Documenting the association between a non-geniculate coralline red alga and its molluscan host

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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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March 2010

I declare that

"*Documenting the association between a non-geniculate coralline red alga and its molluscan host*"

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.

REager

3 March 2010

I would like to dedicate this thesis to my husband, John Eager and my children Gabrian and Savannah for their patience and support. Last, but never least, I would like to thank GOD for sustaining me during this project.

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Abstract

Non-geniculate (encrusting) coralline red algae are widespread in shallow water in all of the world's oceans, where they often cover close to 100 % of rocky substrates. While many molluscs include coralline algae in their diets, some are known to form only passive associations with them without necessarily grazing them. A facultative association between the encrusting coralline alga *Spongites discoideus* and its winkle host *Oxystele sinensis* had been observed at several sites within western False Bay, South Africa. Nearly all adult *O. sinensis* (98.6 ± 1.10 %) encountered had been observed to bear the coralline on their shells. This implied a strong positive relationship between the winkle and the coralline. The coralline was not found to occur on the morphologically similar winkle *Oxystele tigrina*, despite the variable overlap in habitats of the two winkle species.

To better understand the association, various natural data (e.g. invertebrate densities and biomass, algal % cover, algal competitive interactions, coralline attachment strengths, % burrowing of the coralline, etc) were collected at Kalk Bay (34° 08'S, 18° 27'E) from all the habitats (mid-Eulittoral flats, mid-Eulittoral crevices, intertidal rockpools, shallow subtidal zone) occupied by the organisms. The results firstly show that *S. discoideus* was restricted to intertidal rockpools (34.8 ± 7.14 %) and the shallow subtidal zone (1.4 ± 0.33 %) where *O. sinensis* (rockpools – 24.0 ± 3.94 number m^{-2}, 12.2 ± 2.84 g m^{-2}; shallow subtidal – 34.4 ± 2.25 number m^{-2}, 313.7 ± 20.49 g m^{-2}) was the most abundant winkle. Despite the high competitive ranking of *S. discoideus*, the coralline is extremely low in abundance in the shallow subtidal zone. Species that were typically at or near the bottom of the hierarchy in terms of overgrowth competition (interference) were the most abundant suggesting that exploitation competition was important in preventing competitive exclusion. The attachment strength of *S. discoideus* on boulders (8.4 ± 0.77 kg) was greater than that on winkle shells (2.2 ± 0.58 kg) ($p = 0.004$). An inverse relationship with percentage burrowing was evident with the percentage burrowing of the coralline on the winkle shells (44 ± 3.32 %) being greater than that on boulders (25 ± 3.94 %) ($p < 0.001$).

Preliminary data suggested that epilithic and epizoic forms of the coralline showed variably different stages in the life cycle of the coralline alga. To determine whether a difference in reproductive stages existed, a frequency measure was taken of the various reproductive stages occurring both epizoically and epilithically (intertidally and subtidally); these were obtained directly from prepared slides used to identify the coralline. Results showed that sporangial (54.4 ± 16.98 %) and gametangial (45.6 ± 16.98 %) plants contributed more or less equally to the alternating life cycle stages encountered epilithically in intertidal rockpools ($p = 0.821$). A similar trend was observed for the shallow subtidal zone (sporangial – 55.5 ± 7.03 %; gametangial – 44.5 ± 7.03 %; $p = 0.494$). In both of these habitats though, sporangial plants occurred substantially more frequently than either male or female plants. Furthermore, in both these habitats the ratios of male to female plants were identical (5.3:1), but reversed with more male plants occurring epilithically in intertidal rockpools and more female plants occurring epilithically in the shallow subtidal zone. In contrast to intertidal rockpools, plants occurring epizoically showed gametophyte (95.5 ± 2.21 %) dominance over sporophytes (4.5 ± 2.21 %) ($p = 0.003$), with male plants occurring in far greater numbers ($p = 0.008$).

To further investigate the strength of the association and the relative advantages of the association to both organisms, several manipulation experiments were set up. A cage experiment set up in the shallow subtidal zone showed that the coralline survived equally well without the winkle and did therefore not require the winkle or its empty shell for survival. A second controlled laboratory aquarium experiment was designed under both fluorescent (rich in blue light) and incandescent light (rich in red light) to ascertain whether the coralline had a preference for *O. sinensis* over the similar *O. tigrina*. This experiment was inconclusive as no recruitment was obtained under either of the light regimes. A third laboratory experiment was designed to determine whether the extra coralline weight had any possible advantage to the winkle, particularly against predation from the rock lobster *Jasus lalandii*. Results suggested that there were no apparent advantages to the winkle bearing the extra coralline load as adult *O. sinensis* bearing the coralline alga (3.7 ± 2.2 winkles $24hr^{-1}$) were equally prone to predation than those lacking the coralline (2.3 ± 1.9 winkles $24hr^{-1}$) ($p = 0.184$). Observations suggested instead that the convoluted nature of the coralline may indeed have promoted predation.

We ultimately deduced that the high occurrence of the coralline on the shells of *O. sinensis* was probably due to the substantial overlap in the niches of the two organisms. This conclusion was supported by the high densities of juvenile *O. sinensis* combined with the high percent cover abundance of the coralline in intertidal rockpools. Understanding sexual reproduction in coralline algae as well as the life cycle of the winkle, ultimately provided insight into the postulated life cycle of this coralline-winkle association. The interaction between *S. discoideus* and *O. sinensis* shows characteristics of a non-trophic, facultative association. The coralline benefits from the association by having an increased rate of fertilization, dispersal and recruitment, and possible refuge from interspecific competition. The benefit(s) to the winkle, if any, is unclear and all in all, the coralline alga appears advantaged at the expense of the winkle. While we may never fully understand the association between this alga and its winkle host, this study has provided valuable insight into the ecology of both organisms and their association.

Keywords: attachment strength, burrowing, competitive ability, encrusting coralline algae, epilithic, epizoic, exploitation, facultative association, gametangial, interference, overgrowth, *Oxystele sinensis*, *Spongites discoideus*, sporangial, thallus thickness, taxonomy.

1.1 Zonation on rocky shores

The vertical distribution of plants and animals between tide-marks on rocky shores is termed Zonation, and is usually evident by the dominance of various indicator organisms at different heights on the shore (Stephenson and Stephenson 1949, 1972, Lubchenco 1980, Dring 1982, Little and Kitching 1996). Zonation is a universal phenomenon prevalent on most rocky intertidal shores. Stephenson and Stephenson (1949) identified three main intertidal zones namely, the Littorina zone, Balanoid zone and the Sublittoral fringe. Still later, Stephenson and Stephenson (1972) renamed these zones the Supralittoral fringe, Midlittoral zone and Infralittoral fringe respectively.

The Supralittoral fringe, high up on the shore, experiences transitional conditions between land and sea. This zone is variably dominated by small snails (e.g. *Afrolittorina* spp.), encrusting Myxophyceae and lichens. The Midlittoral zone follows this and is partly covered and uncovered every day. This middle zone possesses more animals than the zone above it and is largely dominated by barnacles. In many cases this zone is further subdivided into two or more sub zones (Lubchenco 1980, Underwood 1980, Branch and Branch 1981a, Little and Kitching 1996, Bustamante *et al.* 1997). Low down on the shore is the Infralittoral fringe. This zone is exposed to the air for only short periods of time and rarely dries out. It is common to find foliose red and large brown macroalgae in this zone. The indicator species mentioned above vary from rocky shore to rocky shore, but the distinctive zonation patterns are very obvious.

1.1.1 Factors causing zonation

Physical factors such as high temperatures (Broekhuysen 1940, Evans 1948, Lewis 1954, Wolcott 1973, Branch 1975a) high light intensities (Evans 1948, Connell 1972, Dayton 1975, Underwood 1980) and desiccation stress (Broekhuysen 1940, Evans 1948, Brown 1960, Connell 1961a, b, Wolcott 1973, Branch 1975b, Beer and Eshel 1983, Davenport 1997) were originally thought to be the primary factors structuring rocky shore communities. It is commonly accepted that physical factors tend to be more prevalent at high shore levels where extremes of wave action and water levels, low and high salinity, high solar radiation, and desiccation stress are common (Stephenson and Stephenson 1949, 1972, Castenholz 1961, Frank 1965, Connell 1972, Vermeij 1972, Schonbeck and Norton 1978, Hay 1979, Rafaelli 1979, Lubchenco 1980, Branch and Branch 1981a, Bustamante *et al.* 1997). Biological factors such as competition (Dayton 1971, 1975, Lubchenco 1978, 1980, Branch 1985, Hawkins and Harkin 1985, Paine 1990, Farrell 1991, Steneck *et al.* 1991, Dethier 1994, Steneck and Dethier 1994), herbivory (Paine and Vadas 1969, Dayton 1971, Nicotri 1977, Lubchenco 1980, Lubchenco and Gaines 1981, Underwood and Jernakoff 1981, Chamberlain 1993, Keats *et al.* 1993, 1994a, Anderson and Underwood 1997, Anderson *et al.* 1997, Maneveldt and Keats 2008), predation (Paine and Vadas 1969, Dayton 1975, Lubchenco and Menge 1978, McQuaid 1982, Watanabe 1984), as well as larval settlement (Dayton 1971, Barnes and Gonor 1973, Steneck 1982, Morse and Morse 1984, Petersen 1984, Johnson *et al.* 1991a, b, Kaspar 1992, Little and Kitching 1996, Williams *et al.* 2008) are generally believed to have greater impacts on species at lower shore levels where physical stresses are minimal. Physical factors thus generally set the upper limits of species distributions while biological factors generally set their lower limits (Dayton 1971, Connell 1972, Branch 1976, Raffaelli and Hawkins 1996).

1.2 Plant-animal interactions on rocky shores

1.2.1 Trophic interactions

Herbivory is a common phenomenon influencing marine community structure (Paine and Vadas 1969, Lubchenco and Menge 1978, Menge 1978, Brock 1979, Vance 1979, Ayling 1981, Lubchenco and Gaines 1981, Paine 1984, Johnson and Mann 1988, Chapman and Johnson 1990, Dethier *et al*. 1991, Sousa and Connell 1992, Anderson *et al*. 1993, 1997, Chamberlain 1993, Keats *et al*. 1993, 1994a, Maneveldt and Keats 2008, Maneveldt *et al.* 2009). Among the many types of herbivores in the marine environment, molluscs are by far the most abundant benthic grazers in most rocky intertidal communities and therefore have a major impact on abundance and distribution of algal communities (Underwood 1980, Ayling 1981, Lubchenco 1983, Steneck 1983, Anderson *et al*. 1993, Keats *et al*. 1993, 1994a, Maneveldt *et al*. 2006, Maneveldt and Keats 2008, Maneveldt *et al.* 2009). Intense grazing by molluscs often lead to the exclusion of foliose macroalgae from mid-shore levels (Underwood 1975, 1980, Hay 1979, Underwood and Jernakoff 1981, Jernakoff 1983, Underwood *et al*. 1983, Underwood and Kennelly 1990, Dye 1995, Chan and Williams 2003, Maneveldt *et al*. 2009), resulting in a high proportion of encrusting algae (Adey 1973, Adey and Macintyre 1973, Lubchenco and Cubit 1980, Paine 1980, Steneck 1982, 1986, Steneck and Dethier 1994, Keats *et al*. 1994a, Maneveldt and Keats 2008). Under low grazer density, generalist grazers usually have a preference for the dominant macroalgae, allowing competitively inferior macroalgal species to occupy primary space (Lubchenco 1978, Lubchenco and Gaines 1981, Williams 1990). Under high grazer density, however, it becomes irrelevant whether grazers are generalists or specialists, because all macroalgae are consumed (Ayling 1978, 1981, Lubchenco 1978, Underwood 1980, Lubchenco and Gaines 1981, Noro *et al*. 1983, Steneck 1985, Steneck and Dethier 1994, Maneveldt *et al*. 2009).

Macroalgae do, however, have adaptations to reduce or escape herbivory. Some of these adaptations include: having small sizes (Ayling 1981); possessing short life spans (e.g. temporal escapes) (Keats *et al*. 1993, Rengefors *et al*. 1998, Bell 2005); possessing feeding deterrents (Ayling 1978, 1981, Lubchenco 1978, Steneck and Watling 1982, Steinberg 1985, 1988, Hay *et al*. 1987, 1988a, b, Branch *et al*. 1994); possessing cryptic morphologies (Adey and Spearamani 1971, Adey *et al*. 1974); possessing morphological defenses (e.g. calcification) (Adey and Macintyre 1973, Littler 1976, Cheney and Mathieson 1978, Underwood 1980, Ayling 1981, Steneck 1983, 1985, 1986, Cabioch 1988, Steneck *et al*. 1991, Keats *et al*. 1993, 1994b, Branch *et al*. 1994); and occurring in low abundance (Steneck *et al*. 1991, Kennish *et al*. 1996). Many edible species are even able to escape herbivory by growing in close proximity to inedible, chemically or morphologically defended species (Hay 1986, Littler *et al*. 1986, Duffy and Hay 1990). Whatever the mechanism, a competitive trade-off is usually evident, but this cost through competition is much less than the cost experienced through increased herbivory (Adey 1973, Adey and Macintyre 1973, Adey and Vassar 1975, Hay 1986, Steneck 1982, 1986, Steneck *et al*. 1991).

1.2.2 Non-trophic interactions

Not all plant-animal interactions involve direct feeding. These non-trophic interactions are vitally important to the ecology and evolution of the organisms involved. Mollusc shells are often used by other organisms as a settlement substrate, or as a burrow (Barnes 2003, Nakin and Somers 2007). Numerous intertidal organisms provide settlement substrates for algae and vice versa (Bell 2005). Besides rocky substrates, algae are notorious for settling on bivalves and barnacles and these interactions are often required for the maintenance of high species diversity in such communities (Menge 1976, Hawkins 1981, Underwood *et al*. 1983). One such example is that of *Gelidium pristoides* (Turner) Kuetzing which is often confined to the shells of barnacles, limpets and reef-worm tubes which provide a refuge from grazing by limpets (Branch *et al*. 1994). Similarly *Caulacanthus ustulatus* (Mertens ex Turner) Kützing escapes grazing by growing on reef-worm tubes (Branch *et al*. 1994). These epibionts influence the survival of their hosts in two ways: negatively by increasing the rates of their dislodgement (Hawkins 1981, Witman and Suchanek 1984, D'Antonio 1985); and/or positively by reducing the predation experienced by the host organisms (Bloom 1975, Vance 1978, Wahl 1989, Wahl and Hay 1995, Stachowicz and Hay 1999, 2000, Marin and López Belluga 2005) as well as providing protection from desiccation stress (Menge 1978). Where this association is positive, one or both members of the association may benefit.

1.3 Ecology of winkles

Winkles (Trochidae, Gastropoda, Mollusca), also known as topshells, possess lime shells with a circular or semicircular aperture which is protected by an operculum when the animal retreats into the shell (Day 1969, Kilburn and Rippey 1982, Branch *et al*. 1994). Winkles have a well developed head with tentacles, a radula and a large foot for locomotion (Day 1969, Kilburn and Rippey 1982, Branch *et al*. 1994). These molluscs are more commonly generalist grazers, feeding on benthic microalgae and a wide variety of macroalgae including encrusting coralline algae (Day 1969, Kilburn and Rippey 1982, Steneck 1983, Branch *et al*. 1994).

Winkles have a wide vertical distribution and are found on salt marshes, on coastal cliffs, intertidally on boulder beaches, intertidally in rock pools, in the sublittoral fringe, and the subtidal zone (Moyse and Nelson-Smith 1963, Kilburn and Rippey 1982, Atkinson and Newbury 1984). These gastropods are generally found on flat surfaces on semi-exposed shores, but on more sheltered shores they are able to occupy steeper slopes (Moyse and Nelson-Smith 1963). Unlike sessile organisms that are restricted to one location, winkles are highly motile organisms that are able to ensure a preferred tidal height. Due to the high wave energy experienced in rocky intertidal habitats, food resources are abundant but at the cost of dislodgement of these mobile, benthic organisms (Atkinson and Newbury 1984, Rilov *et al.* 2004). All gastropods generally prevent dislodgement by attaching their foot to the substratum. The rate of dislodgement is usually amplified when foraging time is increased (Denny 1985, Judge 1988, Burrows and Hughes 1989). When the foraging time is decreased to avoid dislodgement (Denny 1985, Judge 1988, Burrows and Hughes 1989), however, growth and development become adversely affected (Etter 1996, Johnson and Black 2008).

Habitat selection by winkles has major impacts on their growth and development (Johannesson *et al.* 1995, Williams 1995, Johnson and Black 2008). Johnson and Black (2008) showed for example, that winkles in a large pond (100 m x 20 m) that was continuously inundated, grew considerably larger and faster, were more mobile, and dispersed more than those found in a smaller pond (10 m in diameter) that was seldom inundated. There is, however, a trade-off as the small pond had a higher abundance and survivorship than the larger pond. The reason for this was due to the intricate differences in the habitats. The smaller pond, being at a higher tidal elevation, experienced reduced inundation and thus reduced grazing time that inevitably affected growth rates. The reduced inundation, however, resulted in lower predation rates, which resulted in higher abundance and survivorship. Winkles tend to overcome these conflicting physiological and biological determinants by migrating up and down the shore.

Winkles migrate for various reasons. Firstly, desiccation stress is a major problem on rocky intertidal shores and winkles cope with this by either retreating into their shells, or by migrating to shelters and gullies to reduce water loss (Lambert and Farley 1968, Underwood 1979, Atkinson and Newbury 1984, Rilov *et al*. 2004). Unfortunately, these adaptations to escape desiccation, can conflict with the adaptations to escape dislodgement (Atkinson and Newbury 1984). After desiccation stress, intraspecific competition for food is the major reason for migrating (Vermeij 1972, Branch and Branch 1981b). Many winkles migrate during or prior to the breeding season to ensure reproductive success (Underwood 1979). Such animals have an added advantage by increasing their growth and reproduction in their new habitat although the risk of being preyed upon before reaching their destination exists (Paine 1969). Consequently, predation is another reason for migrating. Some of these winkles avoid predation by finding refuge on foliose macroalgae of low nutrient status (Watanabe 1984) or other defended macroalgae (Williams and Seed 1992, Williams 1995). The trade-off to such winkles is that they too are then dependent on these low nutrient food sources which adversely impacts on their growth and reproductive development, but reduces the risk of predation (McQuaid 1982, Watanabe 1984). Fluctuating salinity levels, particularly in high shore tide pools, have also been shown to determine the migration and distribution patterns of winkles as these fluctuations result in the cessation of mobility (Broekhuysen 1940).

1.4 Ecology of encrusting coralline algae

Non-geniculate or encrusting coralline algae (Corallinophycidae, Rhodophyta) are amongst the most abundant benthic organisms occupying hard substrata within the photic zone in all of the world's oceans (Adey and Macintyre 1973, Paine 1984, Steneck 1985, 1986, Steneck *et al*. 1991). Corallines generally have a distinctive pinkish to reddish colouration (caused by the protein pigment phycoerythrin) that readily becomes bleached when exposed to high light intensities, sometimes resulting in the death of the organism (Littler 1973, Steneck 1982, Hawkins and Harkin 1985, Irving *et al*. 2004). They are therefore normally restricted to shaded and damp areas in the upper intertidal, to the low shore, to rockpools, and to the subtidal zone in order to reduce desiccation stress (Steneck *et al*. 1991).

Encrusting coralline algae often occupy close to 100 % of primary rocky substrata (Adey and Macintyre 1973, Steneck 1986). This is ironic given the extremely slow growing nature of most of these organisms and the fact that they are overgrown by most other macroalgae (Steneck 1985). Consequently, these algae invest more into mechanical, anatomical and morphological defenses than faster growing marine benthic organisms (Steneck and Watling 1982, Steneck 1983, 1985, Coley *et al*. 1985). One notable adaptation is the presence of one to several outer layers of epithallial cells above the meristematic region. This epithallial layer protects the developing meristematic, reproductive and photosynthetic tissues of these organisms (Steneck 1983). In addition, the epithallial layer serves as a unique antifouling mechanism that has received considerable attention (see Adey 1966, Littler 1972, Masaki *et al*. 1981, 1984, Moss 1982, Steneck 1982, Breitburg 1984, Johnson and Mann 1986, Keats *et al*. 1993, 1997, Pueschel 1988, Pueschel and Keats 1997). It is for this reason that corallines remain largely free of potentially fouling epiphytes.

All coralline algae have a high fecundity and extended reproductive season; this increases their opportunity to occupy space cleared by disturbance (Ayling 1976). They are, however, notably restricted in their capacity to grow on fine-grained materials, granular substrates and sand (Adey 1970a). Encrusting coralline algae are therefore largely epilithic and most abundant in rocky areas where heavy wave activity or strong bottom currents are prevalent

(Steneck 1986). In addition to encrusting primary rocky substrata, these corallines are also found growing unattached as rhodoliths (free-living encrusting corallines), or encrusting unstable substrata such as cobbles and boulders, epizoically on corals and other animals, or epiphytically on other macroalgae and other corallines (Adey 1970a, 1973, Adey and Spearapani 1971, Adey and Macintyre 1973, Littler 1973, Gordon *et al*. 1976, Steneck 1982, 1986, Morse and Morse 1984, Steneck and Paine 1986, Borowitzka *et al*. 1990, Branch *et al*. 1994, Figueiredo *et al*. 1996, Morcom and Woelkerling 2000).

Encrusting coralline algae have often been compared to "bare rock" and therefore referred to as primary substrata (Dayton 1975, Menge 1976). For this reason it was commonly assumed that these algae had no effect on other species. Breitburg (1984) proved to the contrary that the recruitment of sessile invertebrates was considerably inhibited by coralline crusts. Encrusting coralline algae are, however, inferior interference competitors to established invertebrates and other benthic macroalgae when competing for primary space (Steneck 1983, 1985, 1986, Breitburg 1984, Carpenter 1986, Steneck *et al*. 1991). On a positive note though, one should not ignore the fact that due to their calcified nature, coralline algae are efficient resistors to most grazers and are often the only organisms to survive intense herbivory (Bakus 1966, Paine and Vadas 1969, Adey and Macintyre 1973, Lawrence 1975, Vadas 1977, Vance 1979, Steneck 1982, 1983, Breitburg 1984, Sousa and Connell 1992, Dethier 1994, Steneck and Dethier 1994, Maneveldt *et al*. 2006).

It is common to find encrusting coralline algae thriving and dominating in environments prone to intense herbivory (Paine and Vadas 1969, Adey and Macintyre 1973, Lawrence 1975, Vance 1979, Steneck 1982, 1985, 1986, Carpenter 1986, Maneveldt *et al*. 2006). In such environments, the removal of herbivores quickly leads to an increase in foliose macroalgal growth and diversity with the coralline crusts often fouled by such canopy-forming macroalgae (Paine and Vadas 1969, Dayton 1975, Duggins 1980, Paine 1980, Slocum 1980, Ayling 1981, Sousa *et al*. 1981, Steneck 1982, Bertness 1984). Through their variable antifouling mechanisms (epithallial cell sloughing – see Adey 1966, Littler 1972, Masaki *et al*. 1981, 1984, Moss 1982, Steneck 1982, Breitburg 1984, Johnson and Mann 1986, Keats *et al*. 1993, 1997, Pueschel 1988, Pueschel and Keats 1997), however, encrusting coralline algae can have a major impact on recruiting foliose macroalgal communities by slowing or even preventing the settlement of foliose algal sporelings (Paine and Vadas 1969, Masaki *et al*. 1981, 1984, Breitburg 1984, Johnson and Mann 1986, Airoldi 2000).

Within the rocky intertidal environment, primary space is the most limiting resource because it is not easily renewable (Connell 1961a, b, Dayton 1971, 1975, Menge 1976, Lubchenco and Menge 1978, Wu 1980, Ayling 1981, Branch 1985, Bertness 1989, Keats *et al*. 1994b, Airoldi 2000). Space only ever becomes available through some kind of physical disturbance that removes the original occupants (Connell 1972, Underwood 1979, Branch 1984). All encrusting algae (coralline and foliose) compete against each other and other benthic organisms for space through overgrowth (interference) competition (Steneck 1986, Steneck *et al*. 1991, Keats and Maneveldt 1994, Keats *et al*. 1994b, Morcom *et al*. 1997). For encrusting coralline algae, two factors determine competitive success in overgrowth competition namely the thallus thickness, and the degree to which their primary margins are raised (Padilla 1984, Paine 1984, Steneck 1985, 1986, Sebens 1986, Steneck *et al*. 1991, Keats and Maneveldt 1994, Morcom *et al*. 1997). In general, thick crusts and those with raised margins tend to be competitively superior to thin crusts and those with adherent margins of equal crust thickness (Steneck 1983, 1985, 1986, Paine 1984, 1990, Sebens 1986, Steneck *et al*. 1991, Keats and Maneveldt 1994, Keats *et al*. 1994b, Morcom *et al*. 1997, Maneveldt and Keats 2008).

Surprisingly though, thinner crusts often tend to be more abundant than thicker crusts. This suggests that factors other than overgrowth (interference) competition influence the competitive outcomes among competing crusts. It is well documented that thinner crusts grow laterally faster than thicker ones (Steneck 1983, 1985, 1986, Keats and Maneveldt 1994, Keats *et al*. 1994a, b, Wai and Williams 2005, Maneveldt and Keats 2008). Thick crusts maintain a higher percentage of living non-photosynthetic tissue than do thinner ones and this investment in vertical growth is thought to deplete photosynthate that could be used in lateral expansion (Steneck 1983, Maneveldt and Keats 2008). In addition, Keats *et al*. (1994b) showed that crust attachment strength is inversely correlated with overgrowth ranking and that thicker crusts were more heavily burrowed by boring organisms. Thicker crusts are thus generally more easily dislodged by physical factors associated with exposure. *Spongites yendoi* (Foslie) Chamberlain, for example, which is the thinnest species in the mid- to lower Eulittoral zone along the South African southern west coast, is at the bottom of the overgrowth hierarchy, but dominates this zone (Keats *et al*. 1994b, Maneveldt and Keats 2008). The reason for its competitive success has been shown to be due to intense grazing by the territorial gardening limpet *Scutellastra cochlear* Born resulting in the coralline having a fast lateral growth and stronger attachment strength of its thin thallus (Maneveldt and Keats 2008). This shows that not only overgrowth among crusts, but also various exploitation competitive mechanisms, determines competitive outcomes. There is thus a trade-off between being thick and being a superior overgrowth competitor, and being thin and capable of faster lateral growth (Keats and Maneveldt 1994, Maneveldt and Keats 2008). Consequently, one would expect the substrate to be dominated by faster growing thinner crusts if primary space is readily available, or if it is constantly being renewed by disturbance. Conversely, the substrate should be dominated by slower growing thicker crusts if space is limited or seldom renewed (Keats and Maneveldt 1994, Maneveldt and Keats 2008).

Besides occurring epilithically, coralline algae are often found occurring epizoically on the shells of various invertebrates. Invertebrate shells are thus seen as particularly important in providing secondary settlement space when space is limiting (Steneck 1986, Warner 1997, Bell 2005). While desiccation stress is seen as a potential problem for such epibionts, especially if they have a lower desiccation tolerance than their host (Bell 2005), the benefits to the corallines are numerous. Besides the direct advantages of having access to secondary space, there are also the advantages associated with reduced interspecific interference competition and increased dispersal (Buss and Yund 1988). The invertebrates have also been demonstrated to benefit from such associations in that the corallines provide some degree of camouflage as well as a degree of protection from predators by virtue of their calcified nature (Wahl 1989, Wahl and Hay 1995).

1.4.1 Mollusc-coralline interactions

Due to their calcified nature, encrusting coralline algae are often the only seaweeds capable of surviving intense grazing pressures (Paine and Vadas 1969, Adey and Macintyre 1973, Lawrence 1975, Vance 1979, Steneck 1982, 1983, 1985, 1986, Carpenter 1986, Maneveldt *et al*. 2006). Many herbivorous molluscs have, however, been reported to actively graze the surfaces of these corallines (Day 1969, Branch 1971, 1975b, c, 1981, Barnes and Gonor 1973, Kilburn and Rippey 1982, Steneck and Watling 1982, Steneck 1983, 1986, Paine 1984, Steneck and Paine 1986, Steneck *et al*. 1991, Fujita 1992, Keats *et al*. 1993, 1994a, b, Maneveldt *et al*. 2006, Maneveldt and Keats 2008). The literature also shows that these algae are vital food sources for many intertidal herbivores (Steneck 1982**,** 1985, Steneck and Watling 1982**,** Paine 1984, Steneck *et al*. 1991, Fujita 1992, Littler *et al*. 1995) and a number of South African intertidal molluscan herbivores have been demonstrated to consume relatively large amounts of encrusting coralline algae (see Keats *et al*. 1993, Maneveldt *et al*. 2006, Maneveldt and Keats 2008).

Herbivory is often linked to negative associations for the alga, but in the case of corallines, molluscan grazing is largely seen as a positive interaction for a number of reasons. Encrusting corallines are often at risk of fouling by invertebrates and foliose macroalgae in shallow productive zones (Steneck 1982, 1983, 1986, Breitburg 1984). While many corallines have a natural protection mechanism against fouling (epithallial shedding – see Adey 1966, Littler 1972, Masaki *et al*. 1981, 1984, Moss 1982, Steneck 1982, Breitburg 1984, Johnson and Mann 1986, Pueschel 1988, Keats *et al*. 1993, 1997, Pueschel and Keats 1997), herbivory has in many cases been recognized as important in keeping the surfaces of corallines clean of fouling organisms (Adey 1973, Adey and Vassar 1975, Dayton 1975, Wanders 1977, Brock 1979, Vance 1979, Paine 1980, Steneck 1982, 1983, 1986, Kaspar 1992). By selective grazing, herbivory is known to prevent competitor exclusion and even reverse competitive outcomes among corallines competing by overgrowth competition (Quinn 1982, Paine 1984, Steneck 1985, Paine 1990, Dethier *et al*. 1991, Steneck *et al*. 1991, Maneveldt and Keats 2008). Grazing by various molluscs has even resulted in an increase in growth, productivity and biomass of encrusting coralline algae. The chiton, *Choneplax lata* (Guilding) for example, has a positive relationship with the encrusting coralline alga, *Hydrolithon pachydermum* (Foslie) Bailey, Gabel & Freshwater (Littler *et al*. 1995 as *Porolithon pachydermum*). This association results in increased growth, elevated meristematic activity, increased biomass and structural carbonate accretion of the alga. This study also showed that the chiton was not found naturally isolated from the coralline and also needed the coralline for its own fitness and survival. Littler and Littler (1999) observed a similar association between the encrusting coralline alga *Hydrolithon onkodes* (Heydrich)

Penrose & Woelkerling and the chiton *Cryptoplax larvaeformis* (Blaineville & Burrow). Similarly, Steneck (1982) showed that the encrusting coralline alga *Clathromorphum circumscriptum* (Strömfelt) Foslie not only survived frequent grazing from the limpet *Tectura testudinalis* (Müller) (as *Acmaea testudinalis*), but actually benefited from their association.

Besides food for various herbivores capable of consuming these algae, corallines serve a number of other non-trophic functions including: settlement cues for various molluscan larvae (Barnes and Gonor 1973, Rumrill and Cameron 1983, Johnson *et al*. 1991a, b, Johnson and Sutton 1994, Daume *et al*. 1999); and spatial refuges for newly settled larvae as well as juveniles of various grazers (Garland *et al*. 1985, Steneck 1986, Johnson *et al*. 1991a, b, Johnson and Sutton 1994, Tarr *et al*. 1996, Daume *et al*. 1997, 1999). Corallines therefore have major impacts on the life cycles of many molluscan invertebrates and their very presence is often capable of altering community structures (Williams *et al*. 2008).

1.4.2 Winkle-coralline associations

While numerous studies exist on the associations between coralline algae and herbivorous molluscs (e.g. Kitting 1980, Steneck 1982, Steneck and Paine 1986, Steneck *et al*. 1991, Littler *et al.* 1995, Maneveldt 1995, Littler and Littler 1999, Maneveldt and Keats 2008), none exist that have documented the associations between coralline algae and winkles. This appears largely so due to the relatively limited research on the general ecology of winkles despite the fact that these molluscs are often the most abundant intertidal invertebrates in marine benthic communities (Kilburn and Rippey 1982). One observation that certainly appears to be true (Maneveldt *pers. obs*.), is that winkles are often abundant when coralline algal communities are well established, or vice versa (Ayling 1981, Steneck 1983).

2.1 South African west and south coast rocky shore zonation patterns

South African rocky shores have been given a unique terminology by Branch and Branch (1981a). High up on the shore on the west and south coasts is the infratidal (or Supralittoral fringe) zone, locally known as the *Littorina* zone because of the dominance by tiny *Afrolittorina knysnaensis* (Philippi) snails, which were previous known as *Littorina africana*. This zone is followed by the upper Eulittoral zone (upper Balanoid) dominated by barnacles (more so on the south than the west coast) and a variety of limpets. Next is the mid-Eulittoral zone (lower Balanoid), mainly comprising dense beds of macroalgae. The lowest zone in the intertidal is the lower Eulittoral zone. On the south coast this zone is known for having dense assemblages of the territorial gardening limpet, *Scutellastra cochlear* (Born) and is therefore named, the Cochlear zone. The west coast shows a similar zonation pattern, but here the lower Eulittoral zone is known as the Cochlear/Argenvillei zone as *Scutellastra cochlear* shares this zone with the larger *Scutellastra argenvillei* (Krauss) that tends to replace the former limpet further north along the west coast.

2.2 Observation

Kalk Bay, within the greater False Bay, has a typical west-south coast transition zonation pattern bearing elements of both the west and south coasts (Stephenson and Stephenson 1972). Within the intertidal and immediate subtidal zones of this little bay, an interesting association between a non-geniculate (encrusting) coralline alga and the molluscan winkle *Oxystele sinensis* (Gmelin) was observed (Figure 2.1). The coralline has only been observed to occur epilithically and epizoically in intertidal rockpools and in the subtidal zone, and all initial observations suggested that the winkle was the primary substrate for the coralline in the subtidal zone. Numerous juvenile *O. sinensis* that were confined to rockpools were observed to bear a thin coralline while adult winkles found both intertidally and subtidally were observed to bear a lumpy, convoluted encrusting coralline alga. Individuals (both juvenile and adult) of the morphologically similar winkle *Oxystele tigrina* (Anton), which shared many of the habitats with *O. sinensis,* were not found to bear any coralline epizoics.

Figure 2.1 Image of the association between the coralline alga and its winkle host *O. sinensis*.

2.3 Aim of Study

Encrusting coralline red algae are widespread in shallow water in all of the world's oceans, where they often cover close to 100 % of rocky substrates (Adey and Macintyre 1973**,** Paine 1984**,** Steneck 1985, 1986**,** Steneck *et al*. 1991). These algae usually show distinct hierarchies of competitive superiority in which thicker crusts and those with raised margins are superior interference (overgrowth) competitors to thinner crusts and those with adherent margins

(Steneck 1983, 1985, 1986, Paine 1984, Sebens 1986, Steneck *et al*. 1991, Keats and Maneveldt 1994, Keats *et al*. 1994b, Maneveldt and Keats 2008). The nature of the competitive hierarchy can change, however, in relation to the abundance of herbivores and the intensity of their grazing (Steneck 1983, 1985, Steneck *et al*. 1991, Maneveldt and Keats 2008). One observation common to many studies involving encrusting coralline algae is that corallines often thrive under, and have often been postulated to even require, intense herbivory (Adey and Macintyre 1973, Dayton 1975, Steneck 1982, 1983, 1986). Molluscs (Gastropoda) are important grazers and many of them include encrusting coralline algae in their diets (see e.g. Barnes and Gonor 1973, Branch 1975b, c, Steneck 1982, 1985, Steneck and Watling 1982, Paine 1984, Steneck *et al*. 1991, Fujita 1992, Littler *et al*. 1995, Maneveldt *et al*. 2006). Some molluscs are even known to form passive associations with these algae without necessarily grazing them (see e.g. Steneck 1986, Bell 2005). The association between *O. sinensis* and its epizoic coralline appears to be an example of just such an association.

Virtually all adult *O. sinensis* that were encountered in the Kalk Bay study area had the lumpy, convoluted coralline encrusted to their shells. The aim of this research was therefore to identify the thin and lumpy corallines encrusting the shells of both juvenile and adult *O. sinensis* respectively, and to determine the nature of their associations. In order to do so, the following needed to be determined:

1. the taxonomic identities of the thin and thick (lumpy and convoluted) corallines;
2. various ecological parameters of the thick coralline found both intertidally and subtidally;
3. the possible benefits of the association to both the coralline and winkle; and

4. the reproductive ecology of the winkle as already published as well as various ecological parameters of the winkle and other associated invertebrates that co-exist at Kalk Bay.

In trying to obtain plausible reasons for the associations, three manipulation experiments were set up in order to answer the following questions.

1. As a large percentage of the corallines encountered (particularly in the subtidal zone) were found epizoically on the shells of the winkle, do the corallines require the winkles as hosts?
2. Since individuals of the morphologically similar winkle *O. tigrina*, which shares many of the habitats with *O. sinensis,* were not found to bear any coralline epizoics, is there a preference for *O. sinensis* over *O. tigrina*?
3. Since the coralline becomes very lumpy and convoluted on the shells of *O. sinensis*, does the extra coralline weight have any advantage to the winkle?

Ultimately all of these components of the study were envisaged to provide, not only clues as to the nature of the association between the winkle and its associated coralline alga, but also on the general ecology of the winkle and the coralline alga in isolation of each other, information which was found to be sorely lacking.

3.1 Introduction

Winkles (topshells) are abundant in South Africa and are very noticeable intertidal grazers (Lasiak 1987, Anderson *et al*. 1997, Pulfrich and Branch 2002). Most South African winkles are endemic and many are overexploited (Pulfrich and Branch 2002). Winkles are generally very slow growing with a few exceptions common amongst the smaller species (Kilburn and Rippey 1982). After hatching, winkles generally settle high on the shore and gradually migrate downshore with increasing size (Pulfrich and Branch 2002). Although winkles are often the most abundant intertidal molluscs, there is a general lack of research concerning their general ecology and reproductive biology (Kilburn and Rippey 1982).

3.2 General ecology and distribution

There are five species of winkles from the genus *Oxystele* in South Africa namely, *Oxystele impervia* (Menke), *Oxystele sinensis*, *Oxystele tabularis* (Krauss), *Oxystele tigrina* and *Oxystele variegata* (Anton) (Branch *et al*. 1994, Van As and Van As 2001). All *Oxystele* species have a flexible, horny operculum that is yellow-brown in colour with spiral growth rings (Day 1969, Kensley *et al*. 1973, Kilburn and Rippey 1982, Branch *et al*. 1994).

Oxystele variegata is found from Luderitz on the west coast of Namibia to Durban on the east coast of South Africa (Day 1969, Kensley *et al*. 1973, Branch and Branch 1981a, Kilburn and Rippey 1982, McQuaid 1982, Lasiak 1987, Branch *et al*. 1994). The winkles name is derived from the variegated pattern on its shell. This winkle has a pearly aperture and ranges in size from 10 - 26 mm shell diameter (Day 1969, Kensley *et al*. 1973, Kilburn and Rippey 1982, Branch *et al*. 1994). Juveniles are more susceptible to water loss than adults and so it is common to find more juveniles low on the shore where desiccation stress is much reduced (Branch and Branch 1981a, McQuaid 1982, Branch *et al*. 1994). Adult *O. variegata* generally migrate to the high shore where there is less food available, but also fewer predators (Branch and Branch 1981a, McQuaid 1982, Branch *et al*. 1994). The diet of *O. variegata* typically comprises microalgae, cyanobacteria and encrusting fleshy macroalgae (Day 1969, Branch and Branch 1981a, Kilburn and Rippey 1982, Lasiak 1987, Branch *et al*. 1994).

Oxystele impervia is morphologically similar to *O. variegata* but possess bead-like dots running spirally around the coils of their shells (Branch *et al*. 1994). The two species were once thought to be one species, but a morphological (Heller and Dempster 1991) as well as genetic study (Donald *et al*. 2005) have shown them to be distinct species. It is for this reason that ecological information on this species is quite limited. Although *O. variegata* and *O. impervia* have a similar distribution pattern (Namibia to Durban) and habitat, the latter species is found in more sheltered areas and is also found a little higher up on the shore (Branch *et al*. 1994). The diet of *O. impervia* has not been reported on due to it being a relatively recently described species, but we can assume its diet is similar to other species in this genus comprising of microalgae, cyanobacteria and encrusting fleshy macroalgae.

Oxystele tabularis is found from Port Alfred on the South African south coast, to the southern Moçambiquan coast; they are especially abundant along the Transkei coast (Day 1969, Kensley *et al*. 1973, Kilburn and Rippey 1982, Lasiak 1987, Branch *et al*. 1994). This winkle is similar to both *O. variegata* and *O. impervia*, but has distinguishing grey-brown to grey-green bands that run radially across each coil of their shells. Thinner red and green lines alternate with these bands (Kensley *et al*. 1973, Kilburn and Rippey 1982, Branch *et al*. 1994). *Oxystele tabularis* range in size from about 7 - 18 mm shell diameter (Kensley *et al*.

1973, Kilburn and Rippey 1982, Lasiak 1987) and their diets typically comprise encrusting fleshy macroalgae (Day 1969).

Oxystele sinensis has a limited distribution from False Bay along the southern west coast, to Transkei along the southern east coast of South Africa (Day 1969, Kensley *et al*. 1973, Kilburn and Rippey 1982). The density and biomass of this winkle generally increases from west to east (Pulfrich and Branch 2002). *Oxystele sinensis* has a dark purple-black shell bearing a distinctive pink inner lip (Day 1969, Kensley *et al*. 1973, Kilburn and Rippey 1982, Branch *et al*. 1994). This winkle has been reported to grow up to 62 mm in shell diameter (Kensley *et al*. 1973, Branch and Branch 1981a, Kilburn and Rippey 1982, Branch *et al*. 1994). *Oxystele sinensis* has a broad vertical distribution across the intertidal zone, extending into the subtidal zone down to about 7 m depth (Branch and Branch 1981a, Griffiths 1981, Branch *et al*. 1994, Pulfrich and Branch 2002) with the greatest biomass occurring at 0-2 m depth (Pulfrich and Branch 2002). This distribution range suggests that the winkle is incapable of withstanding the harsh physical stresses that other species of *Oxystele* are able to tolerate (Broekhuysen 1940, Brown 1960, Branch and Branch 1981a, Kilburn and Rippey 1982, Branch *et al*. 1994). Compared to other winkles, *O. sinensis* appears to be more adapted to life in wave-exposed habitats (Branch and Branch 1981a) and generally finds refuge from wave action and sand scouring within and between kelp holdfasts (Pulfrich and Branch 2002). The diet of *O. sinensis* typically comprises microalgae, cyanobacteria, encrusting fleshy macroalgae, and even the sporelings of foliose macroalgae (Day 1969, Branch and Branch 1981a, Branch *et al*. 1994, Anderson *et al*. 1997).

Oxystele tigrina occurs from Port Nolloth along the west coast, to Transkei along the southern east coast of South Africa (Day 1969, Kensley *et al*. 1973, Kilburn and Rippey

1982, Branch *et al*. 1994). This winkle is superficially similar to *O. sinensis* in that they both have dark purple-black shells (Figure 3.1) (Day 1969, Kensley *et al*. 1973, Kilburn and Rippey 1982, Branch *et al*. 1994). The only obvious difference between them is the distinctive white inner lip and black border of *O. tigrina* compared to the pink inner lip of *O. sinensis*, both of which are only evident when the winkles are flipped over (Figure 3.2) (Day 1969, Kensley *et al*. 1973, Kilburn and Rippey 1982, Branch *et al*. 1994). *Oxystele tigrina* grows to about 45 mm in shell diameter (Kensley *et al*. 1973, Branch and Branch 1981a, Kilburn and Rippey 1982). While the winkle is generally an intertidal species, it is found moderately low on the shore; it is less desiccation intolerant than high shore winkles, but more so than the low shore *O. sinensis* (Branch and Branch 1981a, Kilburn and Rippey 1982, Branch *et al*. 1994). The diet of *O. tigrina* typically comprises microalgae and encrusting fleshy macroalgae (Day 1969, Branch and Branch 1981a, Branch *et al*. 1994).

Figure 3.1 Juveniles of the morphologically similar *O. sinensis* (left) and *O. tigrina* (right) viewed from their dorsal perspectives.

Figure 3.2 It is only when flipped over that the differences between *O. sinensis* (left) and *O. tigrina* (right) become apparent.

3.3 Factors influencing the vertical distribution of *Oxystele* species

3.3.1 Physical factors

Desiccation stress has long been accepted as being the dominant physical factor controlling the distribution patterns of various intertidal invertebrates (Broekhuysen 1940, Evans 1948, Brown 1960, Connell 1961a, b, Wolcott 1973, Branch 1975a, Beer and Eshel 1983, Davenport 1997). Species from the genus *Oxystele* are known to be variously tolerant of desiccation stress and this has influenced their vertical distribution (zonation) across rocky shores (Broekhuysen 1940, Brown 1960). Those species less tolerant of desiccation stress have evolved to inhabit permanent rockpools and have consequently overcome the problems associated with desiccation stress (Broekhuysen 1940, Evans 1948, Brown 1960).

Of the three closely associated species (i.e. *O. variegata*, *O. sinensis* and *O. tigrina*), *O. sinensis* is the least tolerant of desiccation stress (Broekhuysen 1940, Brown 1960). Consequently, *O. sinensis* is found in damp areas on the low shore where the physical environment is not as harsh and where it is able to limit the amount and rate of water loss (Broekhuysen 1940, Brown 1960). *Oxystele tigrina*, being more desiccation tolerant than *O. sinensis*, occupies areas a little higher up the shore and finds refuge in rockpools and crevices (Broekhuysen 1940). *Oxystele variegata*, being the most tolerant of desiccation stress than either of the previously mentioned species, is typically most abundant in the intertidal zone (Broekhuysen 1940, Brown 1960). In contrast to the other two species, *O. sinensis* is, however, more tolerant of wave exposure (Branch and Branch 1981a) and is also better able to resist dislodgement under wave exposed conditions (Day 1969, Branch and Branch 1981a, Branch *et al*. 1994, Rilov *et al*. 2004).

Winkles are known to migrate to shelters and crevices until the environment is conducive to their survival (Denny *et al*. 1985, Burrows and Hughes 1989). Intertidally, *O. sinensis* and *O. tigrina* are found mainly in rockpools (Broekhuysen 1940) and so problems associated with desiccation stress are eliminated (Evans 1948). They do, however, have to cope with diurnal and seasonal fluctuations in temperature, salinity and oxygen concentrations (Evans 1948, Newell 1979). While the higher occurring *O. variegata* has been reported to have a greater tolerance for salinity stress than either of the other two species, *O. tigrina* copes better with salinity fluctuations (Broekhuysen 1940). This is probably why *O. tigrina* is largely confined to rockpools (Broekhuysen 1940).

3.3.2 Biological factors

Besides the various physical factors, biological factors such as competition and predation also determine the vertical distribution of *Oxystele* spp. As *O. variegata* individuals mature, they become more tolerant of desiccation stress and this allows them to survive higher up on the shore (McQuaid 1982). This migration pattern is primarily due to the intense predation on the low shore (Branch and Branch 1981a, McQuaid 1982, Branch *et al*. 1994). The animals opt rather to forfeit greater body weight due to less food availability and deal with the harsh physical conditions higher up on the shore, than to contend with intense predation. In contrast, juvenile and adult *O. tigrina* find refuge mainly in intertidal rockpools and are thus able to escape predation from subtidal predators (Pulfrich 1997). Interspecific competition between adult *O. sinensis* and *O. tigrina* as well as the higher tolerance of *O. sinensis* to high wave exposure, is what largely restricts adult *O. sinensis* to the low shore and shallow subtidal zone (Day 1969, Branch and Branch 1981a, Branch *et al*. 1994, Rilov *et al*. 2004).

In the absence of their preferred prey (i.e. mussels and sea urchins), the rock lobster, *Jasus lalandii* (Milne-Edwards) preferentially consumes the winkle *O. sinensis* (Van Zyl *et al*. 1998, Pulfrich and Branch 2002). To prevent predation of their juveniles, adult *O. sinensis* migrate into intertidal rock pools to reproduce (Van Zyl *et al*. 1998, Pulfrich and Branch 2002). Here juveniles are able to escape predation from subtidal predators, but become exposed to these predators when they mature and move into the subtidal zone (Pulfrich 1997, Van Zyl *et al*. 1998, Pulfrich and Branch 2002). To minimise predation by subtidal predators, winkles are often observed to clump together in narrow crevices (Lasiak 1987, Pulfrich 1997, Van Zyl *et al*. 1998, Pulfrich and Branch 2002). By virtue of their intertidal habit, both adult and juvenile *O. tigrina* find refuge from subtidal predators (Pulfrich 1997). All these examples show that there is a balance between physiological adaptations to the physical environment, and behavioural adaptations to the biological environment that ultimately zone the various species of *Oxystele* within the intertidal and shallow subtidal zones.

3.4 Reproductive Biology of *Oxystele* species

Information on the reproductive biology of South African winkles is very limited (Pulfrich and Branch 2002). South African winkles are known to have separate sexes and fertilisation occurs externally (Kilburn and Rippey 1982). It has been suggested that winkles are capable of spawning throughout the year (Joska and Branch 1983, Lasiak 1987), but that the major reproductive period appears to occur between September and March with the arrival of new recruits in the intertidal in winter (McQuaid 1983). The reproductive biology of *O. impervia* and *O. tigrina* has not been reported on in the literature, but we can assume that their reproductive biology is similar to most other species in the genus.

Oxystele variegata has a 1:1 sex ratio with no differences in the size frequency distribution between sexes (Lasiak 1987). This winkle displays asynchronous, sporadic gametogenesis and spawning throughout the year, which seems to peak around September and October and then again in February (Joska and Branch 1983, Lasiak 1987). This spawning behaviour ensures that only a small amount of potential recruits are lost should conditions be unfavourable (Lasiak 1987). Clustering by this winkle also ensures the maximisation of reproductive output and thus increases the winkle’s fertilisation success (Lasiak 1987).

Oxystele tabularis also has a 1:1 sex ratio with no differences in the size frequency distribution between sexes (Lasiak 1987). This winkle also displays asynchronous, sporadic gametogenesis and spawning throughout the year, but peaks from February to March and then again in August (Lasiak 1987). Similarly as in *O. variegata*, clustering ensures fertilisation success (Lasiak 1987).

Information of the reproductive biology of *O. sinensis* is limited. Recruitment of this winkle has been suggested to be irregular, but appears to be most intense during late summer through winter (Pulfrich and Branch 2002). This winkle shows a clumping behaviour in the presence of predators (Lasiak 1987, Pulfrich 1997, Zyl *et al.* 1998, Pulfrich and Branch 2002), which may also provide an added benefit by ensuring the close proximity of the sexes during spawning, thus increasing its reproductive success.

4.1 Introduction

Oxystele sinensis is one of the most abundant winkles in benthic communities along the south-Western to the Eastern Cape of South Africa, occurring from the intertidal zone to depths of up to 7 m (Griffiths 1981, Kilburn and Rippey 1982, Anderson *et al*. 1997, Pulfrich and Branch 2002). Within their geographic range, these winkles are very common on rocky shores and adult winkles occur most abundantly near the low spring-tide levels, often where the waves are rough (Branch and Branch 1981a, Griffiths 1981, Kilburn and Rippey 1982, Branch *et al*. 1994, Pulfrich and Branch 2002). Within their geographic range, the density and biomass of these winkles increase from west to east, with the highest densities occurring at 0-2 m depth (Pulfrich and Branch 2002). Low densities and biomass of this winkle generally coincide with high densities of rock lobsters, which are their primary predators (Pulfrich and Branch 2002).

Although *O. sinensis* is widely distributed (from False Bay to Transkei along the southern east coast of South Africa) (Day 1969, Kensley *et al*. 1973, Griffiths 1981, Kilburn and Rippey 1982, Branch *et al*. 1994), in the Western Cape where it is less abundant, the winkle remains largely confined within kelp beds (Pulfrich and Branch 2002). Kelp beds provide these winkles with protection from direct wave action, sand scouring and to a certain degree, predation by rock lobsters (Pulfrich and Branch 2002). Despite their comparatively higher densities within kelp beds, *O. sinensis* recruits intertidally and displays sporadic recruitment patterns, peaking during late summer and winter (Pulfrich and Branch 2002).

While larger *O. sinensis* (> 30 mm shell diameter) generally have a size refuge against predation by small rock lobsters (< 70 mm carapace length), juvenile and small adult winkles are hugely susceptible to predation by all rock lobsters (Van Zyl *et al*. 1998). It is for this reason that adult winkles migrate into the intertidal zone to reproduce because here juvenile winkles find a spatial refuge from predation by rock lobsters (Pulfrich 1997, Van Zyl *et al*. 1998, Pulfrich and Branch 2002). Adult *O. sinensis* are generally inactive and cryptic at spring low tides (Pulfrich and Branch 2002) and are often observed to either rest at the tops of exposed boulders, or to aggregate together in narrow crevices, which are considered to be defense mechanisms to reduce predation and allow co-existence (Lasiak 1987, Pulfrich 1997, Van Zyl *et al*. 1998, Pulfrich and Branch 2002); aggregation in this manner has only been observed to occur in the presence of rock lobsters (Van Zyl *et al*. 1998).

Since virtually all adult *O. sinensis* that we encountered in the Kalk Bay area bore an encrusting coralline on their shells (*pers. obs.*), we looked at various ecological parameters of *O. sinensis* both in isolation and in association with the coralline, as well as the winkle's co-existence with other associated invertebrates. Subsequently, the following questions were posed:

1. How important (density and biomass) are the various resident invertebrates on the Kalk Bay mid-Eulittoral and shallow subtidal zones?
2. How frequent are associations between the winkle and the coralline alga?
3. What effect does the weight of the coralline have on the winkle?

Ultimately, the answers to these questions would provide a better understanding of the association between the winkle and the coralline alga as well as to the general ecology of the winkle, information which is generally lacking in the literature.

4.2 Materials and Methods

4.2.1 Study site

Field work was done at Kalk Bay (34° 08’S, 18° 27’E) in the Western Cape Province, South Africa. The site is moderately exposed to the south-easterly winds as well as to wave action (Figures 4.1 and 4.2).

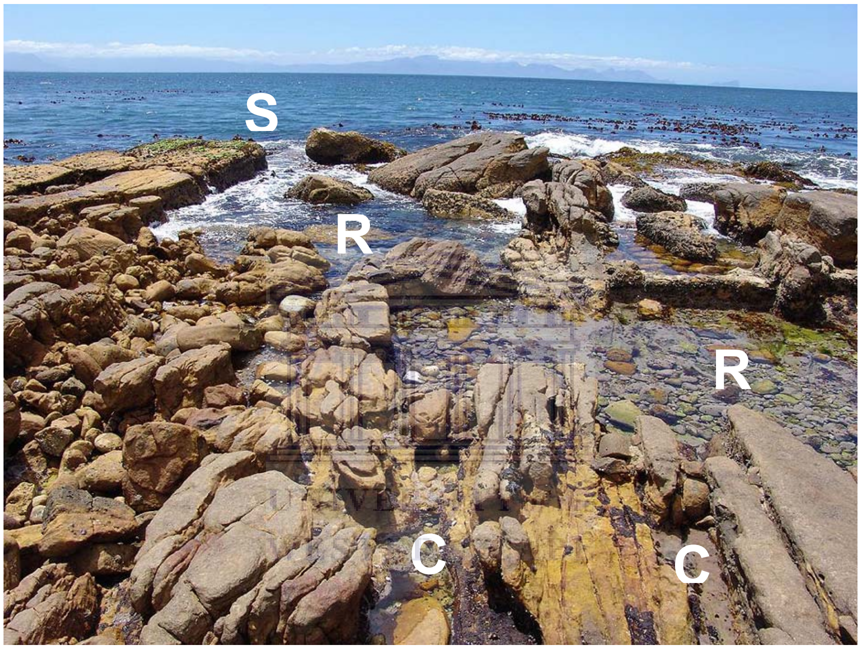


Figure 4.1 Habitats in which data were collected (C = crevices, R = rockpools, S = subtidal zone).

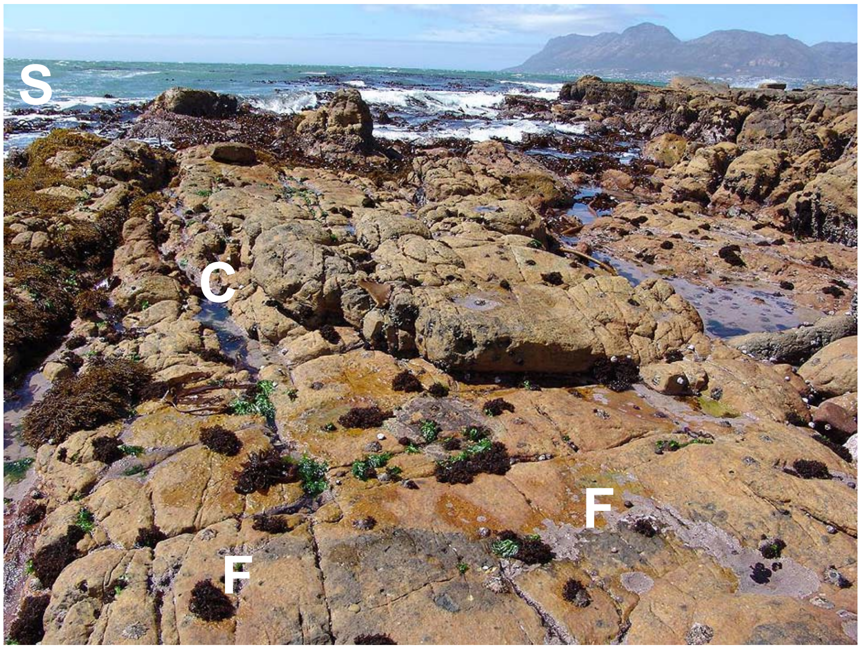


Figure 4.2 Habitats in which data were collected (C = crevices, F = flats, S = subtidal zone).

4.2.2 Natural invertebrate densities and biomass

Invertebrate densities were estimated and then averaged for the mid-Eulittoral zone flats (F), crevices (C), rockpools (R), and for the shallow subtidal zone (S; 2-6 m depth) (Figures 4.1 and 4.2). These were estimated at regular 2 m intervals along transect lines running perpendicular to the zones and spaced 2 m apart, using a 0.2 x 0.25 m (crevices) and a 0.5 x 0.5 m (flats, rockpools, subtidal) quadrat (n = 10 quadrats in subtidal; n = 15 quadrats on flats, in crevices and in rockpools). Animals from these quadrats (Table 4.1) were collected and brought back to the laboratory for biomass determinations. In addition, the shell diameter (at the broadest end) of each of 20 randomly collected individuals of *O. sinensis* and *O. tigrina* was measured in order to determine the size-class variation from each of the habitats in which the winkles occurred. *Oxystele tigrina* was also sampled because it is morphologically similar to *O. sinensis*.

Table 4.1 Invertebrate taxa surveyed during the study and their main features

Species	Main Feature
Oxystele sinensis (Gmelin)	Winkle - herbivore
Oxystele tigrina (Anton)	Winkle - herbivore
Oxystele variegata (Anton)	Winkle - herbivore
Cymbula miniata (Born)	Limpet - herbivore
Cymbula oculus (Born)	Limpet - herbivore
Helcion pruinosus (Krauss)	Limpet - herbivore
Scutellastra barbara (Linnaeus)	Limpet - herbivore
Scutellastra granularis (Linnaeus)	Limpet - herbivore
Scutellastra longicosta (Lamarck)	Limpet - herbivore
Siphonaria capensis Quoy and Gaimard	False limpet - herbivore
Acanthochiton garnoti (Blainville)	Chiton - herbivore
Patiriella exigua (Lamarck)	Sea star - herbivore
Parechinus angulosus Leske	Urchin - herbivore
Burnupena cincta (Röding)	Whelk - scavenger
Chthamalus dentatus Krauss	Barnacle – filter feeder
Octomeris angulosa Sowerby	Barnacle – filter feeder
Tetraclita serrata Darwin	Barnacle – filter feeder

4.2.3 Frequency of the winkle-coralline association

To determine the relative importance of the winkle serving as a secondary substratum for the coralline alga, a frequency measure was taken subtidally from 2-6 m depth during full moon spring low tide of May 2008. Frequencies of the association were recorded within a 0.5 x 0.5 m quadrat placed at regular 2 m intervals along three, 20 m transects running perpendicular to the shore and that were also 2 m apart. Associations were also expressed as a fraction of all winkles encountered (*n* = 21 quadrats, 168 winkles encountered).

4.2.4 Mean coralline load

The weight of the coralline-load was determined by randomly sampling 20 winkles from those animals already collected for biomass determinations. In the laboratory, animals bearing the corallines were blotted dry and their wet weight determined. The coralline was then removed in its entirety from the winkle's shell using a hammer and cold chisel. Thereafter, the wet weight of both the winkle without its coralline, as well as the detached coralline fragments was weighed to determine the relative contribution of the coralline alga to the weight of the association.

4.2.5 Statistical analysis

To show the relative importance of the different invertebrate species in their natural habitats, multiple paired sample *t*-tests were performed on both the density and biomass values for all possible species pairs (28 – flats; 66 – crevices; 28 – rockpools; 15 - subtidal) of invertebrate species encountered. Mean values were sorted in descending order and the *P*-values for the *t*-tests used to assign significance letters (a's, b's, etc). To determine the relative importance of the contributions by only *O. sinensis* and only *O. tigrina* individuals in the various habitats sampled, differences were first evaluated according to one-way ANOVA for three means and then according to *t*-tests for pairs between habitats. For all tests performed a 5 % significance level was applied and so differences amongst treatments were considered statistically significant at $P < 0.05$. Except for the frequency measures, all data are expressed as means ± standard errors (SE).

4.3 Results

4.3.1 Natural invertebrate community structure

Numbers of invertebrate species were highest in intertidal crevices followed by the flats and rockpools. The shallow subtidal zone had the lowest numbers of invertebrate species (Figure 4.3). While a number of other invertebrates (*O. variegata* and *T. serrata*) occurred in equally high numbers, the limpet *C. oculus* (210.96 ± 18.49 g m^{-2}) was by far the dominant invertebrate on the flats ($p < 0.001$, Figure 4.3). This limpet obtained similarly high biomass compared with *O. tigrina* ($p = 0.995$) in intertidal crevices. In contrast to these former two habitats, the sea urchin *P. angulosus* was the co-dominant invertebrate with *O. tigrina* in intertidal rockpools (113.66 ± 38.37 g m^{-2}, $p = 0.060$) and the dominant invertebrate in the shallow subtidal zone (1180.45 ± 169.08 g m^{-2}, $p < 0.001$).

While the winkles *O. sinensis* and *O. tigrina* had overlapping niches, *O. sinensis* was absent from the flats while *O. tigrina* was absent from the subtidal zone. *Oxystele sinensis* increased in both density and biomass down the shore and reproductively mature *O. sinensis* (29.60 ± 0.61 mm) were largely restricted to the subtidal zone, while most juveniles (16.96 ± 1.16 mm) were largely restricted to the intertidal rockpools, with only occasional juveniles (13.89 ± 0.67) found in intertidal crevices ($p < 0.001$) (Figures 4.3. & 4.4). Of all winkles encountered (see Table 4.1) *O. tigrina* was the dominant intertidal winkle with reproductively mature *O. tigrina* (24.09 ± 0.67 mm) most often found in intertidal rockpools and only occasionally on the flats (22.50 ± 0.92 mm), while juveniles (16.80 ± 1.08 mm) were found almost exclusively in intertidal crevices ($p < 0.001$). Biomass data followed closely the density trends except for the intertidal rockpools. This was so largely due to the presence of a few, but large adult *O. tigrina* compared against the relatively many, but small juvenile *O. sinensis* resident in the habitat.

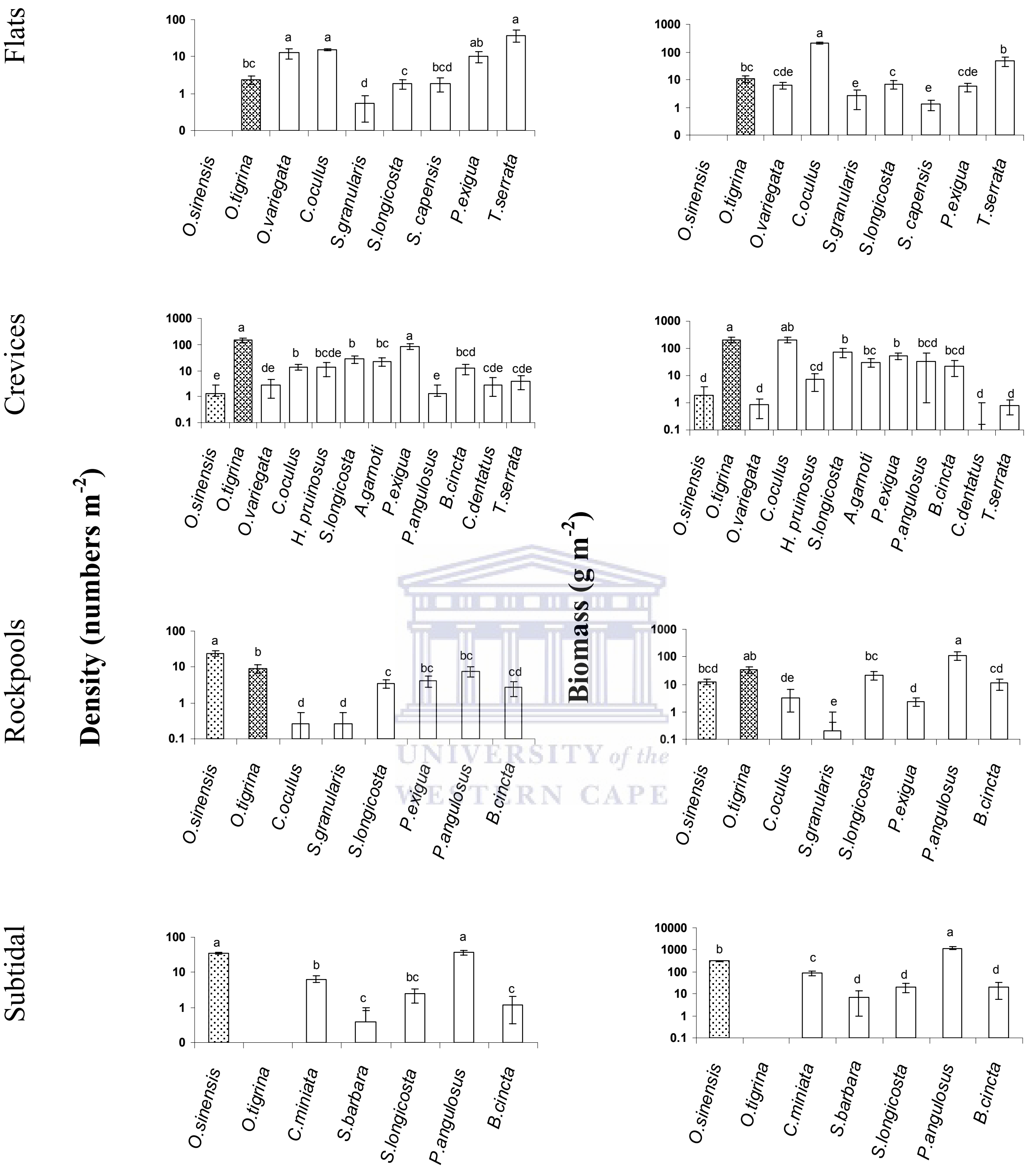


Figure 4.3 Invertebrate densities and biomass in the four habitats sampled. Data for *O. sinensis* as well as the similar looking *O. tigrina* are highlighted. Biomass of subtidal *O. sinensis* includes the weight of the coralline epizoics. Bars with the same letters are not statistically different at $p > 0.05$.

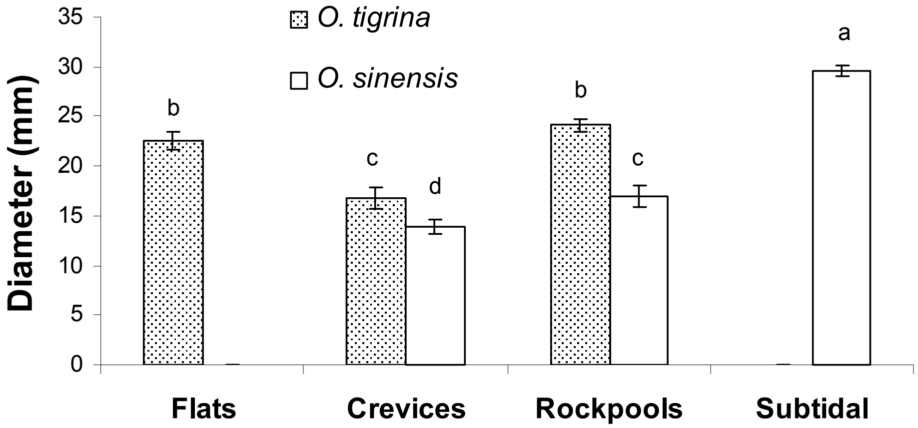


Figure 4.4 Mean size (diameter) of the similar looking *O. sinensis* and *O. tigrina* in the four habitats sampled. Habitats bearing no corresponding data suggest the absence of the species from that habitat. Bars with the same letters are not statistically different at $p > 0.05$.

4.3.2 Frequency and potential burden of the association

The data show that nearly all (98.6 ± 1.10 %, n = 168) adult *O. sinensis* encountered in the subtidal zone were observed to bear the coralline on their shells whereas the remaining (1.4 ± 1.10 %) bore the encrusting fleshy alga, *Ralfsia verrucosa* (Areschoug) Areschoug on its shell (Figure 4.5). The results show that while the winkle on its own (61.1 ± 2.52 % of the weight of the association) weighs more than the coralline, a substantial percentage (38.9 ± 2.52 %) of the association comprises the weight of the coralline (Figure 4.6).

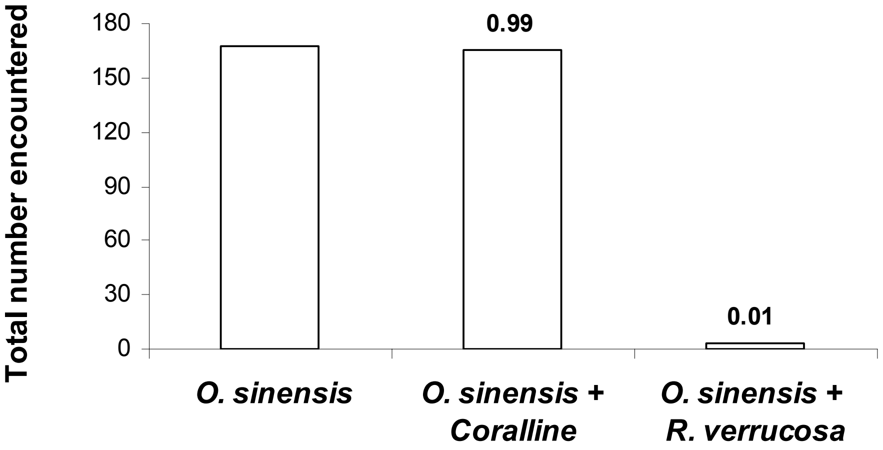


Figure 4.5 Relative frequencies (number of individuals) of *O. sinensis* encountered in the shallow subtidal zone and the proportions of the winkle associated (+) with the coralline and the encrusting brown alga *R. verrucosa*. Numbers above the bars relate to the % occurrences.

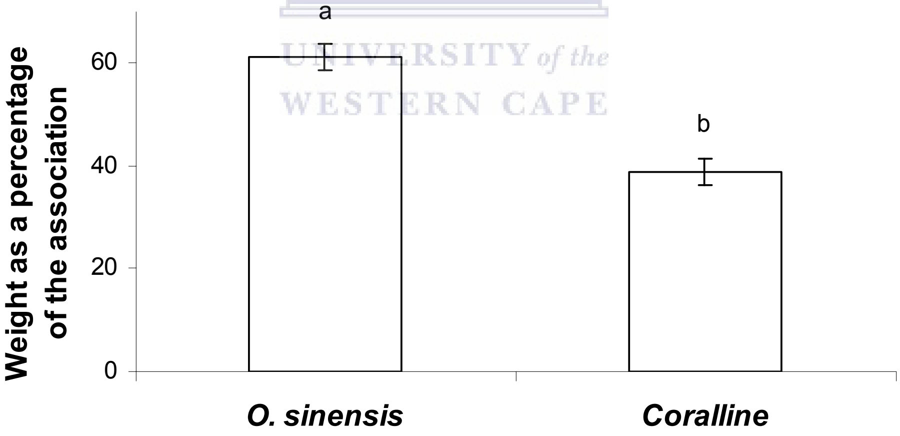


Figure 4.6 Blotted wet weight of the winkle without the coralline as well as the detached coralline alga as a proportion (%) of the total blotted wet weight of the association. Letters above the bars reflect the statistical significance.

4.4 Discussion

From the results of this component of the study, a number of generalisations can be made. Firstly, while many invertebrates were found at Kalk Bay, the habitats sampled were dominated by no more than one or two species. This is consistent with other studies that previously had shown the limpet *C. oculus* (e.g. Maneveldt *et al.* 2006, 2009) and the sea urchin *P. angulosus* (e.g. Anderson *et al*. 1997) to be the dominant invertebrates within the intertidal and shallow subtidal zones respectively. Secondly, intertidal crevices had the highest number of invertebrate species and the subtidal zone the lowest. This was in all probability due to the diminished effects of both desiccation and salinity stress in crevices, and the increased effects of both competition and predation in the subtidal zone. Thirdly, while the winkles *O. sinensis* and *O. tigrina* have strongly overlapping niches, *O. tigrina* is largely restricted to the intertidal zone while *O. sinensis* is for the most part restricted to the subtidal zone and rockpools. This is no doubt due to their variable susceptibilities to desiccation stress with *O tigrina* being far more tolerant of desiccation stress than *O. sinensis* (Broekhuysen 1940, Brown 1960). Intertidal rockpools seem to provide *O. sinensis* with the ideal intertidal conditions to avoid predation of juvenile winkles from subtidal predators and survive desiccation stress during the early juvenile stages. Finally, nearly all *O. sinensis* encountered in the subtidal zone were observed to bear the coralline on their shells with the coralline contributing a significant percentage to the weight of the association. The low percentage cover abundance of the coralline occurring epilithically in the subtidal zone (see chapter 6) suggests that the winkle serves as a very important secondary substrate for the coralline.

Desiccation stress has long been accepted as the primary physical factor controlling the upward migration patterns of various intertidal invertebrates (Broekhuysen 1940, Evans 1948, Brown 1960, Connell 1961a, b, Wolcott 1973, Branch 1975a, Beer and Eshel 1983, Davenport 1997). *Oxystele* species, in particular, are known to be variously tolerant of desiccation stress and this has influenced their vertical distributions on rocky shores (Broekhuysen 1940, Brown 1960). Species that are less tolerant of desiccation stress are observed to occupy intertidal rockpools to overcome the problems associated with desiccation stress (Broekhuysen 1940, Evans 1948, Brown 1960). The results of this study are consistent with the literature (see e.g. Broekhuysen 1940, Evans 1948, Brown 1960, Van Zyl *et al*. 1998, Pulfrich and Branch 2002) showing that *O. sinensis* is probably far less tolerant of desiccation stress than other species of *Oxystele* and consequently is found in greater densities in the infratidal zone, lower intertidal zone and intertidal rockpools. *Oxystele sinensis* is also more tolerant of wave exposure than other species of *Oxystele* (Branch and Branch 1981a) and is also better able to resist dislodgement under wave exposed conditions (Day 1969, Branch and Branch 1981a, Branch *et al*. 1994, Rilov *et al*. 2004).

Biological factors such as competition, herbivory and predation are generally believed to have greater impacts on species at lower shore levels when physical stresses are minimal (Paine and Vadas 1969, Dayton 1971, 1975, Lubchenco 1978, 1980, Lubchenco and Menge 1978, Lubchenco and Gaines 1981, Underwood and Jernakoff 1981, McQuaid 1982, Watanabe 1984, Hawkins and Harkin 1985, Steneck *et al*. 1991, Chamberlain 1993, Keats *et al*. 1993, 1994a, Steneck and Dethier 1994, Anderson and Underwood 1997, Anderson *et al*. 1997, Maneveldt and Keats 2008). Predation by rock lobsters has been shown to limit the downward migration and aggregation of *O. sinensis* in the subtidal zone (Van Zyl *et al*. 1998, Pulfrich and Branch 2002) and adult winkles typically migrate into intertidal rockpools to limit predation on their offspring by such subtidal predators (Pulfrich 1997). The high density of *O. sinensis* in the Kalk Bay shallow subtidal zone was probably due to the reduced numbers of lobsters in the Kalk Bay area (Anderson *et al*. 1997, Leliaert *et al*. 2000).

In conclusion, the results of this and other studies suggest that physical (desiccation stress) and biological (predation) limitations, as well as physiological advantages (increased adaptations to wave exposure and dislodgment) have resulted in *O. sinensis* being a very prominent feature of the shallow subtidal zone, low shore intertidal zone and intertidal rockpools. Adult *O. sinensis* that are largely confined to the shallow subtidal zone perform an important function as secondary substrate for the coralline with the coralline equating to more than one third the weight of the association. The question remains then as to what the advantage is, if any, of carrying such a heavy coralline load?

5.1 Introduction

Despite their ubiquity, coralline algae are a relatively poorly known group of marine algae (Chamberlain 1993, Meneses 1993, Keats *et al*. 1994b, Morcom and Woelkerling 2000, Vidal *et al*. 2003, 2008, Maneveldt *et al*. 2008). Although modern research on this group of algae has been under investigation for some 20 years in South Africa (see Maneveldt *et al.* 2008), ecological information pertaining to the coralline algae is still sorely lacking. This lack of detailed ecological knowledge stems largely from a legacy of poor-quality taxonomic work (Woelkerling and Lamy 1998). However, the ongoing efforts to fully understand their taxonomy and systematics, particularly in light of the many major taxonomic revisions in recent years (see e.g. Penrose and Woelkerling 1988, 1992, Womersley 1996, Harvey *et al*. 2003, 2004) have lead to a greater understanding of the ecology of this relatively poorly known group of algae.

While attempting to address the lack of ecological information on the encrusting coralline algae of South Africa, a number of algal-herbivore interactions involving coralline algae have already been reported (see e.g. Maneveldt *et al.* 2006, Maneveldt and Keats 2008). More recently a species of encrusting coralline algae was found to occur epizoically on the shells of adult *Oxystele sinensis* winkles in the shallow subtidal zone (Figure 5.1). The association was observed to be particularly common along western False Bay rocky shores, but was also observed to occur less frequently at Cape Agulhas and intermittently as far eastward as the Tsitsikamma National Park along the south coast (G.W. Maneveldt *pers. obs*.).

Figure 5.1 The habit of the thick, convoluted coralline occurring epizoically on the shells of the winkle *O. sinensis* in the Kalk Bay shallow subtidal zone.

Initial observations suggested that the epizoic alga was a highly convoluted form of the coralline *Spongites discoideus* (Foslie) D. Penrose et Woelkerling that occurred epilithically in intertidal rockpools (Figure 5.2). To confirm the identity of the coralline occurring epizoically on the winkle shells, a taxonomic study was done to compare this thick, convoluted coralline against *S. discoideus* from the intertidal rockpools. In accordance with recent taxonomic studies of South African encrusting coralline algae (e.g. Chamberlain 1994, Chamberlain *et al*. 1995, Keats and Chamberlain 1993, 1994a, b, 1995, Keats and Maneveldt 1997, Keats *et al*. 2000, Maneveldt *et al*. 2007), the approach of describing coralline algae in complete detail was also adopted in this study to complement any future work that might need to be done on this species.

Figure 5.2 The habit of the coralline occurring epilithically on a boulder in a Kalk Bay intertidal rockpool. Note the typically thin purple-grey primary thallus and the reddish-brown discoid, secondary thalli. Both forms were once considered as different species of coralline algae.

5.2 Materials and Methods

5.2.1 Taxonomy

Thalli were examined as far as possible when fresh. Otherwise they were air-dried or fixed in neutralized 10 % commercial formalin seawater (4 % formaldehyde) and stored in a 70 % ethanol: 10 % glycerol: 20 % distilled water solution. Formalin-preserved specimens were first decalcified in 10% nitric acid. Thereafter, specimens were immersed in 70 %, 90 % and 100 % ethanol solutions respectively for a minimum of 60 minutes each. Specimens were then immersed in Leica Historesin filtration medium (50 ml basic resin [liquid] and 1 sachet [0.5 g] activator) until completely infiltrated. Infiltration was complete when the specimen appeared slightly translucent and sank to the bottom of the infiltration vessel. A hardening solution was added to the infiltration medium (15 ml infiltration solution + 1 ml hardener) and the specimens orientated in this final solution until set. Gelling of the hardener usually occurred within about 15 mins; some specimens were placed in an oven at 60 °C for an additional 5 mins to allow more rapid hardening. All specimens were sectioned at 12 –15 µm thickness using a Bright 5030 microtome. Each individual section was removed from the microtome blade using a fine sable hair brush and transferred to a slide covered with distilled water. Excess distilled water was carefully drained and slides were then air dried for at least 24 hrs. Thereafter, the slides bearing the sections were stained with toluidine blue (0.25 g borax/100 ml and 0.06g toluidine blue/100 ml), left to air-dry and later covered with cover slips using DPX Mountant for microscopy (BDH Laboratory Supplies, England). Photographs were taken from prepared slides using an Olympus BX50 compound microscope equipped with a digital camera.

All anatomical measurements were made using a calibrated eyepiece micrometer. In cell measurements for monomerous thalli, length denotes the distance between primary pit connections, and diameter the maximum width of the cell lumen at right angles to this. For dimerous thalli, the dimensions of the cells of basal filaments are given as follows: height denotes the dimension at right angles to the substratum (technically diameter as defined for monomerous thalli), while width denotes the dimension between successive primary pit connections parallel to the substratum (technically length as defined for monomerous thalli). Conceptacle measurements follow the system of Adey and Adey (1973). Thallus terminology follows Chamberlain (1990). Growth-forms terminology follows Woelkerling *et al*. (1993). Typification data follow Woelkerling (1993).

The location of the relevant specimens is indicated by the herbarium code and specimen number. Herbarium codes are those used in *Index Herbariorum*, previously in print (Holmgren *et al.* 1990) and more recently electronically online (Holmgren & Holmgren 1998, continuously updated).

5.2.2 Frequency of gametangial and sporangial material

Preliminary data suggested that epilithic and epizoic forms of the coralline showed variably different stages in the life cycle of the coralline alga. To determine whether a difference in reproductive stages existed, a frequency (counts) measure was calculated of the various reproductive stages occurring on both rocky substrata and winkle shells; these were obtained directly from prepared slides used to identify the coralline. The frequency of gametangial (gamete producing stages) versus sporangial (spore producing stage) material occurring epilithically in the intertidal rockpools and the shallow subtidal zone, as well as that occurring epizoically on the winkle shells was calculated.

5.2.3 Statistical analysis

As is the norm, all taxonomic measurements are provided as ranges and not means. For frequency measures, paired sample *t*-tests were performed on gametangial and sporangial data in the intertidal rockpools and the shallow subtidal zone. Mean values were sorted in descending order and the *P*-values for the *t*-tests used to assign significance letters (a's, b's, etc). For all tests performed a 5 % significance level was applied and so differences amongst treatments were considered statistically significant at $P < 0.05$; here all data are expressed as means ± standard errors (se).

5.3 OBSERVATIONS

***Spongites discoideus* (Foslie) D. Penrose et Woelkerling** (“*discoidea*”)

(Figs 5.3 – 5.12)

BASIONYM

Lithophyllum discoideum Foslie, 1900:73

SYNONYMS

Pseudolithophyllum discoideum (Foslie) Lemoine, 1913: 46

Hydrolithon discoideum (Foslie) Medoza et Cabioch, 1984: 148

Lithophyllum consociatum Foslie, 1905: 15

Pseudolithophyllum consociatum (Foslie) Lemoine, 1913: 48

Hydrolithon consociatum (Foslie) Mendoza, 1979: 8

Lithophyllum decipiens f. *subantarcticum* Foslie, 1906: 18

Lithophyllum subantarcticum (Foslie) Foslie, 1907a: 23

Pseudolithophyllum subantarcticum (Foslie) Adey, 1970b: 14

Hydrolithon subantarcticum (Foslie) Mendoza et Cabioch, 1986b: 180

Spongites discoideus (Foslie) D. Penrose et Woelkerling, 1988: 173

LECTOTYPE

TRH, A9-499. Mouth of Rio Grande, Tierra del Fuego, Argentina, P. Dusén, February 1896 (see Adey 1970b: 24, for typification).

ETYMOLOGY

‘*discoideus*’ = discoid, with a rounded blade and thickened margin, disk-like (Stearn 1973). Foslie (1900) did not explain the origin of the epithet, but it presumably made reference to the “more or less orbicular crusts, which are, however, apt to be sooner confluent …” (Foslie 1907b: 11). In all likelihood, Foslie (1900, 1907b) may have been referring to the disk-like or discoid secondary thalli referred to by Chamberlain (1994).

REPRESENTATIVE SPECIMENS EXAMINED

Western Cape Province: Kalk Bay - epizoic on shells of the winkle *O. sinensis* in the shallow subtidal zone down to 5 m depth (*G. Maneveldt*, 2.viii.2002, UWC 02/07; 21.v.2008, UWC 08/41; *G. Maneveldt & M. Cocks*, 16.x.2003, UWC 03/31; 29.v.2008, UWC 08/44; 4.vi.2008, UWC 08/50; *G. Maneveldt & R. Eager*, 19.viii.2008, UWC 08/52; 19.viii.2008, UWC 08/53); - epilithic in intertidal rockpools (*G. Maneveldt*, 2.viii.2002, UWC 02/04; 21.v.2008, UWC 08/42; 21.v.2008, UWC 08/43; *G. Maneveldt & M. Cocks*, 29.v.2008, UWC 08/45; 29.v.2008, UWC 08/46; 29.v.2008, UWC 08/48; 4.vi.2008, UWC 08/51; *G. Maneveldt & R. Eager*, 19.viii.2008, UWC 08/56; 19.viii.2008, UWC 08/58; 19.viii.2008, UWC 08/59; 19.viii.2008, UWC 08/60; 19.viii.2008, UWC 08/61); Maasbankerbaai, Pringle Bay - epilithic in a low shore intertidal rockpool (*G. Maneveldt*, 8.x.2002, UWC 02/09).

Eastern Cape Province: Tsitsikamma - epizoic on shells of the winkle *O. sinensis* in a low shore intertidal rockpool (*G. Maneveldt & U. van Bloemenstein*, 4.iv.2008, UWC: 08/02); - epilithic in shallow subtidal zone at 2 m depth (*G. Maneveldt & U. van Bloemenstein*, 4.iv.2008, UWC 08/12).

HABITAT AND PHENOLOGY

Grows epilithically on small and large boulders, as well as attached to the primary substratum in intertidal rockpools and the shallow subtidal zone. Occasionally occurring epiphytically on the stipes of *Ecklonia maxima* (Osbeck) Papenfuss. Also occurs epizoically on the shells of the winkle *O. sinensis* and occasionally on whelks in both intertidal rockpools and the shallow subtidal zone. Conceptacles of all reproductive types were observed to occur during all months sampled i.e. April to November.

DISTRIBUTION

South Africa: Port Nolloth (Northern Cape) to Tsitsikamma (Eastern Cape) (Chamberlain 1994, Silva *et al*. 1996, this study).

World: Antarctica (Mendoza *et al*. 1996), Falkland Islands (Lemoine 1915, Mendoza and Cabioch 1986b, Mendoza *et al*. 1996), Kerguelen (Mendoza and Cabioch 1986a, Mendoza *et al*. 1996), Macquarie Island (Ricker 1987, Mendoza *et al*. 1996), Namibia (Rull Lluch 2002, John *et al*. 2004), Tierra del Fuego (Argentina) (Foslie 1900, Lemoine 1915, Adey and Lebednik 1967, Adey 1970b, Mendoza and Cabioch 1984, 1986a, b, Mendoza *et al*. 1996, Silva *et al*. 1996).

APPEARANCE AND VEGETATIVE STRUCTURE

The following description is based only on plants found to occur epizoically on the shells of *O. sinensis* although sections of epilithic *S. discoideus* were made for comparison (see Tables 5.1 & 5.2). This description was also compared with that of *S. discoideus* described for epilithic plants by Chamberlain (1994).

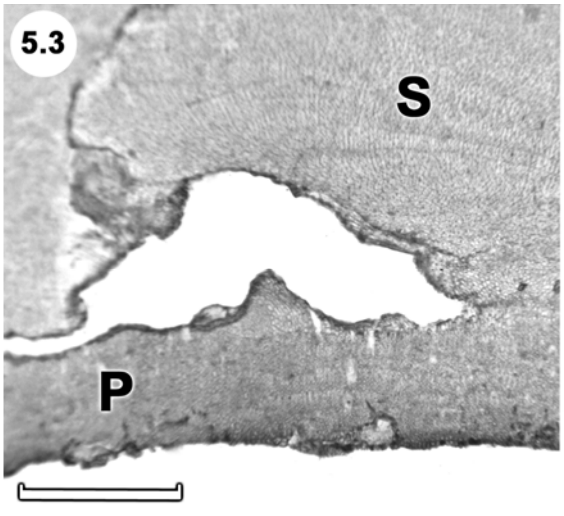
Plants are initially encrusting being firmly attached, but later become discoid and then very convoluted (Figure 5.1). The convoluted form appears to result from the limited space available for growth on the winkle shells. The primary thallus is purple-grey in colour, is very flat and smooth and has a matt texture; their margins are thin and firmly adherent. Primary thalli are seldom visible and are often engulfed by the convoluted secondary thalli (Figure 5.3). Primary thalli are dimerous, are 39 - 461 µm thick and possess numerous cell fusions between cells of adjacent filaments (Figure 5.5). Cells of basal filaments are squarish to elongate and measure 11 - 22 µm in length and 4 - 17 µm in diameter. Cells of erect filaments are squarish to rectangular and measure 4 - 17 µm in length and 2 - 12 µm in diameter. Secondary thalli developing from the primary thalli are reddish-brown in colour, are smooth and slightly glossy. These thalli are monomerous, are up to 10 mm thick, form somewhat circular discs which are rosette-like and become convoluted as the thallus thickness. Cortical cells of secondary thalli are squarish to round and measure 4 - 10 µm in length and 4 - 7 µm in diameter. Medullary cells of secondary thalli are elongate and measure 12 - 34 µm in length and 4 - 10 µm in diameter (Figure 5.6). Subepithallial initials are rectangular and measure 4 - 10 µm in length and 4 - 7 µm in diameter. Epithallial cells typically occur in layers up to 5 cells thick (Figure 5.4) and measure 2 - 6 µm in length and 2 - 9 µm in diameter. Trichocytes occur singly, are rare and measure 4 - 7 µm in length and 3 - 6 µm in diameter. Data on measured vegetative characters are summarized in Table 5.1.

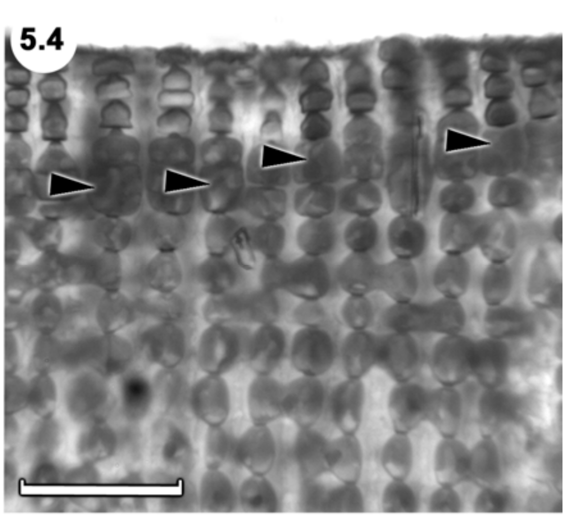
Table 5.1. A comparison of the appearance and vegetative structure of *S. discoideus* from this study compared against previously published records of the species as well as of other species of *Spongites* known to occur in South Africa. Data from previously published records have been taken from both the descriptions and the figures. A single value denotes the maximum recorded value. Unless otherwise stated, all measurements are in micrometres. ND = no data provided. N/A = Not applicable.

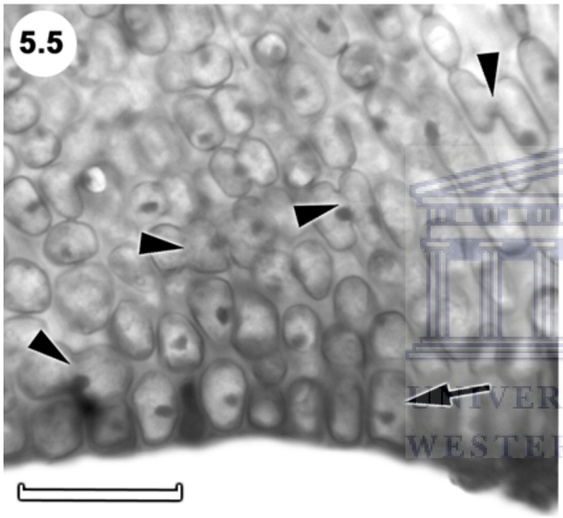
Character	***S. discoideus* (epizoic)** – present study	***S. discoideus* (epilithic)** - present study	***S. discoideus*** (Chamberlain 1994)	***S. impar*** (Chamberlain 1994)	***S. yendoi*** (Chamberlain 1993, Maneveldt 1995)
Habit	Epizoic	Epilithic	Epilithic	Epilithic/epizoic	Epilithic/epizoic
Shape	Flat, becoming highly convoluted	Flat, becoming discoid and convoluted	Flat, becoming discoid	Flat, becoming crested and convoluted	Flat to warty to highly protuberant in the absence of herbivory
Thallus construction	Dimerous & monomerous	Dimerous & monomerous	Dimerous & monomerous	Monomerous	Monomerous
Trichocytes	Rare	Rare	Rare	Absent	Common
Length	4-7	4-6	ND	-	ND
Diameter	3-6	3-5	ND	-	ND
Epithallial cells					
Number	3-5	3-5	4	6	1
Length	2-6	2-7	2-3	3-4	2-7
Diameter	2-9	2-10	4-6	3-6	3-10
Erect filament cells					
Length	4-17	4-17	4-17	N/A	N/A
Diameter	2-12	2-12	4-11	N/A	N/A
Cortical cells					
Length	4-17	2-17	4-17	3-10	5-12
Diameter	4-12	4-12	4-11	3-5	3-10
Medullary cells					
Length	7-20	7-17	ND	5-25	10-37
Diameter	4-10	4-9	ND	3-6	3-9
Basal filament cells					
Length	11-22	10-20	14-16	N/A	N/A
Diameter	4-17	4-17	5-16	N/A	N/A

Table 5.2. A comparison of the reproductive structure of *S. discoideus* from this study compared against previously published records of the species as well as of other species of *Spongites* known to occur in South Africa. Data from previously published records have been taken from both the descriptions and the figures. A single value denotes the maximum recorded value. Unless otherwise stated, all measurements are in micrometres. ND = no data provided.

Character	***S. discoideus* (epizoic) – *present study***	***S. discoideus* (epilithic) - *present study***	***S. discoideus*** (Chamberlain 1994)	***S. impar*** (Chamberlain 1994)	***S. yendoi*** (Chamberlain 1993, Maneveldt 1995)
Plants monoecious or dioecious	Dioecious	Dioecious	Dioecious	Dioecious	Dioecious
Spermatangial conceptacle					
External diameter	76-149	81-154	ND	ND	ND
Chamber diameter	49-98	51-98	52-91	150-200	117-260
Chamber height	17-42	15-44	17-31	35-40	47-62
Roof thickness	17-54	17-51	18-52	35-50	29-62
Carposporangial conceptacle					
External diameter	164-323	162-333	ND	ND	ND
Chamber diameter	137-213	135-221	146-200	ND	138-234
Chamber height	47-78	47-81	52-65	ND	52-109
Roof thickness	69-100	37-103	91-100	ND	39-78
No. cells in gonimoblast	5-7	5-7	7	ND	7
Fusion cell	Wide, thin	Wide, thin	Wide, thin	ND	Continuous
Tetra/bisporangial conceptacle					
External diameter	220-309	215-304	ND	ND	ND
Chamber diameter	169-250	169-255	169-190	180-247	136-303
Chamber height	47-98	52-91	52-65	70-104	62-158
Roof thickness	31-100	32-113	35-100	39-50	26-65
Depth of conceptacle floor (no. cells)	14 - 18	12-18	ND	ND	ND
Pore canal cells	Short, papillate	Short, papillate	Short, papillate	Long, thin papillate	Long, thin papillate
Central columella	Broad	Broad	Broad	Broad	Narrow
Tetrasporangium					
Length	29-74	34-69	35-50	55-119	29-115
Diameter	10-32	12-37	13-26	36-38	15-74
Old tetra/bisporangial conceptacles buried or shed	Buried	Buried	Buried	Shed	Shed







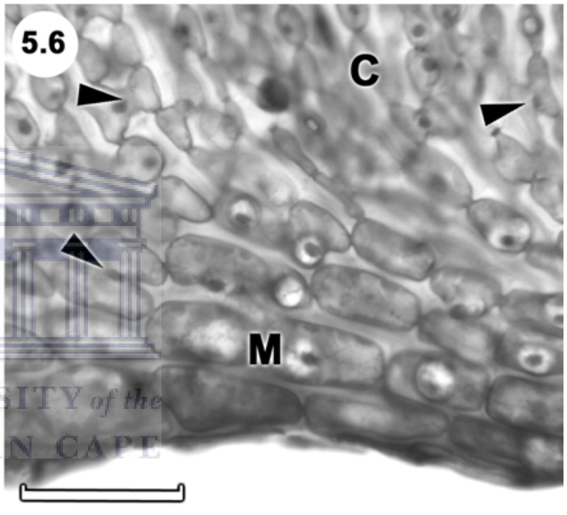


Figure 5.3 Vertical section of the lower thallus showing the primary dimerous thallus (P) giving rise to a discoid secondary, monomerous thallus (S) (scale bar = 150 µm).

Figure 5.4 Vertical section of the outer thallus showing a multi-layered epithallial region located above the meristematic cells (arrow heads) (scale bar = 15 µm).

Figure 5.5 Vertical section of the lower region of a primary thallus showing a dimerous thallus with a single basal layer (arrow) from which erect filaments are arising. Note too the cell fusions (arrow heads) between cells of adjacent erect filaments (scale bar = 15 µm).

Figure 5.6 Vertical section of the lower region of a discoid, secondary thallus showing a monomerous thallus with numerous layers of upward curving filaments. Note too the numerous cell fusions (arrow heads) between cells of both medullary (M) and upward curving cortical (C) filaments (scale bar = 15 µm).

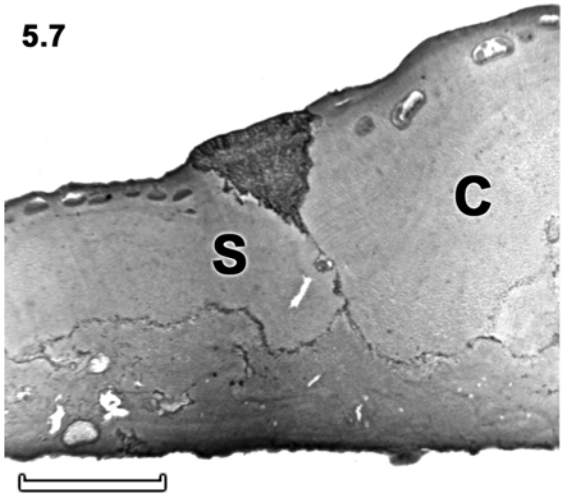
REPRODUCTION

Gametangial plants are dioecious (Figure 5.7). Male conceptacles are comparatively small measuring only about 76 - 149 μm in external diameter (Figure 5.9). Their roofs are more-or-less flush to only slightly raised above the rest of the thallus surface. The conceptacle chamber is shallow and wide, measuring 49 - 98 μm in diameter X 17 - 42 μm high, with the roof 17 - 54 μm thick. Simple spermatangial systems are borne only on the floor of the conceptacle chambers (Figure 5.9).

Carpogonial conceptacles have not been observed, but carposporangia develop in carpogonial conceptacles after presumed karyogamy.

Carposporangial conceptacles are comparatively large, measuring 164 - 323 μm in external diameter (Figure 5.10). Their roofs are somewhat flush to slightly raised above the rest of the thallus surface. Conceptacle chambers are elliptical to dumb-bell shaped and measure 137 - 213 μm in diameter X 47 - 78 μm high with the roof 69 - 100 μm thick. The pore canal is lined with small cells that project as papillae into the canal but do not block it; the pore opening may, however, be partially occluded by a hyaline flange. The central fusion cell is relatively wide and thin, with gonimoblast filaments borne peripherally within the chamber. Gonimoblast filaments are 5 - 7 cells long including a terminal carpospore that measures 32 - 54 μm long X 22 - 37 μm in diameter.

Tetrasporangial conceptacles are somewhat flush to raised above the rest of the thallus surface and measure 220 - 309 μm in external diameter (Figures 5.11). Their chambers are elliptical to dumb-bell-shaped and measure 169 - 250 μm in diameter X 47 - 98 μm high, with the roof 31 - 100 μm (10 - 15 cells) thick. The conceptacle floor is located 14 - 18 cells below the thallus surface. The conceptacle roof is formed from filaments peripheral to the conceptacle chamber (Figure 5.12). Pore canal filaments project into the pore canal as papillae and are orientated more or less parallel to the roof surface (Figures 5.11, 5.12). A large and broad central columella exists and zonately divided tetrasporangia are found to occur peripherally in the conceptacle chamber. Tetrasporangia measure 29 - 74 µm long X 10 - 32 µm in diameter; bisporangia were not seen. Tetrasporangial conceptacles often become buried in the thallus and often contain apparently viable sporangia (Figure 5.8); infilled conceptacles have not been observed. Data on measured reproductive characters are summarized in Table 5.2.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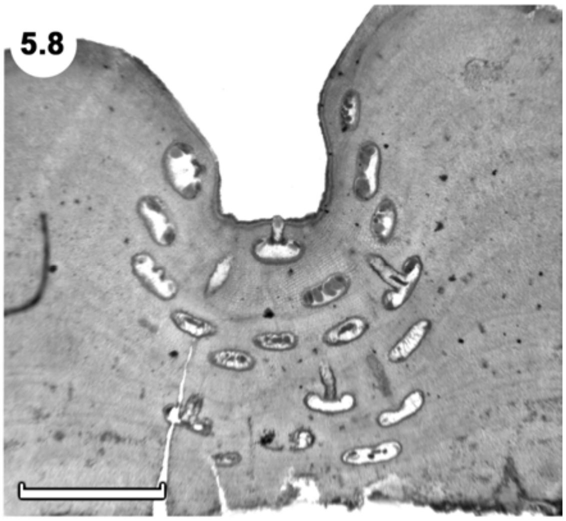
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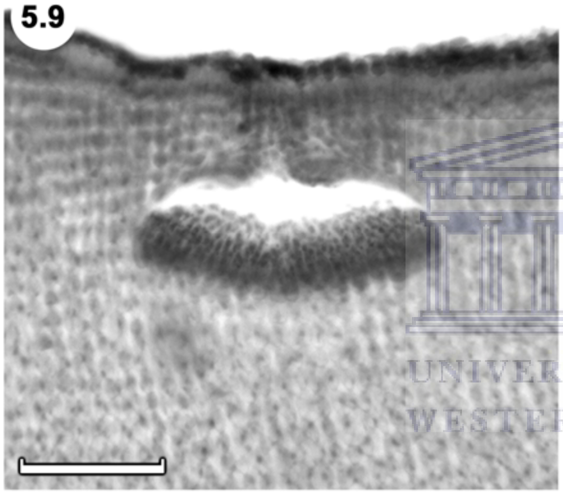
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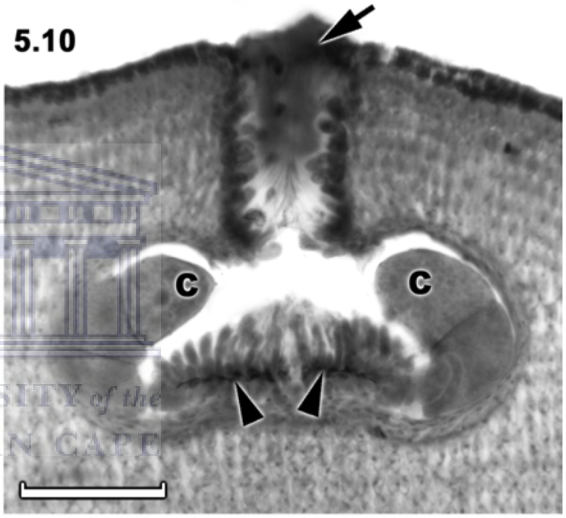
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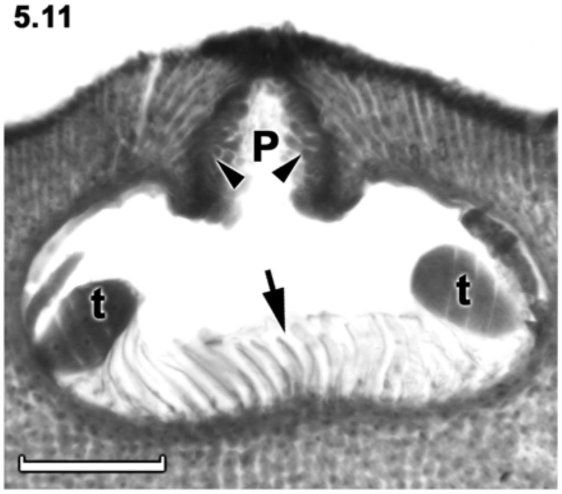
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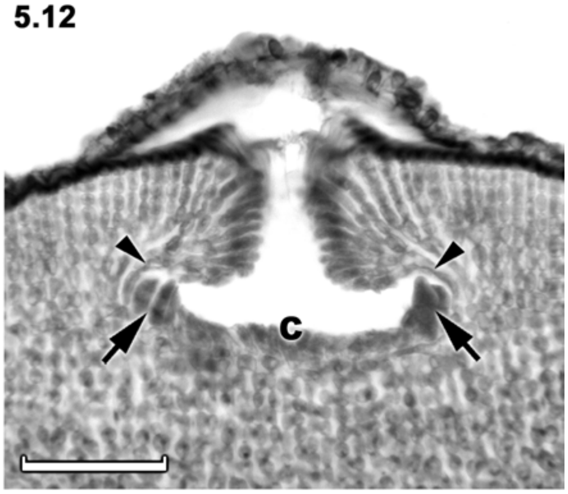
5.12
c

Figure 5.7 Vertical section through two abutting individual fragments showing male (S) and female (C) plants on separate discs (scale bar = 300 µm).

Figure 5.8 Vertical section of a convoluted thallus showing old conceptacles buried in the thallus (scale bar = 300 µm).

Figure 5.9 Vertical section of the outer thallus showing a flush spermatangial conceptacle with simple spermatangial systems borne only on the floor of the conceptacle chamber (scale bar = 30 µm).

Figure 5.10 Vertical section of a mature, raised carposporangial conceptacle showing a discoid fusion cell (arrow heads) with peripheral gonimoblast filaments terminating in carposporangia (c). Note too the hyaline flange (arrow) that occludes the pore opening (scale bar = 30 µm).

Figure 5.11 Vertical section of a mature, raised tetrasporangial conceptacle showing a large central columella (arrow) and peripheral, zonately divided tetrasporangia (t). Note the pore canal (P) lined with short papillate cells (arrow heads) that are orientated more-or-less parallel to the conceptacle roof (scale bar = 30 µm).

Figure 5.12 Vertical section of the outer thallus showing the development of the tetrasporangial conceptacle roof (arrow heads) from filaments peripheral to the conceptacle chamber. Note too the development of the central columella (c) and the peripheral sporangial initials (arrows) (scale bar = 30 µm).

5.4 Results

5.4.1 Taxonomy

Based on our observations, the thick, convoluted coralline occurring on the shells of the winkle *O. sinensis* is confirmed to be *Spongites discoideus*. The coralline firstly possesses all four characters considered diagnostic of the Mastophoroid coralline algal genus *Spongites* Kützing (see Penrose and Woelkerling 1991, 1992, Verheij 1993) namely:

1. tetrasporangial conceptacle roof formed by filaments that arise from the periphery of the conceptacle chamber and sporangial initials;
2. these filaments protrude into the pore canal as papillae and are orientated more-or-less parallel to the roof surface;
3. male conceptacles bearing simple spermatangia that are restricted to the chamber floor; and

4. carposporangial conceptacles bearing a central fusion cell with peripherally arranged gonimoblast filaments.

In addition, we have shown the thick convoluted coralline on the winkle shells to conform to the specific characterisation of that said to be collectively diagnostic of *S. discoideus* (Tables 5.1 & 5.2) as described by Chamberlain (1994), namely:

1. bearing a primary, juvenile thallus that is mainly dimerous;
2. bearing a secondary thallus arising from the juvenile thallus that is mainly monomerous;
3. possessing predominantly cell fusions, secondary pit connections unknown;
4. possessing up to 5 layers of epithallial cells;
5. bearing solitary trichocytes that occur sporadically;
6. bearing carposporangial conceptacle fusion cells that are relatively wide and thin;
7. possessing tetrasporangial conceptacles with a broad central columella.

5.4.2 Frequency of gametangial and sporangial material

While sporangial and gametangial plants contributed more or less equally to the alternating life cycle stages encountered epilithically in both intertidal rockpools (54.4 ± 16.98 %; 45.6 ± 16.98 %; $p = 0.821$) and the shallow subtidal zone (55.5 ± 7.03 %; 44.5 ± 7.03 %; $p = 0.494$) respectively, sporangial plants were far more frequently encountered than either spermatangial (male) or carposporangial (female) plants (Figures 5.13, 5.14). In these two habitats, the ratios of male to female plants were identical, but reversed. Male plants occurred more frequently on intertidal boulders while female plants occurred more frequently on subtidal boulders. In contrast, plants occurring epizoically on subtidal winkles showed gametophyte (95.5 ± 2.21 %) dominance over sporophytes (4.5 ± 2.21 %) ($p = 0.003$), with male plants occurring in far greater numbers (Figures 5.15, $p = 0.008$).

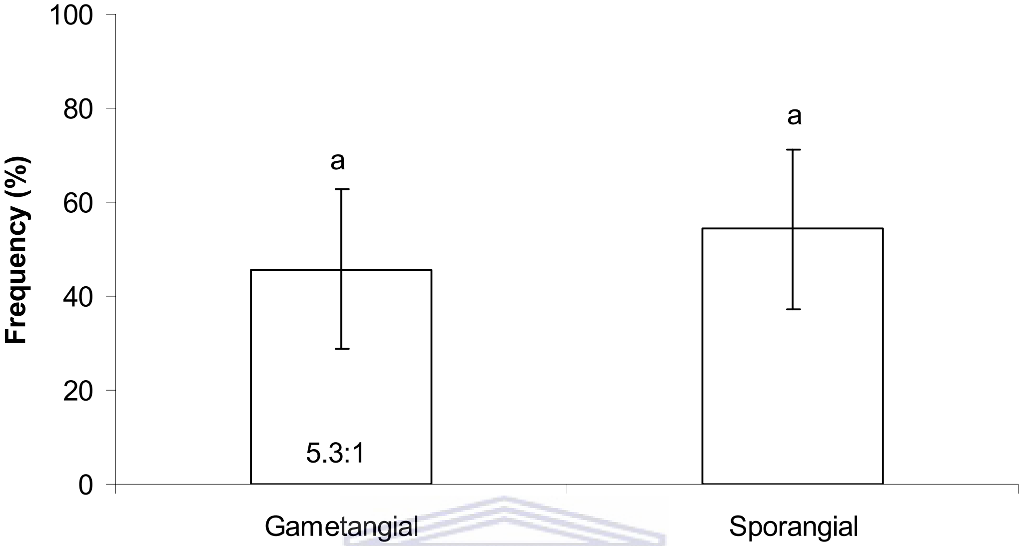

Figure 5.13 Frequency of gametangial versus sporangial material occurring epilithically in intertidal rockpools (the ratio in the gametangial bar represents the proportion of male to female plants encountered). Bars with the same letters are not statistically different at $p > 0.05$.

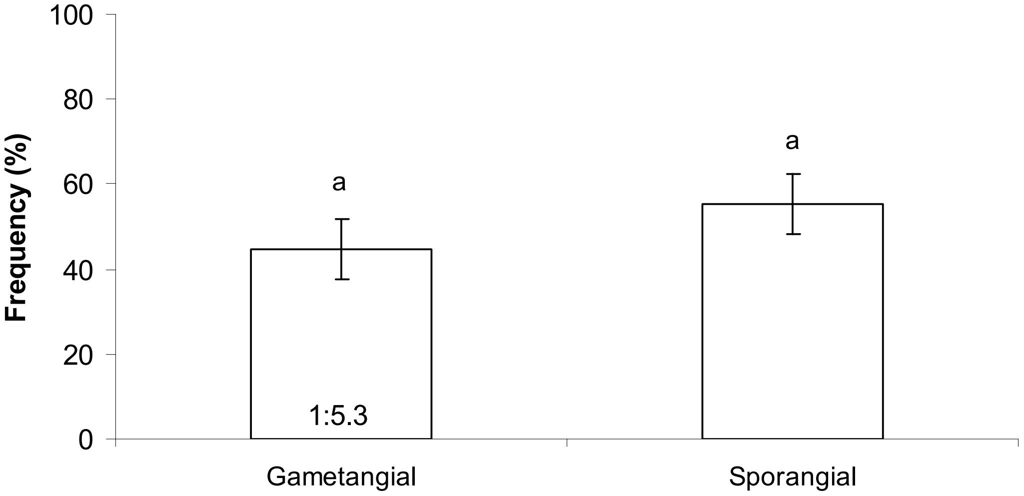

Figure 5.14 Frequency of gametangial versus sporangial material occurring epilithically in the shallow subtidal zone (the ratio in the gametangial bar represents the proportion of male to female plants encountered). Bars with the same letters are not statistically different at $p > 0.05$.

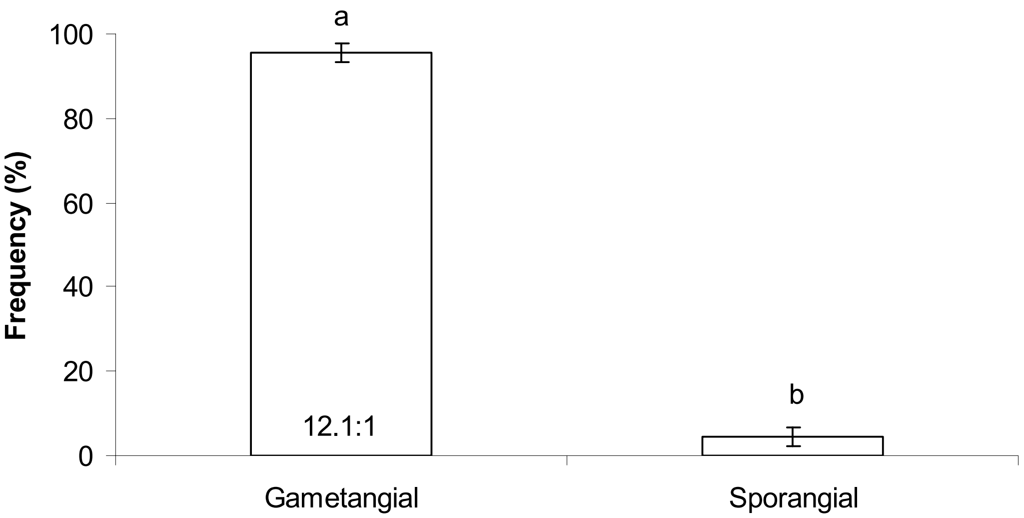

Figure 5.15 Frequency of gametangial versus sporangial material occurring epizoically on winkle shells in the shallow subtidal zone (the ratio in the gametangial bar represents the proportion of male to female plants encountered). Bars with the same letters are not statistically different at $p > 0.05$.

5.5 Discussion

The thick convoluted coralline found occurring epilithically on the shells of *O. sinensis* possessed all the features collectively considered diagnostic of *S. discoideus* (Chamberlain 1994). The coralline is the only species of *Spongites* known to have a dual thallus structure with thin, primary thalli that gives rise to discoid and/or convoluted, secondary thalli. While these forms were once thought to be separate species, Chamberlain (1994) confirmed the dual nature of the species.

Species concepts within the coralline algae are relatively poorly established and only relatively recently becoming more widely known (Penrose and Woelkerling 1992, Woelkerling and Penrose 1988, Keats *et al*. 1994b, Maneveldt and Keats 2008). *Spongites* *discoideus* is one of eleven recognised species within the genus *Spongites* Kützing from the coralline algal subfamily Mastophoroideae (Woelkerling 1985, Maneveldt *et al*. 2008). The species appears to be able to adapt to a range of water temperatures and has been widely recorded from various antarctic, subantarctic, cool and warm temperate regions (Mendoza and Cabioch 1986b, Ricker 1987, Chamberlain 1994, Mendoza *et al*. 1996, Rull Lluch 2002, John *et al*. 2004, Maneveldt *et al*. 2008).

Since encrusting coralline algae portray a range of morphological variability, it is often difficult to say with any degree of certainty to which species a given plant belongs (Johansen 1981, Steneck 1986, Cabioch 1988) especially since crust morphology is so easily affected by a host of biological (see e.g. Steneck and Adey 1976, Steneck and Paine 1986, Littler *et al*. 1995, Maneveldt and Keats 2008) and physical (see e.g. Littler 1976, Steneck and Adey 1976, Adey *et al*. 1982, Steneck 1986) factors. *Spongites discoideus* has been recorded to occur mostly epilithically and until more recently, in a typical discoid form (Adey and Lebednik 1967, Chamberlain 1994). The current study is the first to show that this coralline can commonly also occur epizoically and more importantly, that the morphology is very variable from the typical discoid form. The convoluted form of *S. discoideus* encountered here is in all likelihood due to space limitation on the shells of the winkles.

Besides displaying morphological variability, *S. discoideus* encountered epizoically on winkle shells were represented by vastly different ratios of reproductive stages in the coralline's life cycle. Interestingly, epilithic material (from boulders) from both intertidal rockpools and the shallow subtidal zone had comparatively more sporangial plants. Even more interesting was the fact that intertidal rockpools and the shallow subtidal zone bore contrasting ratios of male to female plants. In contrast to epilithic plants, epizoic plants (from winkle shells) were dominated by gametangial and more so, male plants. In other words, sporangial plants were most frequently found on both intertidal and subtidal boulders, male plants most frequently on winkle shells and female plants mostly frequently on subtidal boulders. There clearly was a separation of the life cycle stages between the three habitats. While the separation of sporangial and gametangial stages is readily understandable (see Figure 5.16), that between the sexes is less obvious and may be due to a number of factors including differences in water temperature between the intertidal and subtidal habitats (see e.g. Santelices 1990). Based on the life cycle of coralline red algae, gametophyte seeding onto winkle shells would thus have originated from the epilithos. Conversely, gametes released from winkle epizoics would have contributed to the epilithic sporophytes.

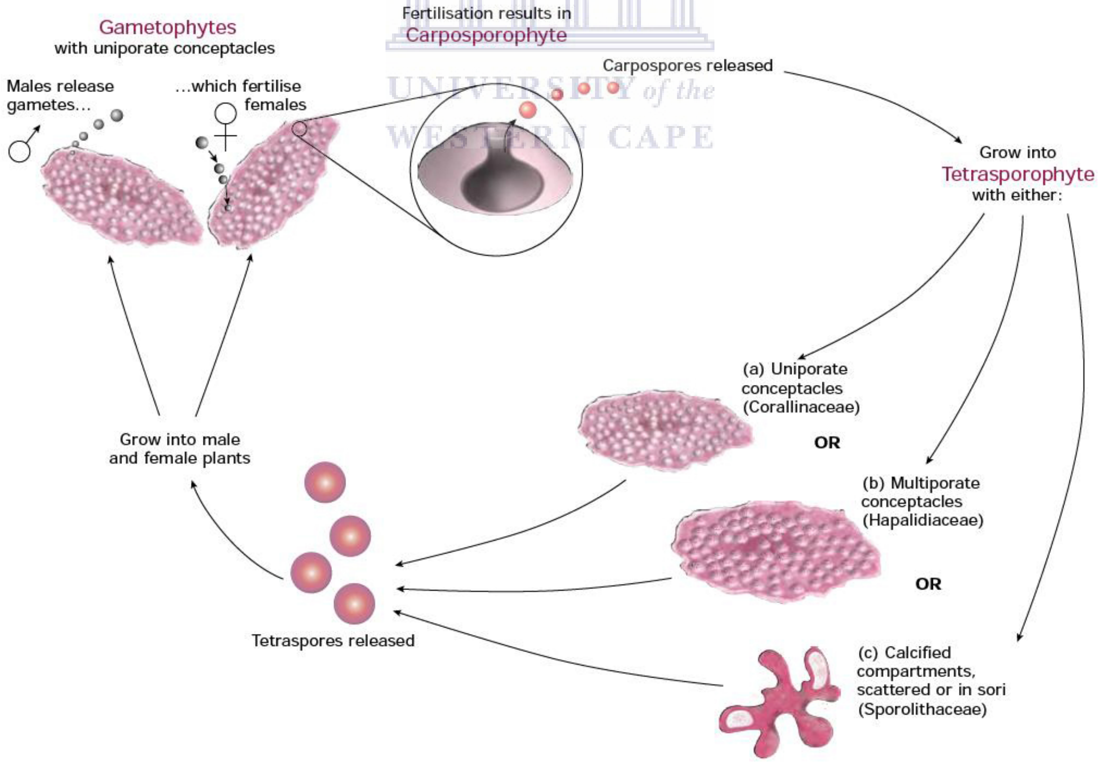

Figure 11.1 Simplified sexual cycle for encrusting coralline algae (Source: Farr *et al*. 2009)

In conclusion, the thick, convoluted encrusting coralline alga occurring epizoically on the shells of the winkle *O. sinensis* was confirmed to be *S. discoideus*. Substrate selection and thus space limitation had in all likelihood resulted in the distinct morphology of the alga. There was a pronounced separation of the algal life cycle stages between the three habitats. This latter observation may possibly be explained by the combined life cycles of the coralline alga as well as that of the winkle.

6.1 Introduction

Encrusting coralline algae are significant occupiers of space in rocky marine environments (Adey and Mcintyre 1973, Lawrence 1975, Vance 1979, Steneck 1982, 1985, 1986, Paine 1984, Dethier *et al*. 1991, Steneck *et al*. 1991, Keats *et al*. 1993, 1994a, b, Keats and Maneveldt 1994, Steneck and Dethier 1994, Fujita 1999, Maneveldt *et al.* 2006). These algae are mostly epilithic and occur most abundantly in rocky areas prone to strong wave action (Steneck 1986) and high grazing intensity (Paine and Vadas 1969, Adey and Macintyre 1973, Lawrence 1975, Vance 1979, Steneck 1982, 1985, 1986, Carpenter 1986, Maneveldt *et al*. 2006). In addition, encrusting coralline algae also occur epilithically on unstable substrata such as pebbles, epizoically on corals and other animals, and/or epiphytically on other macroalgae and other corallines (Adey 1970a, 1973, Adey and Spearapani 1971, Adey and Macintyre 1973, Littler 1973, Gordon *et al*. 1976, Steneck 1982, 1986, Morse and Morse 1984, Steneck and Paine 1986, Borowitzka *et al*. 1990, Figueiredo *et al*. 1996, Morcom and Woelkerling 2000).

Within the benthic marine environment, space is the primary limiting resource because it is seldom renewed (Connell 1961a, b, Dayton 1971, Menge 1976, Wu 1980, Branch 1985, Bertness 1989, Keats *et al*. 1994b). Encrusting coralline algae compete for this limiting resource by overgrowing one another where their leading margins come into contact (Littler 1972, Padilla 1984, Paine 1984, Steneck 1985, Sebens 1986, Olson and Lubchenco 1990, Steneck *et al*. 1991, Chamberlain 1994, Keats and Maneveldt 1994, Keats *et al*. 1994b, Morcom *et al*. 1997, Maneveldt and Keats 2008). In general, thicker crusts and those with raised margins are superior interference (overgrowth) competitors to thinner crusts and those with adherent margins (Steneck 1983, 1985, 1986, Paine 1984, Sebens 1986, Steneck *et al*.

1991, Keats and Maneveldt 1994, Keats *et al*. 1994b, Morcom *et al*. 1997, Maneveldt and Keats 2008). Trade-offs, however, exist and quite often there is an inverse relationship between interference and exploitation competition for crusts competing by overgrowth (Keats *et al*. 1993). Thin crusts that are at the bottom of the hierarchy in terms of overgrowth competition, are quite often most abundant because they have faster lateral growth rates (Steneck 1983, 1985, 1986, Keats *et al*. 1994a, Keats and Maneveldt 1994, Maneveldt and Keats 2008). This is so because thin crusts invest more energy into lateral expansion; it is believed that thick crusts invest more photosynthate into crust thickness that could otherwise have been diverted to lateral growth (Steneck 1983, Maneveldt and Keats 2008).

Spongites discoideus occurs epilithically, epizoically and occasionally even epiphytically (Chamberlain 1994, see also chapter 5). The species has a characteristic dual thallus structure comprised of thin primary thalli as well as thick, discoid secondary thalli (Chamberlain 1994). Chamberlain (1994) reports the primary thalli of the species to be competitively superior to *Spongites yendoi* (Foslie) Chamberlain and *Hydrolithon samoënse* (Foslie) Keats & Chamberlain, but competitively inferior to *Lithophyllum neoatalayense* Masaki and *Mesophyllum engelhartii* (Foslie) Adey (as *M. discrepans*). Discoid, secondary thalli have, however, not been reported to be overgrown by any other species and the coralline consequently has a high overgrowth competitive ranking (Chamberlain 1994).

In order to gain greater insight into the association between the coralline alga *S. discoideus* and the winkle *Oxystele sinensis*, various data on the ecology of the coralline alga were sought. Such data included the distribution and cover abundance of the coralline alga in the four habitats in which winkles are commonly found, and examining the competitive hierarchy and ranking of *S. discoideus* and the other encrusting algae with which it is commonly associated.

6.2 Materials and Methods

6.2.1 Natural algal percent cover abundance

Natural algal percent cover abundance was estimated and then averaged for the mid-Eulittoral zone flats, crevices, intertidal rockpools, and shallow subtidal zone (2-6 m depth). This was performed at regular 2 m intervals along transect lines (spaced 2 m apart) running perpendicular to the zones, using a 0.2 x 0.25 m (crevices) and a 0.5 x 0.5 m (flats, rockpools, subtidal) quadrat (n = 19 quadrats for the flats, crevices and rockpools; n = 21 quadrats for the shallow subtidal zone).

6.2.2 Interference competitive interactions

As *S. discoideus* was only recorded to occur in intertidal rockpools and the shallow subtidal zone, competitive interactions were determined only for these habitats. Competitive interactions were determined from within the same quadrats (n = 19 quadrats for rockpools; n = 21 quadrats for the shallow subtidal zone) used to determine algal percent cover abundance. Approximately 480 contact zones in intertidal rockpools and 341 contact zones in the shallow subtidal zone between species pairs were observed. The overgrowth (symbol ">" on graph) of one species by another was scored as a "win" for the overgrowing species against the overgrown species (sensu Steneck *et al.* 1991). Retaliations were also recorded where species normally overgrown resisted overgrowth or even reversed the normal pattern by regenerating margins and thereby raising their thalli over the encroaching alga (e.g. symbol “A >< B” on graph: A overgrows B, but B retaliates to overgrowth by A; see Keats and Maneveldt 1994).

6.2.3 Diversity

To gain insight into the environment of the competing algae, the algal diversity of the four habitats was calculated using both the Shannon information index as expressed in equation 1, as well as the Simpson's index as expressed in equation 2 (Magurran 2004).

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

Where H' represents the Shannon information index, ln the natural log and p_i the proportion of individuals found in the *i*th species.

$$D = \sum \left(\frac{n_i [n_i - 1]}{N[N-1]} \right) \qquad \text{eq. 2}$$

Where D is the Simpson's index, n_i the number of individuals in the *i*th species and N the total number of individuals. As D increases, diversity decreases and therefore the Simpson's index is usually expressed as 1-D or 1/D (Magurran 2004).

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

$$E_{1/D} = \frac{(1/D)}{S} \qquad \text{eq. 3}$$

Where E is the Simpson's measure of evenness, 1/D the reciprocal form of the Simpson's index and S the number of species in the sample (Magurran 2004).

In determining the diversity indices, rare species (those occurring in less than 5% of the samples) were eliminated following the arguments of Clarke and Gorley (2001). This action therefore necessitated the use of an additional dominance index such as Simpson's and more specifically inverse Simpson's, instead of indices based solely on species richness. Simpson's index is thus more robust than Shannon's index since it is less dependent on rare species (Magurran 2004). Data were consequently also jack-knifed to generate an overall index of diversity (and associated 95% confidence interval) for each sample following the protocols outlined by Magurran (2004).

6.2.4 Statistical analysis

To show the relative importance of the different algal species in the four habitats sampled, multiple paired sample t-tests were performed on the percent cover abundance values for all possible species pairs (0 – flats; 6 – crevices; 28 – intertidal rockpools; 6 – shallow subtidal zone) of the taxa encountered. Mean values were sorted in descending order and the *P*-values for the *t*-tests used to assign significance letters (a's, b's, etc). To show the relative importance of *S. discoideus* in the two habitats sampled, a paired sample *t*-test was also performed on the percent cover abundance values for the species in the intertidal rockpools and the shallow subtidal zone. For all tests performed, a 5 % significance level was applied and so differences amongst treatments were considered statistically significant at $P < 0.05$. Unless otherwise stated, all data are expressed as means ± standard error (SE).

6.3 Results

6.3.1 Natural algal percent cover abundance

Fleshy macroalgae were entirely absent from all habitats sampled; much of the primary substratum was occupied by encrusting algae (Table 6.1, Figure 6.1). The mid-Eulittoral zone flats was primarily comprised of "bare rock" (bare rock here refers to the absence of visible macroalgae, but may include microalgal biofilms) with only a small percentage of the encrusting fleshy brown alga, *Ralfsia verrucosa* (2 ± 0.60 %) evident (Figure 6.1). While intertidal crevices had no clear dominance, intertidal rockpools were co-dominated by the encrusting coralline algae *S. discoideus* (34.8 ± 7.14 %) and *S. yendoi* (29.5 ± 6.81 %) (p = 0.694). The shallow subtidal zone was in turn dominated by the encrusting coralline alga

Leptophytum foveatum Chamberlain and Keats (81.3 ± 3.22 %). *Spongites discoideus* was notably very low in abundance in the shallow subtidal zone (1.4 ± 0.33 %); the species was restricted to intertidal rockpools and the shallow subtidal zone, and there was a significant difference in *S. discoideus*' percent cover abundance between these two habitats ($p < 0.001$).

Table 6.1 Algal taxa surveyed during the study and their main features

Species	**Main Feature**
Heydrichia woelkerlingii (Townsend) Chamberlain & Keats	Encrusting coralline red alga
Hildenbrandia lecanellierii Hariot	Encrusting fleshy red alga
Hildenbrandia rubra (Sommerfelt) Meneghini	Encrusting fleshy red alga
Leptophytum acervatum (Foslie) Chamberlain & Keats	Encrusting coralline red alga
Leptophytum foveatum Chamberlain & Keats	Encrusting coralline red alga
Phymatolithon sp.	Encrusting coralline red alga
Ralfsia verrucosa (Areschoug) J. Agardh	Encrusting fleshy brown alga
Spongites discoideus (Foslie) Penrose & Woelkerling	Encrusting coralline red alga
Spongites yendoi (Foslie) Chamberlain	Encrusting coralline red alga

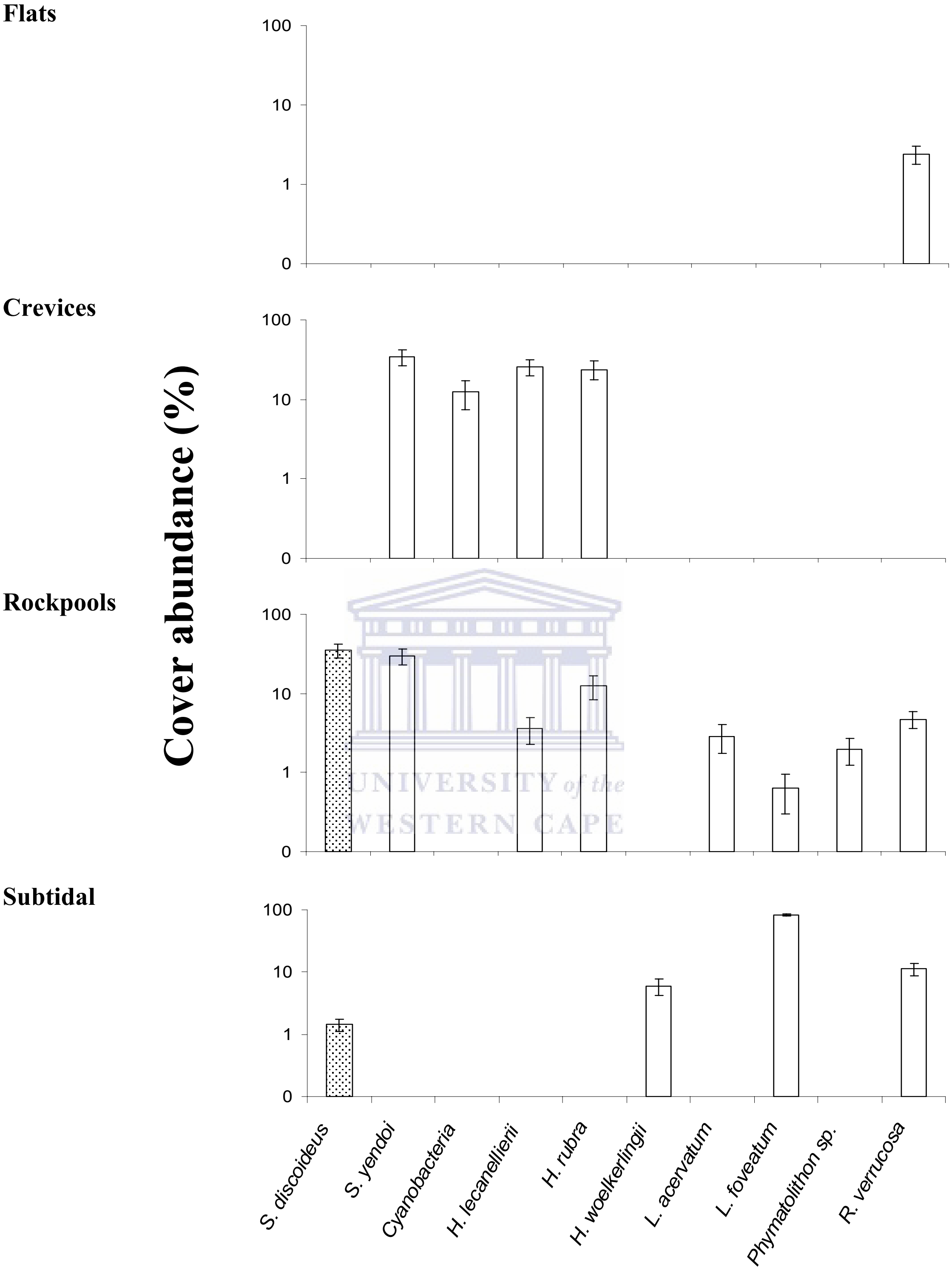

Figure 6.1 Percent cover abundance of macroalgae in each of the four habitats surveyed at Kalk Bay. The remaining unrecorded percentages are "bare rock" ("bare rock" refers to the absence of visible macroalgae, but may include microalgal biofilms).

6.3.2 Interference competitive interactions

Overgrowth interactions were largely unidirectional. Interactions involving *L. foveatum* showed the characteristic competitive retaliations reported on in the literature (see e.g. Keats and Maneveldt 1994, Maneveldt and Keats 2008). *Spongites discoideus* ranked highest in the competitive hierarchy in intertidal rockpools and was only outcompeted by the thicker *H. woelkerlingii* in the shallow subtidal zone (Figure 6.2). Except for *S. discoideus* in intertidal rockpools, species that were most abundant (Figure 6.1) were consistently at or near the bottom of the hierarchy in terms of overgrowth competition. Interestingly, the competitive relationship between *L. foveatum* and *R. verrucosa* was reversed in the two habitats.

Rockpools

Ranking	
DISC	7
FOVE	6
RALF	5
PHYM	4
YEND	3
LECA	2
ACER	2
RUBR	1

Subtidal

Ranking	
HEYD	4
DISC	3
RALF	2
FOVE	1

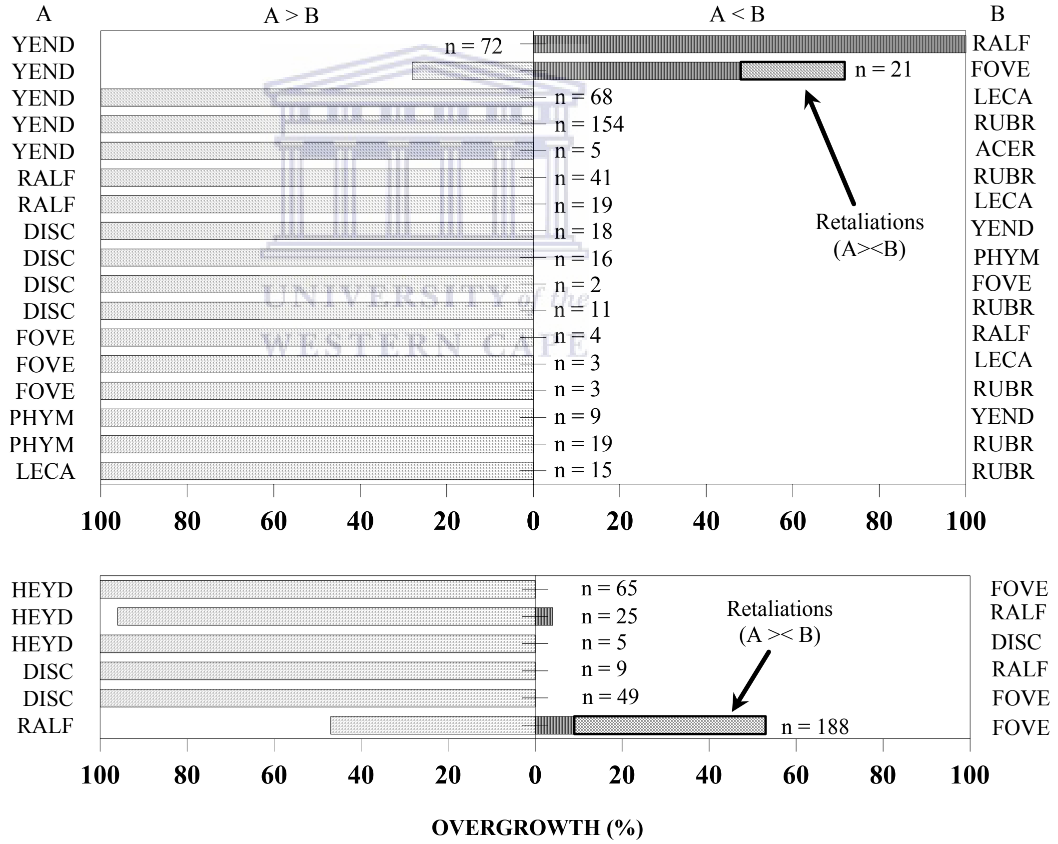

Figure 6.2 The percentage overgrowth interactions among all encrusting algae in the rockpools and shallow subtidal zone (YEND = *S. yendoi*; RALF = *R. verrucosa*; DISC = *S. discoideus*; FOVE = *L. foveatum*; PHYM = *Phymatolithon* sp.; LECA = *H. lecanellierii*; ACER = *L. acervatum*; RUBR = *H. rubra*; HEYD = *H. woelkerlingii*) and their rank within the competitive hierarchy (1 ranks lowest i.e. overgrown by all other species and vice versa; species with the same number are awarded equal ranking because they were not shown to compete).

6.3.3 Diversity

Diversity was notably lowest on the mid-Eulittoral zone flats because only one species of algae was able to colonise this zone (Table 6.2). Although intertidal rockpools had the highest number of algal species present, inverse Simpson's diversity was highest in intertidal crevices. This was so because of greater evenness (in percent cover abundance i.e. exploitative competitive abilities) between algal species in the crevices in which no one species dominated. In contrast, intertidal rockpools and the shallow subtidal zone displayed either co-dominance or clear dominance (in percent cover abundance) respectively.

Table 6.2 Diversity parameters for algae in the different habitats ranked by inverse Simpson's index (1 ranks highest).

Habitat	No. of species	Shannon index	Inverse Simpson's index	Simpson's measure of evenness[2]	Rank
Crevices	4	1.37 ± 0.05	3.82 ± 0.29	0.95	1
Rockpools	8	1.55 ± 0.06	3.75 ± 0.31	0.31	2
Subtidal	4	0.67 ± 0.07	1.49 ± 0.10	0.37	3
Flats	1	0	N/A[1]	N/A[1]	4

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

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

6.4 Discussion

The first noticeable result of this component of the research demonstrates the general absence of fleshy macroalgae from the mid-Eulittoral and shallow subtidal zones at Kalk Bay, these zones being largely dominated by encrusting fleshy and more so encrusting coralline algae. This suggests that the Kalk Bay intertidal and shallow subtidal zones experience high grazer pressure, possibly from the numerous herbivorous molluscs and sea urchins that are so abundant in the area (see also Maneveldt *et al*. 2009). The absence of fleshy macroalgae, in combination with the dominance and co-dominance (exploitation competition) by only a few species in three of the four zones sampled, explains the relatively low algal diversity values obtained for Kalk Bay. Secondly, *S. discoideus* was restricted to intertidal rockpools (in which it was the most abundant alga) and the shallow subtidal zone where *O. sinensis* was the most abundant winkle (see chapter 4). Lastly, despite the high competitive ranking of *S. discoideus*, the coralline was extremely low in abundance in the shallow subtidal zone. Species that were typically at or near the bottom of the hierarchy in terms of overgrowth competition (interference) were generally the most abundant.

Encrusting algae and more so encrusting coralline algae are known to thrive and even dominate in environments prone to intense herbivory (Paine and Vadas 1969, Adey and Macintyre 1973, Lawrence 1975, Vance 1979, Steneck 1982, 1985, 1986, Carpenter 1986, Keats *et al*. 1994b, Maneveldt *et al*. 2006). In such environments, the exclusion of grazers quickly leads to an increase in abundance and diversity of fleshy macroalgae (Paine and Vadas 1969, Dayton 1975, Duggins 1980, Paine 1980, Slocum 1980, Ayling 1981, Sousa *et al*. 1981, Steneck 1982, Bertness 1984, Maneveldt *et al*. 2009). The high density and biomass of grazers was clearly evident at our study site (see chapter 4) which probably accounted for the coralline dominated barrens observed (see Maneveldt *et al*. 2009). The consequence of these factors more than likely resulted in less to no competition with fleshy macroalgae with which encrusting algae cannot successfully compete.

In the absence of competition from fleshy macroalgae, two factors in particular control the competitive abilities of encrusting algae. These include their interference (overgrowth) and exploitative (e.g. growth rate) competitive abilities. Success in overgrowth competition between competing crusts is largely determined by two factors namely, the thallus thickness at the leading edge and the degree to which the growing margins are raised (Steneck 1982, 1983, 1985, 1986, Paine 1984, Sebens 1986, Steneck *et al*. 1991, Keats and Maneveldt 1994, Keats *et al*. 1994b, Morcom *et al*. 1997, Maneveldt and Keats 2008). Any factor that influences the thallus thickness of competing crusts may invariably then alter their overgrowth competitive success. Maneveldt and Keats (2008) showed for example that selective grazing by the territorial gardening limpet *Scutellastra cochlear* reduced the thallus thickness of the coralline *S. yendoi* and consequently also its interference competitive ability. Despite the high interference (overgrowth) competitive ability of *S. discoideus* (see also Chamberlain 1994), the coralline was not very abundant in the shallow subtidal zone. In contrast, those encrusting algae at or near the bottom of the hierarchy in terms of overgrowth competition (i.e. the thinner species), were the most abundant in the shallow subtidal zone, and nearly so in intertidal rockpools. For these latter species, exploitation competition was clearly more important.

It has long been known that crust thickness and lateral marginal extension (growth rate) are inverse related i.e. thicker crusts tend to grow laterally slower than thinner crusts (Steneck 1983, 1985, 1986, Keats and Maneveldt 1994, Keats *et al*. 1994a, b, Wai and Williams 2005, Maneveldt and Keats 2008). Maneveldt and Keats (2008) showed that in reducing their thallus thickness and thus their interference competitive abilities, *S. yendoi* grazed by limpets, grew laterally faster (greater exploitation ability) and consequently occupied more substrata when space was available for growth. The thicker, discoid thalli of *S. discoideus* observed from the shallow subtidal zone, which no doubt would display a slower lateral margin extension rate, probably explains the coralline's low abundance in this zone. Conversely, the abundant *S. discoideus* from intertidal rockpools occurring mostly as primary (thin) thalli would display faster lateral margin extensions and thus greater percent cover abundance. Similarly, *L. foveatum*, a thin crust that appeared at the bottom of the overgrowth hierarchy in the shallow subtidal zone, was the most abundant subtidal coralline. Keats and Maneveldt (1994) reported that in addition to growing laterally fast, *L. foveatum* was able to produce thin, regenerated margins at its thallus surface that could prevent or even reverse overgrowth by thicker competitors. This species is able to benefit from the advantages of being thin as well as being thick. The importance of this latter statement was clearly evident in those overgrowth interactions involving this coralline and *R. verrucosa* in intertidal rockpools in which a large proportion of retaliations probably 'evolved' on to overgrowths.

In conclusion, the benthic environments of the mid-Eulittoral and shallow subtidal zones at Kalk Bay are dominated by encrusting algae with coralline algae being prominent features of this algal guild. While *S. discoideus* is one of the most superior interference competitors, the coralline is conversely the weakest exploitation competitor in the shallow subtidal zone. This outcome is as a result of the thick discoid morphology (displaying slow margin extension) of the alga in the subtidal zone. For thin crusts, overgrowth does not mean competitive exclusion because exploitation competition promotes co-existence among the encrusting algae of the Kalk Bay mid-Eulittoral and shallow subtidal zones.

7.1 Introduction

Encrusting coralline algae are well-known for thriving and dominating in environments prone to intense herbivory (Paine and Vadas 1969, Adey and Macintyre 1973, Lawrence 1975, Vance 1979, Steneck 1982, 1985, 1986, Carpenter 1986, Keats *et al*. 1993, 1994a, Wai and Williams 2005, Maneveldt *et al*. 2006, Maneveldt and Keats 2008). Thinner crusts generally grow laterally faster than thicker ones (Steneck 1983, 1985, 1986, Keats and Maneveldt 1994, Keats *et al*. 1994a, b, Wai and Williams 2005, Maneveldt and Keats 2008). Consequently, thin species often tend to be more abundant than thicker species particularly in areas prone to very high grazer intensity, or under sever physical disturbance regimes (Adey and Macintyre 1973, Steneck 1982, 1985, Steneck *et al*. 1991, Keats *et al*. 1994a, b, Littler *et al*. 1995, Wai and Williams 2005, Maneveldt and Keats 2008). In addition to the opposing lateral growth rates displayed by thin and thick coralline crusts, are also their varying susceptibilities to invasion by burrowing organisms, a factor that invariably also influences their relative abundance (Keats *et al*. 1994b, Maneveldt and Keats 2008).

In contrast to thicker crusts, thinner crusts are less susceptible to invasion by burrowing organisms (Paine 1984, Steneck and Paine 1986, Sebens 1986, Keats *et al*. 1993, 1994a, b, Maneveldt and Keats 2008). Consequently, thinner crusts have significantly higher attachment strengths than thicker ones (Paine 1984, Sebens 1986, Steneck and Paine 1986, Keats *et al*. 1993, 1994a, b, Maneveldt and Keats 2008). This is so because thick, undercut thalli have fewer points of attachment with the substratum than thinner ones and so are more easily dislodged by physical disturbances (Keats *et al*. 1993, 1994b).

In the Kalk Bay shallow subtidal zone, encrusting coralline algae are very abundant, occupying close to 100 % of the primary rocky substrata (Figure 7.1; see also chapter 6). *Spongites discoideus*, however, is epilithically very low in abundance despite occurring so frequently on the shells of *O. sinensis* (see chapters 4 and 6). In order to ascertain possible reasons for this low epilithic abundance, a number of physiological and morphological attributes were determined. Since percentage burrowing and thus attachment strength have been advocated as being important in determining overall crust abundance (Paine 1984, Sebens 1986, Steneck and Paine 1986, Keats *et al*. 1993, 1994a, b, Maneveldt and Keats 2008), we wanted to determine what these attributes were for *S. discoideus* occurring both epilithically (principally on the primary substratum in the subtidal zone, but also to a lesser extent in rockpools) and epizoically (on subtidal winkle shells), and whether this could explain the low abundance of the coralline subtidally.

Figure 7.1 A view of the Kalk Bay shallow subtidal zone at 3 m depth. Note the coralline algal dominated background.

7.2 Materials and Methods

7.2.1 Attachment strength and percent burrowing

Ten separate pieces of rock covered by *S. discoideus* were chipped off from the subtidal as well as ten *Oxystele sinensis* individuals bearing the thick, convoluted form of the coralline were collected from Kalk Bay and returned to the laboratory. High strength Pratley Quickset® epoxy glue was used to attach wire paperclips to the bits of coralline from each of the above samples. Using a fishing scale attached to the wire paperclips, the force at which the coralline was pulled free from the rock substratum and the winkle shells was recorded. Thereafter, the under surfaces of the individual crusts were examined under a dissecting microscope equipped with an eyepiece micrometer with 100 scale bars. Using the scale bars as a "transect" across the thallus undersurface, the degree of burrowing and undercutting by invertebrates was estimated. A scale bar crossing a point that was undercut was taken as 1 % undercutting. The mean primary thallus and discoid, secondary thallus of the individual crusts were then determined to compare these thicknesses against the attachment strengths and percent burrowing.

7.2.2 Primary and secondary thallus thickness

For primary and secondary thallus thickness measurements of *S. discoideus*, air-dried thalli of the material removed in the attachment strength component of the study was used. For variable comparative analyses, thallus thickness measurements were also taken for ten specimens collected from the intertidal rockpools. Crude sections were made perpendicular to the growing margins simply by breaking the crusts between two forceps or using diagonal cutters or a hammer and chisel. The thicknesses of the thalli were measured under a dissecting microscope equipped with an eyepiece micrometer and the mean for 10 fragments was calculated.

7.2.3 Statistical analysis

All data are expressed as means ± standard errors (SE). To show the relationships between the parameters tested, multiple paired sample *t*-tests were performed on coralline crusts occurring on boulders and on those occurring on winkle shells. A 5 % significance level was applied to all tests and so differences were considered statistically significant at $P < 0.05$.

7.3 Results

Except for the crusts occurring on subtidal boulders for which primary thalli were not evident beyond the secondary thalli (i.e. secondary thalli always covered the primary thalli completely), subtidal specimens of *S. discoideus* were generally thicker than those found intertidally in rockpools (Table 7.1). Even though the thicknesses of the convoluted, secondary thalli of the coralline occurring epilithically and epizoically in the shallow subtidal zone were not statistically different ($p = 0.266$), there were pronounced differences in both their percent undercutting ($p < 0.001$) and their attachment strengths ($p = 0.004$), with those crusts occurring on the shells of winkles having a higher percentage burrowing and consequently weaker attachment strengths.

Table 7.1 Parameters associated with attachment strength for *S. discoideus* occurring on boulders and on winkle shells. Comparative values with the same superscript are not statistically different. * = Due to the convoluted nature of the subtidal epilithic crusts, no primary thalli were evident.

Feature	**Intertidal Boulders**	**Subtidal Boulders**	**Subtidal Winkles**
Primary thallus thickness (µm)	626 ± 46.64^{a}	*	746 ± 40.55^{b}
Secondary thallus thickness (mm)	2.39 ± 0.21^{a}	6.02 ± 0.67^{b}	7.24 ± 0.55^{b}
Percentage burrowed / undercut	-	25 ± 3.94^{a}	44 ± 3.32^{b}
Attachment strength (removal force in kg)	-	8.4 ± 0.77^{a}	2.2 ± 0.58^{b}

7.4 Discussion

The results of this study show that the overall thallus thickness of *S. discoideus* was greater in the shallow subtidal zone than in intertidal rockpools. Despite the statistically similar secondary thallus thicknesses of *S. discoideus* on subtidal boulders and on adult *O. sinensis* shells, the percentage undercutting or burrowing of the coralline on the winkle shells was greater than that on boulders. This is in contrast to other findings (see Paine 1984, Steneck and Paine 1986, Sebens 1986, Keats *et al*. 1993, 1994a, b, Maneveldt and Keats 2008) in which thallus thickness was always shown to be positively correlated with percent undercutting. Furthermore, the attachment strength of *S. discoideus* on subtidal boulders was greater than that on winkle shells. Crusts that are generally more weakly attached (as those on winkle shells) are always found to be more undercut by burrowing organisms. This latter finding is consistent with the literature (see Paine 1984, Sebens 1986, Dethier *et al*. 1991, Keats *et al*. 1993, 1994a, b, Maneveldt and Keats 2008).

There is generally a strong negative or inverse relationship between thallus thickness and attachment strength and similarly, so is the relationship between attachment strength and percentage burrowing (Paine 1984, Sebens 1986, Steneck and Paine 1986, Keats *et al*. 1993, 1994a, b, Maneveldt and Keats 2008). This implies then a positive relationship between thallus thickness and percentage burrowing. In contrast to thin crusts, thicker crusts are more susceptible to invasion by burrowing organisms (Paine 1984, Steneck and Paine 1986, Sebens 1986, Keats *et al*. 1993, 1994a, b, Maneveldt and Keats 2008) and so have fewer points of attachment with the substratum than thinner ones. Consequently thicker crusts are generally more easily dislodged by physical disturbances than thinner crusts (Keats *et al*. 1993, 1994b). While the thick, convoluted thalli of *S. discoideus* on winkle shells where more heavily undercut by burrowing organisms (Figure 7.2) and so explaining their weaker attachment strengths, this phenomenon was not observed for crusts on subtidal boulders (that had significantly higher attachment strengths due to significantly less undercutting), which had similar thallus thicknesses. This latter outcome was in all likelihood due to insufficient numbers of crusts of *S. discoideus* collected (i.e. too low a sample size) for this analysis.

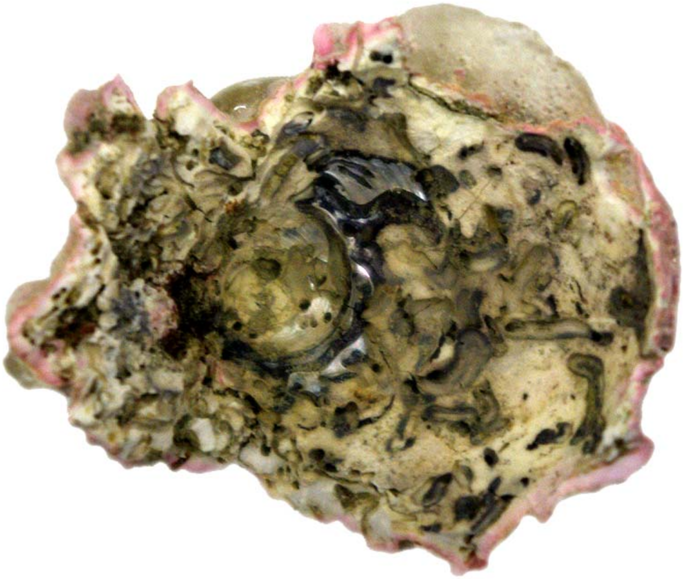

Figure 7.2 The bottom view of an intact coralline fragment removed from a winkle shell showing extensive undercutting by burrowing organisms.

While undercutting by burrowing invertebrates have been advocated as being the primary factor resulting in reduced attachment strength of coralline crusts to their substrate (Dethier *et al*. 1991, Paine 1984, Sebens 1986, Keats *et al*. 1993, 1994a, b, Maneveldt and Keats 2008), other factors may invariably also contribute to a weaker attachment. At times during our investigations, the outer layer of the winkle shells often became detached along with the coralline sooner that the coralline crust did. The weaker attachment strength observed for crusts on winkle shells was probably amplified by the relative weakness of the outer shell, a phenomenon already reported for many winkles (see Mayfield 1998, Van Zyl *et al*. 1998, Pulfrich and Branch 2002).

In conclusion, percentage undercutting and consequently attachment strength have been reported as being important factors influencing overall cover abundance of encrusting coralline algae (Paine 1984, Sebens 1986, Steneck and Paine 1986, Keats *et al*. 1993, 1994a, b, Maneveldt and Keats 2008). It is so largely because undercutting increases the probability of dislodgement and thus wave-induced mortality (Dethier *et al*. 1991, Paine 1984, Sebens 1986, Keats *et al*. 1994b). This probably accounts for the low cover abundance of *S. discoideus* occurring epilithically on the primary substrata. It does, however, not account for the high abundance of the epizoic form of the coralline in the Kalk Bay subtidal, suggesting that factors associated with the association itself probably play the most important role in increasing the cover abundance of the epizoic form of the coralline in the shallow subtidal zone.

8.1 Introduction

Although the coralline *Spongites discoideus* occurs quite commonly epilithically in both intertidal rockpools and the sublittoral fringe, it is not very abundant epilithically in the shallow subtidal zone (see chapter 6). In the shallow subtidal zone (down to about 5 m), the coralline occurs primarily epizoically on the shells of adult *Oxystele sinensis*. Virtually all adult *O. sinensis* encountered in the Kalk Bay shallow subtidal zone (98.6 ± 1.10 %; see chapter 4) had the coralline encrusted to its shell. Due to the high occurrence of the association subtidally, we wanted to determine if the winkle shell was a substrate requirement of the coralline in the subtidal zone.

8.2 Materials and Methods

A caged experiment was set up in the shallow subtidal at 2 m depth in June of 2008. Initial observations and density measurements (see chapter 4) showed this depth to bear the highest concentration of adult *O. sinensis*. The following three hypotheses were established:

H_1 – The coralline requires the live winkle for its survival in the subtidal.

H_0 (null hypothesis) – The coralline survives equally well on the empty winkle shells as well as on the primary substratum.

H_A (alternate hypothesis) – The coralline requires neither the living winkle nor its shell for survival.

Sixty adult winkles bearing the coralline were collected subtidally (at 1.5 – 2.5 m depth) by snorkel diving. Winkles measured 29.6 ± 0.49 mm in shell diameter. Twenty winkles were removed from their shells and the empty shells blotted dry. The empty shells were then glued in pairs diagonally opposite each other using marine silicone, with their intact corallines upright, onto 10 perspex slates (80 X 80 mm) (Figure 8.1). From another 20 winkles, the corallines were removed using a hammer and cold chisel, also blotted dry and then glued onto the same perspex slates opposite to the empty winkle shells (Figure 8.1). The perspex slates where kept out of direct sunlight to prevent the corallines from bleaching and/or dehydrating. After the silicone had set (± 1.5 hrs), the perspex slates were bolted down individually in the center of 10 concrete slabs weighing roughly 30 kg (Figure 8.2). Thereafter the remaining 20 winkles (control winkles) were placed in pairs onto the blocks and were covered along with the perspex slates by bolted-down stainless steel cages using stainless steel screws (Figure 8.3). The caged blocks were then randomly placed at 2 m depth in a nearby subtidal channel that was easily accessible by snorkel diving. The cages were maintained (removal of fouling organisms and sedimentation) and monitored monthly for three months by recording the number of coralline mortalities on the live winkle controls, the empty winkle shells and the fragmented corallines removed from the winkle shells.

Figure 8.1 The experimental design showing empty winkle shells (top left & bottom right) bearing whole corallines as well as individual coralline fragments glued opposite each other onto perspex slates.

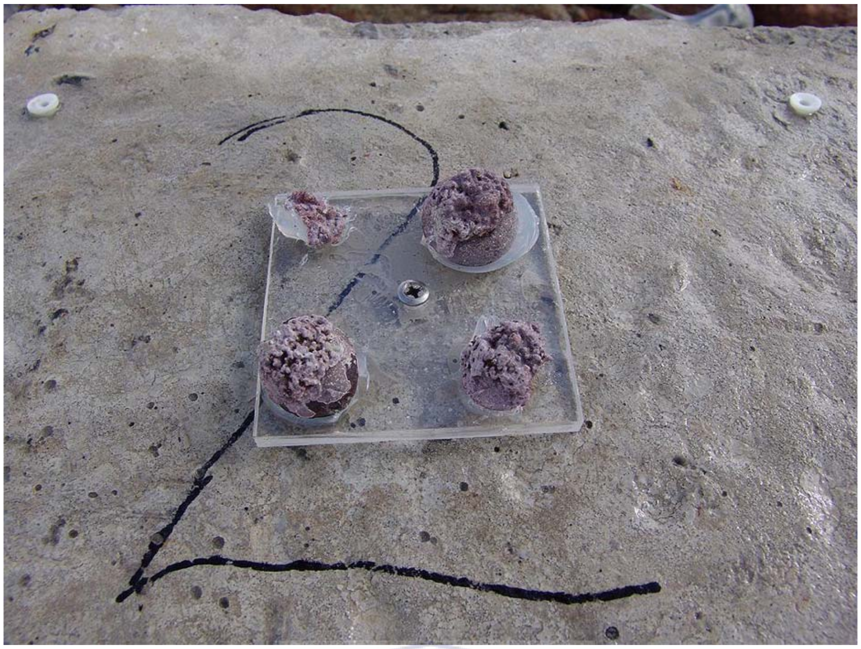

Figure 8.2 Perspex slates bearing the empty winkle shells and whole corallines, and individual coralline fragments, bolted onto concrete slabs.

Figure 8.3 Stainless steel cages were mounted onto the concrete slabs wherein the experiment was housed. Note also the two control winkles that were caged in along with the mounted perspex slate.

Coralline algae have a characteristic reddish or pinkish colouration that becomes readily bleached when the organism is exposed to unnaturally high light intensities, or when it dies (Littler 1972, Steneck 1982, Hawkins and Harkin 1985, Brown 1997, Irving *et al*. 2004, Stobart *et al*. 2005); this usually happens within days of such an occurrence (Littler 1972, Brown 1997, Figueiredo *et al*. 2000, McClanahan *et al*. 2001, Irving *et al*. 2004). Corallines bleached by unnaturally high light intensities are, however, able to restore their original colour if the light intensities are reduced, or revert back to what the coralline had previously been accustomed to (Littler 1972, Figueiredo *et al*. 2000, McClanahan *et al*. 2001, Miller *et al*. 2006). Since the concrete slabs along with the various treatments were placed at a depth range similar to where the winkles were collected, and since the cages would offer a degree of protection from high light intensities, any pronounced and persistent bleaching could be seen to be due to the coralline dying.

8.2.1 Statistical analysis

All data are expressed as means ± SE. Statistical analysis using one-way ANOVA and Tukey test for multiple comparison of means with 5 % significance level was the intended application. Differences amongst treatments were therefore considered statistically significant at $P < 0.05$.

8.3 Results

While all treatments persisted after one month (n = 20), only 17 and then 14 coralline fragments remained intact (three and then six were lost) after two and three months respectively. Consequently, the data presented here report on 20, then 17 and finally 14 sets of treatments although all control animals as well as coralline fragments on empty winkle shells, survived and persisted for the entire three months. Throughout the experimental period, we recorded 0 % coralline mortality in all treatments (Figure 8.4). Consequently the intended statistical tests were no longer applicable. While we did observe some level of bleaching (*pers. obs.*) this was relatively superficial and occurred in all treatments. By the end of the experiment, however, all corallines possessed their healthy, deep pink colouration (Figure 8.5).

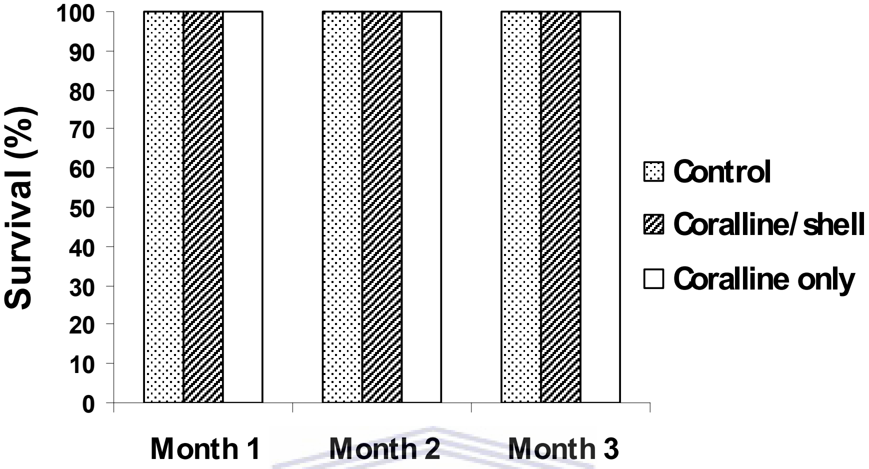

Figure 8.4 Percentage survival of the coralline alga *S. discoideus* on live winkles (control), empty winkle shells and coralline fragments, over the experimental period.

Figure 8.5 After three months, all whole corallines as well as coralline fragments still possessed their healthy, deep pink colouration.

8.4 Discussion

The results of this study clearly show that the coralline survives equally well on its own and therefore does not require the living winkle or its shell as a substrate. The high occurrence of the coralline on the shells of *O. sinensis* is therefore due to some other, as yet unknown reason. Needless to say, the winkle provides the coralline with an important mechanism for increased dispersal and recruitment. The importance of this latter statement is easily understood when ones takes into account the very low abundance of the coralline on the primary substratum within the shallow subtidal zone (see chapter 6).

Historical ecological research suggests that many associations between encrusting coralline algae and herbivores are due to co-evolution (Steneck 1985) and in many of these associations, the benefits to the interacting organisms are fairly well defined (see e.g. Steneck and Adey 1976, Maneveldt and Keats 2008). Plant-animal interactions do not, however, necessarily have to involve feeding and yet these non-trophic associations are still essential to the ecology and evolution of the organisms involved (Bloom 1975, Menge 1976, 1978, Vance 1978, Hawkins 1981, Underwood *et al*. 1983, Witman and Suchanek 1984, D'Antonio 1985, Branch *et al*. 1994, Bell 2005). At this point, we can therefore only speculate as to why the coralline has "chosen" to settle on this particular winkle.

9.1 Introduction

Primary space is the most limiting resource within the rocky intertidal benthic environment because it is often non-renewable (Connell 1961a, b, Menge 1976, Wu 1980, Branch 1985, Bertness 1989, Keats *et al*. 1994b, Lohse 2002). As a consequence, the shells of several intertidal invertebrate organisms are regarded as important because they provide extra settlement substrates for algae, substrates that are often required for the maintenance of high species diversity (Menge 1976, Hawkins 1981, Underwood *et al*. 1983, Barnes 2003, Bell 2005, Nakin and Somers 2007).

Encrusting coralline algae are inferior interference competitors to established invertebrates and other benthic macroalgae when competing for primary space (Breitburg 1984, Carpenter 1986, Steneck 1986, Steneck *et al*. 1991). These algae are, therefore, often found growing epizoically on the shells of molluscs (Steneck 1986, Steneck and Paine 1986, Smyth 1989). While *Spongites discoideus* has been observed to occur largely epilithically on the primary substratum in intertidal rockpools, the coralline is found occurring largely epizoically on the shells of adult *Oxystele sinensis* in the subtidal zone (see chapter 6). Although *O. sinensis* and *Oxystele tigrina* are virtually identical in external appearance, and have overlapping niches, the latter species was not found to bear any *S. discoideus* on their shells. Consequently, the aim of this component of the research was to determine whether the coralline has a recruiting preference for *O. sinensis* over *O. tigrina*.

9.2 Materials and Methods

Two controlled laboratory experiments were set up at the Two Oceans Aquarium in Cape Town, South Africa. Each of the experimental systems used consisted of six experimental aquaria (455 x 230 x 310 mm; length x breadth x height) encompassing a simple flow-through seawater system (0.018 L s^{-1} flow rate) at 16.5 ± 0.71 °C. Both sets of experiments were identical in all respects except that the first was run under fluorescent (rich in blue light) light while the second was run under incandescent (rich in red light) light (Figure 9.1). A timer device was installed to allow for a 10:14 hour, day: night environment.

Into each aquarium, five live juvenile *O. sinensis* (shell diameter - 13.1 ± 0.17 mm under blue-light; 15.0 ± 0.27 mm under red-light) and five live juvenile *O. tigrina* (shell diameter - 13.1 ± 0.17 mm under blue light; 15.3 ± 0.26 mm under red-light), as well as five empty shells (similar shell diameters) from each species were placed. All live winkles and empty shells lacked any visible coralline algae on their shells at the start of the experiment. Boulders bearing reproductively mature *S. discoideus* were placed in each tank as a recruitment source. In addition, and to increase the chances of recruitment, five adult *O. sinensis* (29.6 ± 0.49 mm shell diameter) bearing the coralline were also placed into each aquarium. All aquaria tops were covered with plastic lids (plastic frames bearing plastic mesh of 5 mm mesh size) to prevent the winkles from escaping. In each of the experimental setups, three aquaria were completely covered by the lids creating an artificial intertidal habitat allowing the winkles to migrate above the water line (Figure 9.2); in the remaining three aquaria, the lids were made smaller so as to float on the water in the aquaria, thus simulating a constant subtidal environment (Figure 9.3). This was done to simulate the environments from which the winkles were collected. The set up under fluorescent light was run for three months, while that under incandescent light was run over five months during which the aquaria were cleaned fortnightly of all sediment build-up. Aquaria were monitored on a monthly basis for any potential recruitment of the coralline alga onto shells of the juvenile winkles or their empty shells.

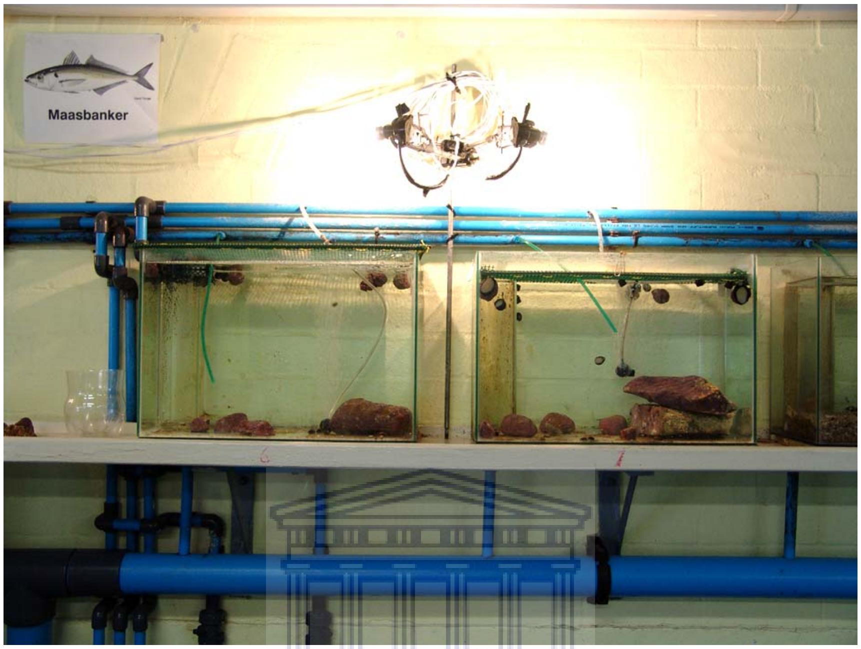

Figure 9.1 Alternating experimental aquaria setups fitted with an artificial light system allowing for a 10:14 hour, day: night cycle.

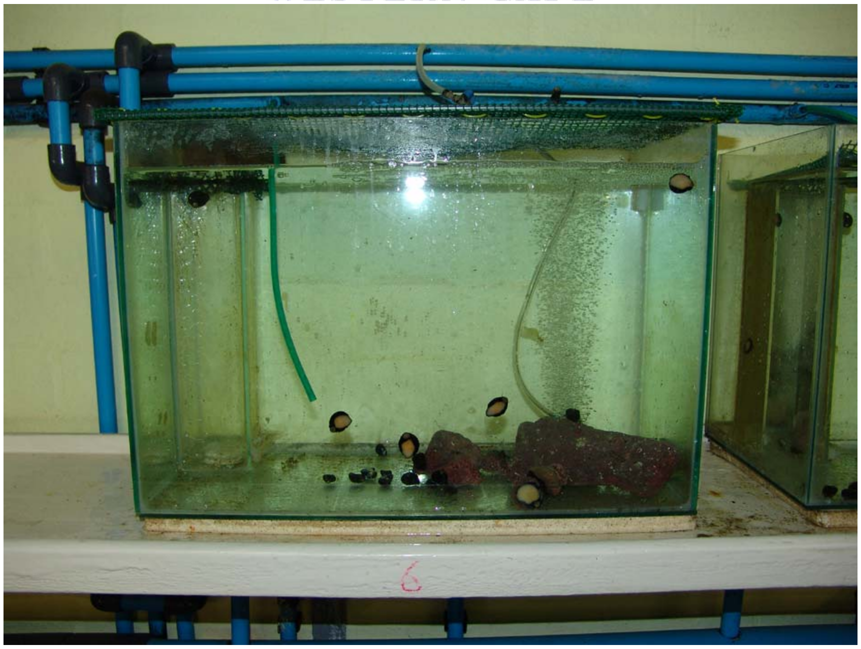

Figure 9.2 Half the experimental aquaria were covered with a mesh frame that was larger than the aquarium, thus creating an artificial intertidal habitat.

Figure 9.3 Half the experimental aquaria bore a floating mesh frame, thus simulating a constant subtidal environment.

9.2.1 Statistical analysis

Except for the temperature data that are expressed as means ± standard deviations (SD); all data are expressed as means ± standard errors (SE). Statistical analysis using one-way ANOVA and Tukey test for multiple comparison of means with 5 % significance level was the intended application. Differences amongst treatments were therefore considered statistically significant at $P < 0.05$.

9.3 Results

While a host of solitary ascidians flourished in all of the aquaria (*pers. obs*.), no recruitment of the coralline was evident on any of the living juvenile winkles or their empty shells in either of the two experimental designs (i.e. under either blue- or red-light conditions) at the end of the trial periods. This was so despite the coralline surviving throughout the trial periods on both the boulders and the adult winkles. In contrast, some winkle mortalities were recorded after about 10 weeks in all treatments, but these were continually replaced to maintain the required experimental numbers originally setup. Consequently the intended statistical tests were no longer applicable.

9.4 Discussion

The results of this experiment are inconclusive since neither of the two experimental trials showed any recruitment of the coralline, despite the survival of the coralline on both the boulders and the adult winkles. The preference for *O. sinensis* over *O. tigrina* could therefore not be determined. This particular component of the study will thus require some additional insights and planning to ensure recruitment and colonisation by the coralline alga.

Encrusting coralline algae are amongst the most abundant benthic organisms occupying hard substrata within the photic zone (Adey and Macintyre 1973, Paine 1984, Steneck 1985, 1986, Steneck *et al*. 1991) despite their extremely slow growing nature (Adey and Vassar 1975, Steneck 1985, 1986). Although coralline algae are amongst the least productive algal groups (Marsh 1970, Littler 1971, Littler and Littler 1984), their abundance is enhanced by a high fecundity and extended reproductive seasons, which enable these seaweeds to rapidly colonize space cleared by disturbance (Ayling 1976). Presently, it is unclear as to why there was no recruitment in the experimental aquaria. We had expected some level of recruitment within at least three months of starting the experiment because we observed recruitment of the coralline alga on the stainless steel cages within only six weeks of starting the subtidal caged experiment (see chapter 8). One possible reason for the lack of recruitment seen here could be that artificial environments are more hostile than natural environments.

Temperature, for example, plays a major role in coralline growth. Coralline algae grow and reproduce faster in warmer water (Adey and Macintyre 1973, Adey and Vassar 1975). The annual mean range of water temperature for False Bay is 15 – 16 °C and has been recorded to reach a maximum of 20 °C (Bolton and Anderson 1990, Leliaert *et al*. 2000). During this experiment, the water temperature at Kalk Bay was approximately 15.3 ± 0.35 °C. Although slightly cooler than the temperature in the experimental aquaria (16.5 ± 0.71 °C), this was within the mean temperature range. Temperature did therefore not appear to be the limiting factor.

Reproductive seasonality has also been advocated to be a limiting factor (Noro *et al*. 1983, Kennish *et al*. 1996, Kennish 1997, Ateweberhan *et al*. 2006) that is usually due to seasonal changes associated with temperature, light intensity, nutrient levels, tide levels and water motion (Santelices 1977, Lüning and tom Diek 1989). Coralline algae are, however, not affected by seasonal changes as much as other functional groups (Ateweberhan *et al*. 2006). Despite this, some encrusting coralline algae show distinct reproductive cycles peaking during certain seasons, while others remain reproductive throughout the year (Noro *et al*. 1983). Annual reproductive cycles, however, appear not to be characteristic to a specific taxon, but appear to be dependant on the habitat or other environmental parameter (Noro *et al*. 1983). Chamberlain (1994) recorded *S. discoideus* from South Africa to be reproductive from October to November. However, all plants collected from May to August during this study (see chapter 5) were reproductively mature. Seasonality *per se* therefore does not appear to be the reason for the lack of recruitment observed in this study.

Another factor postulated to affect coralline recruitment and colonisation is the spore viability (Steneck 1986). Studies on the viability, dispersal and habitat selection of coralline algal spores are, however, lacking (Steneck 1986). Coralline algal spores are uncalcified and are thus vulnerable and detrimentally buoyant when released (Steneck 1986). Despite the relatively slow flow rate in the experimental setup, we may simply have been losing valuable spore production to the filtration system. This suggestion, however, needs to be further evaluated.

Due to a lack of general information on the recruitment environment of coralline algae, we may have omitted to create an environment conducive for coralline algal recruitment. Consequently, we can only speculate as to why the occurrence of the coralline alga is so high on the shells of *O. sinensis* and completely lacking on those of *O. tigrina*. The higher occurrences may simply be due to the sheer numbers (density, see chapter 4) of juvenile *O. sinensis* acting as secondary substrates relative to those of *O. tigrina* abundant in rockpools where the coralline is so abundant (see chapter 6). A similar, caged study performed in the natural environment could possibly provide greater insight into this aspect of the association.

10.1 Introduction

The West Coast rock lobster, *Jasus lalandii* is distributed from Walvis Bay in Namibia, to East London in South Africa (Day 1969, Pollock 1979, Pollock and Beyers 1981) and historically attained its greatest abundance in the cooler waters along the west coast (Field *et al*. 1980, Pollock and Beyers 1981). The abundance of this lobster has notably increased along the South African south-east coast since the 1980's (Tarr *et al*. 1996). This species is a major predator in benthic communities where it is found and is consequently able to drastically alter community structure by negatively affecting prey densities (Pollock 1979, Barkai and Branch 1988, Barkai and McQuaid 1988, Barkai *et al*. 1996, Tarr *et al*. 1996, Pulfrich and Branch 2002).

Jasus lalandii is a highly selective predator (Mayfield *et al*. 2000), feeding primarily on large prey such as ribbed mussels, black mussels and sea urchins (Day 1969, Newman and Pollock 1974, Pollock 1979, Branch *et al*. 1994, Tarr *et al*. 1996, Mayfield 1998). They have, however, been recorded to feed on a host of other species such as barnacles (Barkai and Branch 1988, Barkai *et al*. 1996, Mayfield *et al*. 1999, 2000), winkles (Van Zyl *et al*. 1998, Pulfrich and Branch 2002), sponges (Barkai *et al*. 1996), encrusting coralline algae (Mayfield *et al*. 1999, 2000), and have even been reported to resort to cannibalism when recruitment of prey is low (Barkai and Branch 1988). When mussels and sea urchins are not readily available, the bulk of the prey consumed by these rock lobsters tends to be small molluscan species such as winkles (Mayfield 1998). *Oxystele sinensis* in particular had been shown to be one of the primary prey items whose numbers drastically declined in the presence of *J. lalandii* largely because the winkle has a relatively thin and light shell, making it easily penetrable (Mayfield 1998, Van Zyl *et al*. 1998, Pulfrich and Branch 2002).

Virtually all adult *O. sinensis* (98.6 ± 1.10 %, see chapter 4) encountered subtidally during the current study bore the coralline *Spongites discoideus* on their shells. Since the coralline is characteristically lumpy and convoluted on the shells of adult *O. sinensis*, making up 38.9 ± 2.52 % of the total biomass (see chapter 4), we wanted to ascertain whether the extra coralline weight had any possible advantage to the winkle against predation from rock lobsters. An experiment was thus set up and we hypothesised that the rock lobster *J. lalandii* would prefer consuming adult *O. sinensis* lacking the coralline over those bearing the coralline. The assumption was made that the added coralline load would provide the winkle with some form of protection against predation since earlier research had suggested that the relatively thin and light-weight shell was the reason for the winkle's susceptibility to predation.

10.2 Materials and Methods

10.2.1 Experimental systems design

The experiment was set up at the Marine and Coastal Management (MCM) research aquarium in Seapoint, Cape Town. The experimental system consisted of a simple flow-through seawater system (0.077 L s^{-1} flow rate) with a single reservoir tank and three experimental tanks (Figure 10.1). Temperature in the system was maintained at 17 °C using a 300 watt aquarium heater and the water was well aerated. While the experimental tanks (1 m diameter) had a 513 L volume capacity, they were only operated at 200 L volumes to allow for an intertidal simulation. To prevent the test organisms escaping, mesh netting was placed over the tops of the tanks.

Figure 10.1 Two of the three experimental tanks used during the study.

10.2.2 Predator-prey manipulations

Prey items tested comprised specimens of adult *Oxystele tigrina* lacking the coralline (species control; 25.8 ± 0.21 mm shell diameter), adult *O. sinensis* lacking the coralline (feed control; 28.2 ± 0.37 mm shell diameter), and adult *O. sinensis* bearing the coralline (27.9 ± 0.36 mm shell diameter), all of which were collected from Kalk Bay. Fifteen rock lobsters (77.7 ± 2.64 mm [68.8-102.9 mm] carapace length) that had been in captivity for about five years at the research aquarium were used in the experiment, five of which were randomly placed into each of the three tanks (Figure 10.2). The rock lobsters were allowed to acclimatise to their new environment for 72 hrs prior to commencement of the experiment. During this time they were starved. 48 hrs after first being transferred, the lobsters were offered an opened black mussel to ensure that they were ready to feed. The lobsters were, however, not allowed to consume the mussels and were starved for an additional 24 hours. Thereafter, 10 winkles from each of the three treatments were placed into each of the three tanks (i.e. each tank of five lobsters had access to 30 winkles). Before the winkles were added to the tanks, a partition was placed inside the tank separating them from the lobsters and allowing the winkles to first attach themselves to the tank surface; this ensured that the winkles would not easily be flipped over by the preying lobsters. The partition was subsequently removed and the lobsters were allowed free access to the winkles. Initial observations were then made of the mode of feeding as well as for possible preference of prey treatments. All observations were made under natural ambient light as lobsters are known to feed better under dim to dark conditions because they are nocturnal and their natural feeding behaviour is stimulated with the onset of darkness (Fielder 1965, Dall 1986, Williams and Dean 1989, Thomas *et al*. 2003). After 24 hours, the numbers of surviving winkles from each treatment were counted and the resulting mortalities determined. Fragmented shells of the consumed winkles were also retained to observe the damage and means of penetration used by the lobsters. The entire experiment was repeated and the mean consumption values for each of the two 24 hour periods determined. This was done to eliminate the possibility that the feeding period of 24 hours may have been either too short or too long for the numbers of winkles tested. This experimental design allowed the winkles to migrate above the water line, thus escaping the reach of the lobsters. It was assumed that only those winkle shells that would be too time-consuming to penetrate; these winkles would end up above the reach of the lobsters and thus escape predation.

Figure 10.2 Five rock lobsters were placed into each of the three experimental tanks and offered 10 winkles from each of the three treatments.

10.2.3 Statistical analysis

To show the relative ease of predation of the different treatments offered to the lobsters, paired sample *t*-tests were performed on the numbers of different winkles consumed for all possible treatment pairs (3) of winkles consumed. Mean values were sorted in descending order and the *P*-values for the *t*-tests used to assign significance letters (a's, b's, etc). To determine if there were differences between individual treatment contributions in any of the individual experimental tanks, paired sample *t*-tests were also performed. For all tests performed a 5 % significance level was applied and so differences amongst treatments were considered statistically significant at $P < 0.05$. All data are expressed as means ± standard errors (se).

10.3 Results

The results of this study firstly demonstrate that rock lobsters of the size tested here, typically have low consumption rates (*O. tigrina* = 4.0 ± 2.8 winkles $24hr^{-1}$; *O. sinensis* bearing the coralline = 3.7 ± 2.2 winkles $24hr^{-1}$; *O. sinensis* lacking the coralline = 2.3 ± 1.9 winkles $24hr^{-1}$). Secondly, there was no significant difference between the three treatments (*O. tigrina* vs *O. sinensis* bearing the coralline - $p = 0.423$; *O. tigrina* vs *O. sinensis* lacking the coralline - $p = 0.199$; *O. sinensis* bearing the coralline vs *O. sinensis* lacking the coralline - $p = 0.184$) (Figure 10.3). Casual observations of feeding by the rock lobsters showed, however, that generally more *O. tigrina* individuals were initially approached by the rock lobsters. With regard to *O. sinensis*, there was no clear preference for the winkle with or without the coralline alga attached. What was interesting to note though was that entire intact corallines were detached from the shells of winkles that bore them (Figure 10.4). Winkle shells that typically had their corallines removed showed extensive undercutting of the coralline by burrowing organisms (Figure 10.5). Rock lobsters were observed to completely fragment the shells of their prey, thus making it nearly impossible to identify what they have consumed (Figure 10.6).

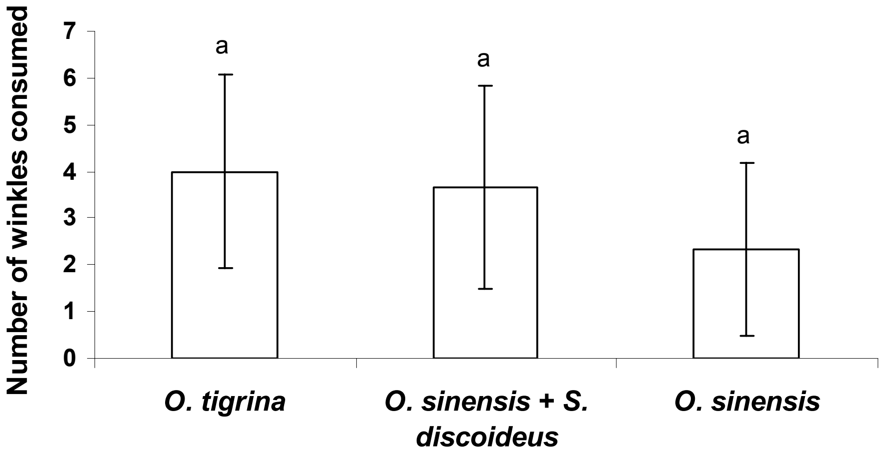

Figure 10.3 Mean number of winkles from each of the three treatments consumed by 15 rock lobsters over successive 24 hour periods. The "+" symbol denoted the presence of the coralline *S. discoideus*.

Figure 10.4 Shell fragments of consumed winkles retained to observe the means of penetration by the lobsters. Note too, the single entire coralline fragment (arrow) removed by one of the lobsters from one of the winkle shells.

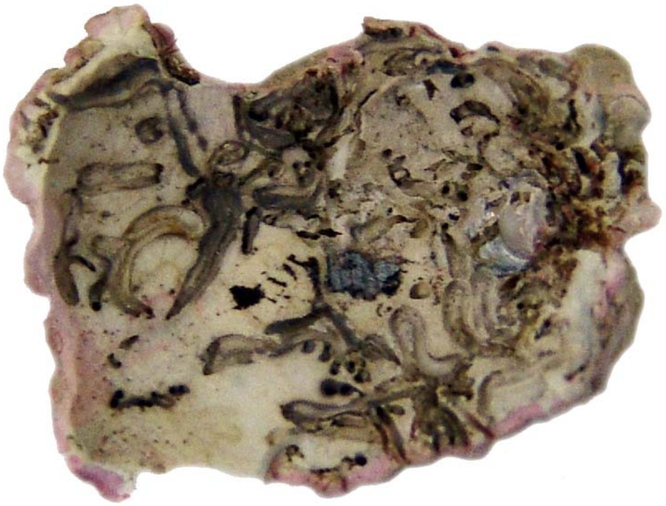

Figure 10.5 An intact coralline removed by a lobster from a winkle shell showing extensive undercutting of the coralline by burrowing organisms.

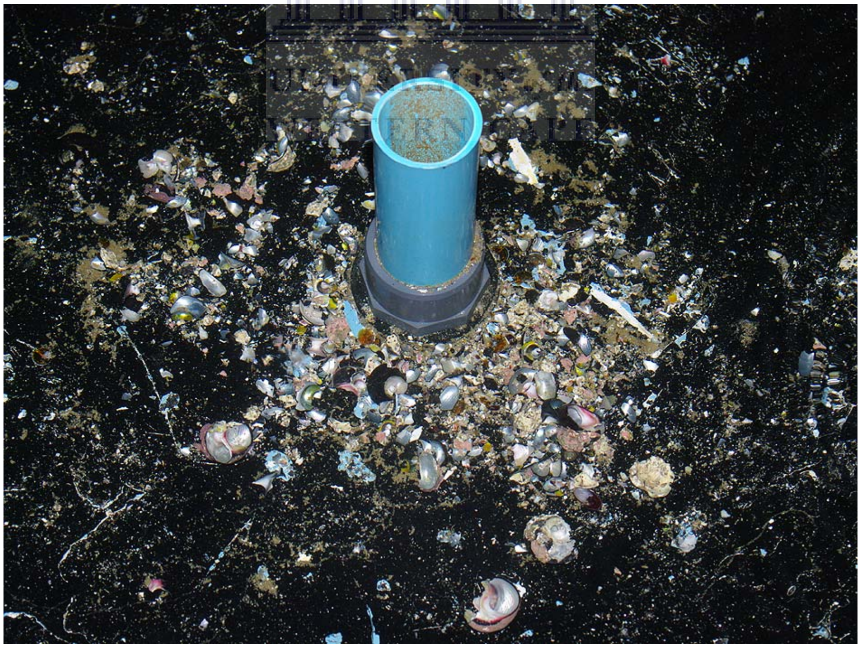

Figure 10.6 Fragmented winkle shells seen in one of the tanks after 24 hours of feeding by rock lobsters.

10.4 Discussion

The results of this study did not support the hypothesis that the rock lobster *J. lalandii* would prefer consuming adult *O. sinensis* lacking the coralline over those bearing the coralline. Our assumption that the added coralline weight would provide the winkle with some form of protection against predation was thus unsubstantiated. The outcome attained in this study was perhaps not unexpected as many epibionts are known to negatively influence the survival of their hosts (Hawkins 1981, Witman and Suchanek 1984, D'Antonio 1985, Willey *et al*. 1990, Chiavelli *et al*. 1993, Threlkeld and Willey 1993, Weissman *et al*. 1993, Stirnadel and Ebert 1997, Visse 2007). The presence of the coralline does, therefore not appear to be an advantage to the winkle against predation. On the contrary, the coralline load is possibly to the detriment of the winkle as it may potentially slow down the winkle and make it more vulnerable to predation due to increased rates of dislodgment (see e.g. Hawkins 1981, Witman and Suchanek 1984, D'Antonio 1985).

Many factors play a role in a predator's choice of prey. Prey handling time, in particular, is important as longer handling times often result in detrimental costs such as opportunities lost to perform other actions, energetic costs and exposure to mortality risks (Rovero *et al*. 2000). When their preferred prey is low in abundance or absent, *Jasus lalandii* prefers *O. sinensis* over the smooth turban shell, *Turbo cidaris* Gmelin as less time and energy is spent in penetrating the thinner winkle shells (Van Zyl *et al*. 1998). Van Zyl *et al*. (1998) observed that smaller *O. sinensis* were generally penetrated at their apex, completely exposing the animal's flesh. Larger individuals tended to be bitten at the rim of the lip. Both these strategies were evident from winkle fragments collected in this study. The presence of the coralline alga, *S. discoideus* may in fact be making it easier for the lobster to handle the winkle because of its uneven and convoluted nature. In addition, the attachment strength of the coralline alga to the shell of the winkle was shown to be significantly lower than that on the primary substratum (see chapter 7). Also, shell fragments showed many corallines that were completely detached from the winkle shells and extensive undercutting of the shells by burrowing organisms. All of these factors probably contribute toward the shell of *O. sinensis* being more vulnerable and more easily penetrable to the lobsters once the coralline is detached.

Juvenile *O. sinensis* are restricted to the intertidal zone and therefore escape predation from subtidal predators such as rock lobsters. As *O. sinensis* ages, however, it moves into the subtidal and is more exposed to predation by rock lobsters (Van Zyl *et al*. 1998, Pulfrich and Branch 2002). Adult winkles are observed to clump together in narrow crevices, which may be a mechanism to escape predation (Lasiak 1987, Pulfrich 1997, Van Zyl *et al*. 1998, Pulfrich and Branch 2002). Unlike juvenile and adult *O. tigrina* that find refuge from predation in the intertidal zone (Branch and Branch 1981a, Griffiths 1981, Branch *et al*. 1994, Pulfrich 1997, Pulfrich and Branch 2002), *O. sinensis* is prone to increased predation rates because of its preferred habitat in the shallow subtidal zone. It may well be though that in the natural environment, bearing the coralline may indeed camouflage the winkle against the coralline dominated background, making the winkle "invisible" to potential predators. This suggestion, however, needs to be further tested.

In conclusion, the results of this study have shown that adult *O. sinensis* bearing or lacking the coralline alga are equally prone to predation by rock lobsters. There thus appears to be no apparent advantage to the winkle bearing the extra coralline load. The high densities of *O. sinensis* bearing the coralline in the Kalk Bay shallow subtidal zone are probably due to the fact that one of the preferred diets of *J. lalandii*, namely the sea urchin *Parechinus angulosus* Leske, was also very abundant (see chapter 4) and so the winkle appears to have a refuge from lobster predation by virtue of the presence of a preferred prey. Also, densities of the rock lobsters in the Kalk Bay area are reported to be very low (Anderson *et al*. 1997, Leliaert *et al*. 2000), which consequently also affords *O. sinensis* the opportunity of attaining high densities in the shallow subtidal zone.

11.1 Introduction

Within its geographic range, *Oxystele sinensis* is one of the most abundant intertidal grazers (Kilburn and Rippey 1982, Anderson *et al*. 1997, Pulfrich and Branch 2002). The winkle is particularly abundant on the Kalk Bay rocky intertidal and shallow subtidal zones (see chapter 4). Adult *O. sinensis* occur most abundantly near the low water level of spring-tides, often where the waves are rough; the winkle, however, finds refuge among kelp holdfasts and stipes (Pulfrich and Branch 2002). Adult winkles characteristically migrate into the intertidal zone to reproduce because here juvenile winkles find a spatial refuge from subtidal predators and wave action (Pulfrich 1997, Van Zyl *et al*. 1998, Pulfrich and Branch 2002). Since juvenile *O. sinensis* are comparatively desiccation intolerant (Broekhuysen 1940, Brown 1960, Branch and Branch 1981a, Kilburn and Rippey 1982, Branch *et al*. 1994), adults lay their eggs in intertidal rockpools. Intertidal rockpools on the Kalk Bay rocky shore are particularly high in juvenile *O. sinensis* numbers (see chapter 4). As the juvenile winkles mature, they migrate back to the shallow subtidal zone (Pulfrich 1997, Van Zyl *et al*. 1998, Pulfrich and Branch 2002). The reason for their migration is unclear, but it is postulated to be due to interspecific competition with adult *Oxystele tigrina* that are also abundant in intertidal rockpools (Broekhuysen 1940, Pulfrich 1997). In migrating, however, the maturing winkles become increasingly exposed to subtidal predators and extreme wave exposure. Mature winkles minimise the effects of these disturbances by clumping together in narrow crevices, as well as finding refuge among kelp holdfasts and stipes (Lasiak 1987, Pulfrich 1997, Pulfrich and Branch 2002).

11.2 Life cycle of the association

Like all red algae, coralline algae have a triphasic life cycle (i.e. three life cycle stages) in which the diploid zygote gives rise to a carposporophyte phase that is essentially “parasitic” on the female gametophyte (Lee 1980) (Figure 11.1). It is this third phase that ultimately produces carpospores that give rise to the sporophyte generation. It is important to note that, although algae may have the ability to reproduce sexually, most algae can also reproduce asexually (Searles 1980, De Wreede and Klinger 1988, Hawkes 1991). In the encrusting coralline algae, it is often the asexual means of reproduction which predominates in nature and this is achieved by simple fragmentation followed by growth (Woelkerling 1988).

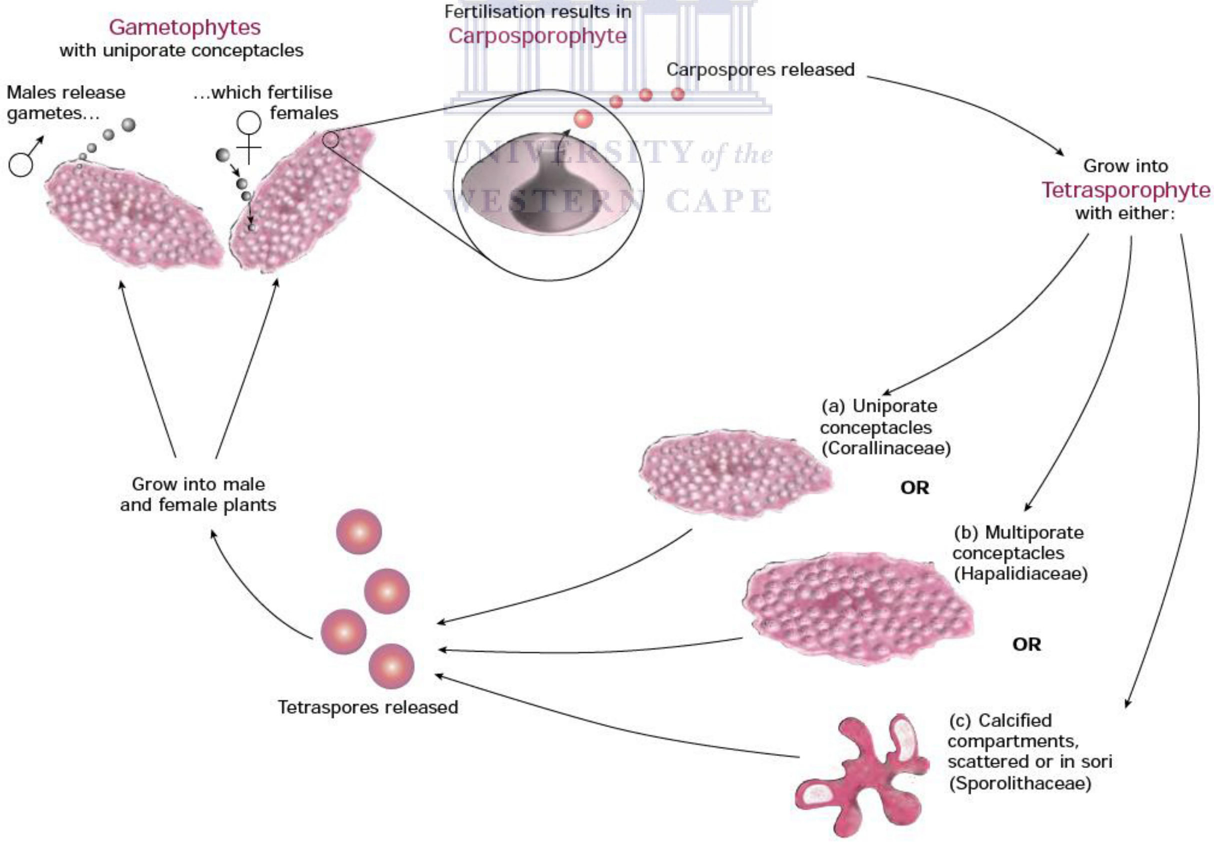

Figure 11.1 Simplified sexual cycle for encrusting coralline algae (Source: Farr *et al*. 2009)

Understanding sexual reproduction in coralline algae as well as the life cycle of the winkle *O. sinensis* ultimately provides insight into the postulated life cycle of this coralline-winkle association (Figure 11.2). The life cycle of the association appears to begin in intertidal rockpools where *Spongites discoideus* occurs largely epilithically and is the dominant encrusting alga. Notably the largest proportion of the coralline alga is tetrasporangial plants producing tetraspores. It is here that juvenile *O. sinensis* are very abundant; only a few adult *O. tigrina* are present. Newly hatched juvenile *O. sinensis* have shells that are free of any coralline crusts. The prolonged residence times of juvenile *O. sinensis* as well as the high percent cover abundance of reproductively mature *S. discoideus* in the rockpools probably account for the juvenile winkles acquiring the products of the dispersed coralline tetraspores (namely primary thallus gametophytes) onto their shells. It is currently unclear as to why the few adult *O. tigrina* do not bear the coralline, but it is assumed that these larger winkles already have acquired a host of other biofilms that may have prevented settlement of the coralline. For example, some adult *O. tigrina* bore the encrusting fleshy brown alga *Ralfsia verrucosa*. This latter seaweed is known to secrete a secondary metabolite that acts as both a feeding deterrent as well as an antifouling agent (Branch and Branch 1981a, Branch *et al*. 1994, Thabard *et al*. 2009). Furthermore, it is also unclear as to why the equally abundant coralline alga *Spongites yendoi* does not show this recruitment pattern. Both species of coralline bear conceptacles of all reproductive stages throughout the year (see Chamberlain 1993) and so timing of reproductive maturity in the coralline, along with that of the winkle, certainly is not the limiting factor for *S. yendoi*.

Maturing winkles, having acquired the developing *S. discoideus* gametophyte thalli, migrate to the shallow subtidal zone (Pulfrich 1997, Van Zyl *et al*. 1998, Pulfrich and Branch 2002), presumably to escape interspecific competition from adult *O. tigrina* (Branch and Branch

1981a). On the shells of these maturing winkles, primary coralline thalli give rise to discoid, secondary thalli that eventually become convoluted due to space limitation on the winkle shells. Developing gametophyte plants occurring epizoically on the subtidal winkles then produce gametes with only male gametes being dispersed into the water column. Fertilization occurs inside female gametophyte conceptacles and this process gives rise to diploid zygotes that grow into the carposporophyte phase, which remains attached to the female gametophyte. These carposporophytes produce carpospores that are released into the water column and eventually settle on the subtidal epilithos to grow into the new sporophyte generation. The high proportion of gametophyte plants on winkle shells and the high proportion of sporophyte plants on the shallow subtidal substratum suggest seeding of the shallow subtidal from adult *O. sinensis* shells. This pattern conforms to the suggestion by Brandano *et al*. (2005) that *Spongites* species typically have their initial growth in shallow water and final growth in deeper waters.

With time, adult *O. sinensis*, having survived in the subtidal zone for some time, now bear large, convoluted specimens of *S. discoideus* on their shells. Due to the high energy environment of the subtidal zone and to prevent predation of newly hatched winkles, reproductively mature winkles now migrate into the intertidal zone to lay their eggs (Pulfrich 1997, Van Zyl *et al*. 1998, Pulfrich and Branch 2002). In doing so, the adult winkles become exposed during low tide; this causes bleaching (whitening) of the coralline which if not exposed for extended periods, does not result in death of the coralline. In this manner the cycle is repeated (possibly several times), i.e. juvenile winkles hatch in rockpools and possibly a new generation of sporophyte plants resulting from those gametophyte plants brought into the intertidal rockpools epizoically.

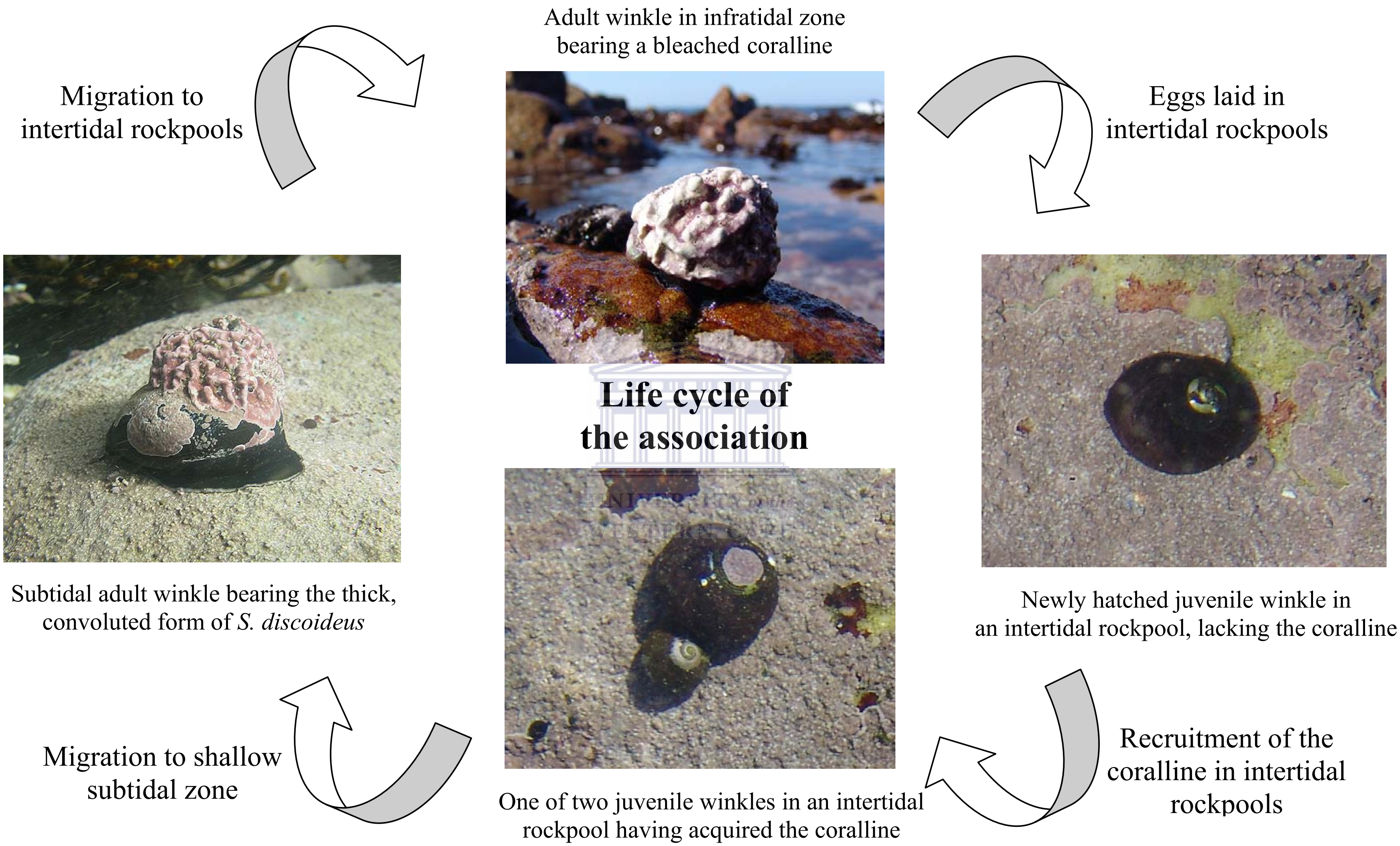

Figure 11.2 Postulated life cycle of the association between the winkle *O. sinensis* and the coralline alga *S. discoideus*

11.3 Possible advantages and disadvantages of the association

Possible advantages for the coralline include: an increased rate of fertilization, dispersal and recruitment; and refuge from interspecific competition (Steneck 1986, Buss and Yund 1988, Bell 2005). Adult winkles are commonly observed to clump together in narrow crevices (Lasiak 1987, Pulfrich 1997, Van Zyl *et al*. 1998, Pulfrich and Branch 2002). This aggregation probably increases the rate of fertilisation for the epizoic plants (Buss and Yund 1988) and is particularly beneficial when shells are colonised largely by only one reproductive stage. The migration patterns of the adult winkles no doubt also result in increased dispersal and recruitment into habitats suitable for the coralline. While *S. discoideus* is superior in overgrowth competition to most other encrusting algae recorded, the exploitation competitive ability of the thick, discoid, convoluted form is weak. Often being the sole inhabitant of an additional substrate (shells) certainly improves the coralline's exploitation competitive ability. Desiccation stress, however, can be a major problem for these epibionts especially if they have a lower desiccation tolerance than their host (Bell 2005). The migration of the winkle from the shallow subtidal zone to the intertidal rockpools causes bleaching of the coralline that may result in death if exposure is prolonged (Littler 1972, Steneck 1982, Brown 1997, Figueiredo *et al*. 2000, McClanahan *et al*. 2001, Irving *et al*. 2004). This potential fatality, however, is far exceeded by the benefits since substantial coralline dispersal would already have occurred before the first migration of a reproductively mature winkle back to the intertidal zone.

In contrast, there appears to be no apparent advantage to the winkle for bearing the coralline load. Epizoics have been reported to afford camouflage to their hosts, to protect them from predation (Bloom 1975, Vance 1978), and to provide protection from desiccation stress

(Menge 1978). The current study has shown that adult *O. sinensis* bearing the coralline are equally prone to predation by rock lobsters as those lacking the coralline. Bearing the coralline is thus not a feeding deterrent. It may well be though that in the natural environment, bearing the coralline may indeed camouflage the winkle against the coralline dominated background, making the winkle "invisible" to potential predators. This suggestion, however, needs to be further tested. From our observations, the coralline load is possibly more to the detriment of the winkle as it potentially slows down the winkle due to extra drag (see Wahl 1996, 1997). This makes the winkle more vulnerable to predation due to increased rates of dislodgment and an inability to escape predators fast enough (see e.g. Hawkins 1981, Witman and Suchanek 1984, D'Antonio 1985). This notion is supported by the many empty winkles shells observed subtidally (presumably consumed) that bore excessively large coralline fragments (Maneveldt *pers. com.*). Increased drag has also been postulated to reduce the growth rate of the winkle due to limited grazing time (see Wahl 1996, 1997). The current study has also shown that the presence of the coralline may indeed be making it easier for predators such as lobsters to handle the winkles because of the uneven and convoluted nature of the coralline. In addition, thicker epizoic crusts were more susceptible to invasion by boring organisms and consequently had weaker attachments strengths. This possibly also increased the vulnerability and penetrability of the winkle shells. All in all, the coralline alga is probably advantaged at the expense of the winkle.

11.4 Other epizoic-mollusc and coralline–mollusc interactions

11.4.1 Epizoic-mollusc interactions

A number of epizoic interactions involving molluscs have been documented. One of these is between the scaly dogwhelk *Nucella squamosa* (Lamarck) and the hydroid *Hydractinia* *altispina* (Millard) (Branch *et al*. 1994). The hydroid coats the shell of the dogwhelk resulting in an orange, prickly shell. This offers protection to the whelk by repelling predators with its stinging cells. Similarly, live specimens of the whelk *Burnupena papyracea* (Bruguière) are coated with the bryozoan *Alcyonidium nodosum* O' Donoghue & de Watteville giving the host a purple or orange appearance with small bumps. *Alcyonidium nodosum* is toxic and by living exclusively on this whelk, it provides the whelk with protection against predators. While the benefits to the epizoics are unknown, the molluscan hosts in both of these associations benefit. Interestingly enough, the bryozoan *A. nodosum* leaves its host shell when the host dies (Day 1969, Branch *et al*. 1994). Unlike these examples, there appears to be no apparent advantage to *O. sinensis* for bearing the coralline *S. discoideus*.

In most other epizoic-mollusc associations reported, more disadvantages than benefits to the host have been reported. In the association between the periwinkle *Littorina littorea* (Linnaeus) and its epibionts (which include barnacles, serpulids, bryozoans and the polychaete *Polydora ciliata* [Johnston]) for example, the extra epizoic weight resulted in increased drag (Wahl 1989, Wahl and Hay 1995, Buschbaum and Reise 1999), extensive undercutting of the host shell (Warner 1997), and ultimately reduced host growth and finally death (Wahl 1996, Warner 1997, Buschbaum and Reise 1999). The periwinkle's association with polychaetes was entirely to the detriment of the host as the extensive boring by the polychaetes weakened the periwinkle's shell making it more vulnerable to predators (Warner 1997). Similarly, *L. littorea* encrusted with the barnacle *Balanus crenatus* Bruguière had its weight increased 4-fold, which resulted in decreased motility, decreased reproductive output and increased mortality (Buschbaum and Reise 1999).

11.4.2 Coralline-mollusc interactions

Nearly all detailed coralline-mollusc interactions recorded involve trophic interactions (e.g. Adey 1971, Adey and Macintyre 1973, Brock 1975, Hagen 1983, Lawrence 1975, Paine 1980, Steneck 1982, 1985, Steneck *et al*. 1991, Keats *et al*. 1994b, Littler *et al*. 1995, Maneveldt and Keats 2008); few non-trophic interactions are recorded in similar detail (Steneck and Paine 1986). While encrusting coralline algae are mainly epilithic (Adey and Macintyre 1973, Steneck 1986), they are also found to occur epizoically on the shells of various molluscs (Steneck 1986, Steneck and Paine 1986, Smyth 1989). Invertebrate shells have mostly been reported to be important in providing secondary settlement space when space is limiting (Steneck 1986, Bell 2005). Steneck and Paine (1986) for example, observed the encrusting coralline alga *Pseudolithophyllum whidbeyense* (Foslie) Steneck et Paine to occur epizoically on the shells of the limpet *Acmaea mitra* Rathke. In this association, the coralline was provided with settlement space. Crusts growing on limpet shells were found to be more fertile than those growing epilithically. Steneck and Paine (1986) argued that epizoic crusts were important for the recruitment of this coralline. No clear benefits or disadvantages were reported for the host limpets. Similarly the encrusting coralline alga *Lithophyllum impressum* Foslie occurs on the apices of the limpet *A. mitra* and the chiton *Katharina tunicata* Wood (Steneck and Paine 1986). It was suggested that settlement of this coralline on these molluscs was possibly to avoid intraspecific vegetative encroachment; again, no benefits or disadvantages of the associations to either the limpet or the chiton were highlighted suggesting that these associations were probably entirely passive. In contrast, Smyth (1989) recorded several advantages to limpets bearing encrusting coralline algal epizoics. In exchange for settlement space, encrusting coralline algae in these examples were shown to: 1) inhibit the larval settlement of various potentially fouling acrothoracian barnacles, clinoid sponges and boring polychaetes; 2) reduce shell undercutting from burrowing organisms by providing a protective coat; and 3) even smothering burrowers that were able to settle on the limpet shells. In the current study, thick convoluted *S. discoideus* was shown to possess a greater degree of burrowing than epilithic crusts. As in all of these examples, the current study has illustrated the importance of winkle shells as extra settlement space for *S. discoideus* especially in the shallow subtidal zone where space is limited. However, as in the former examples, the current study has failed to provide any benefit of the association to the winkle *O. sinensis*.

11.5 Summary and future considerations

As in many other associations (e.g. examples cited in Steneck and Paine 1986, Smyth 1989, Wahl 1989, Wahl and Hay 1995, Warner 1997), *S. discoideus* does not occur exclusively on the shells of *O. sinensis*. Why then does the coralline not occur on the shells of adult winkles of the morphologically similar *O. tigrina*? In all likelihood this is because a host of other epizoics that resist fouling already exist on their shells. We deduced that the high occurrence of the coralline on the shells of *O. sinensis* was probably due to the substantial overlap in their niches. This appears to be supported by the far greater numbers of juvenile *O. sinensis* acting as secondary substrates compared to those of adult *O. tigrina* abundant in intertidal rock pools where the coralline is so abundant. However, this cannot be argued with any degree of certainty because our results on whether *S. discoideus* has a preference for *O. sinensis* over *O. tigrina* were inconclusive. There is thus a need for further study to provide greater insight into this aspect of the association and possible repetition of the experiment under a better manipulated environment.

Although there are numerous studies on plant-animal associations in the marine environment (see e.g. Kitting 1980, Steneck 1982, Breitburg 1984, Steneck and Paine 1986, Steneck *et al*. 1991, Littler *et al*. 1995, Maneveldt and Keats 2008), it is clear that there are still numerous gaps in our understanding of the general ecology of winkles and consequently of non-trophic coralline-winkle associations. There is thus a need for further study and investigation of these organisms that are so abundant within our intertidal and subtidal benthic communities. Along with other studies on benthic marine associations (e.g. Kitting 1980, Steneck 1982, Breitburg 1984, Steneck and Paine 1986, Steneck *et al*. 1991, Littler *et al*. 1995, Maneveldt and Keats 2008), hopefully this study can be used as a point of departure for similar studies involving winkles and the associations they form.

In conclusion, the interaction between the coralline alga *S. discoideus* and the winkle *O. sinensis* shows characteristics of a non-trophic facultative association. Both physical and biological factors play an important role in the occurrence and frequency of the association. While not dependent on the winkle, the coralline clearly benefits from the association. The benefit(s) to the winkle, if any, however, is unclear. While we may never fully understand the association between this alga and its winkle host, we have indeed gained valuable insight into the ecology of both organisms and their association.

Acknowledgements

I gratefully thank my supervisor, Prof. Gavin W. Maneveldt for his invaluable guidance, leadership and criticism during my fieldwork as well as in writing this thesis. 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, the Canon Collins Trust Fund for a top-up bursary, and the South African Department of Environmental Affairs and Tourism (DEAT) for the research permits to carry out the investigation. Many thanks to the management and staff of the Two Oceans Aquarium and Marine and Coastal Management's Seapoint Research Aquarium for their support, space and research facilities utilized during the experimental phase of the research. Thanks to Patrick Africa, Riaan Cedras, Martin Cocks, John Eager, Wayne Florence, Wynn Haupt, Martin Hendricks, Clint-lee Jansen and Deborah Robertson-Andersson for assistance with field work. Thanks to Prof. George M. Branch for assistance with identifying some of the subtidal limpets. Thanks are also due to Frikkie Calitz, Marieta van der Rijst (Biometrics Unit, Agricultural Research Council) and Martin Hendricks (Biodiversity and Conservation Biology Department) for advice with the statistical analyses of the data.

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