Kützing	Turfy red alga	-	-	+	+
Ceramium arenarium Simmons	Filamentous red alga	-	-	+	+
Cladophora capensis (C. Agardh) De Toni	Filamentous green alga	-	-	+	-
Pyrenocollema sp.	Marine lichen	-	+	-	+
Verrucaria sp.	Marine lichen	-	+	-	-
Number of taxa		2	4	10	12
		U-value: 12; p = 0.310		U-value: 112; p = 0.467	

Table 3.3.5: Macroalgae and lichens surveyed from Pearly Beach, their main features and their presence (+) and/or absence (-) on the primary (bedrock) and secondary (shells of 'resident' molluscs) substrata.

Taxa	Main feature	Mid-eulittoral		Lower eulittoral	
		Primary	Secondary	Primar	Secondary
Spongites yendoi (Foslie) Chamberlain	Encrusting coralline red alga	+	+	+	+
Leptophytum foveatum (Foslie) D. Penrose & Woelkerling	Encrusting coralline red alga	-	-	+	+
Leptophytum ferox(Foslie) Y.M. Chamberlain & D.W. Keats	Encrusting coralline red alga	+	+	-	+
Mesophyllum engelhartii (Foslie) W.H. Adey	Encrusting coralline red alga	-	-	+	+
Ralfsia verrucosa (Areschoug) J. Agardh	Encrusting fleshy brown alga	+	+	+	+
Geniculate coralline	Geniculate coralline red alga	-	-	+	-
Ulva intestinalis Linnaeus	Foliose green alga	-	+	-	-
Gelidium pristoides (Turner) Kützing	Turfy red alga	-	+	-	-
Gelidium micropterum Kützing	Turfy red alga	-	-	+	+
Pyrenocollema sp.	Marine lichen	-	+	-	+
Verrucaria sp.	Marine lichen	+	+	-	-
Number of taxa		4	7	6	7
		U-value: 44; p = 0.225		U-value: 55; p = 0.587	

Table 3.3.6: Macroalgae and lichens surveyed from Stinkbaai, their main features and their presence (+) and/or absence (-) on the primary (bedrock) and secondary (shells of 'resident' molluscs) substrata.

Taxa	Main feature	Mid-eulittoral		Lower eulittoral	
		Primary	Secondary	Primar	Secondary
Spongite syendoi (Foslie) Chamberlain	Encrusting coralline red alga	+	+	+	+
Leptophytum foveatum (Foslie) D. Penrose & Woelkerling	Encrusting coralline red alga	-	-	+	-
Leptophytum ferox (Foslie) Y.M. Chamberlain & D.W. Keats	Encrusting coralline red alga	+	-	+	-
Hildenbrandia lecannellieri Hariot	Encrusting fleshy red alga	+	-	-	-
Ralfsia verrucosa (Areschoug) J. Agardh	Encrusting fleshy brown alga	+	+	+	+
Geniculate coralline	Geniculate coralline red alga	+	-	+	+
Ulva intestinalis Linnaeus	Foliose green alga	-	-	+	-
Gelidium pristoides (Turner) Kützing	Turfy red alga	+	-	+	+
Gelidium micropterum Kützing	Turfy red alga	-	-	-	+
Herposiphonia heringii (Harvey) Falkenberg	Turfy red alga	-	-	+	-
Pyrenocollema sp.	Marine lichen	-	+	-	+
Verrucaria sp.	Marine lichen	+	+	-	-
Number of taxa		7	4	8	6
		U-value: 54; p = 0.133		U-value: 60; p = 0.587	

Table 3.3.7: Macroalgal and lichen functional groups surveyed from all sites, and their presence (+) and/or absence (-) on the primary (bedrock) and secondary (shells of 'resident' molluscs) substrata.

Functional group	Mid-eulittoral		Lower eulittoral	
	Primary	Secondary	Primary	Secondary
Encrusting coralline red algae	+	+	+	+
Encrusting fleshy red algae	+	-	-	-
Encrusting fleshy brown alga	+	+	+	+
Geniculate coralline red algae	+	+	+	+
Foliose algae	-	+	+	+
Turfy algae	+	+	+	+
Filamentous algae	-	+	+	+
Marine lichens	+	+	+	+
Number of algal taxa	5	7	7	7
	U-value: 28; p = 0.5874		U-value: 0; p = 1	

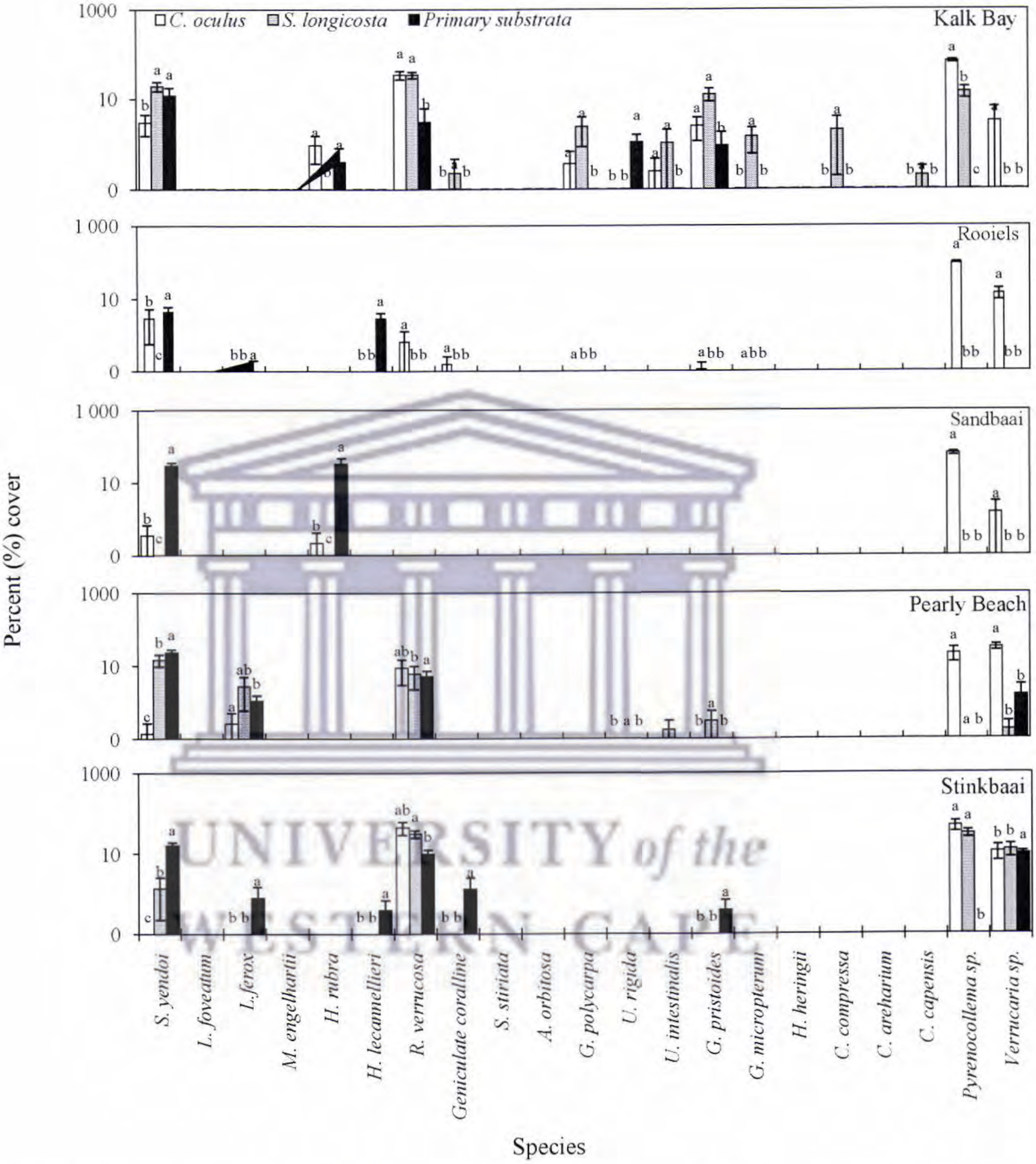

Figure 3.3.6: Algal and lichen percent cover (mean ± SE) within the Mid-eulittoral zone across the primary substratum and the shells of *C. oculus* and *S. longicosta*. Bars with the same letters for a species (on the X-axis) from a site, occurring on a particular substratum, are not statistically different and are based on the ranking of Kruskal-Wallis values (Key to generic names are presented in Table 3.3.1).

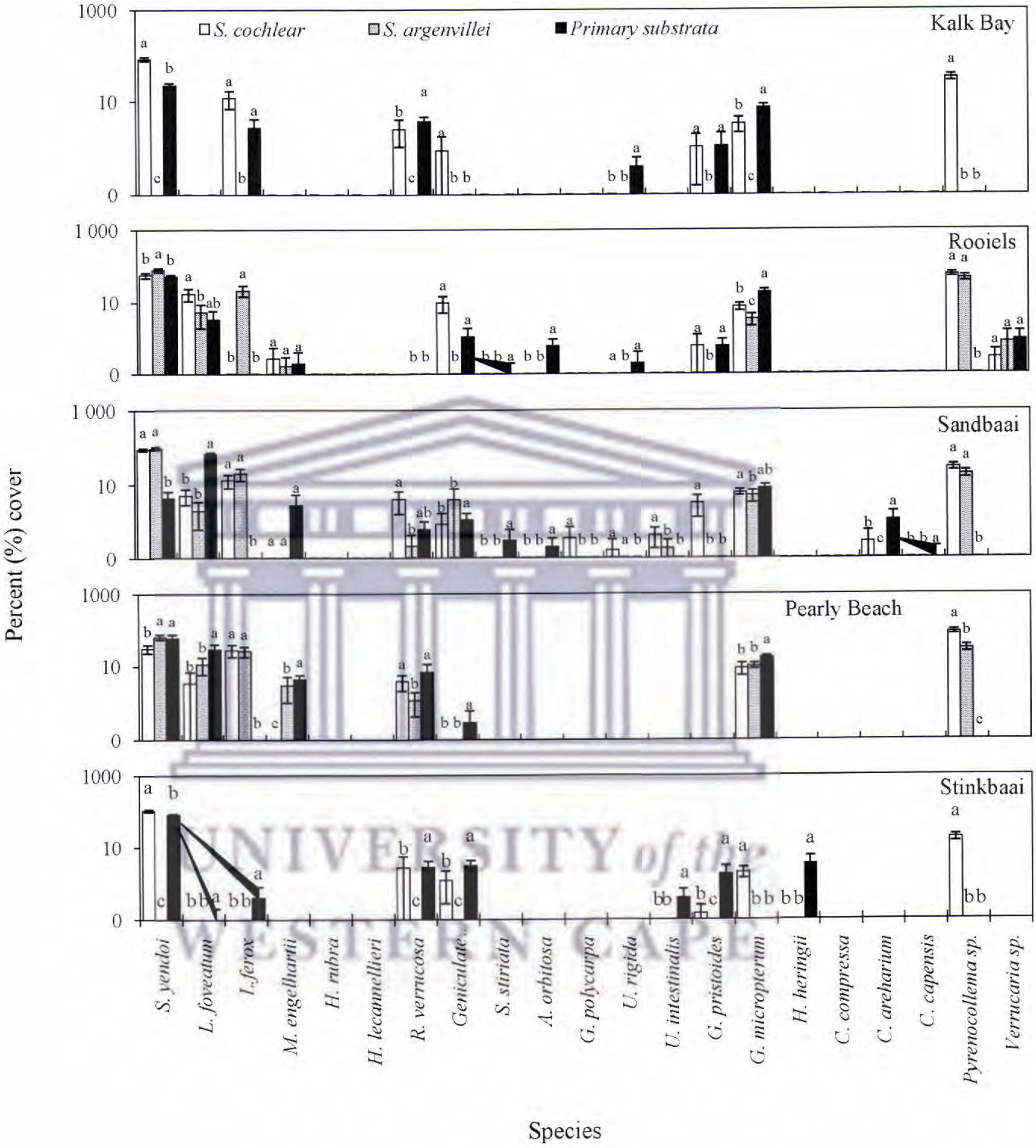

Figure 3.3.7: Algal and lichen percent cover (mean ± SE) within the Lower eulittoral zone across the primary substratum and the shells of *S. cochlear* and *S. argenvillei*. Bars with the same letters for a species (on the X-axis) from a site, occurring on a particular substrate, are not statistically different and are based on the ranking of Kruskal-Wallis values (Key to generic names are presented in Table 3.3.1).

3.3.3 Importance of **Oxystele sinensis** *as a secondary substratum*

Oxystele sinensis provides an important settlement substratum for encrusting algae and lichens (Figure 3.3.8). The coralline alga *Leptophytum foveatum* was the only species to occur on *O. sinensis* at all sites. Species richness of epizoics on the shells of *O. sinensis* was greatest at eastern-most sites (four species at both Pearly Beach and Stinkbaai).

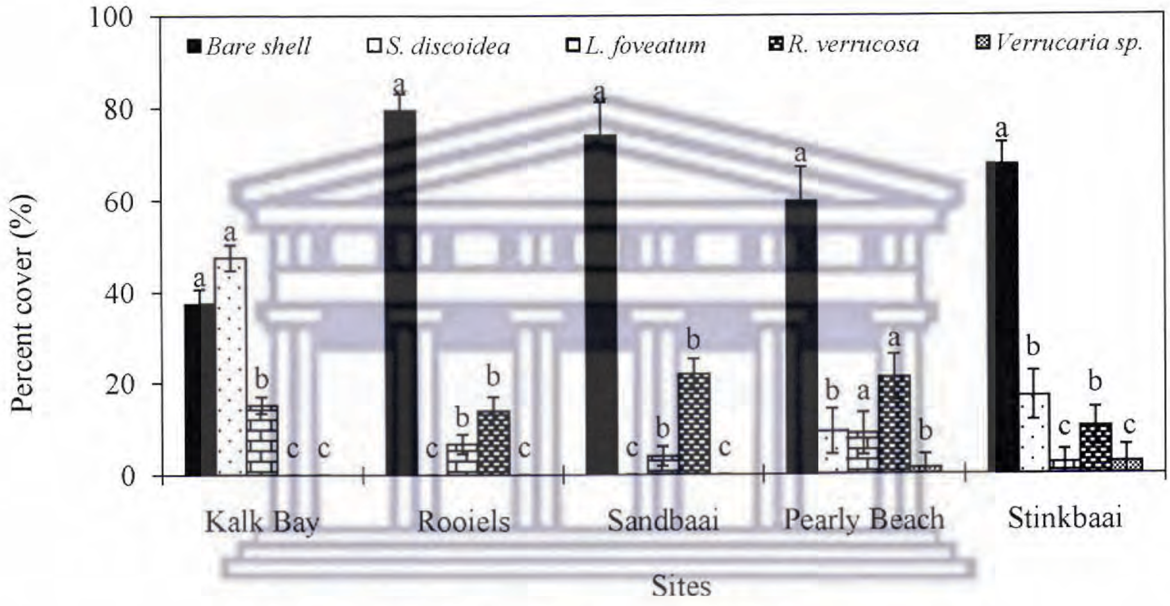

Figure 3.3.8: Algal and lichen percent cover (mean ± SE) abundance on shells of *O. sinensis* at all sites. Bars with the same letters are not statistically different and are based on the ranking of Kruskal-Wallis values (Key to generic names are presented in Table 3.3.1). Sites are presented from west to east.

3.3.4 Diversity

An examination of the diversity indices gives a similar result to what has thus far been reported. Overall, limpets as secondary substrata are more important along the western sites than the eastern-most sites (Pearly Beach and Stinkbaai) (Table 3.3.8). According to the Friedman's 2-way ANNOVA by ranks, at western-most sites, secondary substrata within the mid-eulittoral zone have a greater diversity than their primary counterpart, whereas the eastern-most sites (Pearly Beach and Stinkbaai) show no significant differences between substrata. Also, similarly as reported before, secondary substrata within the Mid-eulittoral zone are more important than within the Lower eulittoral zone. Although ranked higher, statistically eastern-most sites show no difference in the importance of secondary vs. primary substrata. Interestingly, the Lower eulittoral zone at Kalk Bay is the only location where the primary substratum is statistically more important than the secondary substrata at this site.

Table 3.3.8: Diversity parameters on different substrata, ranked according to the Inverse Simpson's index. Diversity indices with the same letters are not statistically different (Friedman's 2-way ANOVA by ranks). The highest value is assigned number 1 and vice versa.

	Habitat	Substrata	No. of species	Shannon index	Inverse Simpson's index	Simpson's measure of eveness^2	Rank
Kalk Bay	Mid-eulittoral	*C. oculus*	6	1.051 ±0.116	2.152± 0.2175^{ab}	0.359	2
		S. longicosta	5	1.661 ± 0.127	3.637 ± 0.436^{a}	0.727	1
		Primary substrata	3	1.205 ± 0.376	1.536 ± 0.678^{b}	0.512	3
	Lower eulittoral	*S. cochlear*	7	1.121 ± 0.085	2.249±0.321^{b}	0.321	2
		Primary substrata	6	1.236 ± 0.092	2.459±0.410^{a}	0.410	1
Rooiels	Mid-eulittoral	*C. oculus*	6	0.590 ± 0.111	1.381± 0.110^{a}	0.230	1
		Primary substrata	1	0	N/A^{1}	N/A^{1}	2
	Lower eulittoral	*S. argenvillei*	8	1.403 ± 0.081	3.329± 0.303^{a}	0.416	1
		S. cochlear	6	1.238 ± 0.083	2.767± 0.275^{ab}	0.461	2
		Primary substrata	7	0.944 ± 0.101	1.895± 0.192^{b}	0.271	3
Sandbaai	Mid-eulittoral	*C. oculus*	3	0.200 ± 0.114	1.063± 0.051^{a}	0.354	1
		Primary substrate	1	0	N/A^{1}	N/A^{1}	2
	Lower eulittoral	*S. argenvillei*	9	1.372 ± 0.091	2.514±0.249^{a}	0.279	1
		S. cochlear	8	1.143 ± 0.142	2.115±0.271^{ab}	0.264	2
		Primary substrata	6	0.893 ± 0.114	1.512±0.121^{b}	0.252	3
Pearly Beach	Mid-eulittoral	*C. oculus*	4	2.649± 0.450	2.649± 0.450^{a}	0.662	1
		S. longicosta	4	1.156 ± 0.285	1.829±0.482^{a}	0.457	2
		Primary substrata	3	0.793 ± 0.185	1.532± 0.184^{a}	0.511	3
	Lower eulittoral	*S. argenvillei*	6	1.354 ± 0.134	2.835±0.436^{a}	0.472	3
		S. cochlear	7	1.530 ± 0.093	3.618±0.527^{a}	0.517	1
		Primary substrata	6	1.349 ± 0.110	3.238±0.544^{a}	0.540	2
Stinkbaai	Mid-eulittoral	*C. oculus*	3	0.954 ± 0.002	2.615± 0.176^{a}	0.872	2
		S. longicosta	4	1.119 ± 0.077	2.853± 0.222^{a}	0.713	1
		Primary substrata	4	1.414 ± 0.128	2.481± 0.107^{a}	0.620	3
	Lower eulittoral	*S. cochlear*	6	0.699± 0.115	1.422±0.115^{a}	0.237	1
		Primary substrata	7	0.623 ± 0.149	1.221±0.057^{a}	0.174	2

[1] Due to the application of the rare species concept, no values were possible for the Simpsons' indices.

[2] The maximum value of 1 reflects the greatest evenness possible.

3.4 Discussion

The findings from this study have shown that limpet shells are important secondary substrata and are particularly so within the Mid-eulittoral zone. Within the Mid-eulittoral zone, limpet shells increase species diversity, allowing grazing susceptible algae and lichens to persist under otherwise intense grazing pressures. Within the Lower eulittoral zone, limpet shells appear to act rather as extensions of the primary substratum. Furthermore, the winkle *O. sinensis* acts as an important secondary substratum for a host of encrusting algae and the lichen *Verrucaria* sp. This latter association is more important at eastern sites (Pearly and Stinkbaai) within this study.

On temperate rocky shores, molluscan grazers are important structural agents (Pain and Vadas 1969, Underwood 1980, Menge 1983, Dye 1993, 1995, Steneck and Dethier 1994, Boaventura *et al.* 2002, Maneveldt *et al.* 2009). On intertidal rocky shores with a healthy population of herbivorous molluscs the high grazing pressures often result in a high percentage of 'bare rock' (Petraitis 1987, Anderson *et al.* 1991, Dye 1993, Berlow and Navarrete 1997, Maneveldt *et al.* 2006, 2009) with largely only grazer-resistant and encrusting algae being able to persist on the primary substratum (Menge 1983, Steneck 1983, Anderson *et al.* 1991, Dye 1995, Maneveldt *et al.* 2006, 2009). Consequently it is highly likely that on such shores, a comparatively high degree of epizoics will be encountered on secondary substrata. The results support this statement as it has shown that, notably within the Mid-eulittoral zone, herbivorous molluscs themselves ironically provide the perfect refuge for herbivore-susceptible algae. A number of other international studies (e.g. Steneck 1986, Warner 1997, Bell 2005, Ayres-Peres and Mantelatto 2010) have already documented this phenomenon with only limited such research (e.g. Zeeman *et al.* 2013) having been reported for the southern African continent. In addition, our results have shown that even at sites and zones along the same shore where diversity was no different between primary and secondary substrata, the importance of limpet and winkle shells as secondary substrata clearly adds value to the diversity of the intertidal communities studied, and particular that of fleshy foliose algae.

Diversity within the Lower eulittoral zone on South African west and southern west coasts is comparatively low (Branch 1975a, 1975b, Branch and Griffiths 1988, Keats *et al.* 1994, Maneveldt *et al.* 2006, this study). This is largely due to the feeding behaviour of the territorial gardening limpet *S. cochlear* that prevents the settlement of most algal species and some invertebrates (Branch 1975a, 1975b, Keats *et al.* 1994, Plaganyi and Branch 2000). One would assume then that the shells of these limpets would provide the ideal settlement substrata for a range of epizoic organisms. However, the densities of these specialist territorial grazers are so high (to several hundred per square meter –Branch 1975a) that their juveniles commonly settle in a tiered layering of still smaller individuals upon larger ones on the shells of more mature individuals (Branch 1975a, Branch 1975b). Consequently, these layered juveniles act much like the mature individuals inhabiting the primary substratum and themselves prevent the settlement of most algae, lichens and other invertebrates on the shells of more mature limpets. Similarly, although *S. argenvillei* shells provide important secondary settlement substrata, the limpet probably does not occur in sufficient densities within the western biogeographic transition zone to make a meaningful contribution. These phenomena more than likely account for the diminished importance of limpet shells as settlement substrata within the Lower eulittoral zone. It should be noted though that, in addition to juvenile *S. cochlear* limpets, the garden algae are also found on the shells of most mature *S. cochlear* and S. *argenvillei* limpets. Limpet shells in the Lower eulittoral zone therefore appear to be more of an extension of the primary rocky substratum and not an alternate settlement substratum for increasing diversity.

Of the algal and lichen species recorded, seven were found to occur in significantly greater percentages on the primary substratum than on limpet shells. Six of these species (*S. yendoi*, *L. ferox*, *H. lacannellierii*, *H. rubra* and *R. verrucosa*, *Verrucaria* sp.) are encrusting species; the first two are encrusting corallines, the next three are encrusting fleshy algae and the last is a lichen. Encrusting algae and lichens are inferior competitors for space and are generally outcompeted by faster growing foliose and turfy algae (Steneck 1983, Paine 1984, Dethier *et al.* 1991, Steneck *et al.* 1991, Keats and Maneveldt 1994, Keats *et al.* 1994, Kaelheler and Williams 1996, Bulleri 2005, Maneveldt *et al.* 2006). In addition, most encrusting algae and lichens either possess grazer-deterrent compounds (Lubchenco and Gaines 1981, Steneck and Watling 1982, Hay and Fenical 1988, Dethier 1994) or are grazer-resistant (Kitting1980, Underwood 1980, Menge and Luchenco 1981, Steneck1986, Pueschel 1988,Chamberlain and Keats 1994, Deither1994), and often regenerate quickly when they are grazed (Fletcher 1973, Branch 1975b, Steneck 1986, 1996, Steneck *et al.* 1991, McQuaid and Froneman 1993, Chamberlain and Keats 1994, Plaganyi and Branch 2000, Dethier and Steneck 2001). Herbivorous limpets tend to consume fast growing, palatable, competitively superior foliose and turfy algae easier thereby allowing inferior, grazer-deterrent and grazer-resistant species to persist (Sousa 1979, Dethier 1981, Lubchenco 1983, Stenecket *al.* 1991). Due to their generally inferior interference competitive abilities it is thus understandable that encrusting species would be generally low in percent cover on secondary substrata as this is where competitively dominant foliose and turfy algae would settle to escape herbivory.

Besides limpets, winkle shells also provide important settlement substrata for some species of algae (Chamberlain 1993, Eager 2010) although notably to fewer species than which occur on limpets shells. It has been recorded that encrusting forms of algae and lichen are often seen on small shelled gastropods (Wernberg *et al.* 2010). The fewer species of epizoics on winkle shells are probably due to the shape and texture of the shell. A number of studies have suggested that winkle shells are not good settlement substrates because of their generally rounded shape and smooth texture (Hummel *et al.* 2001, Vasconcelos *et al.* 2007). It is already well established that algae settle easier on rough surfaces than on smooth ones (Ogata 1953, Watanuki and Yamamoto 1990, Fletcher and Callow 1992). Rough surfaces appear to provide greater settlement advantages in that they have higher water retention rates, which protect algal spores from desiccation (Gonzalez and Goff 1989, Fletcher and Callow 1992). In addition, rough surfaces protect algal spores from detachment by wave action, water currents and herbivory (Vadas *et al.*1990). In any case, at least three species of encrusting algae (*R. verrucosa, S. discoidea, L. foveatum*) and one lichen (*Verrucaria* sp.) were found to colonise the shells of *O. sinensis*. McQuaid and Froneman (1993) suggested that juvenile *S. longicosta* occur on the shells of *O. sinensis* to escape predation by *Marthasterias glacialis* (Linnaeus). As a consequence the encrusting fleshy alga *R. verrucosa* probably recruits to the winkle shells as gardens for juvenile *S. longicosta*. For *S. discoidea*, *O. sinensis* shells appear to largely be an extension of the primary substratum, providing an important mobile secondary substratum within tide pools and the shallow subtidal (Eager 2010). *Leptophytum foveatum* has been recorded to occur on a variety of molluscan shells (e.g. *S. granatina, S. cochlear* and *S. argenvillei* – Chamberlain and Keats 1994). Its range also strongly overlaps with that of *O. sinensis* and therefore, the occurrence of *L. foveatum* on *O. sinensis* shells is most likely due to the high abundance of *O. sinensis* in the intertidal (*pers. obs.*) where there is also a high percent cover abundance of reproductively mature corallines. *Verrucaria* sp. on the other hand has been documented to occur in all zones and on a variety of molluscan shells (Eckman *et al.* 2004) suggesting that the lichen is probably an indiscriminate settler.

In conclusion, limpet and winkle shells act as important secondary substrata in rocky intertidal benthic environments where primary space is the most limiting resource, largely because it is often non-renewable (Dayton 1971, Branch 1985, Bell 2005), and because herbivorous molluscs often denude rocky surfaces of available algae. Within the Mid-eulittoral zone of our sampling sites, mollusc shells provide an important refuge for lichens and other grazer-susceptible algal species, and greatly increases the diversity in this zone. Within the Lower eulittoral zone mollusc shells appear to act largely as extensions of the primary substratum providing increased settlement surface area. It is apparent that on rocky intertidal environments within the western biogeographic transition zone, mollusc shells provide important microhabitats as well as increased surface area for the settlement of a variety of epizoic organisms.

4. General Discussion

4.1 Zonation patterns

With a few notable exceptions (presence of the invasive mussel *Mytilusgalloprovincialis* along the mid to low shore at most sites, general absence of barnacles at most Mid-eulittoral zone sites, and the absence of dense beds of foliose and turfy algae in the Mid-eulittoral zone at all sites), zonation patterns along the shores of the western biogeographic transition zone is largely consistent with the published literature (e.g.Branch and Branch 1981)for South African south coast shores. In general, physical factors associated with desiccation stress limit the upward recruitment and colonisation of algae on rocky shores (Lent 1968, Dayton 1971, Tomanek and Somero 2000, Stillman and Somero 2000).However, grazing by herbivorous molluscs within the rocky intertidal zone is highly effective at controlling the abundance, distribution and diversity of algae across the shore (Paine and Vadas 1969, Lubchenco 1980, Underwood 1980, Underwood and Jernakoff 1984, Kaehler and Williams 1996, Anderson and Underwood 1997, Williams *et al.* 2000, Maneveldt *et al.* 2009). Consequently, most of the intertidal zone has a low percentage of fleshy and turfy algal coverwhen herbivore densities are comparatively high. This phenomenon has been shown for both rocky shores abroad (e.g. Petraitis 1987, Berlow and Navarrete 1997,) and for South African shores (e.g. Dye 1993, 1995,Maneveldt *et al.* 2006, 2009).

4.1.1 Invertebrate densities and biomass

Sites within this study cluster along a strong geographic gradient with each distal cluster presenting well-defined homogenousassociations when total invertebrate densities and biomass are examined. Invertebrate densities and biomass peak along the mid-shore at the western-most sites (Kalk Bay, Rooiels)where the zones are dominated by barnaclesand the invasive mussel, *Mytilusgalloprovincialis*. The densities of predators within the intertidal zonesalong west, southern west and southcoastsare low and this has reportedly resulted in the high densities and biomass of herbivorous molluscs and other invertebrates (Griffiths and Hockey 1987, Bustamante *et al.* 1995, Bustamante and Branch 1996). Due to desiccation stress at upper limits of the shore, grazers are generally unable to effectively control the recruitment and colonisation of sessile organisms (Lewis 1964, Newell 1979, Bustamante *et al.* 1997).At lower limits though, where desiccation stress is reduced, herbivorous molluscs are far more effective at limiting the recruitment and colonisation of a host of invertebrates (Maneveldt *et al.* 2009). The invasive marine mussel *Mytilusgalloprovincialis*, which was found to varying degrees at all sites except the eastern-most Stinkbaai, is the most successful marine invasive species in South Africa. The mussel has the ability to completely change the structure of rocky intertidal shores by displacing key species (Robinson *et al.* 2004, Bownes and McQuaid 2006, Robinson *et al.* 2007) and having already extended its range as far east as East London (Steffani and Branch 2004, Robinson *et al.* 2005), it was not surprising to encounter it in this study.It is strange though that the species was not record at the eastern-most extent (Stinkbaai) of this study.

Invertebrate density and biomass patterns are different for the eastern-most cluster (Pearly Beach, Stinkbaai) of sites. Here totalinvertebrate densities peak in the Supralittoral zone while biomass peaks in the Lower eulittoral zone. Greater densities and biomass in the high and low shore respectively appear to be a consequence of: 1) the much reduced invertebrate densities and biomass within the mid-shore environments at these eastern sites; and 2) the comparatively greater densities of the territorial gardening limpet *Scutellastra cochlear* at the eastern-most shore. This phenomenon will need to be further investigated to ascertain possible other reasons for this finding.

Examining only 'resident' herbivores gave different pictures for both invertebrate densities and biomass. While density data followed a similar site clustering trend to when all invertebrates were pooled, biomass data resulted in a different outcome. For biomass of 'resident' herbivores, sites clustered according to exposure. It is already well established that sites with greater exposure have greaterinvertebrate biomass(McQuaid and Branch 1985, Bustamante and Branch 1996, Bustamante *et al.* 1997, Ricciardi and Bourget 1999). Examining only 'resident' herbivores, our data is consistent with the published literature. However, this phenomenonis not seen when the biomass of all invertebrates is pooled. The reason for this outcome is still unclear and will need further investigation.

4.1.2 Algal diversity and cover abundance

On intertidal rocky shores with a healthy population of herbivorous molluscs the high grazing pressures often result in a high percentage of 'bare rock' (Petraitis 1987, Anderson *et al.* 1991, Dye 1993, Berlow and Navarrete 1997, Maneveldt*et al.* 2006, 2009) with largely only grazer-resistant and encrusting algae being able to persist (Menge 1983, Steneck 1983, Anderson *et al.* 1991, Dye 1995, Maneveldt *et al.* 2006, 2009). Our results are consistent with these findings and are in contradiction to previous older reports (e.g. Branch and Branch 1981) for the South African rocky intertidalbecausewe also found a general absence of foliose and turfy algae down the shore. In general, only encrusting algae and one lichen species were encountered.Encrusting algae and lichens are inferior competitors for space and are generally outcompeted by faster growing foliose and turfy algae (Steneck 1983, Paine 1984, Dethier*et al.* 1991, Steneck*et al.* 1991, Keats and Maneveldt 1994, Keats *et al.* 1994, Kaehler and Williams 1996, Stachowicz and Hay 1996, Bulleri 2005, Maneveldt*et al.* 2006). In addition, most encrusting algae and lichens either possess grazer-deterrent compounds (Lubchenco and Gaines 1981, Steneck and Watling 1982, Hay and Fenical 1988, Dethier 1994,) or are grazer-resistant (Kitting1980,Underwood 1980, Menge and Luchenco 1981, Levings and Garrity 1983,Steneck1986,Pueschel 1988,Dethier1994, Chamberlain and Keats 1994), and often regenerate quickly when they are grazed (Fletcher 1973, Branch 1976, Steneck 1986, 1996, Chamberlain and Keats 1994, Steneck*et al.* 1991, McQuaid and Froneman 1993, Plaganyi and Branch 2000, Dethier and Steneck 2001). Herbivorous limpets tend to consume fast growing, palatable, competitively superior foliose and turfy algae easier thereby allowing inferior, grazer-deterrent and grazer-resistant species to persist (Sousa 1979, Dethier 1981, Lubchenco 1983, Steneck*et al.* 1991). This probably accounted for the high cover abundance of encrusting algae and lichens on the primary substratum.

Algal diversity within the Lower eulittoral zone on South African west, southern west and south coastsiscomparatively low (Branch 1975a, 1975b, 1976, Branch and Griffiths 1988, Keats*et al.* 1994, Maneveldt *et al.* 2006, this study). This is largely due to the feeding behaviour of the territorial gardening limpet *S. cochlear* that prevents the settlement of most algal species and some invertebrates (Branch 1975a, 1975 b, 1976, Keats *et al.* 1994, Plaganyi and Branch 2000). Due to their high densities (to several hundred per square meter – Branch 1975a) juvenile*S. cochlear* commonly settle in a tiered layering of still smaller individuals upon larger ones on the shells of more mature ones (Branch 1975a, 1975b). These layered juveniles act much like the mature individuals inhabiting the primary substratum and themselves prevent the settlement of most algae and other invertebrates on the shells of more mature limpets. This phenomenon more than likely accounts for the low algal diversity on the low shore.

4.2 Space as a limiting resource

Primary space within the marine benthos is an absolute resource because it is not easily renewable (Dayton 1971, Underwood 1978, Branch 1985, Dudgeon *et al.* 1999). Space only ever becomes available when the organism occupying it dies or is forced to leave the area (Connell 1961, Pequegnat 1964, Dayton 1971, Paine 1971, Jackson 1977, Branch 1985, Chadwick 1987, Rossi and Snyder 2001, Barnes 2003, Bell 2005).For most sessile organisms, a physical disturbance (e.g. wave exposure, battering, desiccation stress, etc.), predation, herbivory or competition is required to renew primary space(Connell 1961, Pequegnat 1964, Dayton 1971, Paine 1971, Branch 1975b, 1985, Jackson 1977, Dudgeon *et al.* 1999, Rossi and Snyder 2001, Bell 2005).

It has long been established that herbivores play an important role in freeing up space by structuring the abundance and diversity of benthic organisms along rocky intertidal shores (Underwood *et al.* 1983, Anderson and Underwood 1997). In general, herbivores reduce species diversity by completely denuding intertidal zones of all algae (Petraitis 1987, Anderson *et al.* 1991, Dye 1993, Berlow and Navarrete 1997, Maneveldt*et al.* 2006, 2009). In addition, herbivores have the ability to enhance or inhibit the recruitment of various species by either altering the rates of succession (speeding or slowing it down) (Dayton 1971, Sousa 1979, Lubchenco 1983, Breitburg 1985, Farrell 1991, Maneveldt *et al.* 2009) or by causing completely different communities to emerge (Anderson and Underwood 1997). Herbivore-defended algal species, that are competitively subordinate to faster growing, more palatable algal species, for example, rely heavily on grazers for their co-existence (Steneck 1983, Paine 1984, Dethier*et al.* 1991, Steneck*et al.* 1991, Keats and Maneveldt 1994, Keats *et al.* 1994, Kaehler and Williams 1996, Stachowicz and Hay 1996, Nagarkar and Williams 1999, Bulleri 2005, Maneveldt*et al.* 2006).

4.3 Molluscs as important secondary substrata

The exploitation of microhabitats (secondary space) is known to increase the biodiversity of a particular area (Bell 2005). In marine ecosystems, mollusc shells are known to provide such microhabitats as they increase the available surface area for the settlement of a variety of epizoic organisms (Bell 2005, Nakin and Sommer 2007). Such secondary substrata become particularly important in rocky intertidal benthic environments where primary space is the most limiting resource, largely because it is often not quickly and easily renewed (Dayton 1971, Branch 1985, Bell 2005).

On rocky shores with a high degree of high grazer pressure, a comparatively high degree of epizoicson secondary substrata is expected largely becausesuch secondary substratum might be the only available settlement substrata. The results support this statement as it has shown that, notably within the Mid-eulittoral zone, herbivorous molluscs themselves ironically provide the perfect refuge for herbivore-susceptible algae. A number of other international studies (e.g. Steneck 1986, Warner 1997, Bell 2005, Ayres-Peres and Mantelatto 2010) have already documented this phenomenon with only limited such research (e.g. Zeeman *et al.* 2013) having been reported for the Southern African continent. On the low shore environment of sites examined in this study, however, mollusc shells are not as important as they are in the mid-shore environment. This is largely as a consequence of the territorial gardening nature of the limpet *S. cochlear* and thetiered layering of juvenile limpets one above the other on the shells of more mature individuals (Branch 1975a,1975b, Gosslin and

Qian 1997). Both adult and juvenile *S. cochlear* prevent the settlement of most algae (except for their garden algae) and other invertebrates on the primary substratum and the shells (secondary substrata) of more mature limpets respectively. This phenomenon more than likely accounts for the diminished importance of the secondary (limpet shells) substrata within the Lower eulittoral zone. It is important to note though that, in addition to juvenile limpets, the garden algae are also found on the shells of most adult limpets. Limpet shells in the Lower eulittoral zone therefore appear to act primarily as extensions of the rocky substratum and not necessarily as available substrata for increasing diversity. Similarly, the winkle *O. sinensis* appears largely to act as an extension of the primary substratum, but this time to the benefit of encrusting algae. The phenomenon of mollusc shells acting simply as extensions of the primary substratum is comparatively well recorded in the literature (e.g. Karlson and Shenk 1983, Lohse 1992, Creed 2000, Barnes 2001, Gutierrez *et al.* 2003, Bell 2005, Nakin and Sommer 2007).

4.4 Summary

In conclusion, with a few notable exceptions, the zonation patterns within the western biogeographic transition zone follow that which has previously been reported for South African south coast rocky shores. A host of invertebrate species, besides 'resident' limpets, add huge value to our understanding of community structure and ecosystem dynamics on rocky shores because they provide a picture of geographical relationships between sites that is different to that observed when only 'resident' limpets are examined. Within the mid-shore environment, mollusc shells provide important spatial refuges for a host of grazer susceptible algae and lichens that are otherwise grazed when they recruit there. On the low shore, mollusc shells appear to act largely as extensions of the primary substratum by providing increased settlement surface area. On rocky intertidal environments within the western biogeographic transition zone, mollusc shells provide important microhabitats as well as increased surface area for the settlement of a variety of epizoic organisms.

Acknowledgements

Thank you to my supervisor, Prof. Gavin W. Maneveldt for his guidance, leadership and criticism during my fieldwork and thesis write-up. I thank the University of the Western Cape and the Department of Biodiversity and Conservation Biology for providing funding, research facilities and technical support, the South African National Research Foundation (NRF) for the research grant to GWM and for a bursary I received, the Department of Agriculture, Forestry and Fisheries (DAFF) for the bursary in my third year, and the South African Department of Environmental Affairs and Tourism (DEAT) for the research permits to carry out the investigation. Thank you to Dr. Martin Hendricks and Dr. Vanessa Coulridge for advice with my statistics, Bahia Groenewald for assistance with my fieldwork and Sihaam Boolay for giving up her time to monitor my usage of the camera.

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