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Ecological and biogeographical studies on the rocky shore seagrass *Thalassodendron ciliatum* (Forsskål) den Hartog and its seaweed epiphytes at the southern limit of its distribution in the western Indian Ocean

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Declaration

I declare that this thesis is my own, unaided work and has not been submitted in this or any form to another university. Where use has been made of the research of others, it has been duly acknowledged in the text.

Work discussed in this thesis was carried out under the supervision of Prof. J.J. Bolton of the Department of Botany, University of Cape Town; and Associate Prof. R.J. Anderson of DAFF and the University of Cape Town.

Signed by candidate

Signature removed

Department of Botany, University of Cape Town

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We learn more by looking for the answer to a question and not finding it.
Than we do from learning the answer itself.

-Lloyd Alexander-

To my family

Thank you for all your love, support and encouragement. You are always behind me on all
my endeavours.

University of Cape Town

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Abstract

Seagrass beds play an important role in tropical and temperate inshore marine ecology, supporting a diverse array of macro- and microfauna and flora, as well as being primary producers within both intertidal and subtidal ecosystems. Knowledge on *Thalassodendron ciliatum* (Forsskål) den Hartog and its associated flora is poor in South Africa, the southern extent of its distribution in the western Indian Ocean. This seagrass is unusual in that it grows on the open rocky shores in northern KwaZulu-Natal, South Africa, an atypical habitat for most seagrasses.

The current study aimed to improve knowledge and understanding about the ecology, diversity and biogeography of the South African rocky shore seagrass *Thalassodendron ciliatum* and its associated macroalgal epiphytes. Seagrass populations were sampled at Jesser Point (Sodwana Bay) and at Maphelane, the former being larger and the southernmost populations observed, and the latter being the site of an isolated small population further south. Three habitats were sampled at Sodwana Bay (subtidal seagrass meadows, meadows exposed during low spring tide and permanent intertidal pools) during both autumn (March 2010) and spring (September 2010) and a single collection made at Maphelane from the subtidal fringe (areas exposed during low spring tide) in October 2010.

It was found that the structure of the seagrass beds did not differ significantly, with regard to seagrass stand density and biomass, between the two sampling sites, although the seagrass stem length, and seaweed epiphyte assemblages did. A total of 99 taxa of seaweed epiphytes were identified growing on the 240 individual *T. ciliatum* uprights analysed. The majority of epiphytes were Rhodophyta, exceeding Chlorophyta and Phaeophyceae (Ochrophyta) both in species number and abundance. The most frequently and abundantly observed epiphytes were red algae: *Pneophyllum amplexifrons*, *Hydrolithon farinosum*, *Tiffaniella schmitziana*, *Asterocladon rhodochortonoides*, *Colaonema gracile*, *Polysiphonia coacta* and a single species of brown alga, an unidentified ectocarpoid, was also frequent. Epiphytic seaweeds accounted for an average of 42% of total biomass in seagrass beds at Sodwana Bay and 58% at Maphelane. Average linkage Bray-Curtis cluster analysis and Detrended Correspondence Analysis (DECORANA) ordination plot showed

that the seaweed epiphytes differed seasonally between samples collected in March and September at Sodwana Bay. Taller seagrass plants supported a greater abundance and weight of seaweed epiphytes. Seaweed epiphyte diversity and biomass was observed to be greater on seagrass stems than leaves in general and there were some differences in the assemblages of epiphytes between habitats sampled at Sodwana Bay. Average linkage Bray-Curtis cluster analysis and DECORANA ordination grouped Pool samples as being more similar to each other than the other habitats.

Distribution records for South African seaweeds indicate that the two sampling sites fall within different biogeographic regions, as demonstrated by analysis of a dataset on the distribution of KwaZulu-Natal seaweeds, and a similar pattern was observed when analyzing the biogeography of the epiphytic flora of *Thalassodendron ciliatum*. Average linkage Bray-Curtis cluster analysis and DECORANA ordination plots found that the presence/absence patterns of epiphyte seaweeds differ between the two sites, as well as seasonally at Sodwana Bay.

The non-geniculate coralline red algae epiphytes on South African *Thalassodendron ciliatum* are described in detail. Three species were identified growing on *T. ciliatum* in northern KwaZulu-Natal (*Hydrolithon farinosum*, *Pneophyllum amplexifrons* and *Synarthrophyton patena*). These coralline red algae grow epiphytically on other species of seaweeds and have been recorded as doing so both in South Africa and other localities. This functional group was represented by low species diversity, but the species were all extremely frequent and abundant epiphytes. Coralline red algae (particularly *Pneophyllum amplexifrons*) which dominate at Jesser Point (Sodwana Bay) are much less abundant at Maphelane.

Knowledge of southern seagrass populations and their algal epiphytes is limited. Studies have been conducted further north on the southern African east coast, investigating *Thalassodendron ciliatum* and other seagrass species and their epiphytes in Mozambique, Kenya and Tanzania. None of these studies examined the epiphytes to the level of detail included in the current study, but rather as functional-form groups and many investigated

sandy habitat seagrass beds, which have rather different dynamics to those on exposed rocky shores. The current study differed in that it investigated the seaweed flora of *T. ciliatum* on rocky shores, identifying epiphytic taxa to species where possible and examined multiple aspects of the seagrass and epiphyte ecology and biogeography. The results of the current study indicate that South African rocky shore *T. ciliatum* supports a higher diversity of seaweed epiphytes, compared with these other studies. It also shows that seaweed epiphytes differ on different parts of the seagrass uprights, in different habitats, seasons and biogeographic locations.

Understanding both the geographic positioning of seagrass populations, as well as associated epiphytic algal affinities, can help to understand the effects of climate change, since species on or spanning biogeographic boundaries will be primarily affected. This study focused on a small fringe population of *T. ciliatum* which may respond to threats differently than do other seagrass species in different habitats. The region studied is biologically interesting and important as a boundary between the tropical Indian Ocean and temperate southern African marine regions. Though the seagrass populations in northern KwaZulu-Natal are relatively small, they support a diverse array of other organisms, serving both as a diverse habitat/substratum and a potentially important energy/carbon source in shallow marine systems. This study serves as a detailed baseline for future management and monitoring of *Thalassodendron ciliatum* beds in South Africa and beyond.

Keywords: *Thalassodendron ciliatum*, epiphytes, biogeography, seaweeds, rocky shores, South Africa

Chapter 1

General Introduction

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1.1 Introduction

Seagrasses are specialised marine angiosperms which grow in both temperate and tropical shallow coastal waters, except along Polar shores, probably because ice scouring greatly damages and hinders their growth. (Hemminga & Duarte 2000; Short *et al.* 2001; Gullström *et al.* 2002; Larkum *et al.* 2006; Orth *et al.* 2006; Short *et al.* 2007). They frequently cover extensive areas and are referred to as seagrass beds or seagrass meadows. They are not true grasses. In spite of the fact that they are all monocotyledons, they are a polyphyletic group and do not have a single evolutionary origin. Such a group is defined by the particular ecological niche in which it occurs. Seagrasses have developed certain adaptations allowing them to thrive in such niches. These adaptations include: an ability to live fully submerged (in lowered gas concentrations and rates of diffusion), being capable of surviving in high, and often varying, salinity, a means of stable anchorage withstanding water movements, a submarine pollination technique, and the ability to compete with other species in the marine environment (Green & Short 2003). These adaptations have resulted in numerous morphological characteristics amongst seagrasses, such as flattened leaves and extensive root and rhizome systems.

1.1.1 Taxonomy of seagrasses

The taxa regarded as seagrasses belong to a very few families, all classified within the superorder *Alismatiflorae* (Monocotyledonae) (den Hartog & Kuo 2006). There are 13 genera and 60 species of seagrasses, in the four families *Hydrocharitaceae*, *Cymodoceaceae*, *Posidoniaceae*, and *Zosteraceae* (Short *et al.* 2001). Although there is considerable debate regarding the nomenclature and taxonomic relations of seagrasses, it is probable that accepted classifications will change, together with the numbers of species considered to be seagrasses (Hemminga & Duarte 2000; Green & Short 2003). Seagrass species encompass approximately 0.5% of the total marine macroflora and <0.02% of all angiosperm species (Hemminga & Duarte 2000), representing a very small number of species compared with any other group of marine organisms.

1.1.2 Distribution of seagrasses

The global extent of seagrass beds was estimated to be around 0.3 million km² according to Kennedy & Björk (2009). The global distribution of seagrasses has been separated into 10 regions: North Pacific (Japan to Baja), Chile, North Atlantic, The Caribbean, Southwest Atlantic Region, Mediterranean Region, Southeast Atlantic Region, Tropical Indo-Pacific Region, South African Region and South Australia Region (Short *et al.* 2001).

There are 13 reported seagrass species in the Western Indian Ocean (WIO), which extends across broad areas of ca. 12 000 km of near-shore soft bottom coastline. In general, seagrass meadows are found both inter-tidally and sub-tidally, and are frequently found in close proximity to coral reefs, mangroves and salt marshes (Gullström *et al.* 2002; Green & Short 2003). Seagrasses are typically restricted to protected areas free from strong currents and waves. These areas usually have soft substrata. However, in southern Mozambique and on the north east coast of South Africa the seagrass *Thalassodendron ciliatum* is common on rocky substrata with high wave action, strong water currents and strong winds (Ward 1962; Bandeira 1995, 2002).

1.1.3 Ecological services provided by, economic value of, and threats faced by, the seagrass biome

Despite there being relatively few seagrass species, the complex physical structure and high productivity of these ecosystems sustain an extensive diversity and biomass of associated species (Leliaert *et al.* 2001; Green & Short 2003). They carry out fundamental physical functions, such as stabilizing bottom sediment and serving as effective hydrodynamic barriers (Dauby & Poulicek 1995; Van Elven *et al.* 2004; Corlett & Jones 2007). They offer habitat and nursery areas to inhabitants of the larger ocean and are also a direct and indirect food source for many animals, and are important substrata for attachment of epiphytes (Coppejans *et al.* 1992; Costanza *et al.* 1997; Gullström *et al.* 2002; Vizzini *et al.* 2002; Lavery & Vanderklift 2002; Green & Short 2003; Pardi *et al.* 2006; Larkum *et al.* 2006; Corlett & Jones 2007; Balata *et al.* 2007; Burfeind *et al.* 2009).

Seagrass systems are characterised by high biodiversity, contributed largely by epiphyte assemblages living on them (Moncreiff *et al.* 1992; Nelson & Waaland 1997; Saunders *et al.* 2003; Van Elven *et al.* 2004). They have been considered one of the most important shallow-marine ecosystems for humans since they play a fundamental role in fishery production (Green & Short 2003) and are responsible for approximately 15% of total carbon storage in the ocean (Kennedy & Björk 2009).

Seagrasses provide fundamental ecosystem services, including an estimated \$1.9 trillion per year in the form of nutrient cycling, an enrichment of coral reef fish productivity, a habitat for thousands of fish, birds, invertebrate species, and a key food source for endangered dugong, manatee, and green turtle (Waycott *et al.* 2009). When seagrasses are damaged, restoration is expensive and uncertain, and many of the lost ecological services are not adequately restored (Fonseca *et al.* 2000, 2002).

It often appears that declines in seagrass meadows have resulted not from individual threats but a combination of impacts. Classic collective impacts may include increased nutrient loads, higher turbidity and direct mechanical damage. Seagrasses exist at the land-sea margin and are therefore exceedingly vulnerable to the world's ever-increasing human populations which live disproportionately along the coasts (Green & Short 2003; Orth *et al.* 2006).

Short *et al.* (2008) noted that *Thalassodendron ciliatum* is slow to colonise new areas and therefore does not easily recover in areas from which it has been removed. This seagrass is notably vulnerable to grazing, particularly by outbreaks of urchins (Klump *et al.* 1993, Alcoverro & Mariani 2002), and in Zanzibar (Tanzania) removal of seagrass beds for seaweed farming is a threat (Eklöf *et al.* 2006). Nordlund *et al.* (2010) in a study in Zanzibar, Tanzania showed how invertebrate harvesting altered species composition and local livelihood by altering the East African social-ecological seagrass system balance. This demonstrates that seagrass losses have direct and indirect effects, some of which often go unnoticed. Seagrasses are ecologically threatened: perhaps species do not appear on red

lists of endangered organisms but as a habitat, an ecological entity, or a system, seagrasses are at risk of great losses in the future (Waycott *et al.* 2009).

1.1.4 Research on seagrasses

Seagrass ecosystem understanding has primarily been based upon site-specific studies, typically conducted in and by developed nations. Seagrass distribution is poorly documented and the value of seagrasses in maintaining regional and global productivity, resources and biodiversity requires further research. Seagrasses are rarely included in coastal management strategies and an understanding of seagrass ecosystems is necessary to safeguard this precious global resource (Green & Short 2003). Seagrass research in South Africa, and globally has increased rapidly over the past few decades.

Little is known of southern seagrass populations, their algal epiphytes, and their biogeographic extent in South Africa. The majority of South African seagrass research has focussed on the dominant local seagrass, eelgrass (*Zostera capensis*: e.g. Adams and Bate 1994; Wortmann *et al.* 1997; Siebert and Branch 2005a, 2005b; Bornman *et al.* 2008; Cyrus *et al.* 2008; Pillay *et al.* 2010), which grows in estuaries and sheltered marine bays. Recent seagrass research in South Africa includes an investigation into ecosystem change in a South African marine reserve (1960-2009) investigating the role of seagrass loss and anthropogenic disturbance (Pillay *et al.* 2010), a study on the impact of the intrusion of beach-disposed dredger spoil into the Mhlathuze Estuary, South Africa, on *Zostera capensis* (Cyrus *et al.* 2008), and comparisons between the macrobenthic assemblage structure in cool-temperate intertidal dwarf eelgrass, looking at *Zostera capensis* (as *Nanozostera capensis*) in the Knysna lagoon (Barnes & Farnon Ellwood 2011).

1.2 The genus *Thalassodendron*

Thalassodendron (den Hartog 1970) is a genus of seagrasses in the family *Cymodoceaceae*, order *Alismatales*. The family *Cymodoceaceae* includes five seagrass genera (*Amphibolis*, *Cymodocea*, *Halodule*, *Syringodium*, and *Thalassodendron*). There are two species in the genus *Thalassodendron*, namely *T. ciliatum* and *T. pachyrhizum*. *T. ciliatum* (formerly *Cymodocea ciliata* (Forsk.) Ehrenb. ex Aschers) is widely distributed in the tropical

Indo-West Pacific. This species occurs on the coasts of Egypt, Eritrea, Kenya, Madagascar, Mozambique, South Africa and Tanzania. It has also been recorded in Indonesia, Malaysia, Queensland Australia, the Federated States of Micronesia and the Solomon Islands (Guiry & Guiry 2012). *T. ciliatum* primarily occurs in shallow bays and estuaries, but also on rocky outcrops and coral reefs, where it is exposed to air, swells and waves. The other species, *T. pachyrhizum*, is restricted to the temperate south-western region of Western Australia, where it occurs on open ocean reefs, exposed to swells and waves (den Hartog & Kuo 2006).

Hyde & Wursten (2011) describe *Thalassodendron ciliatum* as being a “dioecious, robust, woody, sympodial rhizomatous, submerged, marine perennial herb, with short erect stems” (for photographs of the species *in situ*, see Figures 2.2 in Chapter 2). Stems are described as being typically unbranched, bearing 6-8 leaves arising at intervals of 4 internodes. Leaves are clasped in a sheath and are linear and parallel-veined. The leaf margin is commonly serrate, with a rounded apex. Flowers are solitary, terminal and enclosed by 3-4 leafy bracts. Fruits consist of a single ovary and a fleshy bract, with germination typically occurring viviparously. The seedlings develop still attached to the mother plant and the dispersal range, which relies on currents distributing the viviparous seedlings is considerable (details follow in section 1.4).

1.3 Taxonomy and biogeographic distribution of *Thalassodendron ciliatum*

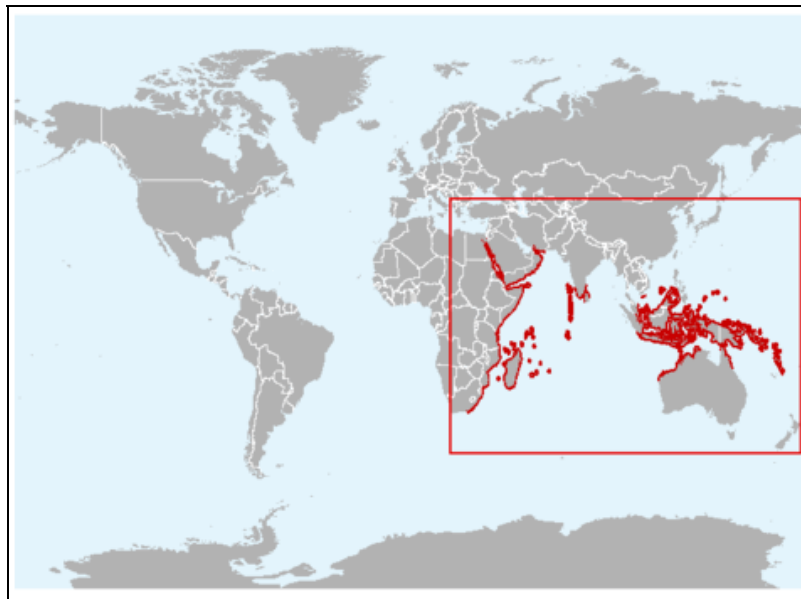


Figure 1: Global distribution of *Thalassodendron ciliatum* (Short *et al.* 2008).

Thalassodendron ciliatum reaches its southwestern limit on the east coast of southern Africa. It is very common on east African coasts, where populations appear to be stable. It is not well studied outside of this region. The distribution of *Thalassodendron ciliatum* on the South African coast was mapped by Ward (1962), who found this species to be restricted to rocky shores along the coast of northern KwaZulu-Natal in the intertidal and shallow subtidal. Patches of seagrass populations were recorded in Sodwana Bay and further northward. However, interestingly *T. ciliatum* was rare further south, with only a single small population recorded in Maphelane, approximately 100 km south of Sodwana Bay.

In Kenya *Thalassodendron ciliatum* generally grows from just below the low water mark down to approximately 10 m depth. It is characterised there by lignified stems up to 70 cm long and terminal tufts of 3-10 distichously placed, recurved, strap-like leaves. The stems are generally densely covered by a diverse array of algal and faunal epiphytes, and the leaves form a good substrate for non-geniculate (encrusting) coralline red algae but tend to be less suitable for other epiphytes (Leliaert *et al.* 2001).

Thalassodendron ciliatum (along with *Thalassia hemprichii*) is the most dominant subtidal seagrass in Mozambique in sheltered lagoons. In Mozambique and on the north-east coast of South Africa *T. ciliatum* also grows commonly on open rocky habitats together with seaweeds. *T. ciliatum* is also the predominant seagrass species in Kenya and Tanzania. Short *et al.* (2008) noted it is typically found at depths from 0-15 m, but has been found down to 33 m in the Seychelles. At higher latitudes plants tend to be shorter and to occur at lower densities. In deeper waters, this often dominant species forms dense mono-specific meadows.

1.4 Epiphytes on *Thalassodendron ciliatum*

Seagrass epiphytes may contribute significantly to the total primary production of their ecological systems (Morgan & Kitting 1984; Moncreiff *et al.* 1992; Nelson & Waaland 1997; Pardi *et al.* 2006) and are typically a major food supply for associated fauna, and via detrital food webs, often distribute energy to adjacent systems.

Seagrasses are ideal substrates and are commonly colonised by a wide variety of epiphytes that play fundamental, complex and dynamic roles in seagrass ecosystems. The epiphytic organisms found on seagrasses depend upon the life-span of the leaves, stems and rhizomes of seagrass and are influenced by seagrass species type, habitat, season and range (Borowitzka *et al.* 2006). The species composition and relative abundance of algal epiphytes is determined by environmental conditions (Kendrick *et al.* 1988; Borowitzka & Lethbridge 1990; Kendrick & Burt 1997). South and Whittick (1987) suggest that many epiphyte species are equally likely to be found on adjacent inorganic substrates and show no particular specificity or affiliation with the seagrass host.

Research on *Thalassodendron ciliatum* and other seagrass ecosystems and epiphytes has been conducted along the East African coast in Kenya (e.g. Coppejans *et al.* 1992); Tanzania (e.g. Leliaert *et al.* 2001); and Mozambique (e.g. Bandeira 2002).

Coppejans *et al.* (1992) studied and recognized a zonation pattern of seagrass and seaweed epiphytes on *Thalassodendron ciliatum* in Gazi Bay (Kenya). This study found that

homogeneous, monospecific meadows of *T. ciliatum* covered large areas of the lagoon from -1 m downward, locally replaced by *Enhalus acoroides*. The leaves and stems of *T. ciliatum* were found to be richly covered by epiphytic algae.

Leliaert *et al.* (2001) studied algal epiphytes on *Thalassodendron ciliatum* in Zanzibar Island (Tanzania) and found that up to 50% of total above-sediment biomass of a seagrass meadow comprised of epiphytes. This study found that epiphyte affinity for certain host plants was primarily linked to the ecological parameters of the host habitat (e.g. depth and tidal level) and also found that epiphytes were better established on perennial stems rather than on ephemeral leaves.

Bandeira (2002) reported that in southern Mozambique *Thalassodendron ciliatum* seaweed epiphytes in rocky areas corresponded to 47.9% of the total seagrass biomass but only 4.7% in sandy habitats. This study found that growth rate dynamics of *T. ciliatum* differed significantly between plants in rocky and sandy habitats.

To our knowledge the only information on macroalgal epiphytes of *Thalassodendron ciliatum* in South Africa are a description of the epiphytic coralline red algae *Pneophyllum amplexifrons* (Chamberlain & Norris 1994) and a picture and a note on the same species in De Clerck *et al.*'s KwaZulu-Natal seaweed guide (2005).

1.5 Background to the current study

Maputaland shores, in the extreme northeast of South Africa, are unique coastal ecosystems and are home to the southern-most coral systems in the Indian Ocean, supporting a diverse array of marine communities (Ramsay & Mason 1990; Riegl *et al.* 1995; Glassom *et al.* 2006). This is a region proposed as being a biogeographical overlap between tropical Indo-Pacific and temperate southern African marine provinces (Bolton *et al.* 2004; Sink *et al.* 2005). The current study investigated an aspect of this ecosystem (the southernmost distribution of *Thalassodendron ciliatum* in the western Indian Ocean). This distinctive region is unique not only from the point of view of its marine biogeographical affinities but also because it is home to a population of the ancient coelacanths, found in deep canyons

off the shores of northern KwaZulu-Natal (Venter *et al.* 2000). Knowledge of southern seagrass populations and their algal epiphytes is very limited. Such information can help to understand the effects of climate change, since species occurring close to biogeographic boundaries will be those primarily affected.

There are many theories on marine biodiversity, for example, latitudinal species-diversity gradients have been proposed. However, empirical evidence is limited and remains uncertain (Grassle *et al.* 1990). Therefore, patterns should be considered as working hypotheses rather than established generalisations (Santelices *et al.* 2009). Particular communities of species characterise each ecosystem and can disclose specific ecological parameters influencing a particular system. It is important to know what species are present in a system and what their biogeographical ranges are in order to understand how a system functions, and the patterns and processes that exist within and around it. Knowing distributional ranges and community composition can allow the monitoring of ecosystem responses to the impacts of natural and anthropogenic change. These changes can result in ecosystem alterations at different spatial and temporal scales. Biogeographical classifications are important for developing ecologically representative systems of protected areas, as required by international agreements (Spalding *et al.* 2007; Anderson *et al.* 2009).

Where does the energy come from that drives the ecosystem in the canyons where the coelacanths live? Stable isotopes, particularly carbon, are being widely used to determine which autotrophs supply energy to food webs (Melville & Connolly 2005). Evidence from isotope studies has indicated that marine animals in systems, such as Jesser Canyon off Sodwana Bay in the extreme northeast of South Africa, where the coelacanths have been found, live on prey that obtains its energy ultimately from intertidal seaweeds and seagrasses (Kaehler *et al.* 2006; Porter 2009). The current study therefore investigates one of the primary producers in an ecosystem supporting high biodiversity and the iconic coelacanths of the region. By gaining knowledge on *T. ciliatum* and its associated flora along the South African north eastern coastline, we may better understand the base of the energy supply being made available to adjacent habitats such as the Jesser Canyon.

1.6 Reproduction and life history of *Thalassodendron ciliatum*

Seagrasses are largely rhizomatous or clonal groups and so the role of sexual reproduction remains somewhat uncertain, although it does exist. Seagrasses can reproduce sexually or asexually through detached or drifting rhizome fragments, although the latter process seems to be rare. Sexual reproduction of seagrasses differs from terrestrial angiosperms with respect to the frequency of dioecious species and the dispersal processes (Hemminga & Duarte 2000). According to Kendrick *et al.* (2012), reproduction in seagrasses may be more important than previously thought, because new evidence indicates gene flow among disjunct populations even hundreds of kilometers apart.

Flowering or fruits have never been reported in *T. ciliatum* growing on rocks in southern Mozambique and *T. ciliatum*, like most seagrasses, demonstrates primarily vegetative growth through its rhizomes (Bandeira & Nilsson 2001). *T. ciliatum* shows an unusual degree of vivipary (produce seeds that germinate before they detach from the parent plant) and it may be assumed that the dispersal range of *T. ciliatum* is therefore limited, with young plants settling in the same areas as their parents.

The flowers of seagrasses in general, as in *T. ciliatum*, are typically much reduced as a result both of their evolutionary origin and specialized nature for submerged abiotic pollination (Ackerman 2006). Most arguments suggest that the low rate of sexual reproduction and the low-range dispersion, coupled with hydrophilous pollination of most seagrasses, have restricted their gene flow, lowering seagrass genetic diversity compared with their terrestrial counterparts (Hemminga & Duarte 2000). However, Kendrick *et al.* (2012) showed that dispersal of seagrasses is far more effective than previously thought? They also noted that seagrass pollen is among the largest for all angiosperms and is modified in terms of shape, buoyancy and size, for water pollination.

A study conducted in Kenya found that the flowering of *T. ciliatum* coincides with very low spring tide (Cox 1991) and staminate plants discharge their flowers under water instantaneously before low tide begins to return. These float to the surface and there release filamentous pollen. The pollen forms floating snowflake-like rafts that collide on the water

surface with female stigmas, with pollination occurring on the surface of the water, noticeably similar to that of *Amphibolis*. Seeds of developing fruit germinate precociously (blossoming before the appearance of leaves) and seedling development is viviparous (producing seeds that germinate on the plant).

Flowering of *T. ciliatum* is both spatially and temporally variable resulting in variability in the occurrence of seedlings (Kamermans *et al.* 2001). Pollen dehiscence occurs on the plant or immediately after anthers detach (Kuo & Kirkman 1987), and it would seem that pollen transport and capture involves within- and below- canopy flow and the interaction of filiform pollen with the local flow environment around female shoots and extended stigmas (e.g. Okubo *et al.* 2002). Dispersal appears to be controlled and seedlings typically take root in their parent's habitat. If the bract breaks off the parent plant prior to complete germination, it floats and currents may carry the seedling further afield (de Koning *et al.* 1995). Detailed studies on the dispersal of *T. ciliatum* are lacking in the primary literature.

1.7 Factors affecting the growth of seagrass, focusing on *Thalassodendron ciliatum*

Seagrasses possess the same primary requirements for growth as all plants: light, inorganic carbon and nutrients - all of which are commonly limited in some way or another (Hemminga and Duarte 2000; Larkum *et al.* 2006). It is thus not unexpected that seagrass growth is frequently suboptimal due to resource limitation.

It is suggested that oceanographic fronts can act as boundaries between seagrass floras by imposing sharp changes in growth conditions, such as water temperature, salinity and nutrient availability (Hemminga & Duarte 2000). Suitable substrate is necessary for seagrasses to occur in a given locality. The majority of seagrass species are restricted to sandy and muddy sediments, although some, such as *Thalassodendron ciliatum*, can grow on rock. Species capable of colonizing and surviving on rocky substrata are characterised by sturdy roots, which penetrate into the crevices of the underlying rocks, effectively anchoring the plants (Hemminga & Duarte 2000). According to Hemminga & Duarte (2000) *Phyllospadix* spp. form dense stands over rocky shelves on the Pacific coast (den Hartog 1970). Other species able to grow over rock include *Posidonia oceanica* and

Thalassodendron spp. *T. ciliatum* grows in a range of habitats from rocky outcrops, where they are exposed to air during low spring tides and to strong swell and wave action, as well as in sheltered estuaries, lagoons and bays.

Duarte (1991) identified the minimum light requirement for seagrasses in the general sense as 10-20% of surface light. This is higher than other marine plants, perhaps due to the high photosynthetic requirement to thrive in anoxic sediments (Short *et al.* 2001). Different species of seagrass have varying light requirements, influencing their depth of distribution (Hemminga and Duarte 2000). *Thalassodendron ciliatum* requires relatively low levels of light. Titlyanov *et al.* (1992) reported from their studies in the Seychelles that the light intensity for saturation of photosynthesis in *T. ciliatum* is 30-50 $\mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. In western Australia *T. pachyrhizum* occurs as a minor species on wave swept subtidal reefs from 5 m to offshore reefs exposed to the force of the Indian Ocean swells from 25 m to >60 m depths. Light compensation levels for this species differ markedly from seagrasses in general. Similarly it is likely that *T. ciliatum* too differs from seagrasses in general, however, little is known regarding the light requirements and compensation levels of *T. ciliatum*. The multifaceted biofilms formed by epiphytic growth of microalgae can create physical barriers to light absorption, gas exchange and nutrient uptake by seagrasses (Zimmerman 2006).

Short *et al.* (2001) found that individual species of seagrass have different thermal tolerances and optimal temperatures for photosynthesis, respiration and growth. Temperature also affects seagrass distribution through effects on flowering and seed germination. A study conducted by Titlyanov *et al.* (1992) in the Seychelles found that the optimum temperature for oxygen exchange, carbon assimilation and primary production in *Thalassodendron ciliatum* blades was 28-30°C.

Long-term observations on seagrass ecosystems are limited and therefore the effect of climate change over longer time scales is not well documented. It has been suggested that expansion and regression of seagrass systems may follow climate changes and it is feasible that widespread distributional changes may result from global change phenomena. The

impacts of climate change are difficult to pinpoint and investigate with certainty, although they will no doubt influence seagrasses. Higher temperatures will alter seagrass growth rates and other physiological functions, shift distributions, and alter sexual reproductive patterns. Changes in tidal variation, water depths and water movement will also increase, along with frequency and intensity of storm events. All these factors will affect seagrass distribution and may influence changes in salinity, affecting seed germination, propagule formation, photosynthesis, growth and biomass. Losses may result from increased diseases, increases in water motion and tidal circulation. These factors may reduce irradiance and enhance turbidity in seagrass systems or may promote epiphytic growth (Short *et al.* 2001).

1.8 Aims, motivation and significance of the current study

While the subtidal turf algal communities have previously been investigated in Sodwana Bay (Anderson *et al.* 2005), *Thalassodendron ciliatum* and its epiphytes have not been studied. Nothing is known about the biogeography and ecology of this seagrass and its macroalgal epiphytes in South Africa, other than that they exist (De Clerck *et al.* 2005). *T. ciliatum*'s distribution was documented in an article in *The Lammergeyer* by Ward (1962), a publication that is not easily available, even in South Africa. The current study goes beyond what Ward reported and investigates the ecology and biogeography of the epiphytes associated with *T. ciliatum* at the southern extreme of its distribution in the western Indian Ocean.

This study aimed to answer the following questions:

1 Distribution and population structure:

1.1 What is the distribution of *Thalassodendron ciliatum* in South Africa?

1.2 Does seagrass height and/or density differ in different habitats (subtidal seagrass meadows, meadows exposed during low spring tide, and permanent intertidal pools) or between Sodwana Bay and Maphelane?

1.3 Does the biomass of seagrass differ temporally (between autumn and spring), in different habitats on the shore (subtidal seagrass meadows, meadows exposed during low spring tide, and permanent intertidal pools), or between Sodwana Bay and Maphelane?

2 Epiphyte diversity and ecology:

- 2.1 Which seaweed epiphytes are found on *Thalassodendron ciliatum*? (A special section will deal with the important non-geniculate coralline red algae in detail).
- 2.2 Do these epiphytes differ temporally (between autumn and spring)?
- 2.3 What are the most common/abundant epiphytic taxa on the *Thalassodendron ciliatum*?
- 2.4 Do algal epiphytes differ between the three colonised habitats on the shore (subtidal seagrass meadows, meadows exposed during low spring tide, and permanent intertidal pools)?
- 2.5 What are the colonisation patterns of epiphytes on South African *T. ciliatum*?

3 Seaweed biogeography:

- 3.1 What are the biogeographical distributional ranges of KwaZulu-Natal intertidal and shallow subtidal seaweeds?
- 3.2 Is the region from the South Africa/Mozambique border to the southernmost extent of the seagrass a crossover region between temperate and tropical algal epiphytes found on *T. ciliatum*, as Bolton *et al.* (2004) found with seaweeds in general?

Chapter 2 deals with the population structure of the seagrass *Thalassodendron ciliatum* and its associated seaweed epiphytes. Within this chapter seagrass biomass, density and height are analysed and the diversity, biomass and abundance of epiphytic species are investigated.

Chapter 3 examines the biogeography of the seaweed species of KwaZulu-Natal in general, and in particular those that grow epiphytically on the seagrass *Thalassodendron ciliatum* in South Africa.

Chapter 4 examines the non-geniculate coralline red algae that grow epiphytically on the South African *Thalassodendron ciliatum*, with a taxonomic approach.

Chapter 5 concludes this dissertation with a discussion and synthesis of all findings covered in Chapters 2-4, reviewing key results and evaluating how the findings improve understanding of South African seagrass systems. It also proposes potential areas of interest for future research.

University of Cape Town

Chapter 2

**Population Structure of the seagrass, *Thalassodendron ciliatum* (Forsskål)
den Hartog and diversity of its associated seaweed epiphytes at the
southern extreme of its distribution in the western Indian Ocean**

2.1 Introduction

Stands of the seagrass *Thalassodendron ciliatum* occur in the intertidal and shallow subtidal waters along the north eastern rocky shores of KwaZulu-Natal, South Africa. Unlike most other seagrasses, *T. ciliatum* has lignified upright stems, as well as terminal leaf clusters and these provide excellent substrata for many epiphytic macroalgae in rocky habitats.

Thalassodendron ciliatum (Forsskål) den Hartog (Cymodoceaceae) (formerly known as *Cymodocea ciliata* (Forsk.) Ehrenb. Ex Aschers) is dioecious and is characterised by having stout, woody rhizomes, 5-10 mm in diameter, with several wiry branching roots arising from each node. Woody branches are erect when supported by water and may grow to 30-40 cm in height at Inhaca Island, Mozambique, whereas in sheltered bays on the east coast of Africa, such as Nacala Bay in Mozambique and Turtle Bay in Kenya, they reach over a meter in height (de Koning *et al.* 1995). Five to seven strap-like leaves cluster at branch ends. Older leaves are shed leaving conspicuous annular scars. Each leaf has a fan-shaped sheath at its base, with older leaves enclosing younger ones. The upper part of the leaf margin is serrated. Male and female flowers occur in the summer months, below the terminal leaf tufts on separate groups of plants (de Koning *et al.* 1995).

It is rare for seagrasses to occur on rocky substrata as they are typically restricted to sheltered bays and/or estuaries and usually to sandy or muddy substrata. However in southern Mozambique and South Africa *Thalassodendron ciliatum* is commonly observed in exposed rocky habitats, where it is prone to strong swells and winds (Ward 1962; den Hartog 1970; Barnabas 1982; 1991; Bandeira 1995; de Koning *et al.* 1995; Bandeira 2002).

Seagrass meadows are highly productive ecosystems in which epiphytes on the seagrasses are an important component (Heijs 1984; 1985; Borowitzka *et al.* 1990; Leliaert *et al.* 2001). Epiphytes play a fundamental role in seagrass ecosystems by contributing to biomass, production and biotic diversity: they are fundamental food and shelter resources for many fishes and invertebrates. There is literature on microalgae (diatoms etc.) which

grow on seagrass (examples include: Uku *et al.* 2007; Gordon *et al.* 2008). Nevertheless macroalgal epiphytes on seagrass remain poorly studied.

The current study is focused on the seagrass *Thalassodendron ciliatum* and its associated macroalgal epiphytes. Samples came from the intertidal and shallow subtidal at Jesser Point (Sodwana Bay) and Maphelane, KwaZulu-Natal, South Africa (Figure 2.1). Jesser Point lies approximately 300 km north-northeast of Durban, South Africa, and 70 km south of Mozambique. Maphelane is approximately 100 km south of Jesser Point. These sites were selected using the distribution of *T. ciliatum* mapped by Ward (1962). This, the only distribution literature on this species in South Africa, indicates that this rocky shore seagrass occurs at Sodwana Bay and further north, as well as at a single outlying population around Maphelane. The seagrass has not been recorded along the approximately 100 km of coast between these two sites. The current study therefore investigates the southern extent of its distributional limit.

It was not previously known that *Thalassodendron ciliatum* occurred as far south as the observed localities in South Africa. Ward (1962) noted that the first record of *T. ciliatum* in South Africa was in the Kosi area as recorded by Robert J. Rodin in 1948. Ward (1962) presented a mapped distribution together with a general description of *T. ciliatum* from his personal sightings in the field. Ward's (1962) and this dissertation are the only known studies on *Thalassodendron ciliatum* in South Africa.

The South African region supporting this southern limit of *Thalassodendron ciliatum* is important in that it includes a biogeographical overlap zone between temperate and tropical waters, and the southernmost coral reef systems in the western Indian Ocean (Reigl *et al.* 1995).

There have been several previous studies of *Thalassodendron ciliatum* on the East African coast. In Gazi Bay, Kenya, Coppejans *et al.* (1992) found *T. ciliatum* to dominate many subtidal and infratidal (lagoon) communities and to occur to 30 m depth, on both sandy and

Chapter 2: Population structure of *T. ciliatum* and diversity of its seaweed epiphytes

rocky substrata. The seagrass bore a rich algal epiphyte flora, and is considered an indicator species recognised as the climax community of the subtidal zone. They determined the general zonation and succession of seagrasses in Gazi Bay.

Leliaert *et al.* (2001) found that in Zanzibar (Tanzania) that average epiphytic cover was 83%, with differences in colonization patterns on different parts of the host seagrass occurring. Their study found epiphyte cover increases with age of the seagrass and is influenced by grazing, presumably by fish. Of the 10 seagrass species sampled, they found *T. ciliatum* to support the highest epiphytic cover, with leaves predominantly covered by crustose coralline algae, and stems by a greater variety of macroalgal epiphytes. Leliaert *et al.* (2001) identified a total of 49 taxa of macroalgae (5 of which were new records for the African East coast) as epiphytes on Zanzibar Island seagrasses and noted that the preference of the epiphytes for certain host plants was primarily linked with ecological parameters of the habitat of the host such as depth and tidal level.

Bandeira (2002) found that in southern Mozambique the growth rate dynamics differed significantly between plants of *Thalassodendron ciliatum* in sandy habitats, with leaf growth rate per shoot generally 100% higher in sandy habitats than in rocky areas. Seaweed epiphytes in rocky areas corresponded to 47.9% of the seagrass biomass while only 4.7% on sand. Plants growing in sandy habitats were observed to have broader and a higher abundance of leaves, while plants in rocky areas were noted as being thinner, with fewer, narrow leaves and they do not bear flowers. Bandeira (2002) found that there were different amounts of various functional-form groups (calcareous articulated algae, calcareous encrusting algae, corticated algae, foliose algae, filamentous algae, and leathery algae) of seaweed epiphytes, while the calcareous articulated algae occurred on *T. ciliatum* on both substrates.

Borowitzka *et al.* (1990) found in Australia that the distribution of epiphytes on the host seagrass *Amphibolis griffithii* is not random but rather related to seagrass height, and therefore age, with different epiphytes occurring on different regions of a host plant. They found epiphyte biomass to increase with seagrass height and the majority of epiphytes to

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occur on the uppermost region of the taller plants in a stand. The stems and leaves provide structurally and temporally different habitats for colonization of epiphytes.

The fundamental aims of this chapter were to investigate the structure of populations of *Thalassodendron ciliatum* and diversity of epiphytic flora at the southern extent of the distribution of the seagrass in the western Indian Ocean. The questions asked were the following:

Do seagrass biomass, height and/or density differ between the two sites sampled?

What is the diversity and biomass of macroalgal epiphytes growing on *T. ciliatum*?

Do these epiphytic assemblages differ between available shore habitats (shallow subtidal, areas exposed during low spring tide and in permanent pools) and/or temporally at Sodwana Bay, or between Sodwana Bay and Maphelane?

Are certain epiphyte species spatially or temporally specific?

Is there a relationship between seagrass length and seaweed epiphyte biomass?

2.2 Materials and Methods

2.2.1 Selection of species and collection sites

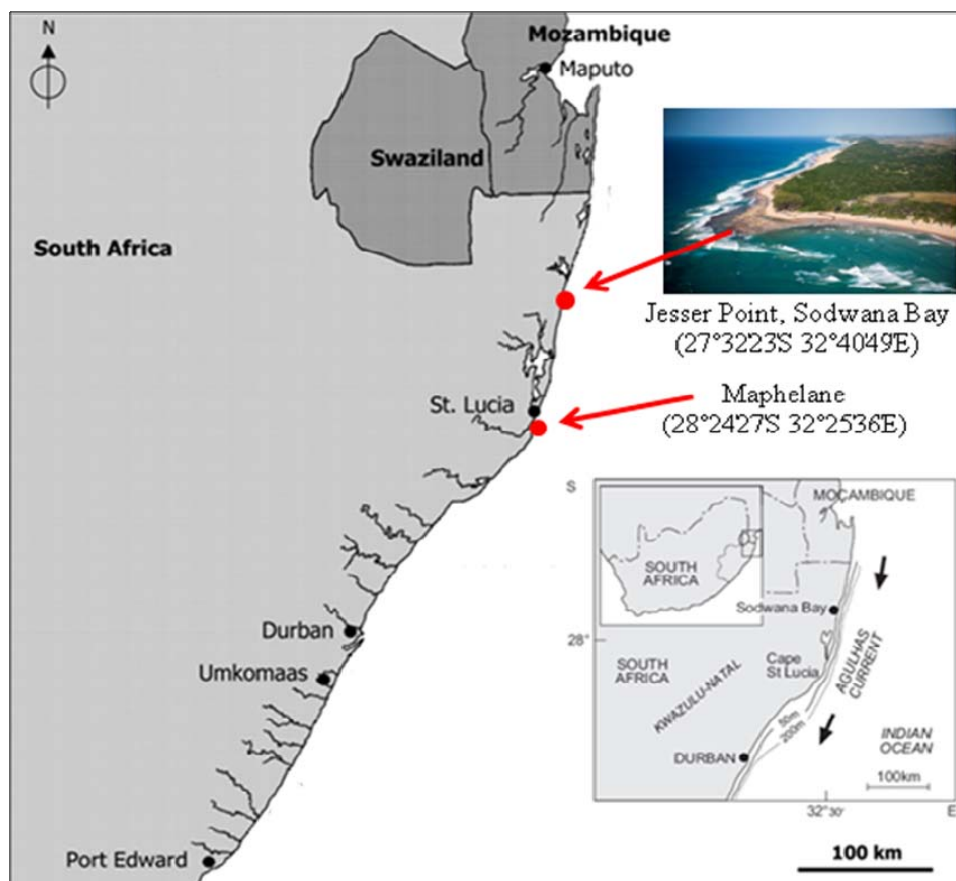


Figure 2.1: Location of sampling sites, Jesser Point and Maphelane, with inset maps of the KwaZulu-Natal coastline, South Africa and photograph of the main sampling site at Jesser Point (Sodwana Bay). (Edited from De Clerck *et al.* 2002; Anderson *et al.* 2005; photograph from www.swimatyourrownrisk.com)

The study sites lie on the coast of northern KwaZulu-Natal (Figure 2.1), a region with a mean annual rainfall of 1000-1100 mm over most of the coast. Summer rainfall dominates and predominant winds are parallel to the coast. The coast in general is very exposed to wave action. Maputaland, the northern region of the KwaZulu-Natal coast lies on a sandy plain extending up the African east coast as far as Somalia. Maputaland has few rivers which gradually drain the vast coastal plain carrying minimal sediment, so that there is negligible terrestrial runoff into the sea. Water temperatures mostly exceed 20°C, and this

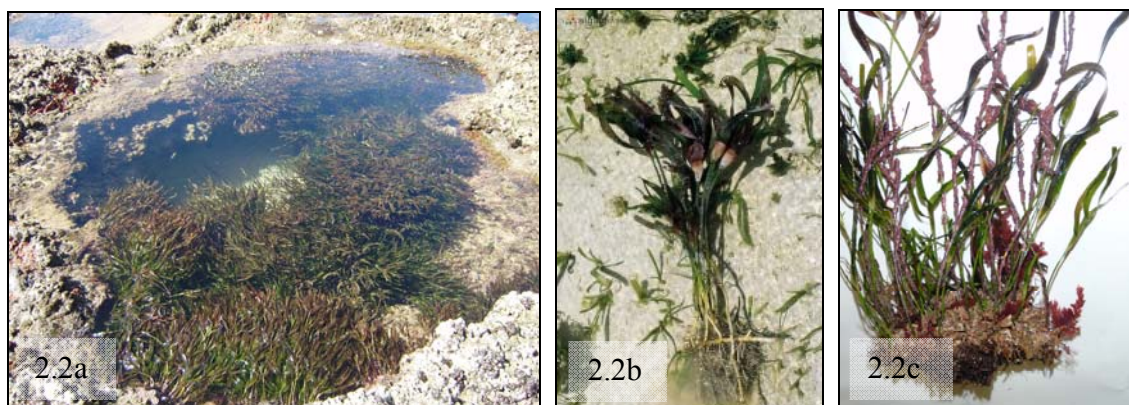
together with the water clarity allows Maputaland to support flourishing coral communities and a highly diverse marine ecosystem (Anderson & Bolton 2005).

The northern KwaZulu-Natal continental shelf is narrow (Ramsay & Mason 1990; Ramsay 1994; Ramsay & Miller 2006): approximately 3 km wide at Sodwana Bay (Ramsay & Mason 1990) compared to the global mean of 75 km wide (Ramsay & Miller 2006), allowing the warm Agulhas Current, the dominant oceanographic feature of this coastline formed by the confluence of surface waters in the Mozambique Channel (Ramsay 1994), to flow close inshore (Ramsay & Mason 1990). The coastline is dominated by high-energy waves and swells from the southeast, which result in a net northward long-shore drift (Ramsay & Mason 1990). Late Pleistocene sediments are present along the northern KwaZulu-Natal coastline in the form of aeolianite/beachrock reef complexes. These consist of carbonate-cemented dune or beach sands, which formed during sea-level low stands during the Pleistocene period (Ramsay & Miller 2006). Many now form marine platforms which are exposed during low tide (Anderson *et al.* 2005), as is the case with Jesser Point, and the rocky outcrops at Maphelane. At Maphelane rocky outcrops are frequently inundated by sand, while the study site at Jesser Point is less sand-affected.

Jesser Point and Maphelane are part of the iSimangaliso Wetland Park (formerly the Greater St. Lucia Wetland Park), a World Heritage Site managed by an independent body known as iSimangaliso Wetland Park Authority. Sodwana Bay is a tropical region, with mean monthly sea temperatures ranging between 21°C and 28°C at a depth of 18 m (Anderson & Bolton 2005; Schleyer *et al.* 2008), and is located within the Indo-West Pacific marine biogeographic realm (Bolton *et al.* 2004; Sink *et al.* 2005; Spalding *et al.* 2007). However, Maphelane, the southernmost location at which *Thalassodendron ciliatum* has been recorded on this coast, lies just south of this tropical area, and within a warm-temperate region (Bolton *et al.* 2004; Sink *et al.* 2005). The mean monthly sea temperature at Maphelane is predicted to range between 21.5°C and 26.5°C (extrapolated, as no data are directly available for Maphelane) (A.J. Smit *pers. comm.* 2010). The two sampling sites are in different biogeographic regions (for biogeographic detail, see Chapter 3). Here ‘tropical’

is defined in a biological sense, where the dominant species in the area have tropical affinities, as used by Bolton *et al.* (2004).

At Sodwana Bay samples were collected from Jesser Point, an approximately 1 km long outcrop of fossilised dune rock, that is relatively flat, with deep permanent pools, raised platforms and gentle slopes encompassing both the intertidal and shallow subtidal zones of the sea shore. The outcrop slopes in a southward direction, where sand cover increases towards the top of the shore. Distances between Jesser Point and other dune rock outcrops are approximately 11 km to the north and 9 km to the south. The outcropping has a relatively shallow slope with large expanses of bare rock and little biodiversity seen along the top of the shore. Raised barnacle platforms are seen approximately halfway down the shore in the mid-eulittoral zone, followed by flatter expanses of rock covered in algal turfs as well as other intertidal organisms such as tubeworms, limpets, reef worms and mussels. Pothole-like pools are found at all heights on the outcrop. Samples were collected from areas where there was relatively little sand, except for around the base of the plants, burying the root system. *Thalassodendron ciliatum* occurs mainly in shallow pools and in crevices, from the intertidal to the shallow subtidal, to depths of approximately 1.5 - 2 m. Seagrass beds are found mostly on the lower shore (below the barnacle platforms), and in pools.



Figures 2.2: (a) Typical rock-pool population of *Thalassodendron ciliatum* in situ Jesser Point (March 2010) (S. Innes), (b) Overview of morphology of *T. ciliatum* plants (Guiry & Guiry 2012), (c) *T. ciliatum* in laboratory illustrating macroalgal epiphyte growth (C. Browne).

2.2.2 Habitats sampled and methods of data collection

The seagrass beds at Sodwana Bay were located on the subtidal fringe (being that part of the extreme low intertidal only exposed at spring low tide and termed as ‘**Exposed**’ in analyses), in shallow subtidal seagrass beds to depths of 2 m (termed ‘**Subtidal**’ in analyses), and in permanent pools (termed ‘**Pools**’ in analyses). Fifteen samples were taken in these habitats during each of two collection trips to Jesser Point (Sodwana Bay) in autumn (March 2010) and spring (September 2010): five replicate samples were collected from each of the three different habitats. Collections were made of the seagrass, its epiphytes, and the sediment below it in 25x25 cm quadrats, scraped to bare rock. Sample quadrats were placed haphazardly. Samples were collected from fairly large seagrass patches in areas that were not inundated by sand, in the different habitats chosen to be investigated. Sample depth (pool depth, where appropriate) and an estimate of seagrass bed size were noted for each sample.

Collecting was done somewhat differently at Maphelane owing to the scarcity of the species and homogeneity of habitat. Seagrass beds that could be identified as separate patches were sampled on 10 October 2010. Ten 25x25 cm quadrats were placed

haphazardly and the seagrass and associated epiphytes collected, scraping samples to bare rock were possible.

Samples were collected at Maphelane from two sites, 7 m apart. Both sites were in gullies on the upper part of the shallow subtidal calcareous sandstone shelf. Since samples were collected from the intertidal/subtidal fringe, and most were exposed to air during low spring tide, the samples were labeled as 'Exposed' for analysis purposes. Depth of water at low tide was up to 20 cm for some samples as the tide starting coming in during collections. Bases of seagrass plants were in sand which was mobile (in that with wave action, much sand transport took place and depth of exposed plant material varied). Wave overwash was frequent, which made collecting from quadrats difficult. *Thalassodendron ciliatum* was much less abundant at Maphelane compared to Jesser Point. Seagrass was not observed at Maphelane during the collection trip for the current study in September 2010 and subsequently R. Ward collected samples for the project in October 2010, from the few localities at Maphelane where he had recorded it before in 1962. More recent checking was carried out during the current project, searches at Mission Rocks, Cape Vidal, and in the drift at St. Lucia. All of these locations lie between the two sampling sites, and *T. ciliatum* has not been observed between the two sites, despite the presence of apparently suitable rocky habitat.

In the field laboratory at Sodwana Bay, each of the samples was rinsed using clean seawater in sorting trays to remove excess sediment and the mesofauna. The mesofauna were collected from the full sample, for a University of Cape Town Zoology Department MSc project by Rebecca Milne. Wet weight of the full seagrass sample was measured using a hand held spring balance and 25% of this wet weight then measured and separated as a subsample. Subsamples were taken due to transport space limitations. Subsamples included different parts of a seagrass plant and where possible included entire uprights. The subsamples were preserved in 5% formalin in seawater, sealed in plastic bags, labeled and stored in the dark to be returned to Cape Town for further analysis. Samples were named based on month sampled, habitat type and replicate number (P: Pools, E: Exposed during low spring tide, S: Subtidal habitats) (e.g. MP1 represents the sample collected from

Sodwana Bay in March from Pool number 1, likewise SP1 represents the sample collected from Sodwana Bay in September from Pool number 1, and OM1.1 represents the sample collected in October from Maphelane, sample number 1.1).

2.2.3 Population structure of *Thalassodendron ciliatum*

The biomass of the seagrass *Thalassodendron ciliatum* was measured as wet weight, to the nearest g., from samples collected from 25x25 cm quadrats. The number of uprights in a sample was determined, to assess the density of a seagrass patch, and the heights of uprights were measured.

2.2.4 Ecology of associated macroalgal epiphytes

In order to assess the diversity of macroalgal epiphytes on *Thalassodendron ciliatum* plants, seagrasses from samples were sorted and epiphyte species put into separate containers. Permanent microscope slides were made of each species for identification and photography. The specimens were identified as accurately as possible using both dissecting and compound microscopes with the aid of field identification guides and available taxonomic literature. Of particular use were Jaasund (1976), Womersley (1987), Stegenga *et al.* (1997), De Clerck *et al.* (2005), Oliveira *et al.* (2005) and many papers on KwaZulu-Natal seaweeds by Norris (as listed in the reference section of Silva *et al.* (1996)). Microscope photographs were taken to develop a visual library (see Appendix). A list of epiphytic taxa identified from leaves and stems was compiled (see Table 2.1). Coralline red algae were also identified using the specific techniques relevant for that group (see Chapter 4 for taxonomic details).

Six uprights of seagrass were randomly selected from each sample for more detailed analysis. The stems and leaves were separated for analysis. The epiphytes were removed by scraping using a scalpel and a pair of forceps. The number of algal epiphytes and their cover were recorded per plant, in relation to the height of each plant measured in cm. Abundances were determined by wet weight recorded to the nearest 0.1 g where feasible or by cover of a stem per taxon. Extremely small and rare species were marked as 'present'.

Chapter 2: Population structure of *T. ciliatum* and diversity of its seaweed epiphytes

Cover was estimated using a scale of 1 to 5 (1= present, 2= rare, 3= common, 4= abundant, 5= dominant), a variation of the Braun-Blanquet cover-abundance scale (Wikum & Shanholtzer 1978). The Braun-Blanquet scale was used because it is not affected by the amount of seagrass in a sample.

2.2.5 Data analyses

Various comparisons were made to determine whether there were temporal or site-related differences in the structure of the seagrass beds sampled at Jesser Point and Maphelane. Parametric Student's t-tests, independent by variables, and non-parametric Wilcoxon matched pairs tests were conducted to determine whether there were significant differences between the averages of measurements of *T. ciliatum* structure. The wet weight (g) of *P. amplexifrons* was measured versus habitat and collections and a one-way Analysis of Variance (ANOVA) and post hoc Tukey HSD test conducted to determine whether there are significant differences between the amounts of this dominant epiphyte between collections and habitat types. These analyses were all conducted using Microsoft Office Excel, and Statistica version 10.0 (StatSoftInc.).

Average linkage Bray-Curtis cluster analyses and Detrended Correspondence Analysis (DECORANA) ordination plots were conducted on all epiphyte abundances per sample for all collections (using Community Analysis Package version 4.0 PISCES Conservation Ltd. 2007). These analyses were also done on data from Sodwana Bay samples alone to determine whether a temporal difference in seaweed epiphytes existed. Analysis of Similarity (ANOSIM) was used on the pre-selected groups tested to establish whether the samples within groups were more similar than would be determined by chance. A Principal Component Analysis (PCA) covariance analysis determined which species were influencing the groups formed between collections and identified influential species.

The percentages of wet weight accounted for by seagrass and epiphytes per collection were graphed and compared with a previous study conducted in Mozambique by Bandeira (2002). Regression analyses were undertaken between seagrass stem length (cm) and

epiphyte wet weight (g) for the three collections made, as well as for the wet weight (g) of the most abundant epiphyte, *Pneophyllum amplexifrons* and upright length (cm).

2.3 Results

The seagrass beds extended to a depth of about 2.5 m below mean low water spring (MLWS, the lowest level to which spring tides retreat on average over a period of time). Stoloniferous bases of plants were denser in some areas than others and were easily removable only from some sites. The depth of pools ranged between 0.3 m and 1 m.

The seagrass beds at Maphelane were located on the low water mark of spring tide and were inundated with sand. The degree of sediment inundation varied between samples and was difficult to measure as sand was washed away by swells during collection.

2.3.1 Population structure of *Thalassodendron ciliatum*

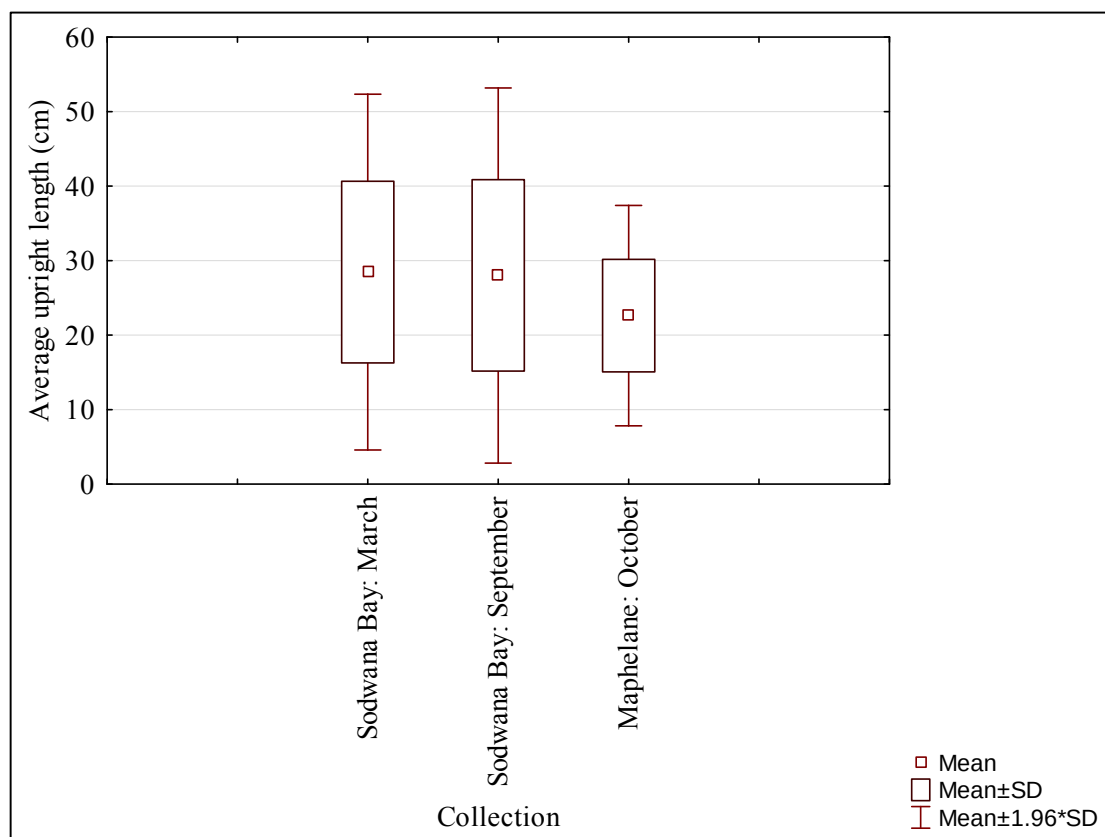


Figure 2.3: Average *Thalassodendron ciliatum* upright length from samples collected from Jesser Point (Sodwana Bay) in March and September 2010, and from Maphelane in October 2010. (Sodwana Bay: March n= 90, Sodwana Bay: September n= 90, Maphelane: October n= 60).

There was no significant difference between the lengths of *T. ciliatum* uprights (Figure 2.3) sampled from Sodwana Bay in March and September 2010 ($t= 0.245$, $df= 178$, $p= 0.807$). A Levene test indicated that variances were homogeneous ($F(1,178)= 0.005$, $p= 0.942$). The lengths of uprights sampled from Maphelane were significantly different from those sampled from Jesser Point in March 2010 ($t= 3.311$, $df= 148$, $p= 0.001$). However, a Levene test showed that the variances in this comparison were not homogeneous ($F(1, 148)= 15.672$, $p= 0.0001$). Therefore the nonparametric Wilcoxon matched pairs test was conducted to compare the upright lengths between these two collections, which found that they were significantly different to one another ($N= 60$, $T= 602.5$, $Z= 2.3$, $p= 0.021$).

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Similarly, the lengths of uprights sampled from Maphelane were significantly different from those sampled from Jesser Point in September 2010 ($t= 2.924$, $df= 148$, $p= 0.003$). However, a Levene test showed that the variances in this comparison were not homogeneous ($F(1, 148)= 13.122$, $p= 0.0004$), therefore the nonparametric Wilcoxon matched pairs test was conducted and found that they were significantly different to one another ($N= 60$, $T= 422.5$, $Z= 3.635$, $p= 0.0002$).

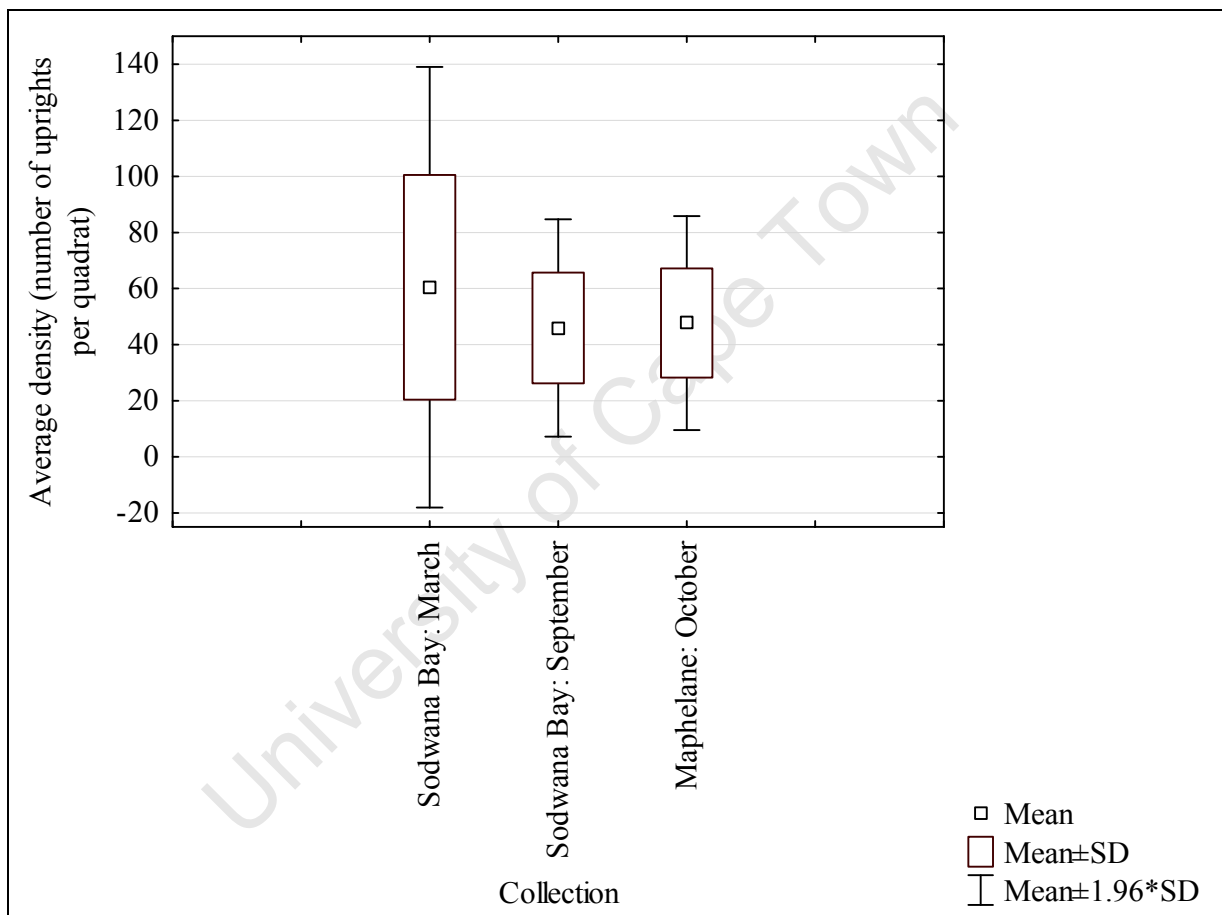


Figure 2.4: Average *Thalassodendron ciliatum* density per 25x25 cm quadrat sampled from Jesser Point (Sodwana Bay) in March and September 2010, and from Maphelane in October 2010. (Sodwana Bay: March $n= 15$, Sodwana Bay: September $n= 15$, Maphelane: October $n= 10$).

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The density of seagrass (Figure 2.4) collected from Sodwana Bay in March and September 2010 did not differ significantly ($t = 1.259$, $df = 28$, $p = 0.218$). A Leven test indicated that the variances were non-homogeneous ($F(1,28) = 4.441$, $p = 0.044$). Therefore the nonparametric Wilcoxon matched pairs test was conducted and indicated that the densities of *T. ciliatum* in these two collections did not to differ significantly from one another ($N = 15$, $T = 41$, $Z = 1.079$, $p = 0.281$).

The density of seagrass patches sampled from Maphelane in October 2010 was also not significantly different from those collected from Sodwana Bay in both March ($t = 0.932$, $df = 23$, $p = 0.361$) and September ($t = 0.220$, $df = 23$, $p = 0.827$) 2010. The variances of the Maphelane and Jesser Point March collections were non-homogeneous ($F(1,23) = 4.015$, $p = 0.057$), and a Wilcoxon matched pairs test indicated that the densities from these two collections did not differ significantly from one another ($N = 10$, $T = 18.5$, $Z = 0.917$, $p = 0.359$). The variances of the Maphelane and Jesser Point September collections were shown to be homogeneous ($F(1,23) = 0.27$, $p = 0.608$).

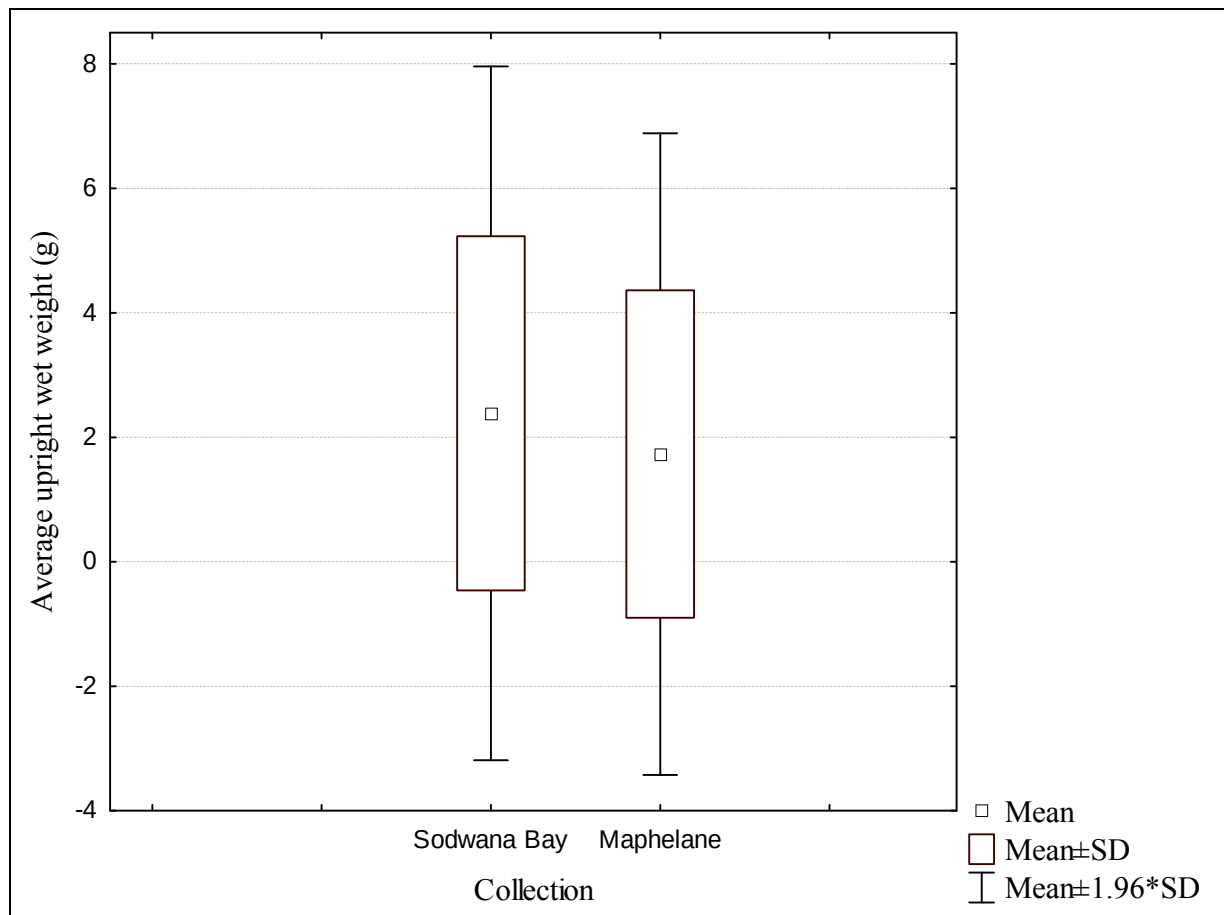


Figure 2.5: Average upright wet weight of 'Exposed' collections from Sodwana Bay in September 2010, and from Maphelane in October 2010. (Sodwana Bay $n=30$, Maphelane $n=60$).

When comparing only the Exposed samples collected from Sodwana Bay in September 2010 to those collected from Maphelane in October 2010 (excluding pool and subtidal samples and a different season), Maphelane did not support a significantly lower average biomass of *T. ciliatum* (1.73 g) than Sodwana Bay (2.39 g) ($t=1.085$; $df=88$; $p=0.281$), and a Levene test showed that variances are homogeneous ($F(1,88)=0.854$, $p=0.358$), (Figure 2.5).

2.3.2 Associated macroalgal epiphytes

Observations suggest that the majority of epiphytes occur on *Thalassodendron ciliatum* stems, with fewer occurring on the leaves. A total of 99 taxa of epiphytic macroalgae were identified on the 240 individual *T. ciliatum* plant uprights sampled. It would appear that most epiphyte diversity was located on the upper stems (>25 taxa of seaweed epiphytes) and different epiphytes were found not only in the different habitats but also on the different parts of the seagrass stems and leaves. The Rhodophyta exceeded the Chlorophyta and Phaeophyceae (Ochrophyta) both in diversity and abundance (Table 2.1, Figures 2.6 and 2.7).

Of the identified seaweed epiphyte taxa, >70, and <50, were observed growing on stems and leaves respectively. It appears that stems tended to support larger seaweeds and hence greater biomass, measured as wet weight, of epiphytes. Stems were notably covered by *Pneophyllum amplexifrons* and *Colaonema gracile*. Taxa that contributed to the greatest epiphyte biomass on stems were *Pneophyllum amplexifrons* and *Jania* spp. *Hydrolithon farinosum* and smaller seaweed taxa (predominantly Ectocarpoid sp.1, *Asterocladon rhodoortonoides* and *Colaonema gracile* in Sodwana Bay, and *Herposiphonia secunda* f. *tenella* and *Polysiphonia coacta* in Maphelane) grew on the leaves, all of which had a wet weight less than 0.1 g on each leaf.

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Table 2.1: List of the taxa identified as seaweed epiphytes growing on *Thalassodendron ciliatum* sampled from Jesser Point (Sodwana Bay) in March 2010 (autumn), as well as in September 2010 (spring) and from Maphelane in October 2010 (spring). 1= present
0= absent

Group/ Taxa	Species	Season/ site/month		
		Autumn	Spring	
		Sodwana Bay: March	Sodwana Bay: September	Maphelane: October
Rhodophyta	<i>Acrosorium acrospermum</i> (J.Agardh) Kylin	1	1	1
	<i>Acrosorium maculatum</i> (Sonder ex Kützing) Papenfuss	0	0	1
	<i>Amphiroa beauvoisii</i> J.V.Lamouroux	1	0	0
	<i>Ceramium</i> <i>centroceratiforme</i> Simons	0	0	1
	<i>Champia parvula</i> (C.Agardh) Harvey	1	1	1
	<i>Chondria armata</i> (Kützing) Okamura	1	1	1
	<i>Chondria collinsiana</i> M.A.Howe	1	0	0
	<i>Colaconema gracile</i> (Børgesen) Ateweberhan & Prud'homme van Reine	1	1	1
	<i>Crouania attenuata</i> (C.Agardh) J.Agardh	1	0	0
	<i>Dichotomaria tenera</i> (Kjeilman) Huisman, T.J.Harper & G.W.Saunders	0	1	0
	<i>Gayliella flaccida</i> (Harvey ex Kützing) T.O.Cho & L.J.McIvor in Cho <i>et al.</i>	0	1	0
	<i>Gayliella taylorii</i> (E.Y.Dawson) T.O.Cho & S.M.Boo in Cho <i>et al.</i>	0	1	0
	<i>Gelidiopsis intricata</i> (C.Agardh) Vickers	1	0	0
	<i>Gloiocladia iyoensis</i> (Okamura) R.E.Norris	0	1	0

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Group/ Taxa	Species	Season/ site/month		
		Autumn	Spring	
		Sodwana Bay: March	Sodwana Bay: September	Maphelane: October
Rhodophyta	<i>Gracilaria cf tuticorinensis</i> V.Krishnamurthy & Rajendran	1	1	0
	<i>Gracilaria corticata</i> (J.Agardh) J.Agardh	0	1	1
	<i>Griffithsia confervoides</i> Suhr	1	1	1
	<i>Griffithsia subbiconica</i> Stegenga	0	1	0
	<i>Herposiphonia secunda f.</i> <i>tenella</i> (C.Argardh) M.J.Wynne	1	1	1
	<i>Hypnea rosea</i> Papenfuss	1	1	1
	<i>Jania intermedia</i> (Kützinger) P.C.Silva	1	0	1
	<i>Jania rosea</i> (Lamarck) Decaisne	0	1	0
	<i>Jania subulata</i> (Ellis & Solander) Sonder	0	1	1
	<i>Kentrophora natalensis</i> (J.Agardh) S.M.Wilson & Kraft in R.J.F.Henderson, S.M.Wilson & Kraft	1	1	1
	<i>Laurencia tenera</i> C.K.Tseng	0	0	1
	<i>Lomentaria amplexans</i> R.E.Norris	1	1	0
	<i>Lomentaria corallicola</i> Børgesen	0	0	1
	<i>Nemastoma gelatinosum</i> M.A.Howe	0	1	0
	<i>Placophora binderi</i> (J.Agardh) J.Agardh	1	0	1
	<i>Platysiphonia delicata</i> (Clemente) Cremades in Cremades & Ferez Cirera	1	1	1
	<i>Pleonosporium caribaeum</i> (Børgesen) R.E.Norris	0	0	1

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Group/ Taxa	Species	Season/ site/month		
		Autumn	Spring	
		Sodwana Bay: March	Sodwana Bay: September	Maphelane: October
Rhodophyta	<i>Pleonosporium filicinum</i> (Harvey ex J.Agardh) De Toni	1	1	0
	<i>Plocamium beckeri</i> F.Schmitz ex Simons	1	1	1
	<i>Plocamium gromeratum</i> J.Agardh	1	1	1
	<i>Plocamium mertensii</i> (Greville) Harvey	1	0	1
	<i>Plocamium suhrrii</i> Kützing	1	1	1
	<i>Plocamium telfairiae</i> (W.J.Hooker & Harvey) Harvey ex Kützing	1	0	0
	<i>Polysiphonia coacta</i> C.K.Tseng	0	1	1
	<i>Polysiphonia urbana</i> Harvey	0	0	1
	<i>Polyzonia elegans</i> Suhr	0	0	1
	<i>Predaea feldmannii</i> Børgesen	1	0	0
	<i>Pterocladia</i> <i>caloglossoides</i> (M.A.Howe) Santelices	0	1	0
	<i>Rhodmelopsis africana</i> M.A.Pocock	0	0	1
	<i>Rhodymenia natalensis</i> Kylin	0	1	0
	<i>Symphyocladia</i> <i>marchantioides</i> (Harvey) Falkenberg in Schmitz & Falkenberg	1	1	0
	<i>Synarthrophyton patena</i> (D.J.Hooker & Harvey) R.A.Townsend	0	1	0
	<i>Tiffaniella schmitziana</i> (E.S.Barton) Bolton & Stegenga	1	1	1

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Group/ Taxa	Species	Season/ site/month		
		Autumn	Spring	
		Sodwana Bay: March	Sodwana Bay: September	Maphelane: October
Rhodophyta	<i>Tricleocarpa fragilis</i> (Linnaeus) Huisman & R.A.Townsend	0	1	0
	<i>Acrochaetium</i> sp.	0	0	1
	<i>Callithamnion</i> sp.1	1	1	1
	<i>Callithamnion</i> sp.2	1	0	0
	<i>Callithamnion</i> / <i>Pleonosporium</i>	0	0	1
	<i>Ceramium</i> sp.	1	1	1
	cf <i>Spermothamnion</i>	0	1	0
	<i>Champia</i> sp.	1	0	0
	<i>Chondria</i> sp.	1	1	0
	<i>Dasya</i> sp.	1	1	1
	<i>Delesseriaceae</i> indet.	0	0	1
	<i>Griffithsia</i> sp.2	1	0	0
	<i>Griffithsia</i> sp.3	1	0	0
	<i>Griffithsia</i> sp.4	1	1	1
	<i>Hypnea</i> cf <i>hamulosa</i>	1	0	0
	<i>Jania</i> sp.	1	1	0
	<i>Laurencia</i> sp.	0	0	1
	Pink blade	1	0	0
	Pink tube	0	1	0
	<i>Solieriaceae</i> indet.	0	1	0
	<i>Solieriaceae</i> indet.2	0	0	1
Phaeophyceae	<i>Asterocladon</i> <i>rhodochortonoides</i> (Børgesen) Uwai, Nagasato, Motomura & Kogame	1	1	0
	<i>Dictyopteris delicatula</i> J.V.Lamouroux	1	1	0
	<i>Dictyota ciliolata</i> Sonder ex Kützinger	0	0	1
	<i>Dictyoteris ligulata</i> (Suhr) O.C.Schmidt	0	1	1
	<i>Ectocarpus siliculosus</i> (Dillwyn) Lyngbye	1	1	0

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Group/ Taxa	Species	Season/ site/month		
		Autumn	Spring	
		Sodwana Bay: March	Sodwana Bay: September	Maphelane: October
Phaeophyceae	<i>Hincksia terminalis</i> (V.Krishnamurthy & Buluswani) P.C.Silva in P.C.Silva, E.G.Meñez & Moe	0	1	1
	<i>Hinksia conifera</i> (Børgesen) I.A. Abbott	0	1	0
	<i>Sphacelaria rigidula</i> Kützinger	0	1	1
	<i>Colpomenia</i> sp.	1	0	0
	Ectocarpoid sp.1	1	1	1
	Ectocarpoid sp.2	1	0	0
	Ectocarpoid sp.3	0	0	1
	Ectocarpoid sp.4	0	0	1
	<i>Caulerpa lentillifera</i> J.G. Agardh	0	1	0
Chlorophyta	<i>Caulerpa scalpelliformis</i> (R.Brown ex Turner) C. Agardh	0	1	0
	<i>Chaetomorpha aerea</i> (Dillwyn) Kützinger	0	1	0
	<i>Chamaedoris delphinii</i> (Harriot) Feldman & Børgesen	0	1	0
	<i>Cladophora herpestica</i> (Montagne) Kützinger	1	0	0
	<i>Cladophora prolifera</i> (Roth) Kützinger	0	1	1
	<i>Cladophora saviniana</i> Børgesen	1	1	1
	<i>Cladophora sibogae</i> Reinbold	0	1	0
	<i>Halimeda cuneata</i> Hering in Krauss	1	1	0
	<i>Pseudocodium de-vriesii</i> Wever-van Bosse	0	1	0
	<i>Valonia fastigiata</i> Harvey ex J. Agardh	1	0	0

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Group/ Taxa	Species	Season/ site/month		
		Autumn	Spring	
		Sodwana Bay: March	Sodwana Bay: September	Maphelane: October
	<i>Ulva cf intestinalis</i>	0	1	1
	<i>Boodlea</i> sp.	1	0	0
	<i>Cladophora</i> sp.1	0	1	1
	<i>Cladophora</i> sp.2	0	1	0
	<i>Ulva</i> sp.	1	1	1
	Unknown green	1	1	0
Cyanobacteria	<i>Cyanobacteria</i> cf <i>Lyngbya</i> sp.	1	1	0
Total number of species	99	52	63	48

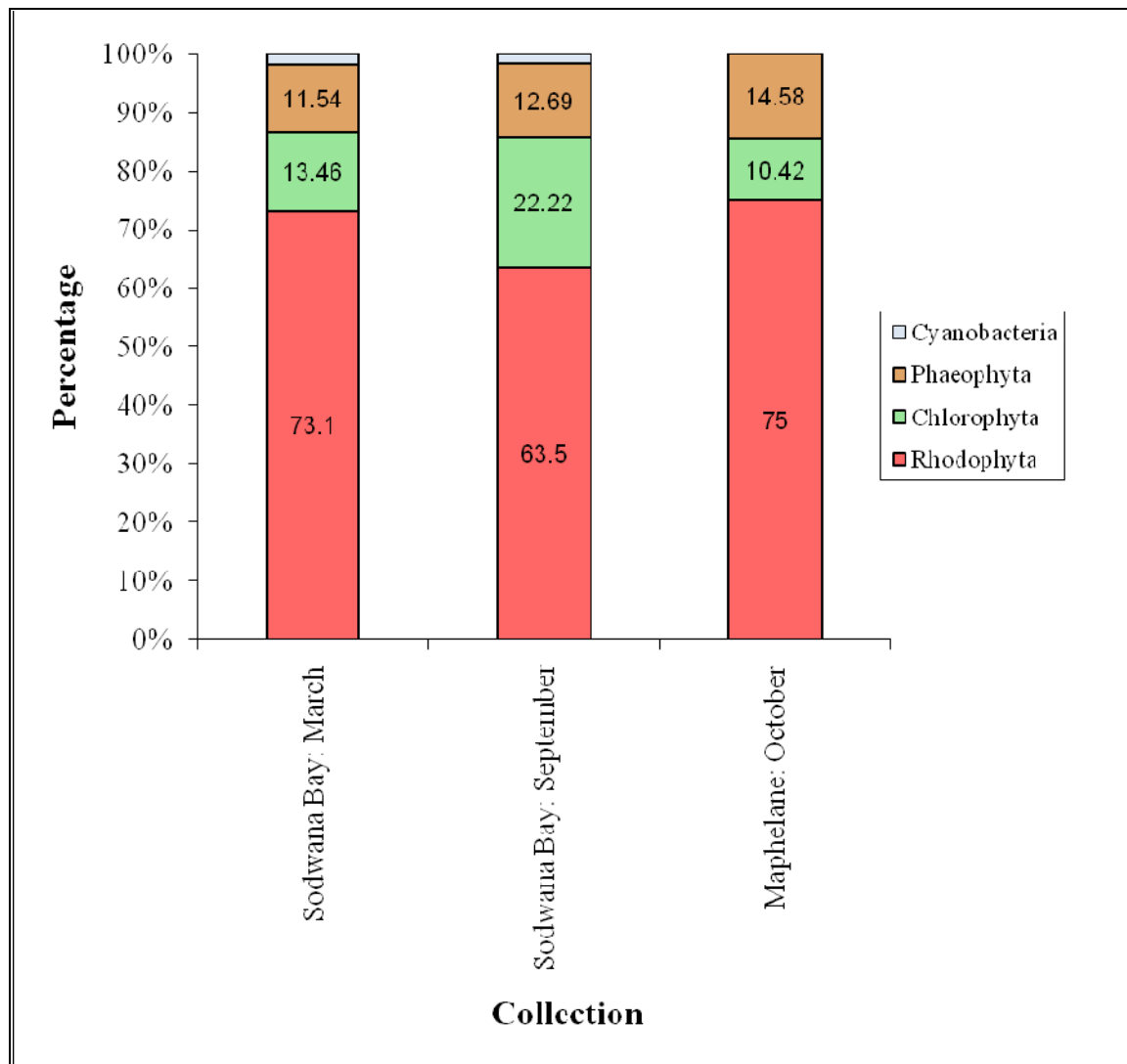


Figure 2.6: Macroalgal epiphyte species (diversity) in different seaweed groups collected from Jesser Point (Sodwana Bay) and Maphelane.

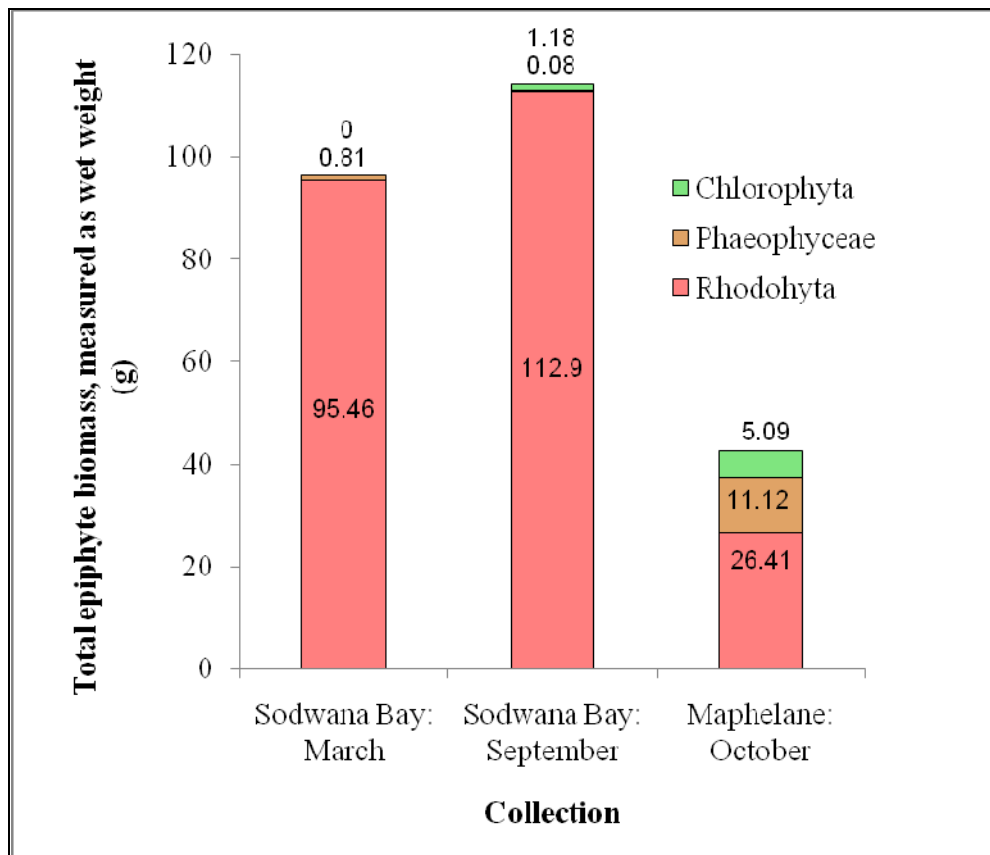


Figure 2.7: Total biomass, measured as wet weight , of macroalgal epiphyte species in different seaweed groups collected from Jesser Point (Sodwana Bay) and Maphelane.

The relative proportions of the seaweed groups identified from each collection are seen in Figures 2.6 and 2.7, illustrating that Rhodophyta are the dominant contributors to the epiphyte flora. This can also be seen in Table 2.1. It is interesting to note that the macroalgal epiphyte weight at Maphelane had very much more Phaeophyceae (Ochrophyta) and Chlorophyta, when compared to samples collected from Sodwana Bay.

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Table 2.2: Average cover, measured by adapted Braun-Blanquet cover-abundance scale, of the most abundant species recorded as epiphytes on *Thalassodendron ciliatum* from collections made from Jesser Point (March and September 2010) and from Maphelane (October 2010).

	Average cover						
Collection	Jesser Point: March 2010			Jesser Point: September 2010			Maphelane: October 2010
Habitat	Pools	Exposed	Subtidal	Pools	Exposed	Subtidal	Exposed
Species							
<i>Pneophyllum amplexifrons</i> (Harvey) Y.M.Chamberlain & R.E.Norris	3.40	2.40	3.20	4.75	4.00	3.60	2.57
<i>Hydrolithon farinosum</i> (J.V.Lamouroux) D.Penrose & Y.M.Chamberlain	2.00	2.25	3.40	4.25	4.20	3.60	2.11
Ectocarpoid sp.1	2.50	1.33	1.67	2.50	2.20	1.00	0.00
<i>Tiffaniella schmitziana</i> (E.S.Barton) Bolton & Stegenga	2.00	1.00	1.00	2.67	0.00	2.00	1.50
<i>Asterocladon rhodochoortonoides</i> (Børgesen) Uwai, Nagasato, Motomura & Kogame	3.00	2.40	1.50	0.00	1.00	1.00	0.00
<i>Colaconema gracile</i> (Børgesen) Ateweberhan & Prud'homme van Reine	1.00	2.00	1.67	1.00	2.00	1.00	0.00
<i>Polysiphonia coacta</i> C.K.Tseng	0.00	0.00	0.00	0.00	0.00	0.00	4.25

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The average cover of the most abundant seaweed epiphyte species (Table 2.2) indicates that *Pneophyllum amplexifrons* and *Hydrolithon farinosum* covered the majority of uprights. Cover of these species was greater at Sodwana Bay compared to Maphelane.

P. amplexifrons cover was observed to be greatest in Pool habitats, and that of *H. farinosum* greatest in Subtidal habitats. The relative cover of *Ectocarpoid* sp.1, *Tiffaniella schmitziana* and *Asterocladon rhodochortonoides* was higher in Pool environments at Sodwana Bay and minimal at Maphelane. *Colaonema gracile* cover of seagrass uprights was greatest in Sodwana Bay Exposed habitats and absent from Maphelane. While the cover of *Polysiphonia coacta* was negligible in Sodwana Bay samples but high in Maphelane samples.

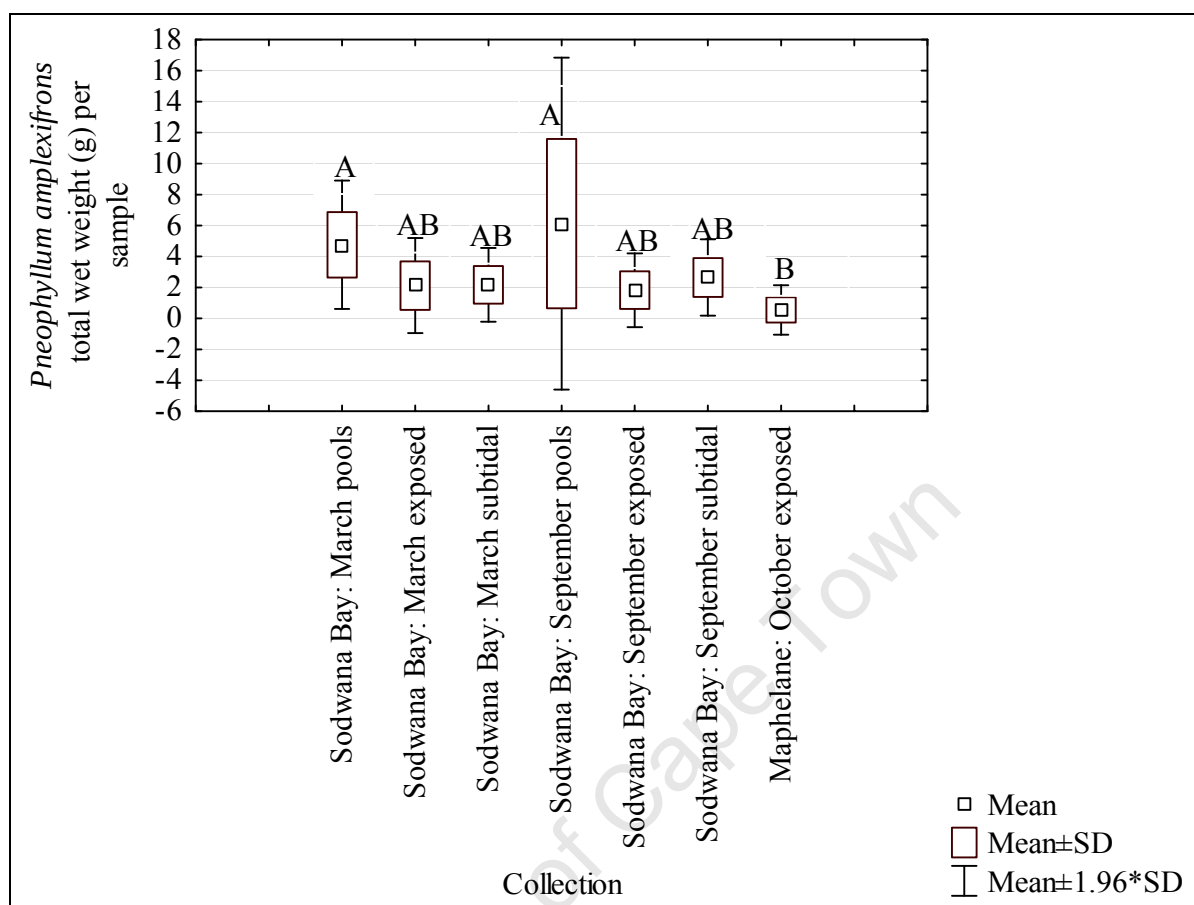


Figure 2.8: Comparison of the total wet weight of *Pneophyllum amplexifrons*, measured as wet weight per sample, between collections from Sodwana Bay in March and September 2010 and from Maphelane in October 2010. Those significantly different from one another are indicated with different letters.

Examination of 240 individual *Thalassodendron ciliatum* uprights studied showed that while most bore the encrusting red coralline alga, *Pneophyllum amplexifrons*, the area of coverage varied (see Table 2.2). The most abundant seaweed epiphyte was identified as being *P. amplexifrons*, however, its wet weight varied between habitats (Figure 2.8). A one-way ANOVA showed that there are significant differences in the total wet weight (g) of *P. amplexifrons* sampled from collections made in different habitats from Jesser Point in March and September 2010 and from Maphelane in October 2010 ($F(6,33)= 4.25$, $p= 0.003$). A post-hoc Tukey HSD test revealed that *Pneophyllum amplexifrons* wet weight

(g) was significantly higher in collections from Sodwana Bay: March Pools (4.752±2.117) compared to collections from Maphelane: October Exposed (0.544±0.813) ($p= 0.288$). Collections from Sodwana Bay: September Pools (6.12±5.472) were also revealed as having significantly higher *P. amplexifrons* wet weight (g) compared to collections from Maphelane: October Exposed (0.544±0.813) ($p= 0.002$).

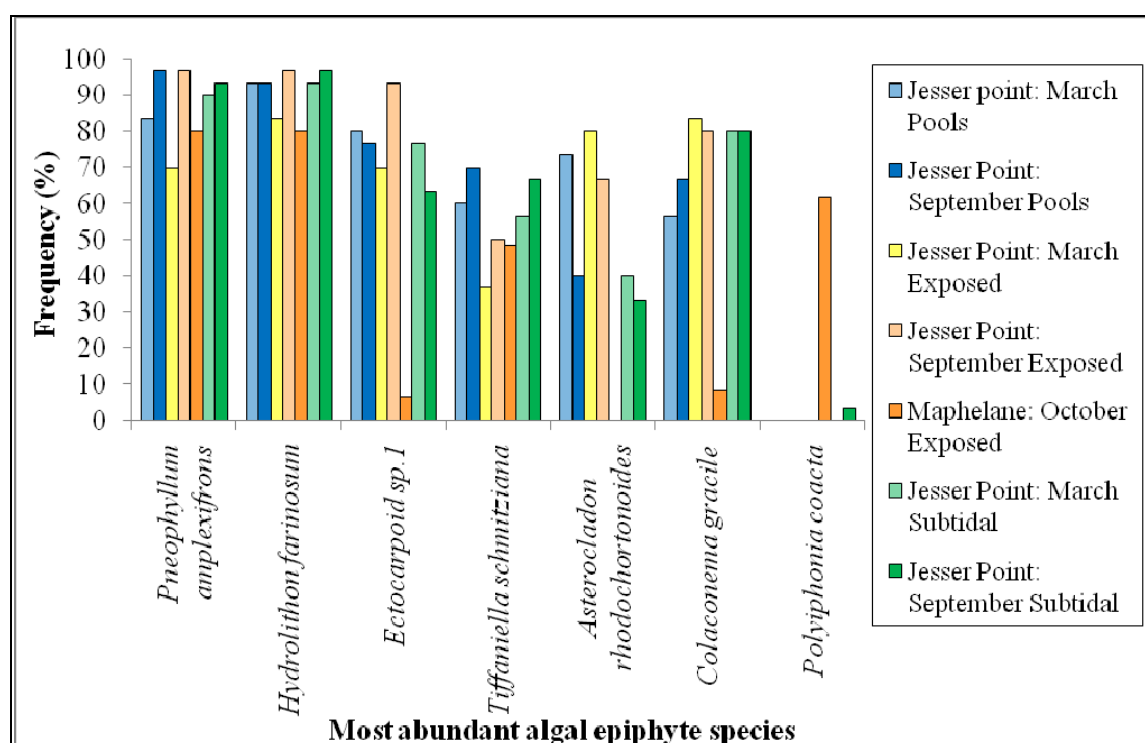


Figure 2.9: Most frequent seaweed epiphyte species growing on *Thalassodendron ciliatum* in differing habitats obtained from Jesser Point in March and 2010, and from Maphelane in October 2010.

The most frequently observed epiphytes growing on *Thalassodendron ciliatum* were predominantly Rhodophyta and were common among collections (Figures 2.9 and Table 2.2). The crustose red coralline algae *Pneophyllum amplexifrons* and *Hydrolithon farinosum* were highly frequent in all samples (Figures 2.9), with *P. amplexifrons* commonly observed on the stems, and *H. farinosum* commonly observed on the leaves. The frequency of *Ectocarpoid sp.1* was noticeably lower at Maphelane (being $\geq 60\%$ in Sodwana Bay samples and $<10\%$ in Maphelane samples). *Tiffaniella schmitziana* occurred

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more frequently in Pool and Subtidal habitats at Sodwana Bay in both March and September, and occurred at similar frequencies in all Exposed habitats sampled (irrespective of season and/or location). *Asterocladon rhodochortonoides* occurred most frequently in Pools at Sodwana and was not observed at all in the Maphelane collection. The frequency of *Colaenema gracile* was less at Maphelane. *Polysiphonia coacta* plants were only observed in spring samples (from Sodwana Bay in September, and Maphelane in October 2010), and were far more frequent at Maphelane.

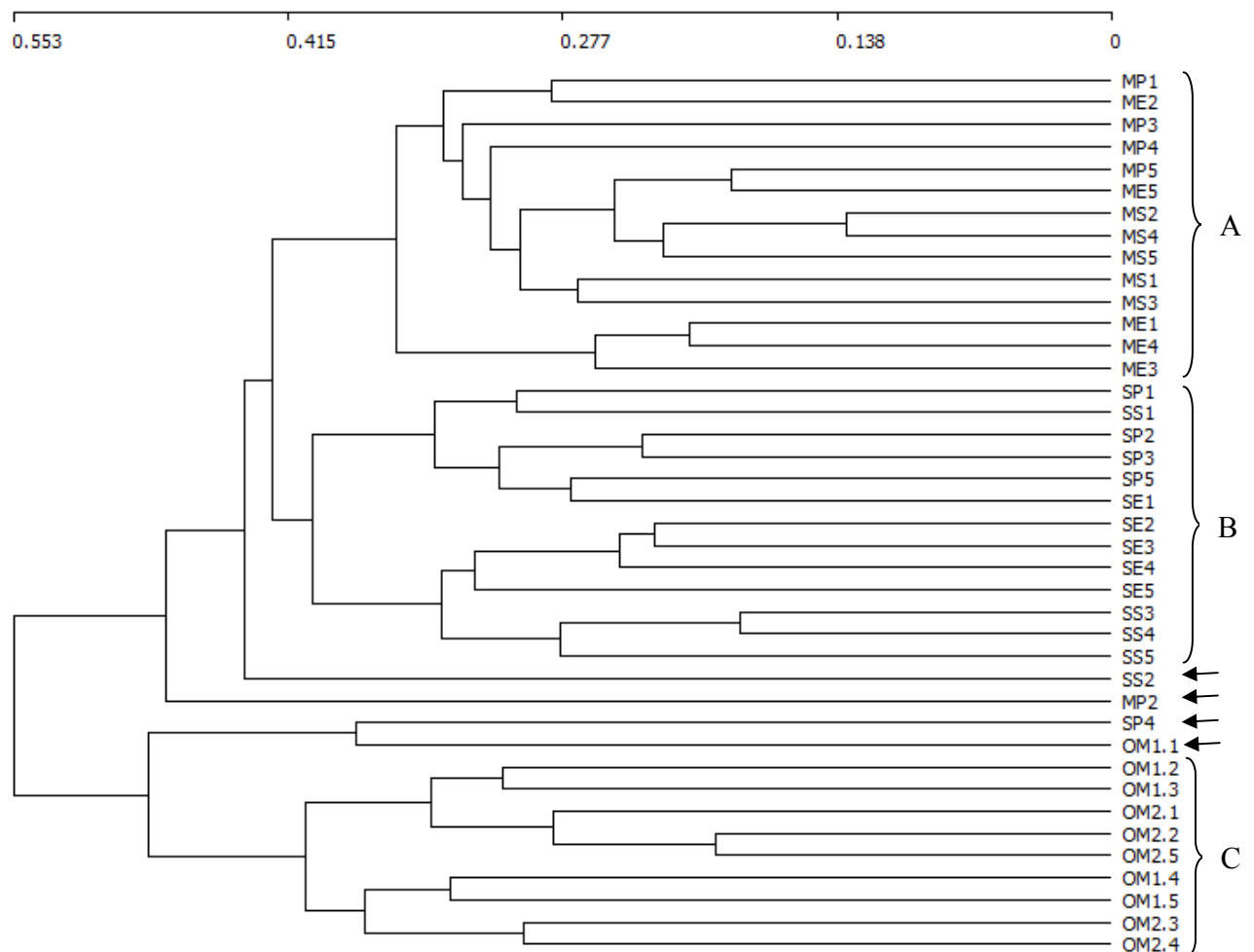


Figure 2.10: Average linkage Bray-Curtis cluster analysis of all samples, based on species abundances, based on adapted Braun-Blanquet cover-abundance scale, of all seaweed epiphytes occurring on *Thalassodendron ciliatum* in samples collected in March 2010 (M) from Jesser Point, in September 2010 (S) from Jesser Point (Pools P, Exposed E, Subtidal

S), and in October 2010 (OM) from Maphelane. Letters indicate clusters at the 0.415 level of dissimilarity. Outliers are indicated by arrows.

An average linkage Bray-Curtis cluster analysis of the data of species abundances (Figure 2.10) found that the primary division was between the Maphelane samples (OM, denoted in C) and those from Jesser Point (A and B), with the exceptions of samples SS2, MP2, SP4 and OM1.1, which are outliers. At the next level of dissimilarity, the Jesser Point samples split into 2 groups, namely those collected in March 2010 (A) and those collected in September 2010 (B). In the Sodwana Bay groups, Pool samples separated out from the Exposed and Subtidal samples. Pools are very different to other habitats and characterised by the dominant seaweed epiphyte species graphed in Figure 2.9.

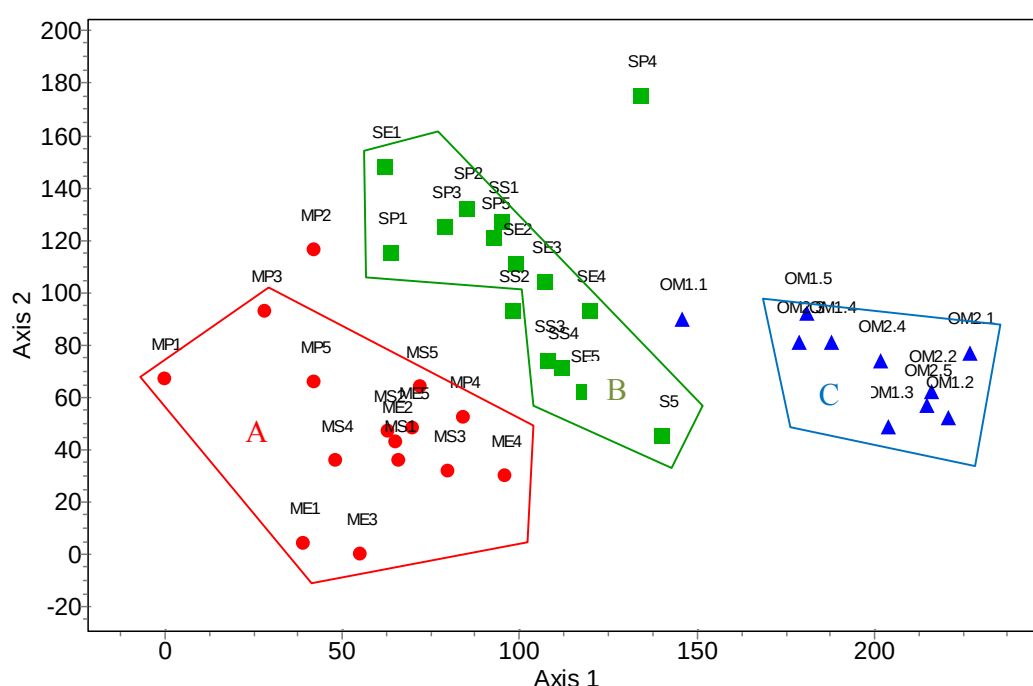


Figure 2.11: DECORANA ordination plot of all samples, based on species abundances, based on adapted Braun-Blanquet cover-abundance scale, of all seaweed epiphytes occurring on *Thalassodendron ciliatum* in samples collected in March 2010 (M) from Jesser Point (red dots) (A), in September 2010 (S) from Jesser Point (green squares) (B) (Pools P, Exposed E, Subtidal S), and in October 2010 from Maphelane (OM) (blue

triangles) (C) (Eigen-values: Axis 1= 0.30837, Axis 2= 0.134952). Shapes include samples identified as similar in Figure 2.10 (Cluster analysis) and exclude those samples identified as outliers.

Abundances of seagrass epiphytes differ significantly both geographically and temporally (Figures 2.10 & 2.11). Figure 2.11 supports the observations described above relating to Figure 2.10, displaying that Axis 1 separates Jesser Point (Sodwana Bay) (A and B) from Maphelane (C) samples, whereas a combination of Axes 1 and 2 separates the two Jesser Point clusters (A and B). Abundances of epiphytes differed between Sodwana Bay and Maphelane samples (ANOSIM $p=0.001$), (Figures 2.10 & 2.11).

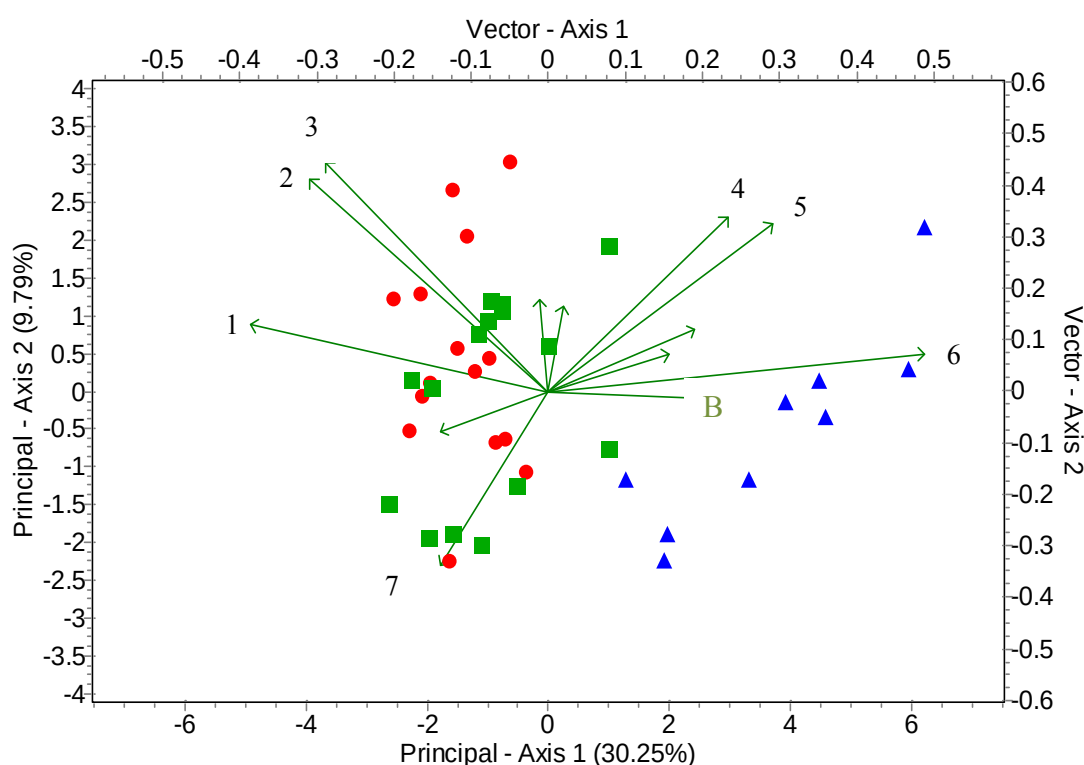


Figure 2.12: PCA covariance analysis of all samples, based on species abundance, based on adapted Braun-Blanquet cover-abundance scale, of all seaweed epiphytes occurring on *Thalassodendron ciliatum* from samples collected in March 2010 from Jesser Point (red dots), in September 2010 from Jesser Point (green squares), and in October 2010 from

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Maphelane (blue triangles). Vectors indicate influential species (see Table 2.3 for species names).

Table 2.3: Influential macroalgal epiphyte species determining the groupings identified between samples collected in March and September 2010 from Jesser Point and in October 2010 from Maphelane (corresponds with Figure 2.12)

Code	Species
1	<i>Ectocarpoid</i> sp.1
2	<i>Asterocladon rhodochortonoides</i> (Børgesen) Uwai, Nagasato, Motomura & Kogame
3	<i>Colaconema gracile</i> (Børgesen) Ateweberhan & Prud'homme van Reine
4	<i>Ceramium</i> sp
5	<i>Platysiphonia delicata</i> (Clemente) Cremades in Cremades & Ferez Cirera
6	<i>Polysiphonia coacta</i> C.K.Tseng
7	<i>Pneophyllum amplexifrons</i> (Harvey) Y.M.Chamberlain & R.E.Norris

Figure 2.12 (together with Table 2.3) illustrates which species are influencing the patterns observed between collections made in March and September 2010 from Jesser Point, and in October 2010 from Maphelane.

The PCA covariance plot (Figure 2.12) clearly indicates differences between Jesser Point and Maphelane along axis 1. For temporal differences in macroalgal epiphyte species occurring, refer to Table 2.1. Maphelane samples are strongly influenced by *Polysiphonia coacta* and to a lesser degree by *Cladophora saviniana*. Sodwana Bay samples were primarily influenced by the presence of *Ectocarpoid* sp.1, *Asterocladon rhodochortonoides*, *Colaconema gracile* and *Pneophyllum amplexifrons*.

2.3.3 Relationships between *Thalassodendron ciliatum* and its macroalgal epiphytes

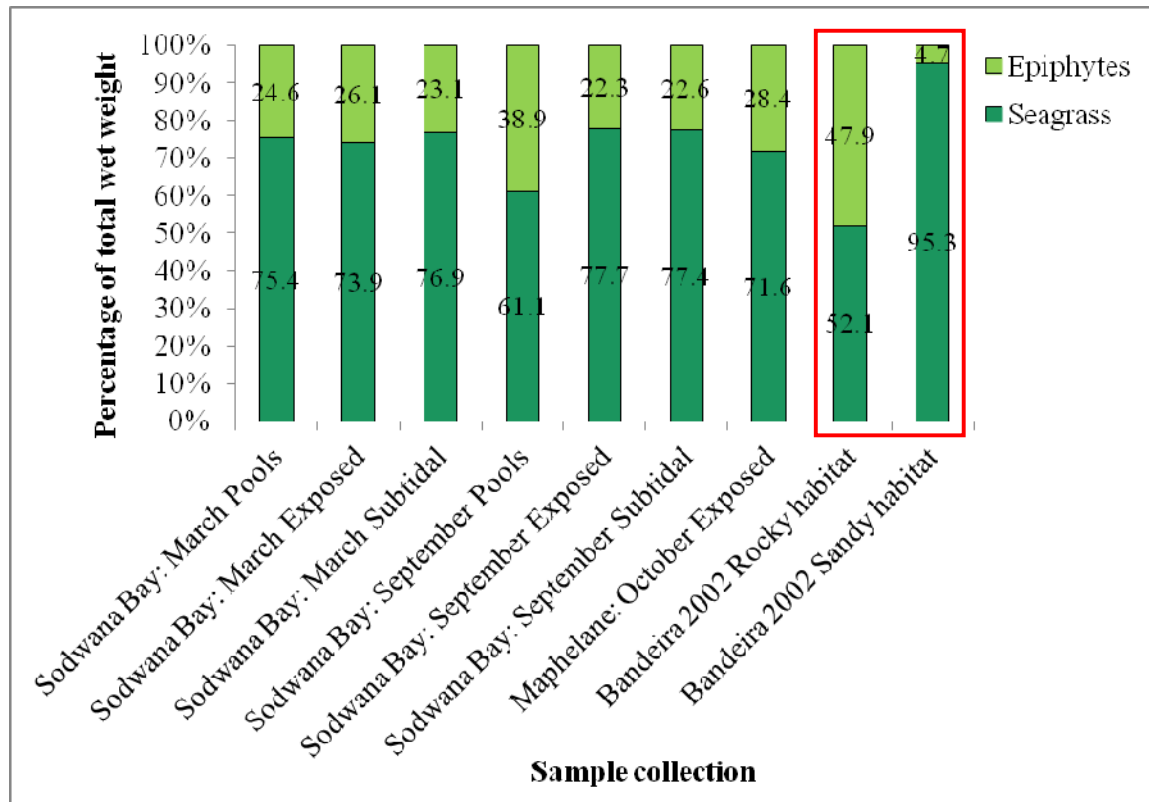


Figure 2.13: Percentages of wet weights (g) of epiphytes and seagrass, obtained from the different collections, and compared with the data of Bandeira (2002) (outlined in red).

Epiphyte cover accounted for approximately 42% of total biomass in seagrass beds off Jesser Point, and 58% in Maphelane. Epiphyte biomass in the sandy habitat in Mozambique (Bandeira 2002) was considerably lower (Figure 2.13).

When comparing similar habitats in the same season (Sodwana Bay: September Exposed, $n = 30$, and Maphelane: October Exposed, $n = 60$), there was no significant difference in the average percentage of biomass of seagrass and of epiphytes between the two sites ($t = 0.407$, $df = 88$, $p = 0.684$).

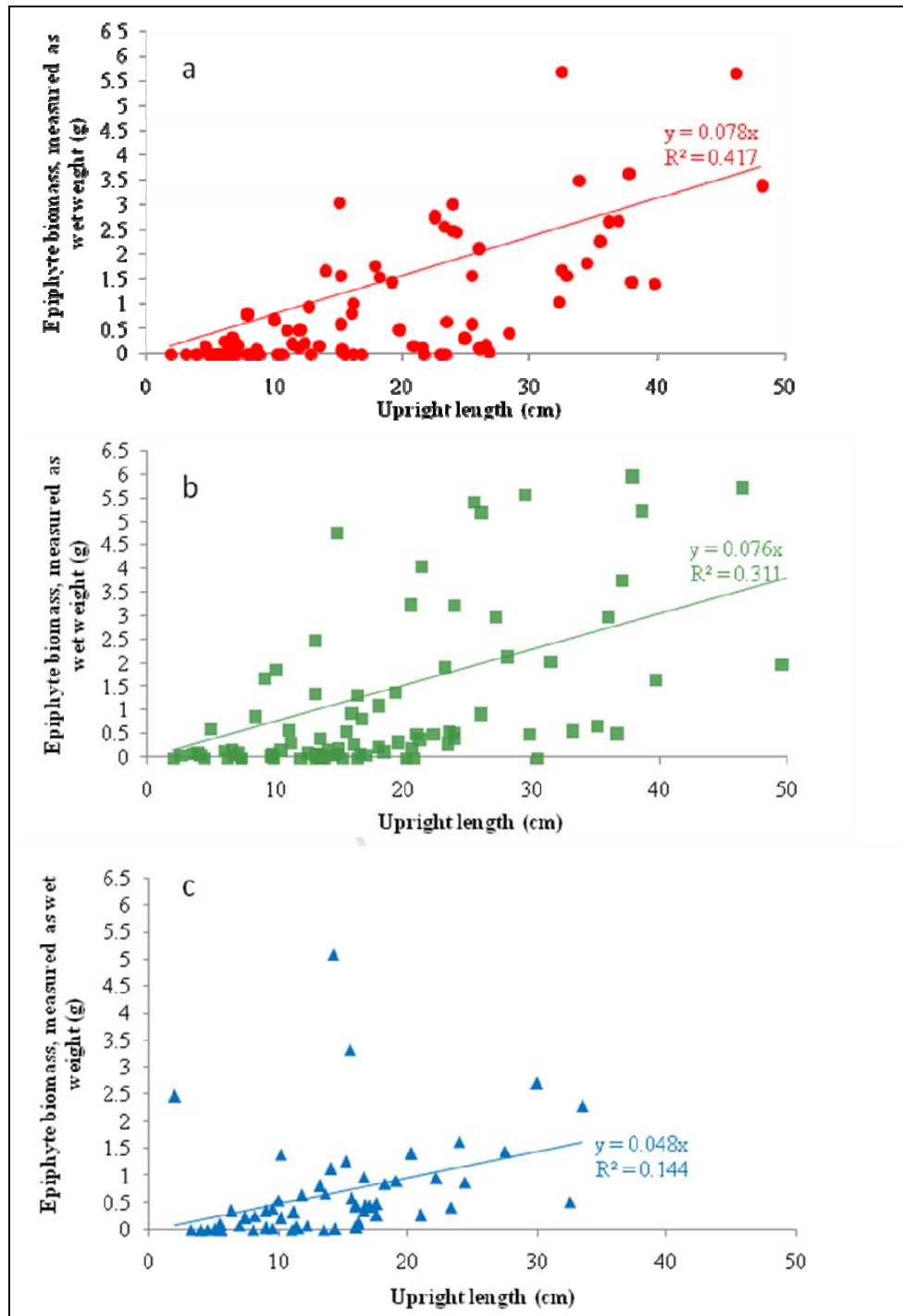


Figure 2.14: Relationship between seagrass upright stem length and epiphyte biomass for collections from a) Jesser Point in March 2010, b) Jesser Point in September 2010, and from c) Maphelane in October 2010.

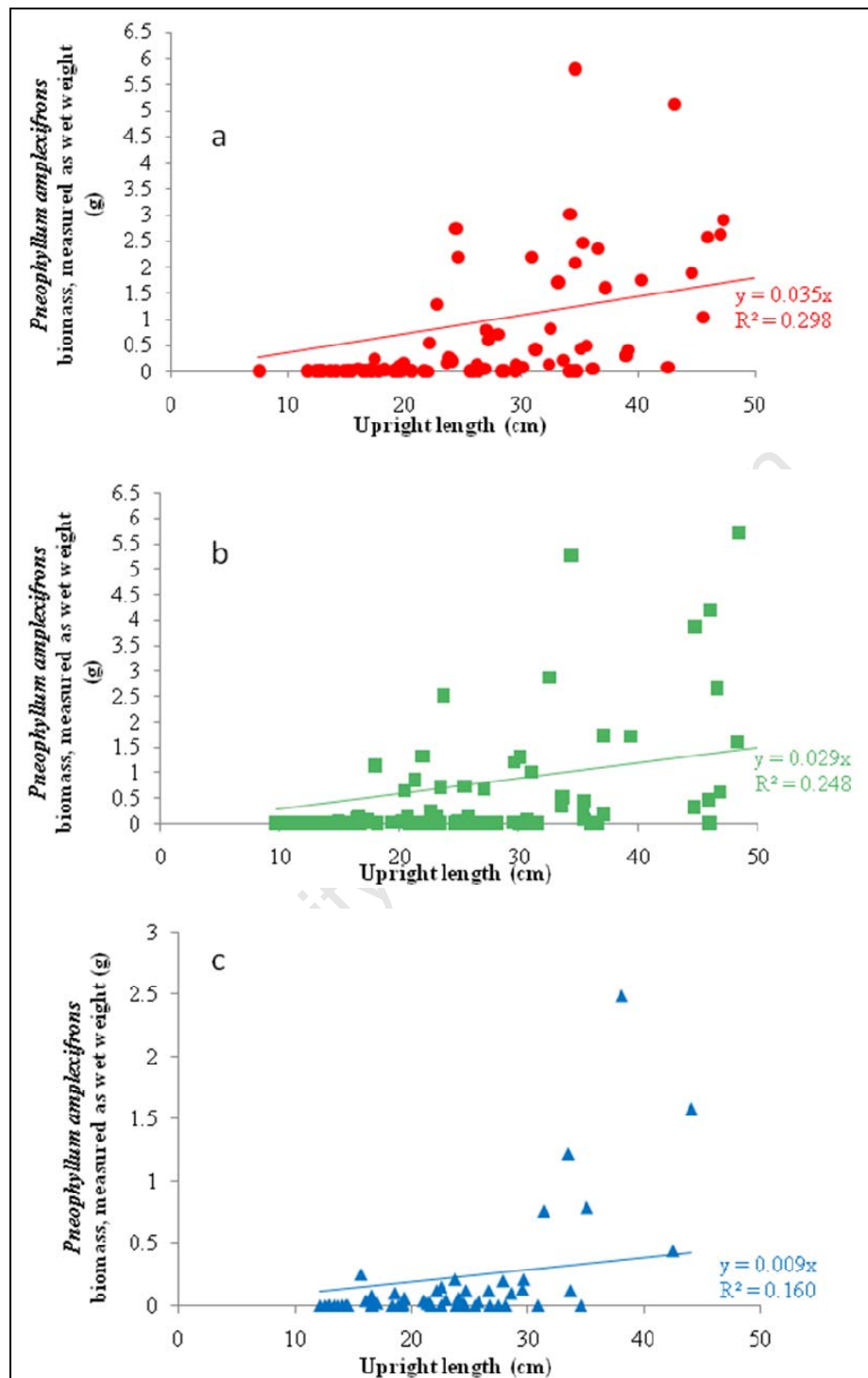


Figure 2.15: Relationship between seagrass upright length and biomass of the common epiphyte, *Pneophyllum amplexifrons*, for collections from a) Jesser Point in March 2010, b) Jesser Point in September 2010, and c) from Maphelane in October 2010.

Epiphyte biomass, measured as wet weight (g) increased with increasing seagrass upright length (cm) (Figure 2.14). This relationship was found to be weak but significant for all three collections ($p < 0.05$). The wet weight (g) of *Pneophyllum amplexifrons*, one of the most abundant (Table 2.2) and highly frequent (Figure 2.9) epiphytic species, was also found to increase with increasing upright length (Figure 2.15) and significantly so for each collection despite the correlations being weak ($p < 0.05$).

2.4 Discussion

Thalassodendron ciliatum provides a substrate for a large biomass of epiphytic organisms. The large number of species epiphytic upon *T. ciliatum* is probably related to the morphology and life history of the host, as well as the habitat type and environmental parameters. Seagrasses do not grow in isolation but form an essential and often crucial part of highly intricate ecosystems. These seagrasses could be called ‘ecosystem engineers’, a term defined as being ‘an organism that causes changes in the physical environment sufficient to influence the structure of the landscape, ecosystem, or community’ (Jones, Lawton, and Shachak 1994). Before *T. ciliatum* can be considered an ecosystem engineer with respect to its epiphytes, some questions would have to be answered. Are the species observed at the sampled sites there because of the presence of *T. ciliatum* and, would they occur in the same areas in its absence? General observation appears to indicate that many of the epiphytes were growing on the seagrass and not the surrounding rocky substrate. However, there is no evidence supporting the suggestion that the majority of these epiphytic species are obligate epiphytes or obligatorily associated with *T. ciliatum*. However, the biomass of seaweed epiphyte species is much more than if the seagrass was not there. Therefore *T. ciliatum* can be seen as an ‘ecosystem engineer’ influencing the structure of the community, and not just the species composition.

The seagrasses produce organic matter into the system, but the productivity of these systems is typically increased by the other primary producers (epiphytic microalgae and macroalgae) living on and among the seagrass itself. The abundant plant material of seagrass beds forms a vital component of many food chains (Green & Short 2003). Previous work in the region has found that some of the energy that drives deep canyon

systems, the homes to the coelacanths of the KwaZulu-Natal coast, is derived from intertidal plant material (Porter 2009). Similar studies have shown that shoreline seaweeds export energy/carbon to adjacent marine environments (Melville & Connolly 2003, 2005; Kaehler *et al.* 2006).

Thalassodendron ciliatum shoot biomass and density were found to be similar between the temporal comparisons of samples collected from Jesser Point in March and September 2010, as well as spatially between samples collected from Jesser Point and those from Maphelane. The average length of shoots was similar between collections from Jesser Point in March and September 2010, which were found to be taller on average than Maphelane shoot lengths. *T. ciliatum* densities in the current study ranged from 40 – 60 uprights per 25X25 m quadrat (on average approximately 200 uprights m⁻²). In Western Australia *T. pachyrhizum* has been found to have a ramet density of 667±28 m⁻² (Marbà and Walker 1999). Other Cymodoceaceae have been observed to grow in much denser stands. For example, a study in Kenya recorded *Cymodocea rotundata* shoot densities of up to 1500 shoots m⁻² occurring in lagoons (Uku and Björk 2005). There are a few possible reasons for the lower densities in our populations.

Seagrass uprights may be expected to be smaller at the limits of their distribution, where they may be struggling to exist. De Koning *et al.* (1995) report that *Thalassodendron ciliatum* at Inhaca Island, Mozambique grows to heights of 30-40 cm and further north in sheltered bays on the African east coast (e.g. Nacala Bay in Mozambique and Turtle bay in Kenya) it may reach heights >1 m. This notion that plants at the furthest extent of their distribution are smaller is supported by the current research, as Maphelane plants are shorter than Jesser Point plants, and South African plants are much shorter than the Mozambique plants as measured by Bandeira (2002). Bandeira (2002) found that stem biomass per unit area was not significantly different between the two substrates sampled in southern Mozambique. However, he noted that despite this, the plants on rock occurred in very dense mats with nearly always a 100% cover, while plants in sandy habitats usually displayed less cover. It could then be suggested that wave action is important in determining the density of seagrass beds rather than biogeography. The degree of wave

action and current was found to be a primary influencing factor determining the composition and extent of seagrass meadows in southern Western Australia (Kirkman 1985). If greater wave action causes dense, mono-length stands of seagrass, perhaps these beds may also be more susceptible to epiphyte settlement and growth. Such denser seagrass beds may have fewer large grazers because they are exposed to greater wave action. Alternatively, small scale disturbances and wave action may play an important role in the structuring of seagrass beds by increasing interactions between abiotic and biotic processes as suggested by Binning *et al.* (2007) from their research on seagrasses in the Caribbean. Seagrass beds have a high supply of both light and nutrients on the rocky shore, thereby perhaps promoting the growth of multiple seaweed epiphyte species. Borowitzka *et al.* (1990) recorded 150 species of multicellular algae epiphytes on the seagrass *Amphibolis* at three sites in South Western Australia. Only a small number of Borowitzka *et al.*'s (1990) species were commonly observed on individual plants because the majority of epiphytes were patchily distributed between plants and between sites. Both the present study and that of Borowitzka *et al.* (1990) found more epiphyte diversity and wet weight associated with seagrass stems than leaves.

A total of 99 taxa of macroalgae were identified, a high diversity with respect to other East African studies. Leliaert *et al.* (2001) studied the epiphytes of 10 seagrass species in Zanzibar Island waters (Tanzania) and identified a total of 49 epiphytic macroalgal species (27 Rhodophyta, 14 Chlorophyta, 6 Phaeophyceae, and 2 Cyanophyta). Only two taxa were common between Leliaert *et al.*'s (2001) and the current study, namely: *Gracilaria corticata* and *Herposiphonia secunda* f. *tenella*. Crustose coralline red algae were noted but not identified to species in Leliaert *et al.* (2001). Leliaert *et al.*'s (2001) and the current study are in the same biogeographical realm, yet analyses of the same seagrass identified very different epiphytes. This may be as the result of the very different habitats, lagoon versus exposed rocky shore.

Bandeira (2002) did not specify the exact number of seaweed epiphytes observed in his study on *Thalassodendron ciliatum* in southern Mozambique, but of the 15 most dominant

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species mentioned 4 were common epiphytes noted herein (*Jania subulata*, *Halimeda cuneata*, *Pneophyllum amplexifrons*, and *Hypnea rosea*).

This dissertation identified Rhodophyta as dominant in species number and cover, as well as accounting for the greatest biomass in all collections. This is primarily due to the cover by red coralline algae (primarily *Pneophyllum amplexifrons* and *Hydrolithon farinosum*), but also the frequent presence of *Jania* species. On average Sodwana Bay supported a higher biomass of Rhodophyta (>90 g) than Maphelane (26.41 g). However, interestingly Maphelane supported a greater biomass of Phaeophyceae (11.12 g) and Chlorophyta (5.09 g) compared with Sodwana Bay which supported <1 g and <2 g respectively. This demonstrates that the two collection locations support different amounts of the different seaweed groups as well as species. Maphelane is perhaps more temperate and Jesser Point (Sodwana Bay) more tropical. Reasons for this may be as a result of the region south of the Natal Bight (in which Maphelane falls) experiencing cooler seawater temperatures than north of that position, where the warm Agulhas current runs close inshore near Jesser Point.

The large number of species epiphytic upon *T. ciliatum* may be related to its morphology and distribution. The stems and leaves provide structurally and temporally different habitats for colonization by epiphytes. The lignified stems survive for several years unlike the leaves, which in *T. ciliatum* are shed on average every 60 days (Hemminga *et al.* 1999). Stems therefore, provide a stable substratum, as is the case with the Australian species of *Amphibolis* studied by Borowitzka *et al.* (1990).

Stems also provide multiple habitats as mentioned in Borowitzka *et al.* (1990). Stems pass from a region of low water motion and lower irradiances near the substratum to a region of high irradiance and high water movement at the seagrass apex. The distributions of epiphytes on the seagrass were also recognized as not being random. This is in keeping with previous observations of epiphytes on other seagrasses (e.g. Willcocks 1982; Heijs 1985; Borowitzka *et al.* 1990). Epiphyte biomass increased with seagrass height and different assemblages of species tend to colonise the stems and leaves.

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Further explanations for this observed pattern (as suggested by Leiaert *et al.* 2001) may be that the smooth surface of the leaves prevents spore attachment. Leaves experience more shear stress and are densely packed together, thereby preventing colonisation on all surfaces and leaves also abrade each other. On the other hand, seagrass stems are an optimal substratum for epiphytic growth as they offer a rough surface (leaf scars) thereby aiding spore attachment, they are less subject to motion, their spacing optimizes spore supply in the water currents, they are often shaded by leaves (therefore experiencing lower irradiation) and stems tend to be slow-growing and perennial.

The crustose coralline red algae are primary colonisers of both leaves and stems of *Thalassodendron ciliatum*, as are they on other seagrass species (e.g. Humm 1964; Borowitzka *et al.* 1990). Observations made suggest that the crustose coralline red algae seem to act, at least in part, as pioneer plants, possibly providing a suitable substratum for other epiphytes. It was observed that smaller epiphytes grew on the epiphytes on *T. ciliatum*. Total epiphytic cover on the stems was greater than on the leaves of *T. ciliatum* confirming previous observations, for example those noted in studies conducted on seagrasses and their seaweed epiphytes in Australia and Tanzania (Borowitzka *et al.* 1990; Leliaert *et al.* 2001).

The most abundant species by both cover and wet weight was *Pneophyllum amplexifrons*. Although abundant in all three collections, the wet weight of *P. amplexifrons* per sample in differing habitats, seasons and locations did not differ significantly in general. The only samples that were found to be significantly different from others were the Sodwana Bay Pool samples (both collected in March and September 2010) compared with those of the Maphelane samples collected from Exposed seagrass beds (October 2010). This indicates that seagrasses and their associated epiphytic algal counterparts, in a Pool habitat, are notably different from those on the open shore ('Exposed') or subtidal zone.

When analyzing the percentage frequency of occurrence of the most abundant species of epiphytes, differences emerged between habitats, and general comparisons were possible between frequencies in the different collections. In the March collections *Pneophyllum*

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amplexifrons, *Hydrolithon farinosum*, *Ectocarpoid* sp.1, and *Tiffaniella schmitziana* were more frequent in the Pool and Subtidal habitats than in samples from Exposed seagrass beds.

Polysiphonia coacta was not frequently observed in the March collections but was highly abundant and frequent in the Maphelane collections in October and was observed in the Sodwana Bay samples collected in September 2010. *P. amplexifrons* and *H. farinosum* were the most abundant epiphyte species in all collections made and occurred with a frequency over 70% in all habitats and all collections. The Maphelane collection showed a notably lower abundance frequency of *Ectocarpoid* sp.1, compared to the Sodwana Bay collections, thereby indicating that it may be a more tropical species. *Asterocladon rhodoortonoides*, though frequently abundant at Sodwana Bay in all habitats in both seasons sampled, was not frequently observed at Maphelane. There are clearly habitat and temporal differences. *Polysiphonia coacta* would appear to be a spring species, since it occurred at both sites later in the year and was absent in the March collection.

Analyses illustrated that the seaweed epiphytes differed between Sodwana Bay and Maphelane collections, showing dissimilarity between different biogeographic regions. There were also temporal differences between samples from Sodwana Bay. Analyses also showed similarity between the different habitats, with Pool samples grouping together more so than the other two habitat types sampled, indicating that the seagrass and associated seaweed epiphytes living in a pool environment differ from those occurring on the open shore and sub-tidally.

Analyses identifying influential species determining these groups show that *Polysiphonia coacta* has a strong influence in separating the Maphelane samples from those collected from Sodwana Bay. Other seaweed epiphytes influencing the separation of Maphelane samples were *Ceramium* sp. and *Platysiphonia delicata*. Sodwana Bay samples were strongly influenced by species such as *Ectocarpoid* sp.1, *Asterocladon rhodoortonoides*, *Colaconema gracile* and *Pneophyllum amplexifrons*. This suggests that the Sodwana Bay

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species are more tropical and those at Maphelane more a mixture of tropical and temperate affinities, supporting Bolton *et al.* (2004)'s overlap theory.

The findings that seaweed epiphytes made up approximately 42% of the seagrass/epiphyte total biomass at Jesser Point and 59% at Maphelane are very similar to the finding of Bandeira (2002) that seaweed epiphytes in rocky areas corresponded to 47.9% of the total above ground seagrass/epiphyte biomass, whereas he reported a value of only 4.7% in a sandy habitat in southern Mozambique. These differences could be because lagoon and sandy habitats support more grazers, as they are more sheltered environments, and grazers reduce the diversity and biomass of epiphytes. Sand inundation may also reduce epiphytes via burial and abrasion. It is reasonable to suppose that exposed rocky habitats support fewer grazers but have a vast diversity of algal species (including epiphytes) because water movement increases nutrient and light availability, supporting plant growth. Another explanation could be that more seaweed species are present on rocks, resulting in more propagules: many of the epiphytes identified are also found epilithically.

The current data showed that epiphyte biomass increased proportionally with seagrass stem length. Bandeira (2002) noted, in his study on *Thalassodendron ciliatum* in southern Mozambique that the increase in epiphyte biomass on taller stems was due to the proliferation of only one or two species on each stem. This finding is supported by this dissertation, where the major contributors to algal biomass were usually made by *Pneophyllum amplexifrons* and *Jania* species, as previously discussed.

Borowitzka *et al.* (1990) found there was a clear relationship between the number of epiphyte species and heights of plants on *Amphibolis* in Australia. It might be assumed that plant height is a function of plant age and therefore older plants support a higher number of epiphytes. This suggestion is supported, since epiphyte wet weight was found to increase with increasing seagrass stem length. This is expected, as over time, as the seagrass grows, there is further recruitment of epiphytes and the epiphytes themselves increase their biomass with time. Older, taller seagrass uprights support higher epiphyte loads as they have survived longer, allowing for epiphyte settlement. They also have developed thicker

stems with more branching and leaves, allowing more substrate onto which epiphytes may attach.

The young leaves are epiphyte-poor, partly because they are protected by older leaves of the same shoot. Leliaert *et al.* (2001) found in their studies in Kenya that total epiphyte cover on subtidal seagrass was much higher than that on intertidal specimens indicating permanent submersion was creating a more stable environment which is a crucial factor influencing epiphyte growth. In contrast, the current study found that *Thalassodendron ciliatum* in both intertidal and shallow subtidal habitats supported similar epiphytic cover.

If epiphytes are too abundant on leaves, seagrass photosynthesis can be inhibited (Sand-Jensen 1977; Borum & Wium-Andersen 1980; Bulthuis & Woelkerling 1983) and epiphytic cover may lead to negative impacts on the host plant, as reported for the rocky intertidal red alga *Rhodomela larix* on the Oregon coast (D'Antonio 1985). A study in Brazil by Papini *et al.* (2011) found that the epiphytic macroalga *Hinckesia mitchelliae* (Phaeophyceae) killed the shoalgrass *Halodule wrightii* (Cymodoceaceae), by adhering to and shadowing the surface and disrupting its osmoregulatory system. At the epiphyte loads observed herein, this may be of less concern for *Thalassodendron ciliatum* as its leaves are relatively short lived (Hemminga *et al.* 1999) and shed together with adherent epiphytes. The relatively short leaf lifespan in seagrasses may be linked to the elevated stresses imposed upon the leaves in an aquatic environment as compared to leaves growing in air, as is the case with their terrestrial counterparts. Another explanation for short longevity in seagrass leaves may be the gradual coverage of the leaf blades by silt and epiphytes in the aquatic environment.

This chapter deals with the structure of the seagrass *Thalassodendron ciliatum* and its associated seaweed epiphytes. *T. ciliatum* stand density and average biomass were found to be similar between all three collections made, however seagrass uprights were found to be taller in general in samples collected from Jesser Point compared with those collected from Maphelane. The epiphyte species in *T. ciliatum* show differences both spatially and temporally. The seaweed epiphytes observed on *T. ciliatum* from Mahelane differ from those collected from Jesser Point. Differences were also observed between the epiphytic

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flora from *T. ciliatum* samples collected from Jesser Point in March and September 2010. The results of the current chapter are of practical use to managers in the region of the study as well as future researchers, as they provide baseline information of the *T. ciliatum* epiphytic flora diversity, biomass and distributions. This information can be used both for monitoring change within the region sampled, as well as for comparison with other seagrass communities.

University of Cape Town

Chapter 3

Biogeography of seaweed species epiphytic on the seagrass *Thalassodendron ciliatum* (Forsskål) den Hartog in South Africa

University of Cape Town

3.1 Introduction

3.1.1 Definitions of “biogeography”

The necessary data for studies of the geographic distributions of marine plants have been accumulating progressively since the first seaweed was named. Biogeography is “the science that attempts to document and understand spatial patterns of biological diversity” (Lomolino *et al.* 2010). Traditionally, biogeography has been based upon organisms’ distributions, both past and present, while the modern approach incorporates studies of all patterns of geographic variation in nature, and biological diversity elements that differ over geographic gradients (Lomolino *et al.* 2010).

Although biogeography can be described simply as the study of the geographical distribution of organisms (Bustamante & Branch 1996), the apparent straight-forwardness of this definition is misleading, for it hides the importance of historical events and processes which may strongly influence modern biogeographic distribution patterns. Spalding *et al.* (2007) defined biogeographic provinces as being large areas defined by the existence of distinct biota that have at least some consistency over evolutionary time periods and that hold some level of endemism (mainly at the level of species). In the ecological context, biogeographic provinces are considered as units likely, for example, to include the broader life history of numerous constituent taxa of both mobile and dispersive species. It is important to note that biogeographic regions (sometimes called provinces) are not just separated by disjunctions in species distributions, but also that they contain a significant number of endemics for that region.

Bolton *et al.* (2004) describe a marine biogeographic province as an extent of coastline that fulfills two criteria. Firstly, it has a homogenous biota which differs from adjacent coastlines with different biota in terms of floristic and/or faunistic discontinuities. Secondly, it displays a significant proportion of its biota endemic to it, thus shaped to a considerable degree by the geographically limited evolution of new species, rather than primarily by dispersal from other regions with comparable temperature regimes.

3.1.2 What is known on the biogeography of:

a. seagrasses and specifically *Thalassodendron ciliatum*?

Seagrasses grow everywhere from deep coastal wave swept areas to sheltered bays and estuaries. There appears to be nothing specific about their ‘global’ distribution. For example, seagrasses of south-west Australia occur from shallow subtidal to 50+ m water depths and in many estuaries along the coast (Carruthers *et al.* 2007). In contrast, *T. ciliatum* on the north eastern South African coast was observed only to occur in the intertidal to shallow subtidal to depths of approximately 3 m. The northernmost seagrasses (*Zostera marina*) are recorded in Norway (70°30’N), Russia (67°30’N) and Alaska (66°33’N). The southernmost seagrasses are *Zostera capricorni* in New Zealand, with the southernmost record being at 46°55’S on Stewart Island, and *Ruppia maritima* in the Straits of Magellan (54°S). Distribution maps are however limited in that sometimes no distinction is made between coasts that have not been surveyed and coasts where no seagrasses are found. For example, the coasts of western South America and West Africa may have more seagrass than reflected in the literature (Spalding *et al.* 2003).

All of the centres of high seagrass diversity which have been identified fall in the eastern hemisphere. The first and largest of these is insular Southeast Asia. The other two centres are around Japan/ Republic of Korea and the other southwestern Australia. Other areas of significant diversity include southern India and eastern Africa (Spalding *et al.* 2003).

Seagrasses recorded in South Africa include *Zostera capensis*, *Syringodium isoetifolium*, *Thalassodendron ciliatum* and *Halophila ovalis* (Branch *et al.* 2010). *Zostera capensis* is the most widespread and the dominant seagrass species in South Africa. It primarily occurs in estuarine waters from KwaZulu-Natal to the Western Cape region. The distribution of *Zostera capensis* in southeastern South Africa is well recorded and it has been reported to grow in 17 estuaries. Individual *Zostera capensis* beds are small, generally only a few hectares, and the total area covered by this seagrass in South Africa is estimated at 7 km² (Green & Short 2003). Other seagrass species cover smaller areas and the exact total cover of seagrass in South Africa remains unknown at present. The coast of eastern Africa, particularly of eastern South Africa, is of interest as little research has been focused on

seagrasses, especially rocky shore communities in these areas. In a few sites off KwaZulu-Natal, the lower intertidal of some rocky shores are dominated by *T. ciliatum* that is adapted to live in a rocky habitat together with seaweeds, although this is atypical of seagrasses in general (Bandeira & Gell 2003). To date the only records of *T. ciliatum* in South Africa are Chamberlain & Norris (1994), who described the epiphyte *Pneophyllum amplexifrons* on this species, and a study of the distribution and description of *T. ciliatum* along the KwaZulu-Natal coast by Ward (1962). Ward's study (1962) is published in a limited distribution local journal which is difficult to obtain even in South Africa.

Thalassodendron ciliatum is a tropical seagrass species, with a distribution in South Africa that is seemingly restricted to rocky shores in northern KwaZulu-Natal. Ward (1962) noted a single population of *T. ciliatum* at Maphelane, 100 km south of Sodwana Bay, and fairly well-developed populations from Sodwana Point northwards. There is no record of *T. ciliatum* being recorded in South African estuaries or enclosed bays or lagoons (Prof. Jeanine Adams, Nelson Mandela Metropolitan University, *pers. comm.* 2010).

b. KwaZulu-Natal seaweeds

The region where the current study was undertaken has been proposed (at least for the seaweed flora) to be a biogeographic overlap between the temperate South African Agulhas and the tropical Indo-West Pacific regions (Bolton & Anderson 1997; Bolton *et al.* 2004).

Bolton *et al.* (2004) found that the southern and central KwaZulu-Natal Province is populated by a mixture of tropical and temperate seaweed elements, representing a true overlap region between the tropical Indo-Pacific and the temperate South African south coast (Agulhas Marine Province), rather than a distinctive subtropical marine province as previously suggested by Stephenson (1948) and subsequent authors. Northern KwaZulu-Natal (Maputaland), by contrast, supports primarily tropical seaweeds (Bolton *et al.* 2004). These authors concluded that the change-over from a tropical Indian Ocean flora to a temperate South African flora occurs most rapidly in the vicinity of Cape St. Lucia, 135 km south of the Mozambique border. Bolton *et al.* (2004) analysed their data into six coastal sections, focused on major collecting areas along the Kwazulu-Natal coastline (known as

“Palm Beach” (site 4), “Durban” (5), “Zinkwazi” (6), “St. Lucia” (7), “Sodwana Bay” (8), and “Bangha Neck” (9)). Maphelane falls between sites 6 and 7 of Bolton *et al.* (2004). Bolton and Stegenga (2002) compiled a dataset on the diversity of South African seaweed species and their distribution in adjacent 50 km sections of the South African coast (they divided the coast into 58x50 km sections), showing the present information of the flora in different coastal regions. Their data have been updated and made available herein. This dissertation analysed these updated records of KwaZulu-Natal seaweeds, to present the biogeographical patterns, and then analysed the biogeography of the seaweed epiphyte species found on *Thalassodendron ciliatum* (detail follows in section 3.2.1).

3.1.3 Aims

One of the main initial aims of this study was to compare the seagrass epiphytes at Jesser Point and Maphelane (the extreme southern limit of its distribution in the western Indian Ocean) with the few tropical Indian Ocean sites where similar studies have been done (e.g. from Mozambique (Bandeira 2002), Tanzania (Leliaert *et al.* 2001) and Kenya (Coppejans *et al.* 1992)). This dissertation aimed to answer whether epiphytes growing on South African *Thalassodendron ciliatum* are different from those further north, and whether they have different biogeographical affinities.

This chapter aims to investigate the South African *Thalassodendron ciliatum* macroalgal epiphyte diversity and their biogeography, as well as whether temporal differences in presence/absence of species exist. The hypothesis tested was that the macroalgal epiphyte species on the rocky shore seagrass, *T. ciliatum* differ between Jesser Point and Maphelane. Distribution records for South African seaweeds (Bolton *et al.* 2004) indicated that these sites fall within different biogeographic areas and this dissertation aimed to determine whether such a pattern held true for the epiphyte flora of *T. ciliatum*.

Presence/absence data is ideal for biogeographic studies as it is fundamental to the ecology of organisms and relates to fundamental niche theory. The word ‘niche’ to the ecologist, summarises the environmental factors that influence the growth, survival, and reproduction of a species (Molles 2008). Hutchinson (1959) called the physical conditions under which a

species might live, in the absence of interactions with other species, the ‘fundamental niche’. He recognized that competition with other species restricted the environments in which a species may live, and termed these restricted conditions as the ‘realised niche’, which is the actual niche of the species whose distribution is limited by biotic interactions such as predation or competition. The current study examined the realized niche of *T. ciliatum* and its associated epiphytic flora in a biogeographic context.

3.2 Materials and Methods

3.2.1 Data collection

Specimens of *Thalassodendron ciliatum* and its seaweed epiphytes were collected from intertidal and shallow subtidal locations at Jesser Point (Sodwana Bay) (27°32′23″S 32°40′49″E) in March and September 2010, and intertidal locations at Maphelane (28°24′27″S 32°25′36″E) in October 2010. For site and collection details, and a list of all seaweed epiphyte taxa identified (see sections 2.2.1 and 2.2.2, and Table 2.1, in Chapter 2). Most of the taxa collected are illustrated in the Appendix (reproductive structures were illustrated if present).

The records of South African seaweeds (Bolton and Anderson *pers. comm.* 2011) are based on records in the literature and collections made primarily by Bolton and Anderson and their associates (specimens in herbaria, either: The Bolus Herbarium, University of Cape Town (BOL) or the herbarium at the University of Ghent in Belgium (GENT)). The diversity of South African seaweed species and their distribution in contiguous 50 km coastal sections was compiled in a study by Bolton and Stegenga (2002). This has been continuously updated from the literature and collections since then (particularly those in the KwaZulu-Natal project, now in the herbarium in GENT), and the dataset used in the current study is this latest update. This updated dataset is comprehensive for the east coast of South Africa. The geographical species distributions were determined by subdividing the South African coastline into 58x50 km sections (Bolton & Stegenga 2002), and scoring the sections for the presence of a species if it had been collected from that section or from localities on either side of it (interpolated). For this study only coastal sections 48 to 58

were analysed as they include the entire coastline of the KwaZulu-Natal Province of South Africa (Table 3.1).

Table 3.1: Global Positioning System (GPS) co-ordinates and localities corresponding to the 50 km sections of the KwaZulu-Natal coastline (sections 48 to 58), as described in Bolton and Stegenga (2002). Samples were collected from sections *55 (at Maphelane) and *57 (at Jesser Point (Sodwana Bay)).

Code	Longitude (E)	Latitude (S)	Limits	Including
48	30.4116	-30.80858	To just north of St Michaels-on-Sea	Mzamba, Port Edward, Southbroom, Margate
49	30.67698	-30.41392	To just south of Pennington	Port Shepstone, Mzumbe, Sezela
50	30.93173	-30.01205	To just south of Isipingo Beach	Scottburgh, Park Rynie, Umkomaass, Illovo, Amanzimtoti
51	31.14903	-29.62306	To Desainagar	Durban, Umhlanga Rocks, Umdloti Beach
52	31.46025	-29.26026	To just north of Zinkwazi Beach	Westbrook, Ballito, Blythdale Beach
53	31.81668	-28.94383	To just east of Mtunzini	Tugela River, Dunn's Reserve
54	32.2117	-28.69975	To Mbonambi Beach	Richards Bay
*55	32.46202	-28.31805	To just north of First Rocks	Dawson's Rocks, Maphelane, Cape St. Lucia, St. Lucia
56	32.58902	-27.86866	To Bhukwini	Mission Rocks, Cape Vidal, Leven Point
*57	32.71765	-27.41544	To just north of Gobey's Point	Liefeldts Rocks, Sodwana Bay
58	32.87288	-26.97485	To Kosimeer	Hulley Point, Black Rock

3.2.2 Data analyses

The data for KwaZulu-Natal species were compiled and two biogeographic analyses were carried out. Firstly, the presence/absence of KwaZulu-Natal seaweeds in 50 km sections of the South African coastline were compiled and extracted from records based on existing literature and collections (Bolton and Anderson *pers. comm.* 2011) (dataset 1). Secondly, the presence/absence (as opposed to relative abundance cover data used in Chapter 2) of *Thalassodendron ciliatum* macroalgal epiphyte species per sample, identified from collections made in the current study.

This epiphyte records were compared to their known distributions in the 50 km sections of the South African coastline (dataset 2). Those epiphyte species that were identified to species level that are recorded on the existing South African seaweed list (dataset 1), were used to create dataset 2. These two datasets were then analysed separately by average linkage Bray-Curtis cluster analyses and Detrended Correspondence Analysis (DECORANA) ordination plots (Community Analysis Package version 4.0 PISCES Conservation Ltd. 2007). ANOSIM analyses were run on the pre-selected groups to test whether the samples within groups were more similar than would be determined by chance.

Average linkage Bray-Curtis cluster analysis and DECORANA ordination plots were conducted on all recorded epiphyte macroalgae presence/absence data per sample to explore biogeographic and temporal differences between the Jesser Point and Maphelane seagrass epiphyte collections (Community Analysis Package version 4.0 PISCES Conservation Ltd. 2007).

3.3 Results

Ninety nine epiphyte taxa were identified in this dissertation (see Chapter 2, Table 2.1 and Appendix). Of these, the Rhodophyta were represented by 68 taxa, the Phaeophyceae by 13 taxa, the Chlorophyta by 17 taxa, and Cyanobacteria by a single taxon. Thirty four taxa could not be indentified to species. Thirty nine of the seaweed epiphytes out of the 70 identified to species are included in the existing list of seaweed species distributions, leaving 31 potential new records for South Africa.

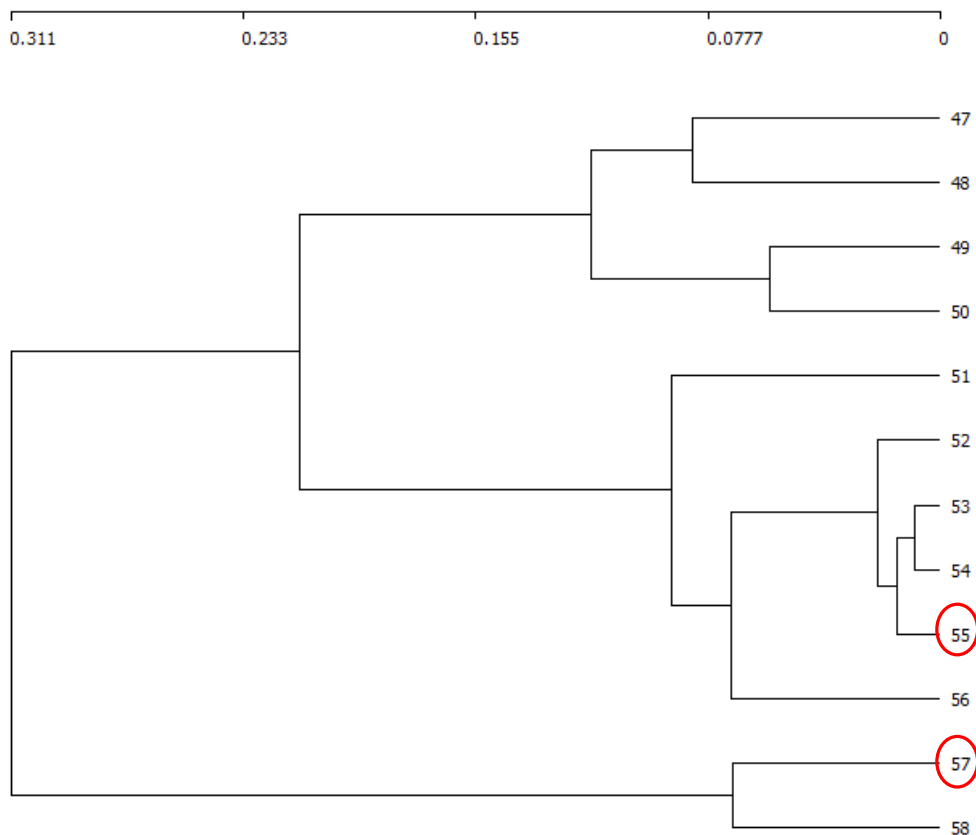


Figure 3.1: Average linkage Bray-Curtis cluster analysis of all recorded seaweed species occurring in 50 km sections of the KwaZulu-Natal coast (dataset 1, Bolton and Anderson *pers. comm.* 2011). Maphelane falls into section 55 and Sodwana Bay into section 57 (circled), in separate clusters at the 0.311 level of dissimilarity.

Analysis of seaweed records along the coast of KwaZulu-Natal (Figure 3.1) produced a primary division between sections 47-56 (St Michaels-on-Sea to Bhukwini) and 57-58 (just north of Gobey's Point to Kosi Bay). The division at the next level was between sections 47-50 (Isipingo Beach to Desainager) and 51-56 (just north of Desainager to Bhukwini). Maphelane falls into coastal section 55 and Jesser Point (Sodwana Bay) into coastal section 57, thereby indicating marked differences between algal communities in these two locations, in different groups at the first separation, in separate clusters at the 0.311 level of dissimilarity. A DECORANA ordination plot (Figure 3.2) supports the differentiation in

seaweed epiphytes between the two locations of interest, showing this separation on Axis 1 between Maphelane (section 55) and Sodwana Bay (section 57).

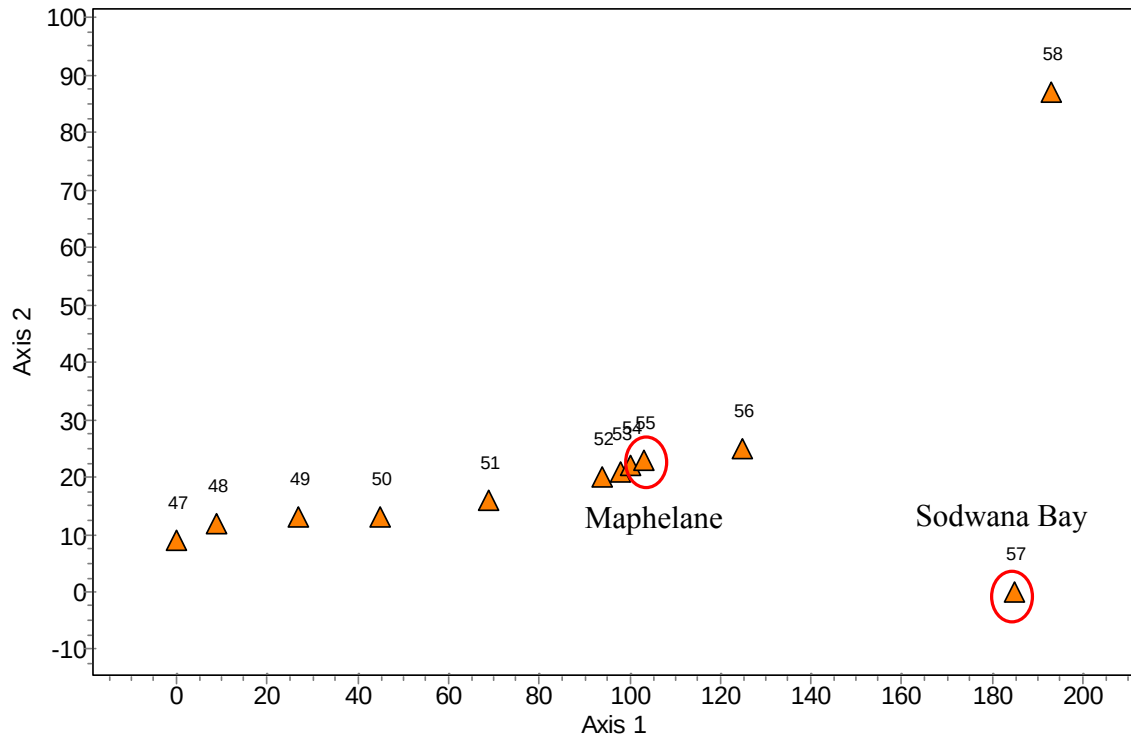


Figure 3.2: DECORANA ordination plot of recorded seaweed species occurring in 50 km sections of the KwaZulu-Natal coast (dataset 1, Bolton and Anderson *pers. comm.* 2011). (Eigen-values: Axis 1= 0.288788, Axis 2= 0.0438585).

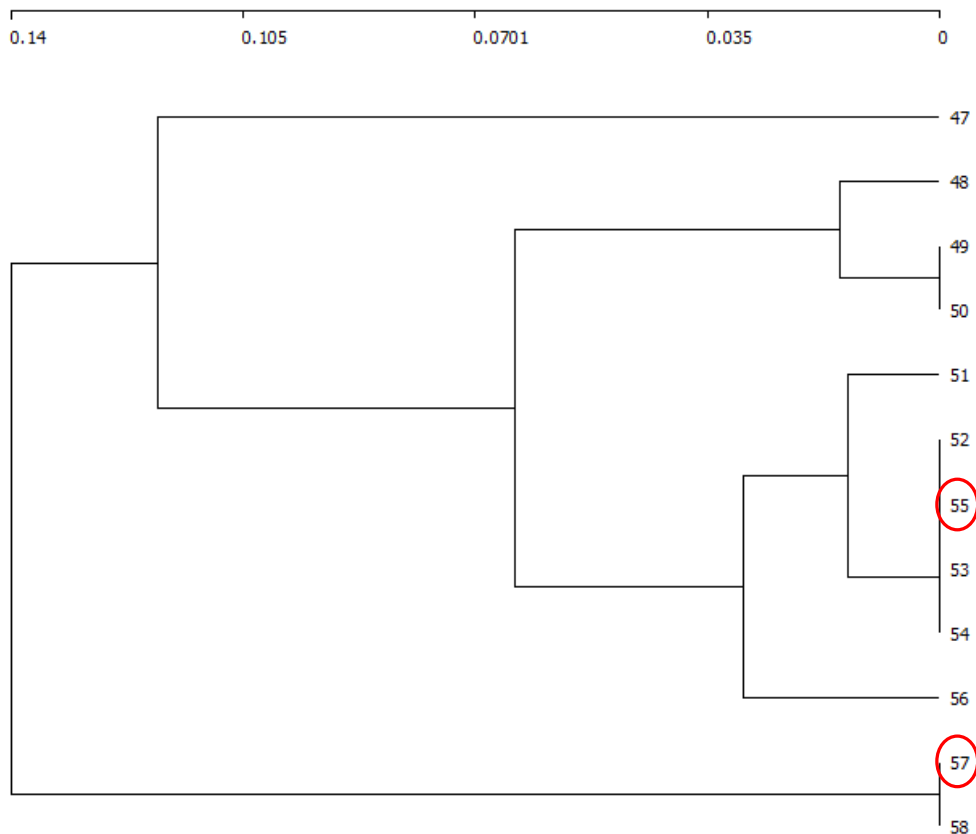


Figure 3.3: Average linkage Bray-Curtis cluster analysis of all species (presence/absence) of seaweed epiphytes listed in South African records (dataset 2) growing on *Thalassodendron ciliatum* occurring in 50 km sections of the KwaZulu-Natal coast (based upon a subset of dataset 1). Maphelane falls into section 55 and Sodwana Bay into section 57 (circled), in separate clusters at the 0.14 level of dissimilarity.

Similar analyses of the epiphytic macroalgae associated with the South African rocky shore seagrass, *Thalassodendron ciliatum* (all identified epiphytic species recorded on the South African database included, dataset 2) showed even stronger separation between 57/58 and the other sections in KwaZulu-Natal, with Maphelane (section 55) differing from Sodwana Bay (section 57) with regard to the macroalgal epiphytes growing on *T. ciliatum* (Figure 3.3). The two collection sites fall into separate clusters at the 0.14 level of dissimilarity. The data suggests that the seaweed epiphytes are from the regions assessed, with the epiphytes (dataset 2, Figures 3.3 & 3.4) displaying a similar pattern to that of the South African seaweed data (dataset 1, Figures 3.1 & 3.2). In Figure 3.4, section 47 is seen as an

outlier, differing from 48-56 (just north of St Michaels-on-Sea to Bhukwini (including Mission Rocks, Cape Vidal and Leven Point)). This was followed by a division between sections 48-50 (from just north of St Michaels-on-Sea to just south of Isipingo Beach) and 51-56 (between Durban and Bhukwini). This was again supported by a DECORANA ordination plot (Figure 3.4) which confirms the split, illustrated on axis 1, between the sections in which Maphelane and Sodwana Bay fall.

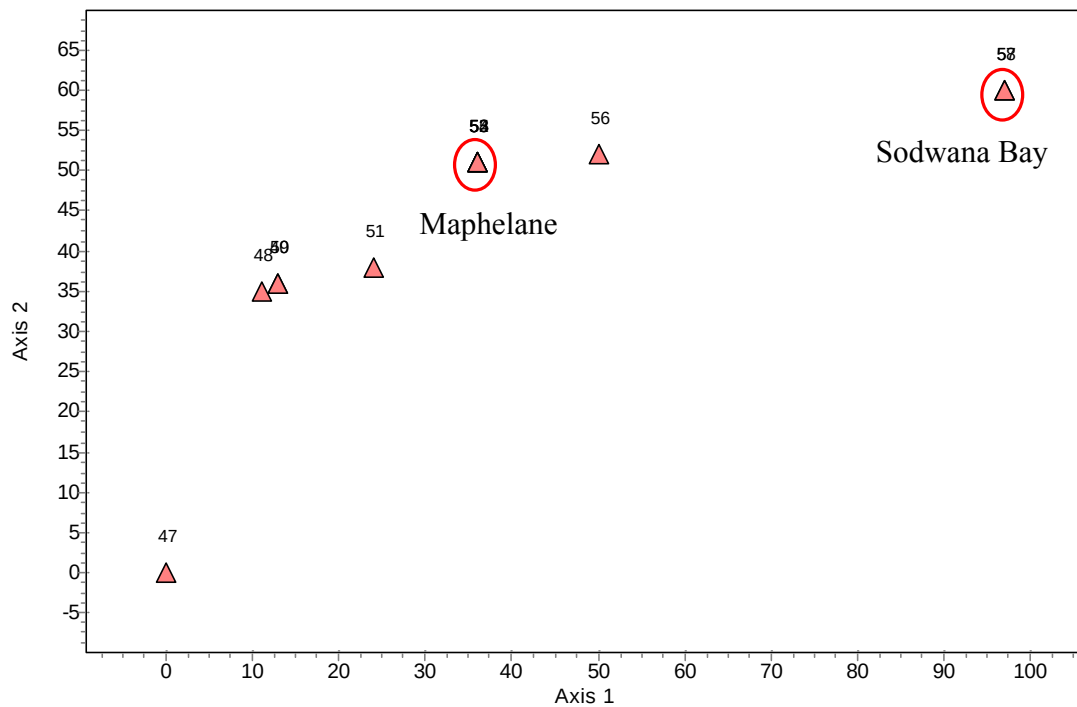


Figure 3.4: DECORANA ordination plot of the predicted occurrence of all species (presence/absence) of seaweed epiphytes growing on *Thalassodendron ciliatum* occurring in 50 km sections of the KwaZulu-Natal coast (dataset 2) (based upon a subset of dataset 1). (Eigen-values: Axis 1= 0.118487, Axis 2= 0.00195027).

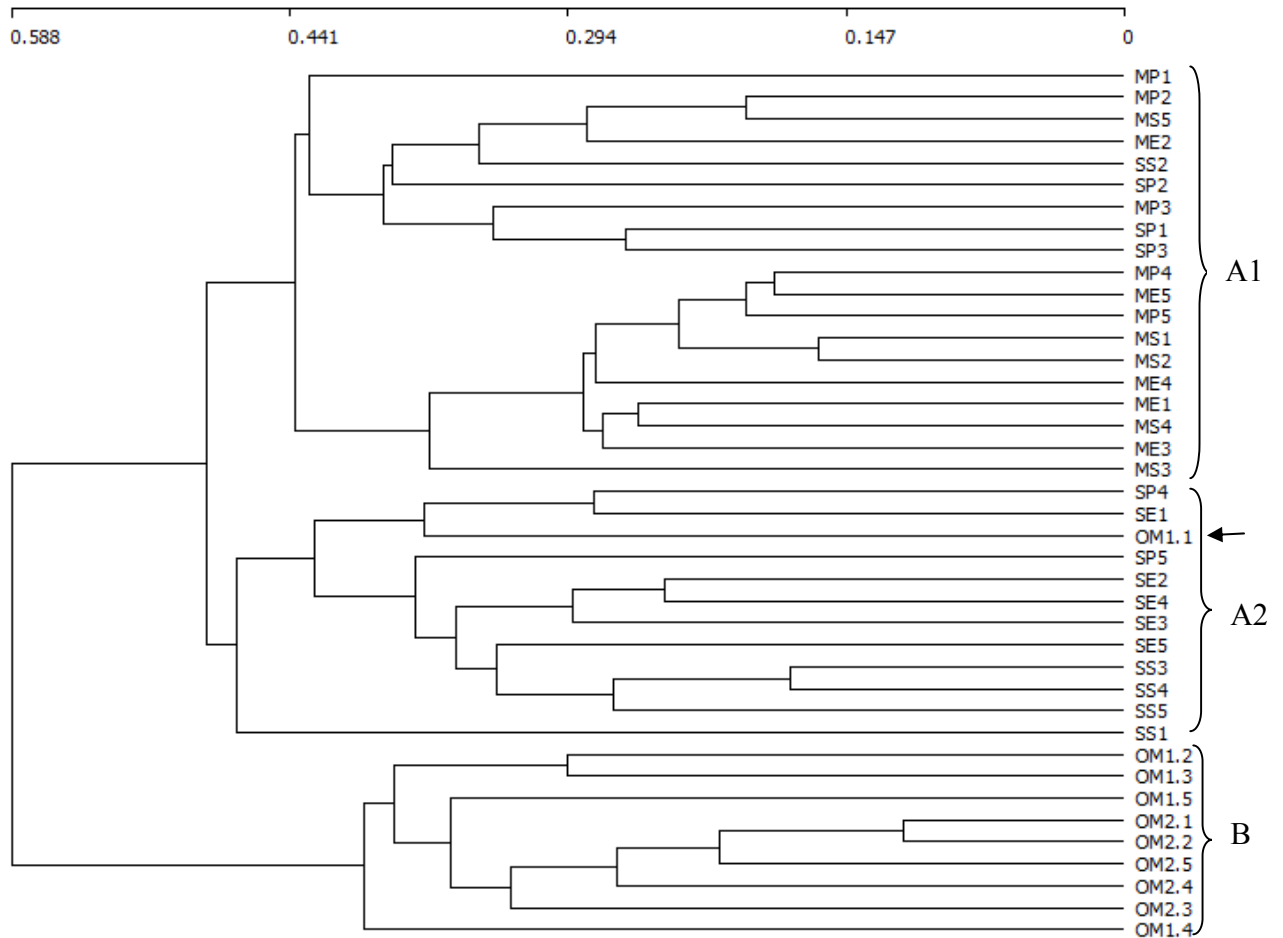


Figure 3.5: Average linkage Bray-Curtis cluster analysis of all samples, based on species presence/absence of all seaweed epiphytes occurring on *Thalassodendron ciliatum* from collections in March 2010 (M) from Jesser Point (Pools P, Exposed E, Subtidal S), in September 2010 (S) from Jesser Point (Pools P, Exposed E, Subtidal S), and in October 2010 (OM) from Maphelane.

Jesser Point samples (A1 & A2) separate from those collected from Maphelane (B) at the 0.588 level of dissimilarity. Jesser Point samples collected in March (A1) separate from those collected in September (A2) at the 0.478 level of dissimilarity.

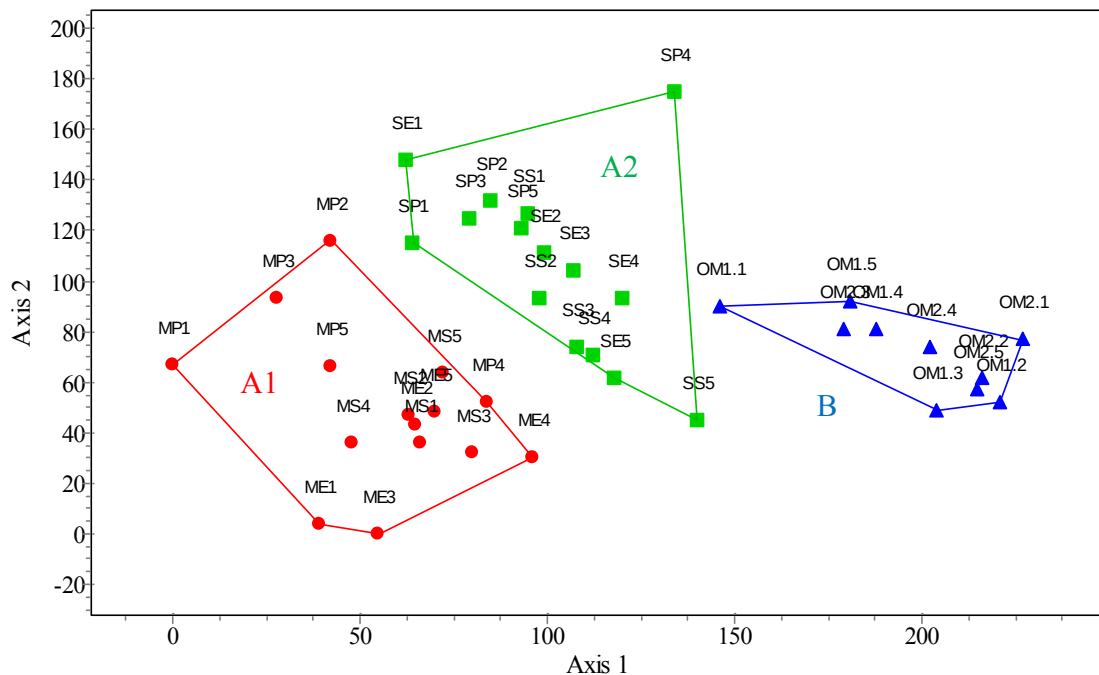


Figure 3.6: DECORANA ordination plot of all samples, based on species presence/absence of all seaweed epiphytes occurring on *Thalassodendron ciliatum* from collections in March 2010 (M) from Jesser Point (Pools P, Exposed E, Subtidal S) (red dots), in September 2010 (S) from Jesser Point (Pools P, Exposed E, Subtidal S) (green squares), and in October 2010 from Maphelane (OM) (blue triangles). (Eigen-values: Axis 1= 0.30837, Axis 2= 0.134952). Shapes include samples identified as similar in Figure 3.5 (Cluster analysis).

An average linkage Bray-Curtis cluster analysis on the presence/absence records of all identified and recorded epiphytic macroalgae sampled on *Thalassodendron ciliatum* during three collections showed both temporal and biogeographic differences (Figures 3.5 & 3.6). Figure 3.6 indicates that samples collected from Jesser Point (A1 & A2) differed from those collected from Maphelane (B), with the exception of sample OM1.1, collected from Maphelane. The division at the next level in Figure 3.5 shows temporal differences between Jesser Point samples collected in March (A1) and September (A2) 2010. Again there are exceptions with samples Subtidal 2 (SS2), Pools 1 to 3 (SP1, SP2 and SP3) collected from

Jesser Point in September 2010. The DECORANA ordination plot (Figure 3.6) supports these patterns. Although Eigen-values are relatively low, with individual samples not being very similar to each other, they do still cluster together and separate along axis 1. In the DECORANA ordination plot it appears that axis 2 displays the temporal difference since the September Jesser Point samples are nearer the Maphelane October samples than the March Jesser Point samples (Figure 3.6).

3.4 Discussion

3.4.1 General epiphyte diversity

The South African *Thalassodendron ciliatum* seaweed epiphytic flora recorded in this dissertation comprises 99 taxa. This is a high figure, in keeping with the biogeographical position of the northern KwaZulu-Natal region, falling into the Indo-West Pacific, the most species-rich world marine coastal region (Lüning 1990; Van den Hoek 1984). Borowitzka *et al.* (1990) recorded 150 macroalgal epiphytes on the seagrass *Amphibolis* in south western Australia. Coppejans *et al.* (1992) recorded 33 epiphytic taxa on seagrasses in Kenya. Leliaert *et al.* (2001) recorded 49 seaweed epiphytes on 10 seagrass species sampled in Tanzania.

When comparing the macroalgal epiphytes identified in previous studies in other localities, few species found in the current study were recorded further north on the southern African east coast. Coppejans *et al.* (1992) had two species in common with the species observed herein: *Sphacilaria rigidula* and *Gracilaria corticata*. Species in common with this study and that in Tanzania by Leliaert *et al.* (2001) are *Gracilaria corticata* and *Herposiphonia secunda* f. *tenella*. Bandeira (2002), although not specifying the total number of epiphytes observed in his study, listed the 15 most abundant seaweed epiphytes observed on *T. ciliatum* in southern Mozambique, of which 4 were found in the current study (*Jania subulata*, *Halimeda cuneata*, *Pneophyllum amplexifrons*, *Hypnea rosea*). Both Bandeira (2002) and the current study identified species of *Griffithsia*, *Ulva*, *Plocamium* and *Cladophora*. Bandeira (2002) noted that there were more epiphytes on rocky habitat *Thalassodendron ciliatum* compared to sandy habitat plants and found that *P. amplexifrons*

made up 80% of epiphyte dry weight biomass. This species was also identified as the most frequent and highly abundant epiphyte species on South African rocky shore *T. ciliatum*.

The current research was unable to determine whether any species are exclusively epiphytic on *Thalassodendron ciliatum*, perhaps because so little is known about many of the species. Chamberlain and Norris (1994) previously described *Pneophyllum amplexifrons*, in KwaZulu-Natal. They examined, described and compared *P. amplexifrons* to type specimens of *Melobesia amplexifrons* confirming that they are indeed the same species, and their study thus concluded that *P. amplexifrons* grows epiphytically on numerous host species in different regions of the world.

Certainly the more abundant epiphytic species on KwaZulu-Natal rocky shore *Thalassodendron ciliatum* do not grow epiphytically on this species exclusively and are not obligate epiphytes. One example is: *Pneophyllum amplexifrons* has been recorded as epiphytic on *Gelidium pteridifolium* (Chamberlain & Norris 1994). *P. amplexifrons* has an unusual growth form, growing as collars around the stems of *T. ciliatum*. Perhaps then, it is more likely to be a specific epiphyte of seaweeds with stiff axes (as is the case with *G. pteridifolium*). Another example is: *Hydrolithon farinosum* on *Sargassum linearifolium* (Penrose & Chamberlain 1993). Presumably also *H. farinosum* grows best on seaweeds with broad flat leaves or blades.

3.4.2 Seaweed biogeography patterns in KwaZulu-Natal

The distributions of known seaweeds from KwaZulu-Natal showed a distinct break between coastal sections 55 and 57, confirming previous findings of Bolton *et al.* (2004) that the seaweed compositions in these regions differ. Maphelane lies south of St. Lucia, within an area that encompasses a mixture of temperate and tropical seaweed species. North of Cape St. Lucia, the continental shelf is narrow and the shelf break near inshore, therefore the southward flowing Agulhas Current dominates and warms the coastal environment. At Cape St. Lucia, the shelf widens and the coast indents, forming the fairly shallow Natal Bight (up to 50 km wide). This diverts the current from the coast and upwelling occurs, thereby making the coastal environment south of Cape St. Lucia, including the area in

which Maphelane falls, slightly cooler than the Agulhas Current (Anderson & Bolton 2005). Since seawater temperature strongly influences species diversity and composition, this is a plausible reason for the separation in the presence of species recorded in Maphelane and Jesser Point. Other explanations may include the influence of differences in turbidity and presence of different grazers in the two areas of interest, although there is little evidence for this.

Similarly, in Figures 3.3 and 3.4, when only species known as epiphytes on *Thalassodendron ciliatum* (dataset 2) were analysed, on the basis of dataset 1, a similar pattern to the above was obtained. This indicates that the distribution of these epiphytes is also determined by the conditions that control the flora as a whole.

3.4.3 Spatial and temporal patterns

When data from individual samples were analysed, the general pattern that emerged was that of separation into localities (separation between those from Jesser Point and those from Maphelane), again confirming this biogeographical pattern. There was an outlier for which explanations remain uncertain. This outlying sample contained *Ectocarpoid* sp.1, which was observed to occur more frequently in the Jesser Point samples and in only two of the Maphelane samples.

The second general pattern that emerged was a difference between the March and September samples collected from Jesser Point. Thus, at least some of the more important species appear to display temporal differences. Some examples are: *Polysiphonia coacta* and *Gracilaria corticata* which were frequently observed in spring but rare in autumn samples, and *Jania intermedia* which was observed in autumn samples but not spring, with *Jania subulata* being observed in spring but not autumn samples. The use of temporal comparisons may suggest possible seasonal differences. However, further sampling would be required to determine this.

3.4.4 Conclusions

The epiphytes on *Thalassodendron ciliatum* in KwaZulu-Natal show the same biogeographic pattern of distribution as the seaweed flora in general. The epiphyte flora on *T. ciliatum* at Maphelane, south of St. Lucia and Cape Vidal and on the edge of the Natal Bight, differs from the flora on this seagrass at Jesser Point (Sodwana Bay), which lies well north of Cape Vidal. Seaweed biologists believe the region north of Cape Vidal to form part of the greater tropical Indo-West Pacific marine province, whereas southward, the KwaZulu-Natal coast appears to be an area of gradual overlap with the south coast flora (Agulhas marine province) (Lüning 1990; Bolton & Anderson 1997; Bolton *et al.* 2004; Anderson *et al.* 2009).

Furthermore, seaweed epiphytes were shown to vary somewhat temporally at Jesser Point. The results of the current study are also of practical use to managers in the iSimangaliso Marine Protected Area, as they provide a baseline for future studies and a foundation against which to compare future populations and/or communities and monitor changes within them in light of global climate change, as result of both natural and anthropogenic influences.

Chapter 4

Non-geniculate coralline red algae epiphytic on South African *Thalassodendron ciliatum* (Forsskål) den Hartog

4.1 Introduction

The coralline red algae (Corallinophycidae, Rhodophyta) are a unique group of algae and among the most abundant marine organisms found within the photic zone on rocky shores (Steneck 1986; Maneveldt *et al.* 2008). Non-geniculate (encrusting) coralline red algae are widespread in all of the world's oceans, where they frequently occupy much of the primary rocky substratum (Maneveldt *et al.* 2008). These corallines are typically adherent on hard primary substrata (epilithic, e.g. *Spongites fruticulosus* (Ringeltaube & Harvey 2000) and *Leptophytum ferox* (Chamberlain & Keats 1994), or grow as epibionts on other plants (epiphytic, e.g. *Hydrolithon farinosum* (Ringeltaube & Harvey 2000)) and animals (epizoic, e.g. *Synarthrophyton papillatum* (Maneveldt *et al.* 2007)).

Coralline red algae have been separated into geniculate (articulated) and non-geniculate (non-articulated or encrusting). Geniculate corallines are typically branching, tree-like plants which attach to the substratum by crustose or calcified holdfasts. These plants have non-calcified sections (genicula) separating longer calcified sections (intergenicula), making them flexible. On the other hand, non-geniculate corallines lack the uncalcified sections and are impregnated with calcium carbonate throughout, with the exception of the outer most walls of their epithallial cells which are weakly calcified. These non-geniculate corallines are typically encrusting, hence the common name of encrusting corallines.

However, 'articulated' and 'encrusting' are not ideal common names since a few non-geniculate corallines are not crustose, such as the genus *Metamastophora*. The South African rocky intertidal and shallow subtidal zones are rich in diversity of non-geniculate coralline algae (Maneveldt *et al.* 2008). Despite their widespread distribution in South Africa, limited work was conducted on them prior to 1993. Seaweed biologists do not often collect these algae. Consequently, coralline algal collection records are comparatively poorly represented and their taxonomy generally poorly understood in South Africa. This is mainly as a result of specific collection requirements (hammer and chisel in most cases) and special laboratory techniques of identification (dissolving away of the calcium carbonate) using histological methods (Maneveldt *et al.* 2008; Maneveldt & van der Merwe 2012). Apart from these factors, corallines are no more complicated to work with than other

seaweeds. Research on this group, although relatively limited in South Africa, has however, increased drastically over the past few years, with numerous publications from the research group based at the University of the Western Cape, initially led by Derek Keats, and now Gavin Maneveldt (e.g. Keats & Chamberlain 1997; Maneveldt *et al.* 2008; Maneveldt & van der Merwe 2012)

Seagrasses support a great diversity of epiphytic organisms (see studies e.g. Coppejans *et al.* (1992) in Kenya, Leliaert *et al.* (2001) in Tanzania, and Bandeira (2002) in Mozambique). *Pneophyllum amplexifrons* was reported as an abundant epiphyte on *Thalassodendron ciliatum* growing on rocky substrates in southern Mozambique, accounting for 80% of the dry weight biomass of epiphytes in Bandeira's (2002) study. Leliaert *et al.* (2001) recorded crustose corallines as being common epiphytes on the seagrasses around Zanzibar Island, Tanzania, although they did not identify them further.

There is no published data specifically on coralline red algae epiphytic on seagrass in South Africa. No coralline red algae species have specifically been noted as epiphytes on *Thalassodendron ciliatum*, apart from a brief mention on *Pneophyllum amplexifrons* in De Clerck *et al.* (2005) and records of *P. amplexifrons* in Chamberlain and Norris (1994). The seagrass *Thalassodendron ciliatum* is unique in that it occurs on exposed rocky outcrops along the Mozambique and north eastern South African coast, whereas most other seagrasses are restricted to sheltered bays and estuaries. Most of the older literature (e.g. Seagrief 1967) simply called all corallines '*Lithothamnion*' indiscriminantly. The aim of the current study was to identify the non-geniculate coralline red algae that occur epiphytically on South African *T. ciliatum*.

4.2 Materials and Methods

In situ collections were made in 2010 and came from open rocky shores where plants ranged from the intertidal zone (in permanent pools) to subtidal zone seagrass beds approximately 1.5-2 m deep at Jesser Point (Sodwana Bay) (27°32'23"S 32°40'49"E) and Maphelane (28°24'27"S 32°25'36"E), along the northern coast of KwaZulu-Natal, South Africa (see sections 2.2.1 and 2.2.2 in Chapter 2 for further site and collection details).

Plants were examined as far as possible when fresh, or preserved in neutralized 5% commercial Formalin seawater solution. Histological methods follow Maneveldt & van der Merwe (2012) and are summarized below.

In the laboratory specimens were examined under a dissecting microscope, and an area chosen from which to remove a piece for further study. Pieces must be carefully selected and include a small piece of the margin so that details of the medulla can be seen in section. Different sizes and stages of conceptacle development are crucial to achieve a reasonable chance of obtaining multiple life cycle stages in section.

Once a suitable 5 mm diameter or smaller piece was selected, the specimen was placed in 10% nitric acid to decalcify. Once decalcified, the material was placed in 70% ethanol to harden it to a manageable state and then cleaned of any debris or sand with the use of a fine brush. The cleaning process is fundamental as it makes sectioning easier and the final microslide product more useful.

After cleaning, the specimen was transferred from a 70% to a 90% and then a 100% ethanol solution respectively for a minimum of 60 minutes each. Specimens were then air dried for a couple of seconds and immersed in Leica Historesin filtration medium until fully infiltrated. A hardening solution was added to the infiltrate medium upon completion and specimens orientated in the final solution until set. Hardener typically sets within 15-25 minutes and can then be placed in a 60°C oven for an addition 5 minutes.

The specimens were then sectioned 10-15 µm thick using a resin microtome. Each individual section was removed from the microtome blade and immersed in distilled water and arranged on a slide. Once slides were dry, they were stained with toluidine blue. When the stained slides were dry, they were covered with cover slips using DPX mountant for microscopy and placed on a warmer for 2-3 days. Finally, once slides were dry they were examined using 4-40X objectives and the specimens identified using the online identification guide.

Herbarium codes are those used in *Index Herbariorum*, previously in print (Holmgren *et al.* 1990) and now electronically online (Thiers 2011, continuously updated).

4.3 Observations

Three species of non-geniculate coralline algae were identified growing epiphytically on *Thalassodendron ciliatum* (see Table 2.1 in Chapter 2, for all epiphytes identified). *Hydrolithon farinosum* and *Pneophyllum amplexifrons* were commonly observed in samples from both, Jesser Point and Maphelane. Ninety percent of seagrass plants analysed from Sodwana Bay and 98% of plants from Maphelane had *H. farinosum* growing on them, and 88% and 73% of plants had *P. amplexifrons* growing on them, respectively. *Synarthrophyton patena* was less common and only observed on the upper stems of a few plants from the Sodwana Bay September and the Maphelane collections. Taxonomic descriptions and comments on these non-geniculate coralline records follow.

***Hydrolithon farinosum* (J.V.Lamouroux) D.Penrose & Y.M.Chamberlain**

(Figures 4.1- 4.2.7)

BASIONYM: *Melobesia farinosa* J.V.Lamouroux, 1816: 315

SYNONYMS: See Guiry & Guiry (2012). This species has relatively recently been recorded in South Africa, and has not been reported by any other name in this country. Homotypic synonyms: *Melobesia farinosa* J.V. Lamouroux 1816, and *Fosliella farinosa* (J.V. Lamouroux) M.A. Howe 1920. Heterotypic synonym: *Melobesia granulata* (Meneghini) Zanardini 1843.

LECTOTYPE: Epiphytic on *Sargassum acinarium* (Linnaeus) Setchell (formerly *Sargassum linifolium* C.Agardh. CN Herb. Lamouroux) (Chamberlain 1994: 123). See Penrose & Chamberlain (1993: 296) for more information on the lectotype.

TYPE LOCALITY: Mediterranean, unspecified locality (Chamberlain 1994: 123).

REPRESENTATIVE SPECIMENS EXAMINED: In total, 40 samples were examined.

South Africa. KwaZulu-Natal: Jesser Point (Sodwana Bay) (27°32'23"S 32°40'49"E), epiphytic on *Thalassodendron ciliatum* (01.iii.2010, C.M. Browne & J.J. Bolton, UCT ME1, ME2, ME3, ME4, ME5), (02.iii.2010, C.M. Browne & J.J. Bolton, UCT MS1, MS2, MS3, MS4, MS5), (03.iii.2010, C.M. Browne & J.J. Bolton, UCT MP1, MP2, MP3, MP4, MP5), (06.ix.2010, C.M. Browne & J.J. Bolton, UCT SP1, SP2, SP3, SP4, SP5), (08.ix.2010, C.M. Browne & J.J. Bolton, UCT SE1, SE2, SE3, SE4, SE5), (09.ix.2010, C.M. Browne & J.J. Bolton, UCT SS1, SS2, SS3, SS4, SS5), Maphelane (28°24'27"S 32°25'36"E), epiphytic on *T. ciliatum* (10.x.2010, C.J. Ward & A. Connell, UCT OM1.1, OM1.2, OM1.3, OM1.4, OM1.5, OM2.1, OM2.2, OM2.3, OM2.4, OM2.5).

DISTRIBUTION: *Hydrolithon farinosum* has a cosmopolitan distribution. It has been recorded on all continents and in most oceans, with the exception of Antarctica. See Guiry & Guiry (2012).

In South Africa, from Maphelane (approximately 100 km south of Sodwana Bay) to Lala Neck (north of Sodwana Bay), KwaZulu-Natal. Commonly observed growing on the leaves of *T. ciliatum* (Manevelde *et al.* 2008). There have been no formal descriptions of this species for South Africa and so no published records of what the species grows on are available.

DESCRIPTION:

Hydrolithon farinosum is a cosmopolitan species found epiphytic on various algae and on seagrasses. The species is characterised by the following **combination** of features:

- 1) tetra/bisporangia simultaneously cleaved, zonately arranged (Figure 4.2.5), and borne in uniporate conceptacles that lack apical pore plugs (Figure 4.2.3),
- 2) cells of contiguous (adjacent) vegetative filaments joined primarily by cell fusions (Figure 4.2.2); secondary pit connections absent or comparatively rare,
- 3) all plants non-geniculate,
- 4) thallus non-endophytic and lacking haustoria,

- 5) epithallial cells present on vegetative thallus filaments (Figure 4.2.2),
- 6) growth form not arborescent (tree-like),
- 7) thallus lacking a basal layer of predominantly palisade cells throughout (Figure 4.2.2),
- 8) pore canals of tetra/bisporangial conceptacles lined by a ring of conspicuously enlarged cells (Figure 4.2.3) that arise from filaments interspersed among and peripheral to the developing sporangia (Figure 4.2.4), these cells do not protrude into the pore canal, but are oriented more or less perpendicular to the conceptacle roof surface,
- 9) spermatangial (male) conceptacles containing simple (unbranched) spermatangial systems that are confined to the conceptacle floor (Figure 4.2.7), and
- 10) gonimoblast filaments borne only from the margins of the central fusion cell i.e. they are arranged peripherally in the carposporangial conceptacle (Figure 4.2.6).

Character 1 places the taxon within the order Corallinales and family Corallinaceae, characters 2 and 3 within the subfamily Mastophoroideae, and the remaining 7 features collectively within the genus *Hydrolithon*. Within the genus *Hydrolithon*, South African plants ascribed to *H. farinosum* are characterised by being:

- 1) thin (up to 150 μm thick, reproductively mature thalli no more than 2-5 cells thick),
- 2) epiphytic (Figure 4.1), and
- 3) possessing dimerous internal construction (Manevelde *et al.* 2008).

All 13 of these characters were clearly evident in this study's samples for this taxon.

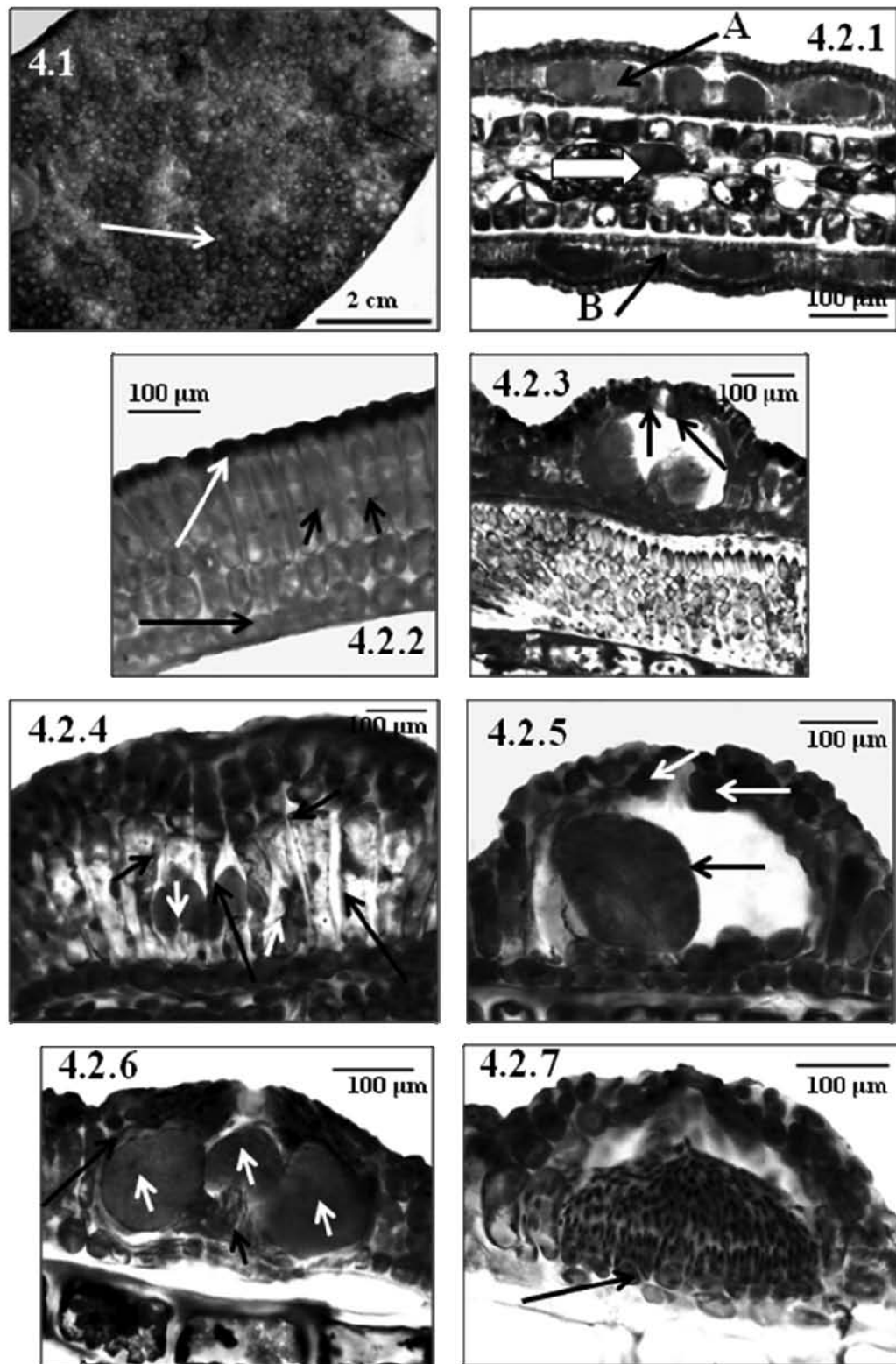


Figure 4.1: External appearance of *Hydrolithon farinosum* (arrow) growing on a *Thalassodendron ciliatum* leaf.

Figures 4.2: Vegetative and reproductive anatomy of *H. farinosum* growing on *T. ciliatum*.

Figure 4.2.1: Cross section through a leaf of *T. ciliatum* (white arrow) showing the general habit of *H. farinosum* (black arrows A & B).

Figure 4.2.2: Vertical section of the dimerous thallus of *H. farinosum* showing a single basal layer of non-palisade cells (long black arrow), a thallus comprised of no more than five cell layers, and a single layer of rounded epithelial cells (white arrow). Note the cell fusions between cells of continuous filaments (arrow heads).

Figure 4.2.3: Vertical section through the thallus of *H. farinosum* showing a uniporate tetrasporangial conceptacle lacking an apical pore plug. Note the conspicuously enlarged cells lining the pore canal (arrows).

Figure 4.2.4: Immature tetrasporangial conceptacle showing the development of the conceptacle roof from filaments interspersed among (long black arrows) and peripheral (arrowheads) to the sporangial initials (white arrowheads).

Figure 4.2.5: Vertical section through a tetrasporangial conceptacle of *H. farinosum* showing zonately arranged tetraspores (black arrow). Note the enlarged vertically orientated cells (white arrows) lining the base of the pore canal.

Figure 4.2.6: Vertical section through a carposporangial conceptacle of *H. farinosum* showing peripherally arranged gonimoblast filaments (long black arrow) terminating in large carpospores (white arrowheads). Note the unfertilised remains of the carpogonial branches at the centre of the chamber floor (black arrowhead).

Figure 4.2.7: Vertical section through a male conceptacle of *H. farinosum* showing simple spermatangia (arrow) distributed across the conceptacle floor.

***Pneophyllum amplexifrons* (Harvey) Y.M.Chamberlain & R.E.Norris**

(Figures 4.3- 4.4.7)

BASIONYM: *Melobesia amplexifrons* Harvey, 1849: 110

SYNONYMS: See Guiry & Guiry (2012). In South Africa no other names have been reported.

LECTOTYPE: Epiphytic on *Gelidium pteridifolium*. TCD (unnumbered). See Chamberlain & Norris (1994: 10) for more information on the lectotype. Isolectotype material also exists at TCD and BM (see Woelkerling & Campbell 1992, fig 63B).

TYPE LOCALITY: Port Natal (i.e. Durban), South Africa (Chamberlain & Norris 1994: 10)

REPRESENTATIVE SPECIMENS EXAMINED: In total, 40 samples were examined.

South Africa. KwaZulu-Natal: Jesser Point (Sodwana Bay) (27°32'23"S 32°40'49"E), epiphytic on *Thalassodendron ciliatum* (01.iii.2010, C.M. Browne & J.J. Bolton, UCT ME1, ME2, ME3, ME4, ME5), (02.iii.2010, C.M. Browne & J.J. Bolton, UCT MS1, MS2, MS3, MS4, MS5), (03.iii.2010, C.M. Browne & J.J. Bolton, UCT MP1, MP2, MP3, MP4, MP5), (06.ix.2010, C.M. Browne & J.J. Bolton, UCT SP1, SP2, SP3, SP4, SP5), (08.ix.2010, C.M. Browne & J.J. Bolton, UCT SE1, SE2, SE3, SE4, SE5), (09.ix.2010, C.M. Browne & J.J. Bolton, UCT SS1, SS2, SS3, SS4, SS5), Maphelane (28°24'27"S 32°25'36"E), epiphytic on *T. ciliatum* (10.x.2010, C.J. Ward & A. Connell, UCT OM1.1, OM1.2, OM1.3, OM1.4, OM1.5, OM2.1, OM2.2, OM2.3, OM2.4, OM2.5).

DISTRIBUTION: *Pneophyllum amplexifrons* has been recorded in the Cape Verde Islands (Atlantic), India (South-west Asia), and in Madagascar, Mozambique and South Africa. See Guiry & Guiry (2012).

In South Africa: Palm Beach (south of Port Shepstone, KwaZulu-Natal) northward into Mozambique (Manevelde *et al.* 2008). Abundant intertidally in rock pools, epiphytically on leaves and stems of the seagrass *T. ciliatum*, and also epiphytic on other intertidal algae, including *Gelidium pteridifolium*, *Chamaedoris delphinii* and *Halimeda* spp. (Chamberlain & Norris 1994: 10).

DESCRIPTION:

Pneophyllum amplexifrons is an epiphytic species that forms successive, trumpet-like thalli around its host plant (Figure 4.3) that may overlap or fuse at the rims to create dumb-bell shapes. The thallus surface is sometimes noticeably ribbed.

Pneophyllum amplexifrons is characterised by the following **combination** of features:

- 1) tetra/bisporangia simultaneously cleaved, zonately arranged (Figure 4.4.6), and borne in uniporate conceptacles that lack apical pore plugs (Figure 4.4.3),
- 2) cells of contiguous (adjacent) vegetative filaments joined primarily by cell fusions (Figure 4.4.2), secondary pit connections absent or comparatively rare,
- 3) all plants non-geniculate,
- 4) thallus non-endophytic and lacking haustoria,
- 5) epithallial cells present on vegetative thallus filaments,
- 6) growth form not arborescent (tree-like),
- 7) thallus primarily dimerous, but may be secondarily monomerous, but lacking a basal layer of predominantly palisade cells throughout (Figure 4.4.2),
- 8) pore canals of tetra/bisporangial conceptacles lined by cells that arise from filaments interspersed among and peripheral to the developing sporangia; these cells protrude into the pore canal as papillae and are orientated more or less parallel, or at a steep angle to the conceptacle roof surface (Figure 4.4.4),
- 9) spermatangial (male) conceptacles containing simple (unbranched) spermatangial systems that are confined to the conceptacle floor (Figure 4.4.7),
- 10) gonimoblast filaments borne only from the margins of the central fusion cell i.e. they are arranged peripherally in the carposporangial conceptacle

Character 1 places the taxon within the order Corallinales and family Corallinaceae, characters 2 and 3 within the subfamily Mastophoroideae, and the remaining features collectively within the genus *Pneophyllum*. Within the genus *Pneophyllum*, South African plants ascribed to *P. amplexifrons* are characterised by:

1) forming thick, trumpet-shaped adjoining thalli encircling seagrasses and green algal stalks (Manevelde *et al.* 2008), and

2) being commonly epiphytic on *T. ciliatum* (Figure 4.3).

Except for character 10 above (no female plants were observed in this study) all of these characters were clearly evident in this study's samples for this taxon.

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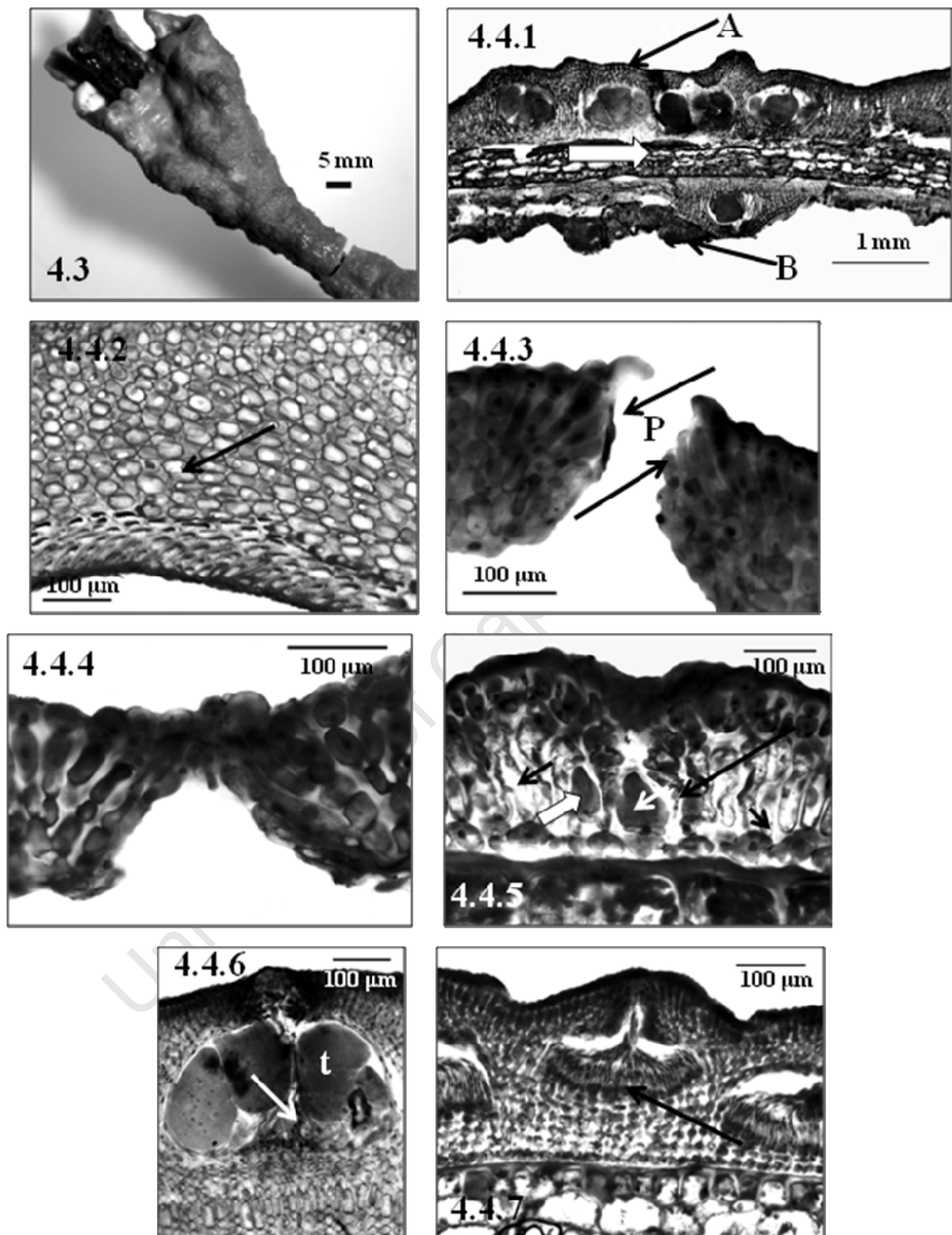


Figure 4.3: External appearance of *Pneophyllum amplexifrons* growing on *Thalassodendron ciliatum*. Note the trumpet-shaped appearance of the alga and how it encircles the seagrass stem.

Figures 4.4: Vegetative and reproductive anatomy of *P. amplexifrons* growing on *T. ciliatum*.

Figure 4.4.1: Cross section through a leaf of *T. ciliatum* (white arrow), showing the general habit of *P. amplexifrons* (black arrows A & B).

Figure 4.4.2: Vertical section of the secondarily monomerous thallus showing a single basal layer of non-palisade cells. Note the cell fusions between cells of continuous filaments (arrow).

Figure 4.4.3: Vertical section through the pore canal (P) of a tetrasporangial conceptacle showing the absence of an apical pore plug and papillate cells (arrows) lining the pore canal.

Figure 4.4.4: Pore canal filaments orientated inward rather than perpendicular to the tetrasporangial conceptacle roof.

Figure 4.4.5: Immature tetrasporangial conceptacle showing the development of the conceptacle roof from filaments interspersed among (arrow) and peripheral (arrowheads) to the sporangial initials (white arrowheads).

Figure 4.4.6: Tetrasporangial conceptacle showing zonately arranged tetraspores (t) arranged peripherally around a central columella (arrow).

Figure 4.4.7: Male conceptacle showing simple spermatangia (arrow) distributed across the conceptacle floor.

***Synarthrophyton patena* (D.J.Hooker & Harvey) R.A.Townsend**

(Figures 4.5.1- 4.5.4)

BASIONYM: *Melobesia patena* D.J.Hooker & Harvey in Harvey 1849:111, fig.40.

SYNONYMS: See Guiry & Guiry (2012). No previous names have been used in South Africa.

LECTOTYPE: Colenso 1331; TCD (Womersley 1996: 209). Notes: Designated by Chapman & Parkinson (1974, pl. 72).

TYPE LOCALITY: Flat Point (near Castlepoint), New Zealand (Townsend 1979)

REPRESENTATIVE SPECIMENS EXAMINED: In total, 7 samples were examined. South Africa. KwaZulu-Natal: Jesser Point (Sodwana Bay) (27°32'23"S 32°40'49"E), epiphytic on *Thalassodendron ciliatum* (03.iii.2010, C.M. Browne & J.J. Bolton, UCT MP1); Maphelane (28°24'27"S 32°25'36"E), epiphytic on *T. ciliatum* (10.x.2010, C.J. Ward & A. Connell, UCT OM1.2, OM1.3, OM1.4, OM2.2, OM2.3, OM2.4).

DISTRIBUTION: *Synarthrophyton patena* has been recorded in the Falkland Islands (Atlantic), Chile (South America), South Africa, Heard Island (Indian Ocean Islands), as well as in Australia and New Zealand: New South Wales, New Zealand, Norfolk Island, South Australia, Tasmania, Victoria, and Western Australia. See Guiry & Guiry (2012).

In South Africa: from Robben Island (Table Bay, off the Cape Peninsula) to Sodwana Bay (KwaZulu-Natal) (Manevelde *et al.* 2008).

DESCRIPTION:

Occurs epiphytically on a variety of green, brown and red algae, and on seagrasses, tunicates, molluscs and sponges, found in intertidal pools and subtidally to depths of 37 m (Womersley 1996).

Synarthrophyton patena is characterised by the following **combination** of features:

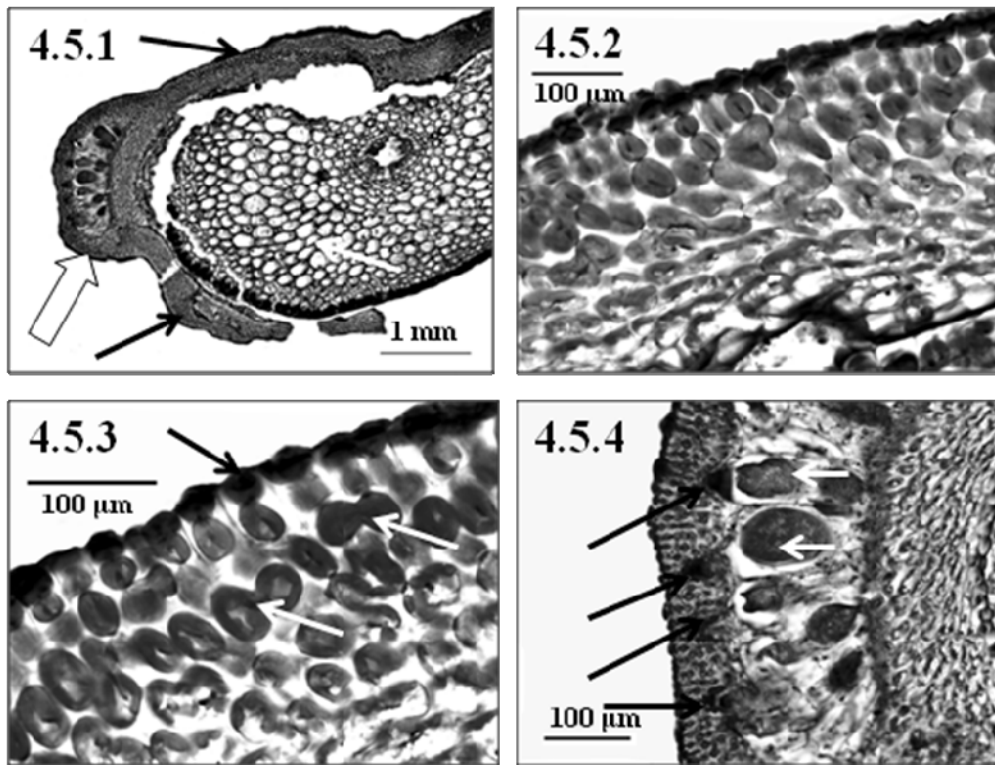
- 1) tetra/bisporangia simultaneously cleaved, zonately arranged, and borne in multiporate conceptacles that have apical pore plugs (Figure 4.5.4),
- 2) all plants non-geniculate,
- 3) cells of contiguous (adjacent) vegetative filaments joined primarily by cell fusions (Figure 4.5.3), secondary pit connections absent or comparatively rare,
- 4) tetra/bisporangial conceptacle pore plate of cellular construction
- 5) thallus non-endophytic and lacking haustoria,
- 6) growth form not arborescent (tree-like),

- 7) thallus construction monomerous throughout (Figure 4.5.2),
- 8) outermost walls of terminal epithelial cells are rounded or flattened, but without flared corners (Figure 4.5.3),
- 9) subepithelial initials as long as, or longer than their immediate inward derivatives (Figure 4.5.2).

Characters 1 and 2 place the taxon within the order Corallinales and family Hapalidiaceae, characters 3 and 4 within the subfamily Melobesioideae and the remaining features variously within the genera *Clathromorphum*, *Mesophyllum* and *Synarthrophyton*. The only way to separate these three genera based on traditional anatomical characters, is with the presence of male conceptacles. This study, however, did not find male plants among its material. Fortunately, among these three genera, South African plants ascribed to *S. patena* are characterised by being:

- 1) epiphytic on a host of fleshy, turf algae (not restricted to *Amphiroa* spp. or *Ecklonia maxima*), but not on geniculate corallines, and
- 2) discoid in appearance with conceptacle roofs raised and dome-like (rather than flush to somewhat sunken) (Figure 4.5.1).

These characters were clearly evident in this study's samples for this taxon.



Figures 4.5: Vegetative and reproductive anatomy of *Synarthrophyton patena* growing on *Thalassodendron ciliatum*.

Figure 4.5.1: Cross section through a stem of *T. ciliatum* (white arrow), showing the general habit of *S. patena* (black arrows). Note that conceptacles are raised and dome-like rather than flush or sunken (thick outlined white arrow)

Figure 4.5.2: Vertical section of the monomerous thallus showing a single basal layer of non-palisade cells

Figure 4.5.3: Vertical section of *S. patena* showing a single layer of rounded epithelial cells (black arrow). Note the cell fusions between cells of continuous filaments (white arrows).

Figure 4.5.4: Vertical section through a multiporate tetrasporangial conceptacle showing incompletely formed apical pore plugs (black arrows) and zonately arranged tetrasporangia (white arrow heads).

4.4 Discussion

The results of the present study have shown that at least three species of coralline red algae are present as epiphytes on the seagrass *Thalassodendron ciliatum* from intertidal and shallow subtidal locations on the north eastern coast of South Africa. This is perhaps not surprising as several authors have shown that species of *Hydrolithon* and *Pneophyllum* are common epiphytes on seagrasses in numerous parts of the world (e.g. Humm 1964; Bramwell & Woelkerling 1984; Jones & Woelkerling 1984; Harlin *et al.* 1985). In our collections, on *T. ciliatum*, *P. amplexifrons* is restricted to the seagrass' stems, *H. farinosum* to the leaves, and *S. patena* to the upper stems.

The three epiphytic species are not restricted to South Africa. *Hydrolithon farinosum* is a cosmopolitan species. *Pneophyllum amplexifrons* occurs in the Atlantic and Indian Oceans. *Synarthrophyton patena* occurs in the Atlantic and Indo-Pacific Oceans (Guiry & Guiry 2012).

To discuss the epiphytic nature of these three species the following questions were asked: are they solely epiphytic, and if not, are they exclusively epiphytic in South Africa? Are they found together like this as epiphytes in other locations of the world?

H. farinosum has been recorded as exclusively epiphytic in Australia (Ringeltaube & Harvey 2000). *H. farinosum* is primarily found in the sublittoral to lower sublittoral zones (Penrose & Chamberlain 1993). This cosmopolitan species is found commonly in southern Australian waters on various algae and on the seagrass *Amphibolis antarctica* (Womersley 1996). In South Africa *H. farinosum* has been reported to have a purely epiphytic habit (Manevelde *et al.* 2008). The species has only ever been reported to be epiphytic.

P. amplexifrons is documented as being epiphytic in South Africa (Chamberlain & Norris 1994; Manevelde *et al.* 2008). Various species of *Pneophyllum* are reported growing on seagrasses in Australia (see Womersley 1996). The genus as a whole has only been reported to be epiphytic in South Africa and most other places in the world (e.g. Australia, New Zealand).

S. patena has only been recorded as an epiphyte in South Africa (Gavin Maneveldt *pers. comm.* 2011). However, in Australia it has a range of habitats (Womersley 1996; Harvey *et al.* 2003). May and Woelkerling (1988) report that in southern Australia *S. patena* is found to only grow on the genus of red alga *Ballia* (Ceramiaceae). However, Harvey *et al.* (1994) report from their study in Australia that *S. patena* has been observed to grow epiphytically on a number of seaweeds and has not been noted to occur epilithically. So, from current evidence it seems that this species is an obligate epiphyte, but grows on several species of larger algae as well as seagrasses. *S. patena* interestingly appears to be a temperate seaweed species, not growing in the tropics except for Sodwana Bay. There are no records of *S. patena* in Mozambique, Kenya and Tanzania, and this may be the explanation as to why.

Possible effects these coralline red algal epiphytes may have on their seagrass hosts are that that they block light from reaching the seagrass directly thereby hindering photosynthesis and growth. The distribution of these coralline epiphytes on the seagrass could be explained due to the longevity of the components of the seagrass. The leaves are regularly shed and tend to be epiphytised by the thinner coralline forms, whereas the thicker coralline, *Pneophyllum amplexifrons* was commonly observed on the stems of the seagrass. Since the seagrass stems are longer living, this allows time for the colonisation of *P. amplexifrons* and thickening and growth thereof.

Not all three of the species were observed on every seagrass plant analysed. *Pneophyllum amplexifrons* and *Hydrolithon farinosum* were most abundant and ecologically important, since it was frequently observed that other epiphytes grow on the coralline algae rather than the seagrass itself. It was noted particularly that *Jania* spp. grew out of the collars of *P. amplexifrons* on the seagrass stems. On the leaves of *Thalassodendron ciliatum* it was also observed that Ectocarpoid spp. And other small seaweed taxa grew over the *Hydrolithon farinosum*. The coralline algae offer a rougher substratum, perhaps more susceptible to attachment of other epiphytic seaweeds, compared to the seagrass surface. Therefore these coralline epiphytes offer a surface for other epiphytes, supporting a greater diversity within the seagrass bed ecosystems.

South African records of coralline algae are increasing (e.g. Maneveldt & van der Merwe 2012). Many species have yet to be studied, especially the less common ones. South Africa has similar numbers of non-geniculate coralline algal species to regions where comparable research has been conducted (Maneveldt *et al.* 2008). No-one can dispute South Africa's high coralline diversity, but it is still a debate as to whether South Africa's diversity is higher than most other regions. Firstly, in light of ongoing molecular studies (e.g. Bittner *et al.* 2011) the taxonomy of the coralline algae globally requires reassessment and thus global species lists would need to be revisited. Secondly, these algae are often very cryptic (easily mistaken for other encrusting organisms such as corals, sponges, etc.). This said, it is not surprising that most taxonomic advances have primarily focused on the more abundant species (Maneveldt *et al.* 2008). Thirdly, the group as a whole has not been well studied globally and species-rich areas such as Brazil and the tropics (Amado-Filho *et al.* 2007, Amado-Filho *et al.* 2010; Villas-Boas *et al.* 2009) may prove to hold an even greater diversity. The regions with the highest diversity of seaweeds in general are Southern Australia, and the tropical Indo-Pacific, and these too may support greater levels of diversity than are currently known. Finally, most detailed descriptions of coralline algae are based on collections from epilithic and epizoic habitats. Greater sampling of epiphytic habitats could reveal a greater diversity of coralline algae that might otherwise have been overlooked on such algal and seagrass hosts.

Chapter 5

General discussion and conclusions

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This dissertation provides the first description of the population structure, diversity and biogeography of *Thalassodendron ciliatum* and its associated macroalgal flora in South Africa and provides new information on this poorly understood seagrass ecosystem.

The findings conclude that South African *Thalassodendron ciliatum* supports a high diversity (99 taxa) of seaweed epiphytes. These macroalgal epiphyte assemblages differ on different parts of the host plant, in differing habitats, temporally, as well as biogeographically. Seaweed epiphytes identified on *T. ciliatum* sampled from Jesser Point (Sodwana Bay) differed from those sampled from Maphelane. The current findings improve our knowledge and understanding of *T. ciliatum* populations at the southern limit of their distributional range in the western Indian Ocean by providing a baseline data record of what occurs in this ecosystem. While it might be assumed that seagrass populations near the edges of their distributional range, such as those in this study, would be in poor condition, which does not seem to be the case with this species. The plants were healthy, numerous, and although the populations sampled are relatively small, they are apparently in good condition.

Thalassodendron ciliatum density was found to be similar between collections made from Jesser Point in March and September 2010, and from Maphelane in October 2010. When comparing seagrass stand densities with *T. pachyrhizum*, the other species in the *Thalassodendron* genus, it was found that densities on *T. ciliatum* in South Africa are lower than those of *T. pachyrhizum* in Western Australia (Marbà and Walker 1999).

In the light of changing global climatic conditions (for example expected increases in temperatures and carbon dioxide levels) many marine environments will experience changes that might affect the distributional ranges of species. It is reasonable to assume that species on the borders of biogeographic regions will be most affected, because the positions of boundaries are likely to change. How might these seagrass populations be affected by such environmental changes?

A study on coastal oceanic climate change and variability around South Africa between 1982 and 2009 by Rouault *et al.* (2010) shows that KwaZulu-Natal seasurface temperatures are warming, and have increased by up to 1.5°C since the 1980s. They argue that the warming is a result of a strengthening of the Agulhas Current in response to a pole-ward shift of westerly winds and an increase in trade winds in the South Indian Ocean at relevant latitudes. Rouault *et al.* (2010) also reported that this strengthened Agulhas Current could have contributed to coastal cooling further south in the Port Alfred dynamic upwelling region.

The shelf break (zone where the shelf begins a steep descent at depths 40-50 m) lies near the KwaZulu-Natal shore, especially north of Cape St. Lucia (2-4 km from shore). Between Cape St. Lucia and Durban lies the Natal Bight, an area where the continental shelf widens (to 50 km at most) and the shoreline indents. This area has a significant influence on coastal oceanography of the region. At the northern end of the Bight a “topographically-driven upwelling cell” (Lutjeharms *et al.* 2000) forms and drives cooler water up through valleys in the edge of the continental shelf, lowering water temperatures in the Bight and creating something of a “biogeographic boundary” to the spread southwards of tropical species (Bolton *et al.* 2004).

If the Natal Bight becomes warmer (for example by weakening of the topographic upwelling) then *Thalassodendron ciliatum*, as a warm water tropical species, may extend its distribution further south down the South African coast. There is not much rocky habitat along the KwaZulu-Natal coast: only about 10% of the total shore between the Mozambique border and the Tugela River mouth comprises rocky outcrops (Anderson & Bolton 2005) and these are separated by long sandy, exposed shores. Therefore there is very limited suitable substrate on which this seagrass can grow. South of the Tugela River mouth, along the 300 km of coast to the southern KwaZulu-Natal border the situation changes and up to 25% of the shoreline comprises extensive wave cut platforms and rocky headlands, where there is potential habitat for seagrass, should it extend its distribution that far south.

Since *Thalassodendron ciliatum* got to Maphelane (which is a rocky outcrop just south of a very long sandy beach), why could this species not extend its' distribution to the next rocky outcrop further south along the eastern South African coast? *T. ciliatum* disperses by viviparous seedlings that typically develop attached to the mother plant and are released and take root in the parent's habitat. It is thus hypothesized that such a seedling(s), or plant(s) with seedlings attached, was transported via coastal currents and landed at Maphelane. Molecular population studies should be undertaken to determine whether the Maphelane population is genetically homogeneous and thus to investigate whether the Maphelane population resulted from a single dispersal event. Either the environmental conditions are not suitable, or it has not managed to disperse to sites between Jesser Point (Sodwana Bay) and Maphelane. There is a rocky point at Cape Vidal, and a considerable stretch of rocky shore at Mission Rocks, however, *T. ciliatum* has not been observed in these locations.

If the Agulhas current strengthens, as reported to be doing so by Rouault *et al.* (2010), increased upwelling in the Natal Bight may continue to lower the temperature of water there, reinforcing its "biogeographic boundary" effect and possibly eliminating the *T. ciliatum* population at Maphelane. Such strengthening might be expected to increase water temperatures from Cape Vidal northwards (where the shelf is very narrow), and it might be speculated that *T. ciliatum* populations could increase if temperature is mainly that which is controlling their distribution. Because the shelf narrows again south of the Natal Bight, and particularly in southern KwaZulu-Natal and northern Transkei, a strengthening of the Agulhas Current might be expected to warm inshore waters there and lead to greater numbers of tropical species on those coasts. Conversely, in the event that waters off southern KwaZulu-Natal were to cool, this overlap region should become more dominated by Agulhas province species and lose some tropical elements. Judging from the data presented herein, in the event of the latter, the epiphytic flora of *T. ciliatum* may become dominated by more temperate Agulhas province species and lose tropical ones.

Whatever the outcome of any climatic changes in the area the information in herein should assist scientists and managers to better understand, and if necessary to conserve, these

populations. Conservation usually involves the preservation of individual species or species-rich areas (habitats). These seagrass beds are both, as they support high species diversity. The detailed analysis of a seagrass bed community greatly improves understanding of a region's diversity and conservation status. This may very well become necessary since globally, seagrasses have been declining at a rapid rate and are clearly threatened. The current marine protected areas in KwaZulu-Natal are mainly on the northern coast (Anderson & Bolton 2005). There is a large marine reserve including Sodwana Bay northwards, as well as Cape Vidal and Mission Rocks (part of isiMangaliso). Maphelane is also a reserve. The southern section of KwaZulu-Natal being an overlap region between the tropical Indo-West Pacific and the temperate Agulhas marine provinces should be monitored to assess changes caused by global warming. Further protected areas may be proposed there, subject to findings of monitoring projects addressing both natural and anthropogenic effects on these systems. The coast from Maphelane to Kosi Bay is already protected.

The *Thalassodendron ciliatum* populations on Jesser Point (Sodwana Bay) are relatively small, however, there are more populations just north of this location (notably so at Mabibi, approximately 25 km north of Sodwana Bay). In terms of energy supply to neighbouring habitats, it is believed that *T. ciliatum* may export carbon across the continental shelf. A study in the vicinity of the Prince Edward Islands by Kaehler *et al.* (2006) found, using microscopic and stable isotope analyses, that the chlorophyll signal in offshore location was largely derived from the residual chlorophyll in fresh and decaying particles of the abundant shoreline seaweed, *Macrocystis laevis*. They directly traced the flow of organic matter from source through to consumers and established the relative contribution of coastal macroalgal carbon in various food webs. A similar study was conducted in the western Indian Ocean by Porter in 2009. He used carbon, nitrogen and sulphur isotopes to characterise the isotopic signals of seaweed-derived suspended particulate organic matter (POM) and measured the relative contribution this source made to the uptake of POM by a suite of filter feeders. His study highlighted the importance of inshore inputs on marine communities and trophic links between adjacent inshore, riverine and pelagic ecosystems. Therefore it can be speculated that northern KwaZulu-Natal *T. ciliatum* and its seaweed

epiphytes are exporting carbon/energy to the reef canyons off Jesser Point and neighbouring areas. This is of particular interest as these canyons are home to the only population of South African coelacanths. The shoreline seaweeds and seagrass (including *T. ciliatum* and its epiphytes) may be supplementing carbon through broader food webs.

Thalassodendron ciliatum beds contribute to the overall diversity of the ecosystem, especially as regards habitats on a small scale. Seagrasses provide a high diversity of habitat and food and the seagrass ecosystem (seagrass plus epiphytes) has been found to support over 400 species of mesofauna in the Sodwana Bay beds sampled (Rebecca Milne, Zoology Department, University of Cape Town *pers. comm.* 2011) as well as the 99 species of seaweed epiphytes. The two major sessile groups of macrofauna are the bryozoa and hydrozoa, observed predominantly on the seagrass stems and blades. It appears that few of the fauna are obligate epiphytes on the seagrass. Many of the bryozoa and hydrozoa also grew on the rhizomes, rocks and understorey algae in the seagrass beds (Rebecca Milne *pers. comm.* 2011). These seagrass beds also provide habitat for benthic seaweeds. There were plants of the large *Plocamium telfairiae* at Jesser Point which appeared to live exclusively under the seagrass.

The total of 99 taxa identified on *T. ciliatum* on rocky shores in KwaZulu-Natal is far higher than the 33 taxa recorded on seagrasses in Gazi Bay (Kenya) by Coppejans *et al.* (1992), or the 49 taxa recorded on 10 seagrass species in Zanzibar (Tanzania) by Leliaert *et al.* (2001). At present this diversity cannot be compared with *T. ciliatum* populations in southern Mozambique, since there Bandeira (2002) recorded epiphytes only as “6 functional groups”. It would appear that there are fewer macroalgal epiphyte species on *T. ciliatum* in Kenya and Tanzania because in these studies it was growing in sheltered lagoon environments, whereas the South African *T. ciliatum* populations are growing on an exposed rocky shore.

Whether all of these epiphytes occur in an area because of the seagrass (obligate seagrass epiphytes) or if they would occur there in the absence of the seagrass (either as epiphytes on other larger seaweeds or growing directly on the rock) will only be known when the

biology of most of these small seaweeds is better known. During collections for the current study the dominant epiphyte *Pneophyllum amplexifrons* was not seen elsewhere on the shore.

Three coralline red algae (*Pneophyllum amplexifrons*, *Hydrolithon farinosum* and *Synarthrophyton patena*) were identified as epiphytes on *Thalassodendron ciliatum*. This low diversity may be because seagrasses regularly shed their leaves. The majority of other studies including seagrass epiphytes have not fully identified coralline red algal epiphytes but recorded them rather as a functional form group. *Pneophyllum amplexifrons* is an exception, having been previously recorded (Chamberlain & Norris 1994, De Clerck *et al.* 2005), probably due to it having a fairly distinctive appearance of forming trumpet-shaped structures that encircle stems of hosts (see Figures 2.2 in Chapter 2, Figure 4.3 in Chapter 4 and Figure 31 in the Appendix). It appears that these coralline red algae tend to be pioneer epiphytes and form additional surfaces onto which other seaweed epiphytes can attach and grow. *Jania* species were observed to often grow from inside the *Pneophyllum* collars.

A few specimens of the white-spined sea urchin *Tripneustes gratilla* were observed in the seagrass beds sampled. A study in the Mombasa lagoon (Kenya) found that sea urchins control *T. ciliatum* density by grazing its exposed apical tips (Alcoverro & Mariani 2002). Future studies could investigate the effects of sea urchin, and other fauna, grazing on the KwaZulu-Natal seagrass beds in order to determine if this is affecting seagrass densities (which appear to be lower than in the other *T. ciliatum* beds studied) or the epiphytes on the seagrass.

Integrated research initiatives, such as the African Coelacanth Ecosystem Project (ACEP), are fundamental in achieving a fuller understanding of multi-faceted systems. What this research has contributed to ACEP is information on the diversity of intertidal seagrass and seaweeds, biologically both interesting and important, as they provide diverse habitats and energy/carbon supply to a number of other organisms and to a degree to adjacent habitats.

Future research could map the full distribution of *Thalassodendron ciliatum* and other species of seagrasses along the southern African coastline and determine areal extent. Such information would assist determining and monitoring whether populations are declining, expanding and how they are responding to changing conditions resulting from natural and anthropogenic influences. Molecular studies could also shed light on how *T. ciliatum* can disperse over large distances such as between Jesser Point and Maphelane. Perhaps it has ‘jumped’ sandy areas in other regions too and investigation into the effects currents have on the distribution of this species could be explored. Studies of rocky shore seagrass populations are limited. Does *T. ciliatum* grow on exposed rocky shores further north on the southern African east coast (other than southern Mozambique)?

Molecular studies to determine whether *Thalassodendron ciliatum* in pools are in fact an individual plant, closely related or genetically different, as well as studies comparing the genetics of populations at Maphelane, Jesser Point and further north, would shed light on how far this species can disperse and its relative dispersal success.

Some molecular work shows that apparently cosmopolitan species may in fact consist of sister species. There are local examples of this among seaweeds: *Grateloupia capensis* (De Clerck *et al.* 2005), and two taxa identified in *Laurencia flexuosa* (Caitlynne Francis, Botany Department, University of Cape Town *pers. comm.* 2011). This highlights that in many cases molecular systematic studies across the biogeographic distribution of taxa are often needed. This has been done for very few species and could be focused on *Thalassodendron ciliatum* in the western Indian Ocean.

Comparative studies on the population structure and biogeography of *T. ciliatum* and other seagrasses and their seaweed epiphytes at the level of detail included herein should be undertaken in other east African countries, to determine how this and other seagrass species are surviving and gain further knowledge on the biodiversity they support. If seagrasses continue to decline at the rapid rate which they currently are on a global scale, the biodiversity they support may also be lost.

Chapter 5: General discussion and conclusions

During the course of the current study, it became apparent that there are still large gaps in our knowledge of seaweeds of this region. Evidence for this is the large number of apparent new records for South Africa. A specific and very practical requirement is for the publishing of comprehensive guides on the seaweeds of this region (the western Indian Ocean) - no doubt a requirement that extends to many other marine organisms as well.

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References

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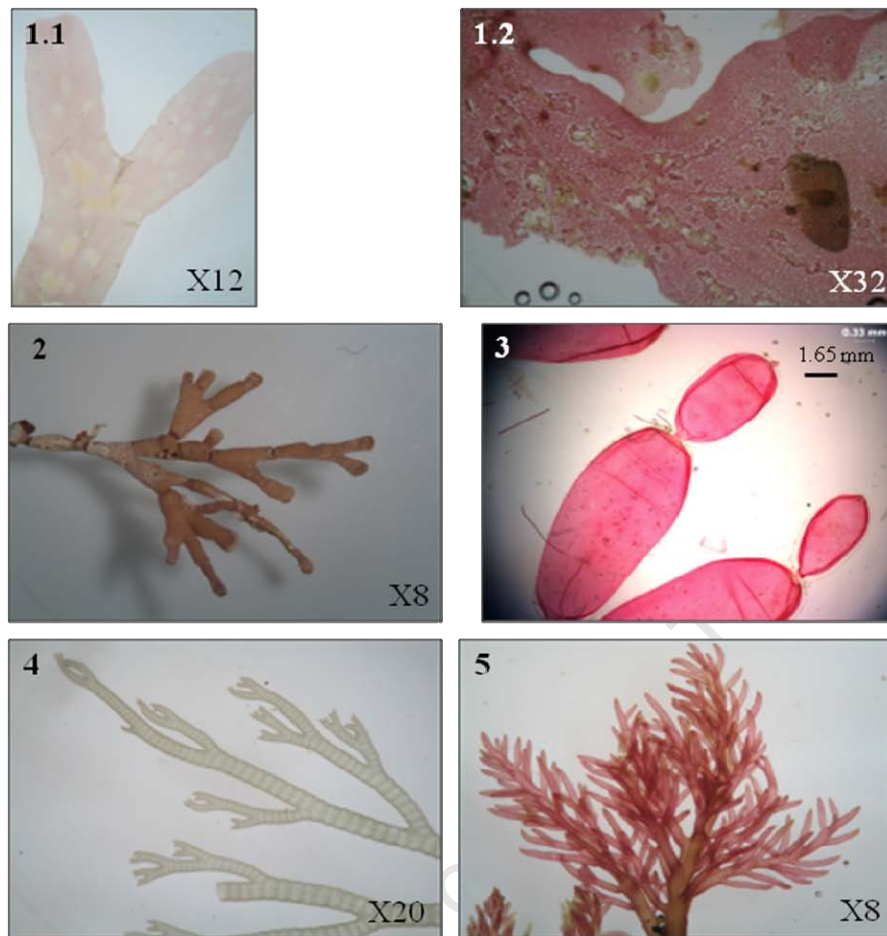
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Appendix

Photos have been taken of most specimens to aid future studies with identification. Only those for which representative photographs could be obtained are included. Scales are approximate. The photographs are arranged firstly displaying the Rhodophyta, followed by the Phaeophyceae, then the Chlorophyta, and lastly the single representative of the Cyanophyta.

University of Cape Town



Approximate scales:

	5 mm
X8	_____
X12	_____
X20	_____
X32	_____

Figures 1-59: Epiphytic seaweed species (with approximate scales) growing on KwaZulu-Natal intertidal and shallow subtidal populations of rocky shore *Thalassodendron ciliatum*. Figures 1-44 include Rhodophyta, Figures 45-49 Phaeophyceae, Figures 50-58 Chlorophyta and Figure 59 Cyanophyta

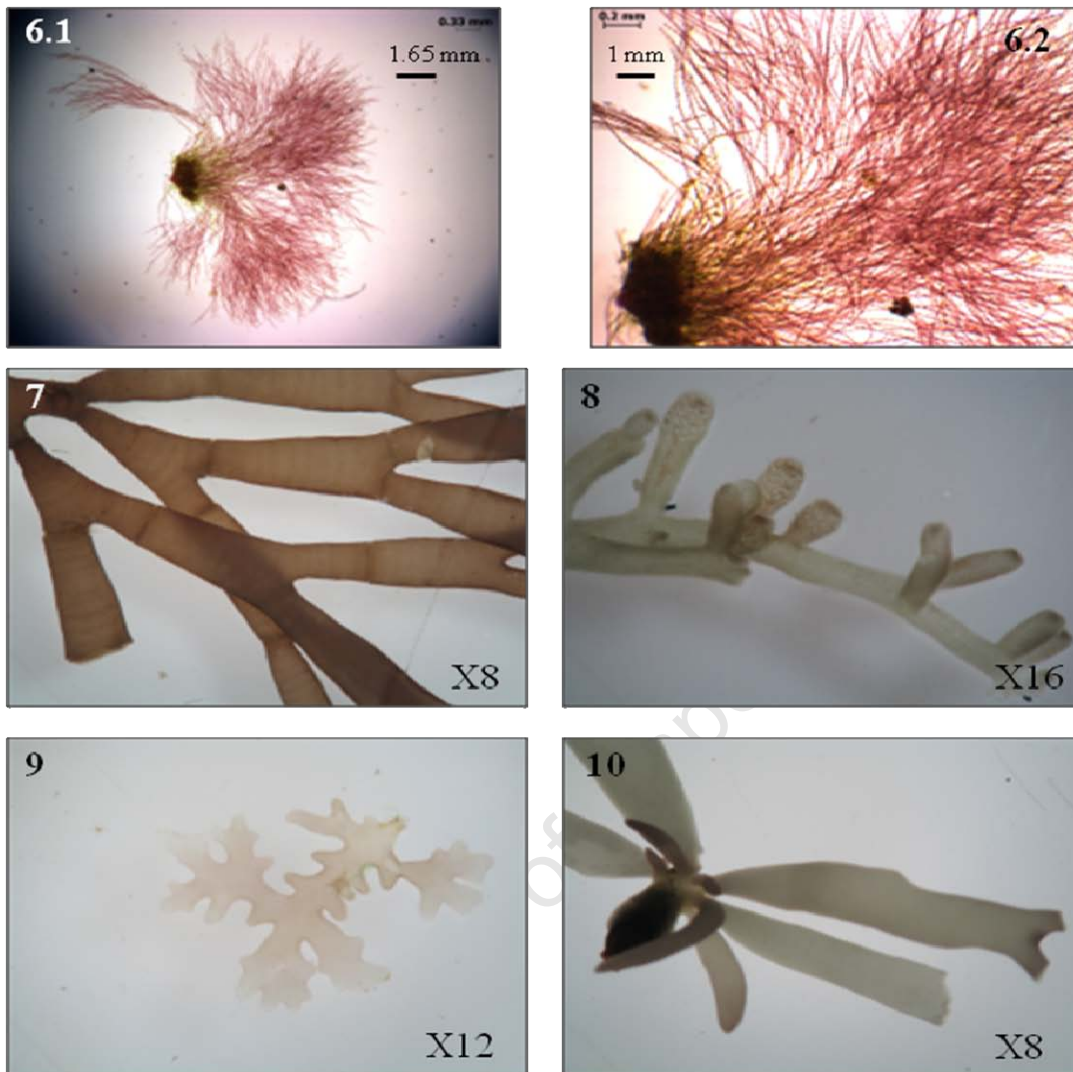
Figure 1.1 & 1.2: *Acrosorium maculatum* (Sonder ex Kützinger) Papenfuss. Note the characteristic yellow patches on the ribbon-like, complanate blade.

Figure 2: *Amphiroa beauvoisii* J.V. Lamouroux. Pale chalky-pink, attached by a crustose holdfast, di- to polytomously branched, with calcified intergenicula.

Figure 3: *Anotrichium secundum* (Harvey ex J. Agardh) G. Furnari in Cormaci, Furnari & Pizzuto

Figure 4: *Ceramium centroceratiforme* Simons showing unequal dichotomously branched axes, cortical bands evident.

Figure 5: *Chondria armata* (Kützinger) Okamura showing irregular branching, composed of closely packed upright cylindrical axes.



Approximate scales:

	5 mm
X8	_____
X12	_____
X16	_____

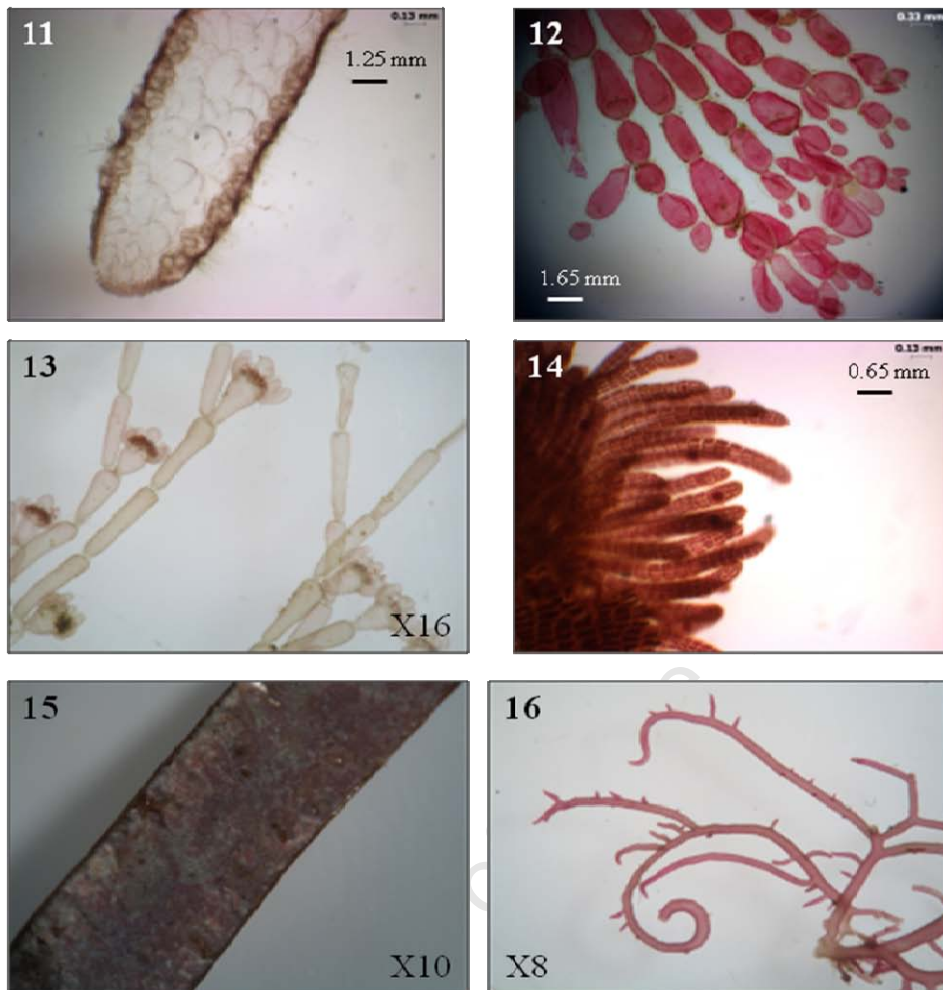
Figure 6.1 & 6.2: *Colaconema gracile* (Børgesen) Ateweberhan & Prud'homme van Reine, showing tuft structure in which it appears, as well as braching.

Figure 7: *Dichotomaria tenera* (Kjeilman) Huisman, T.J. Harper & G.W. Saunders, showing dichotomously branched, erect axes with compressed thalli.

Figure 8: *Gelidiopsis intricata* (C. Agardh) Vickers

Figure 9: *Gloiocladia iyoensis* (Okamura) R.E. Norris

Figure 10: *Gracilaria corticata* (J. Agardh) J. Agardh. Colour depicted altered due to preservation. Plant dark purple/red in colour, axes compressed, elongate straps with smooth margins.



Approximate scales:

	5 mm
X8	_____
X10	_____
X16	_____

Figure 11: *Gracilaria tuticoriensis* V. Krishnamurthy & Rajendran. Cross section through the blade.

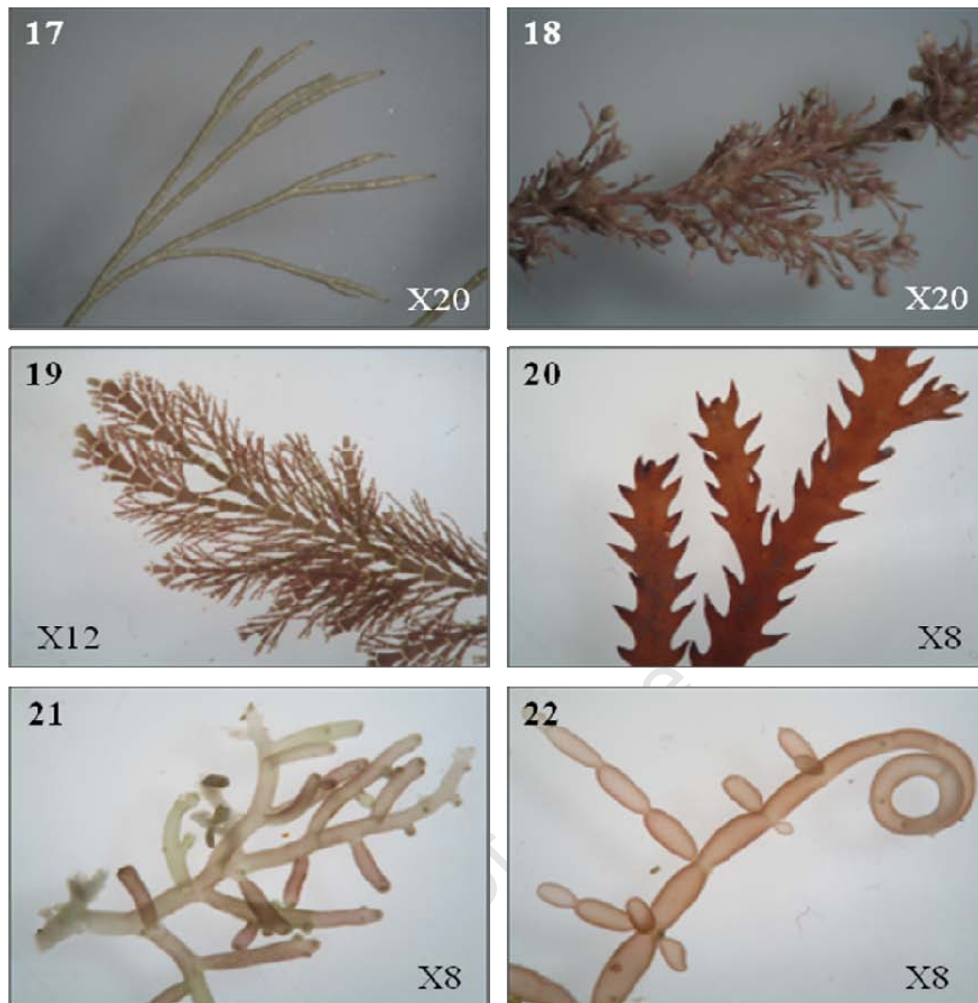
Figure 12: *Griffithsia confervoides* Suhr

Figure 13: *Griffithsia subbiconica* Stegenga

Figure 14: *Herposiphonia secunda* f. *tenella* (C.Argardh)M.J. Wynne. Observed growing as mat over stems of *Thalassodendron ciliatum*.

Figure 15: *Hydrolithon farinosum* (J.V. Lamouroux) D. Penrose & Y.M. Chamberlain growing epiphytically on a leaf of *Thalassodendron ciliatum*. The bumps are raised conceptacles.

Figure 16: *Hypnea rosea* Papenfuss forms a loose tangle of irregularly branched axes, without a percurrent main axis.



Approximate scales:

	5 mm
X8	_____
X12	_____
X20	_____

Figure 17: *Jania intermedia* (Kützinger) P.C. Silva. Note cylindrical, articulated axes with calcified intergenicula, branching in various planes.

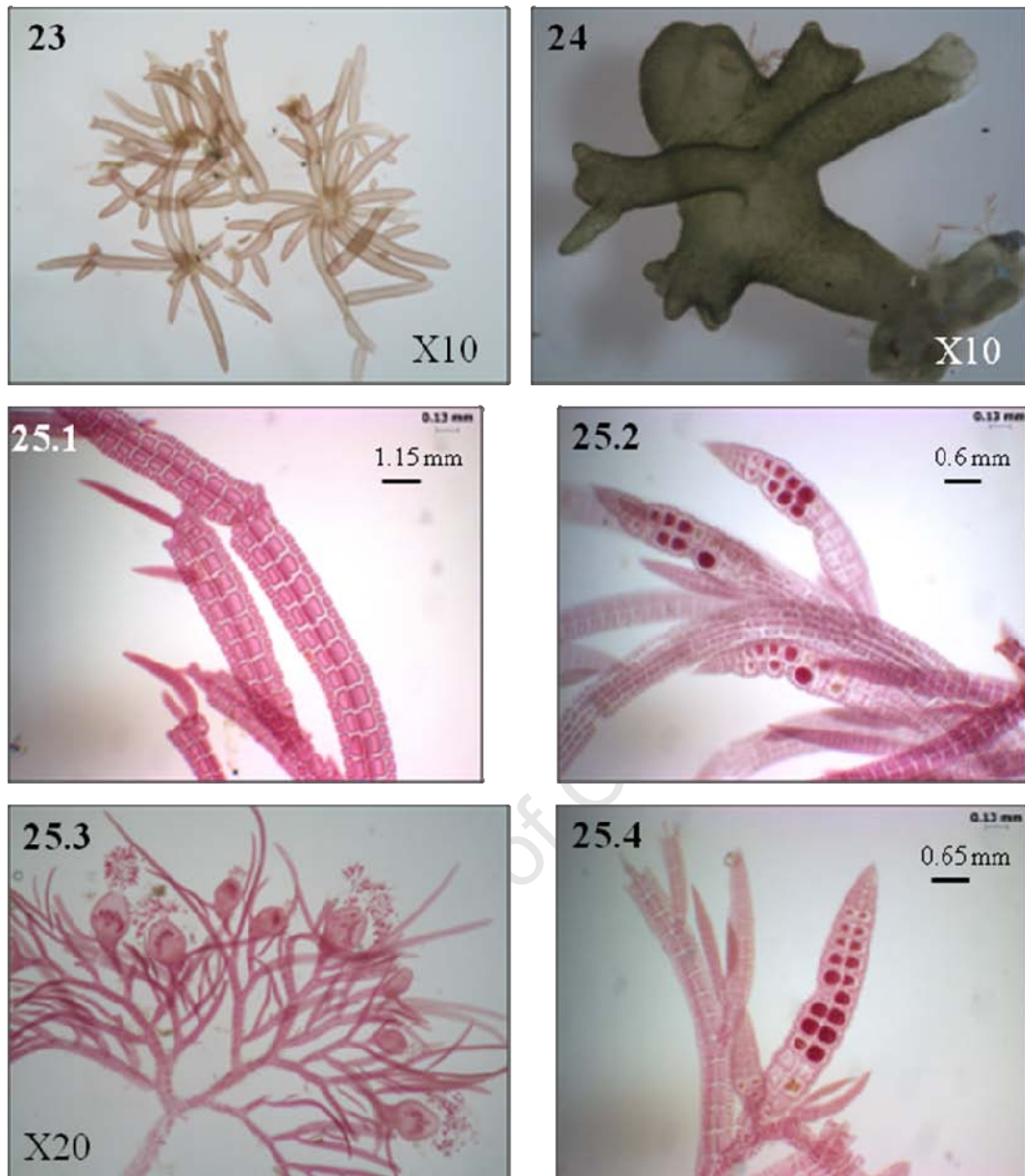
Figure 18: *Jania rosea* (Lamarck) Decaisne. Pinnately branched from every intergeniculum, sparsely branched near the base, irregular whorls of branches.

Figure 19: *Jania subulata* (Ellis & Solander) Sonder

Figure 20: *Kentrophora natalensis* (J. Argardh) S.M. Wilson & Kraft in R.J.F. Henderson, S.M. Wilson & Kraft. Bushy in appearance due to branches loosely twisting and bending in multiple planes. Complanate with dentate margins, irregularly branched, with marginal teeth.

Figure 21: *Laurencia tenera* C.K. Tseng

Figure 22: *Lomentaria amplexans* R.E. Norris. Characteristic sausage-like appearance.



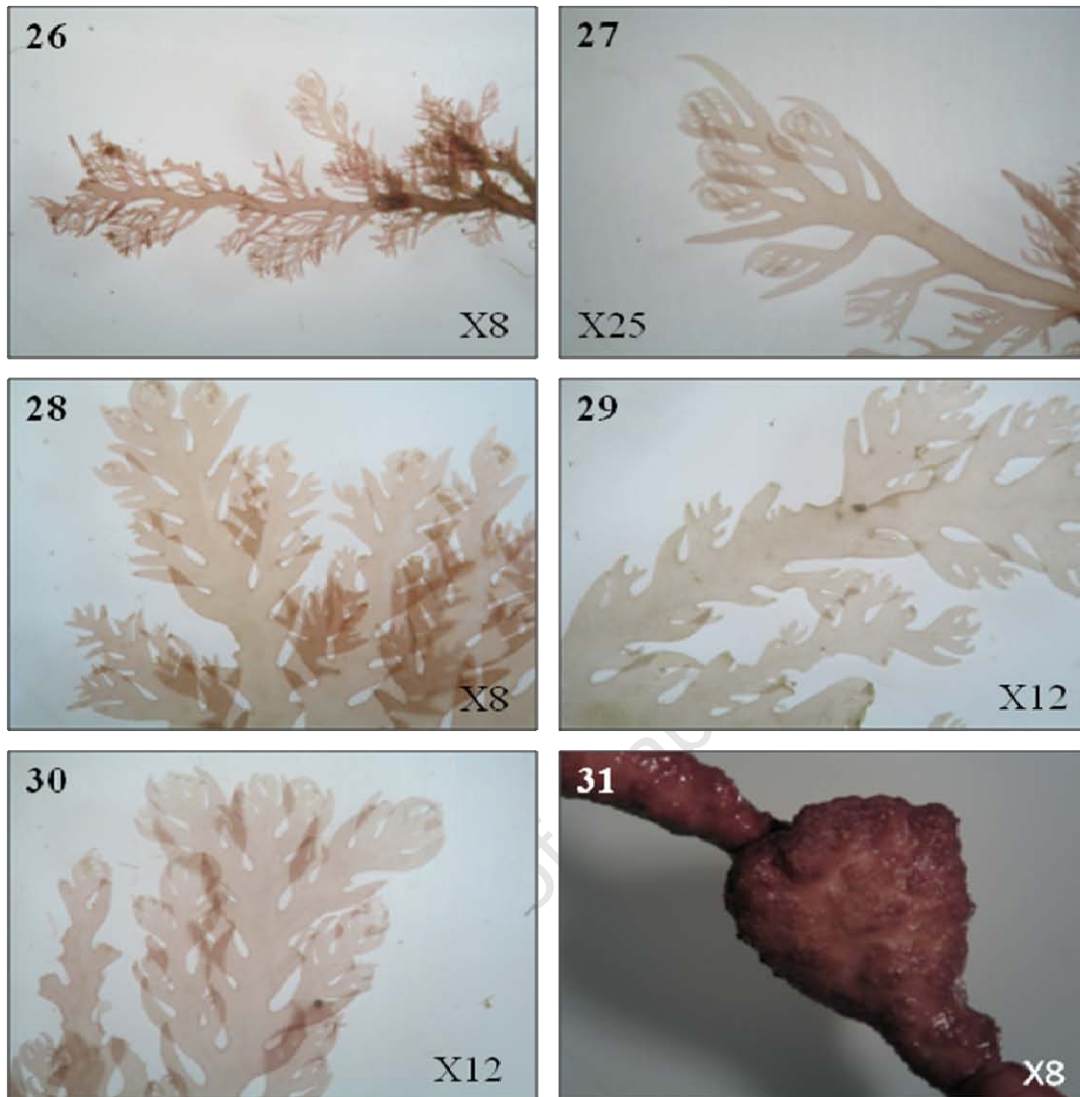
Approximate scales:

5 mm
X10 _____
X20 _____

Figure 23: *Lomentaria corallicola* Børgesen

Figure 24: *Nemastoma gelatinosum* M.A. Howe

Figure 25.1- 25.4: *Platysiphonia delicata* (Clemente) Cremades in Cremades & Ferez Cirera. Delicate plants form turf-like mats. Tetrasporangial stichidia can be seen, fertile segments bearing distichously arranged tetrasporangia.



Approximate scales:

	5 mm
X8	_____
X12	_____
X25	_____

Figure 26: *Plocamium beckeri* F. Schmitz ex Simons

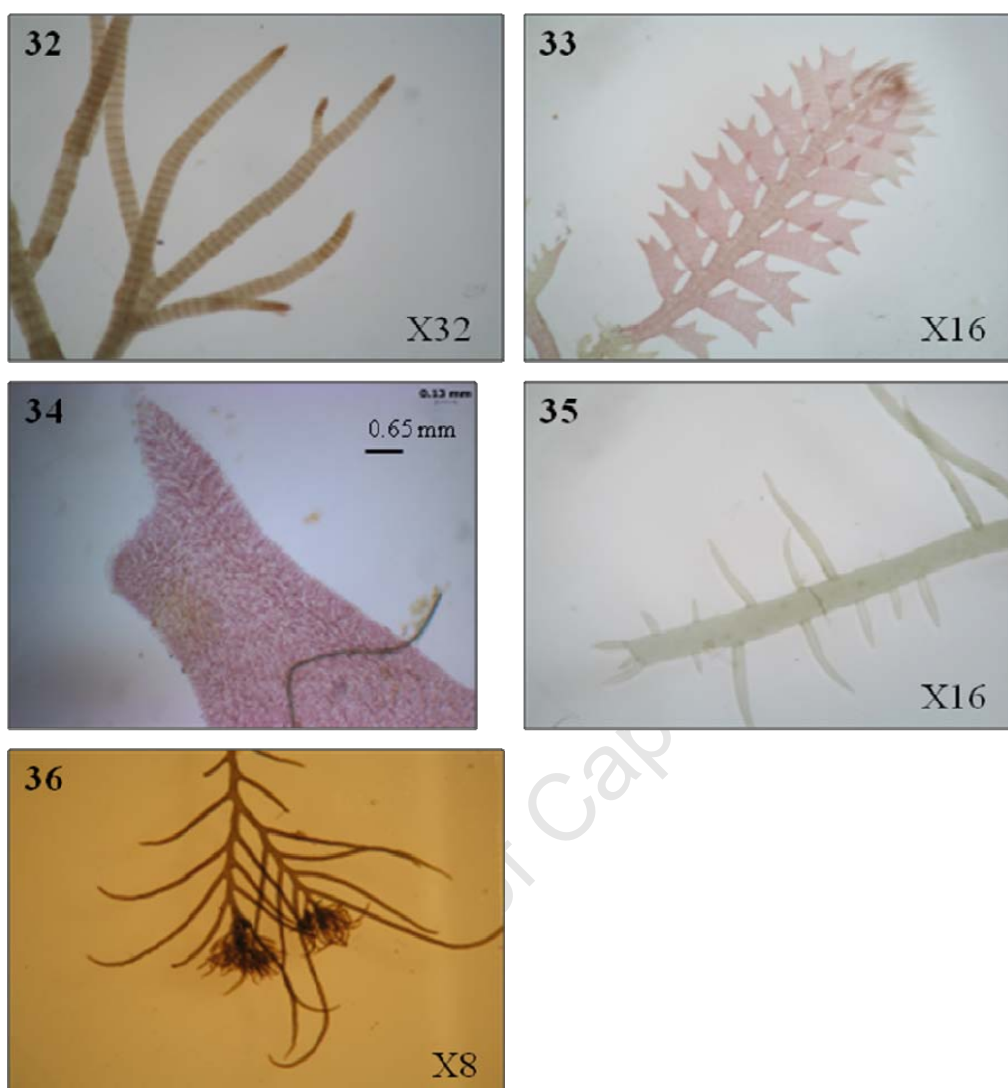
Figure 27: *Plocamium glomeratum* J. Agardh

Figure 28: *Plocamium mertensii* (Greville) Harvey

Figure 29: *Plocamium suhrii* Kützing

Figure 30: *Plocamium telfairiae* (W.J. Hooker & Harvey) Harvey ex Kützing

Figure 31: *Pneophyllum amplexifrons* (Harvey) Y.M. Chamberlain & R.E. Norris. Forms distinctive calcareous rings (and trumpet-shaped collars) enveloping the stems of *Thalassodendron ciliatum*.



Approximate scales:

X8 5 mm
 X16 _____
 X32 _____

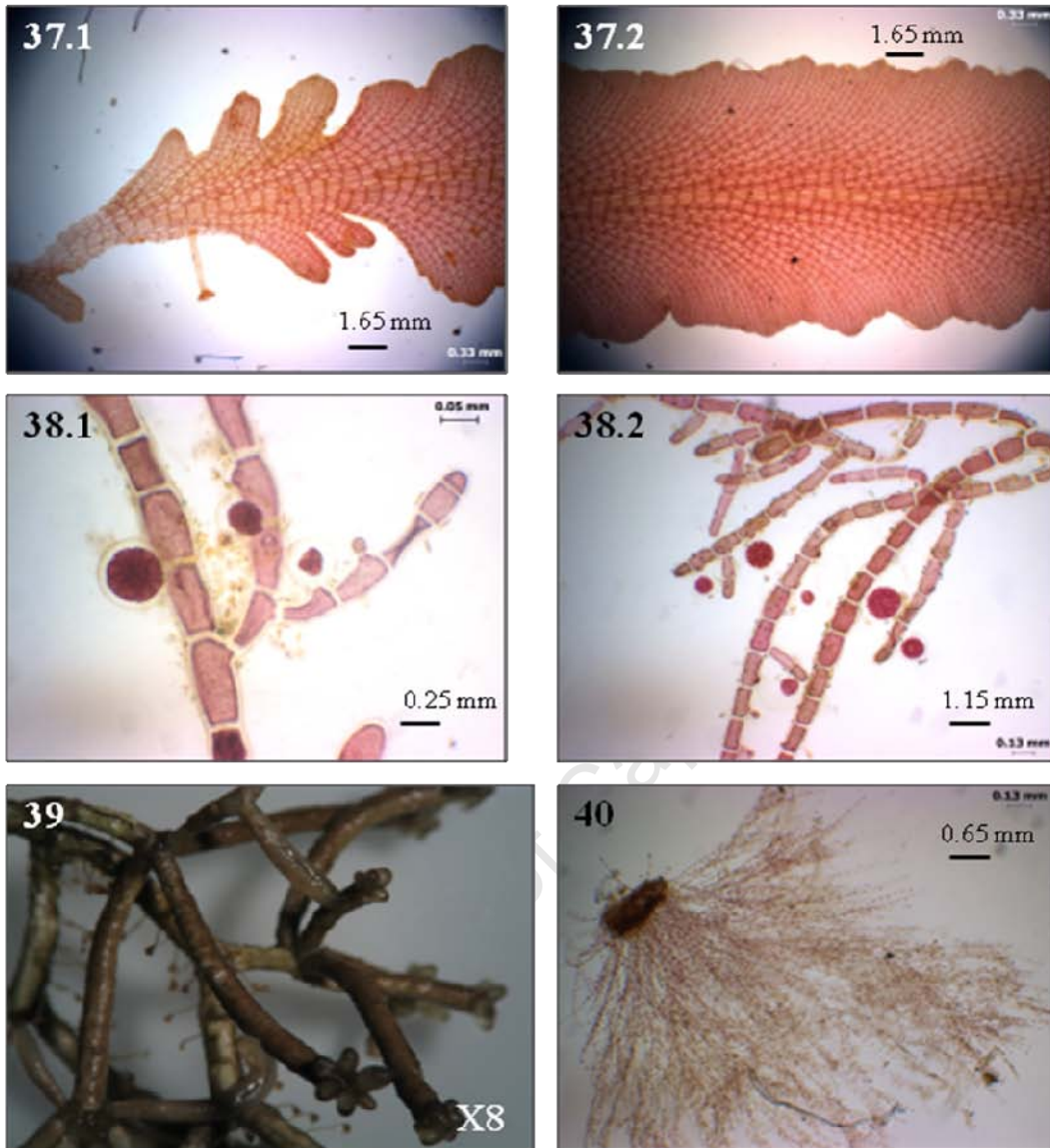
Figure 32: *Polysiphonia urbana* Harvey

Figure 33: *Polyzonia elegans* Suhr. Polysiphonous axes branched, bearing distichously arranged leaf-like determinate laterals.

Figure 34: *Predaea feldmannii* Børgesen. Gelatinous matrix with filamentous medulla and cortex.

Figure 35: *Pterocliadiella caloglossoides* (M.A. Howe) Santelices

Figure 36: *Rhodomelopsis africana* M.A. Pocock. Bushy plant, dark in colour, axes cylindrical, sympodially branched, determinate laterals unbranched.



Approximate scale:

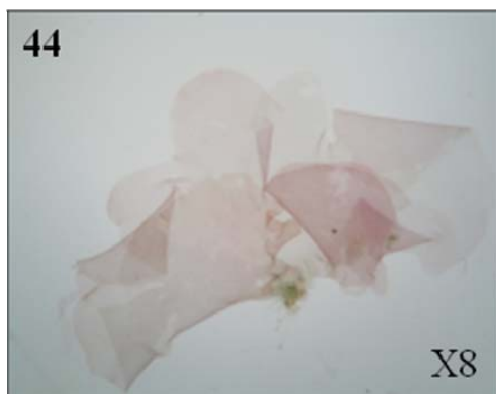
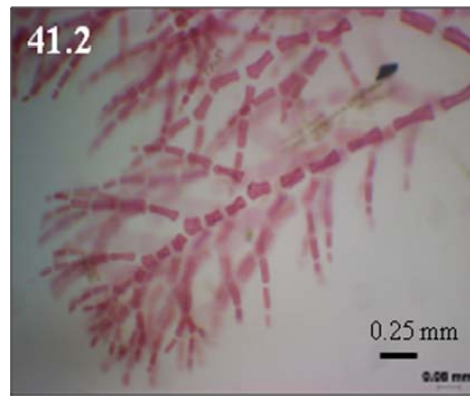
X8 5 mm

Figure 37.1 & 37.2: *Symphyocladia marchantioides* (Harvey) Falkenberg in Schmitz & Falkenberg.

Figure 38.1 & 38.2: *Tiffaniella schmitziana* (E.S. Barton) Bolton & Stegenga. Sporangia can be seen.

Figure 39: *Tricleocarpa fragilis* (Linnaeus) Huisman & R.A. Townsend

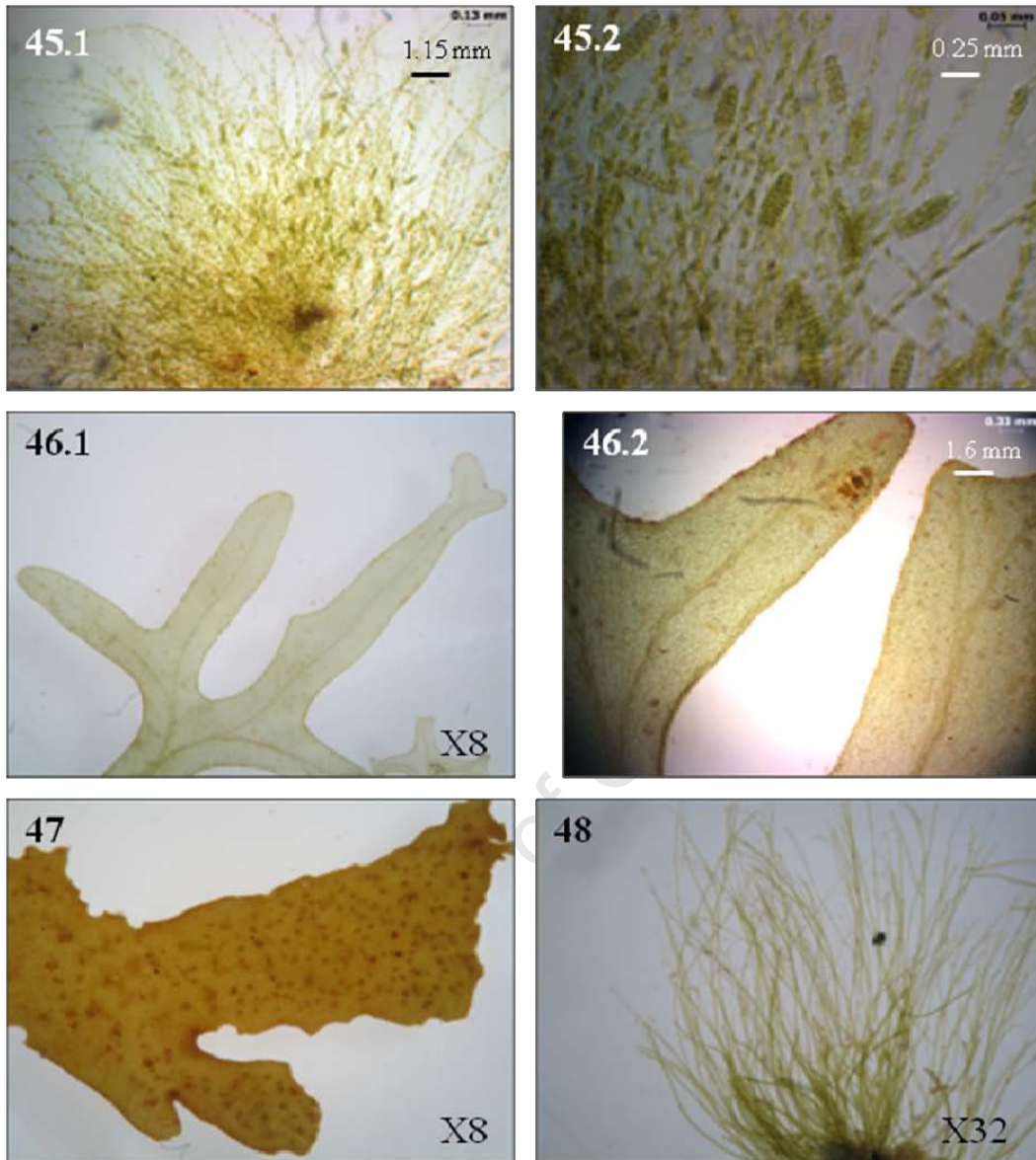
Figure 40: *Acrochaetium* sp.



Approximate scales:

5 mm
X8 —————
X16 —————

Figure 41: *Callithamnion* sp.
Figure 42: *Champia* sp.
Figure 43: *Dasya* sp. Fox-tail appearance.
Figure 44: *Delesseriaceae* indet.



Approximate scales:

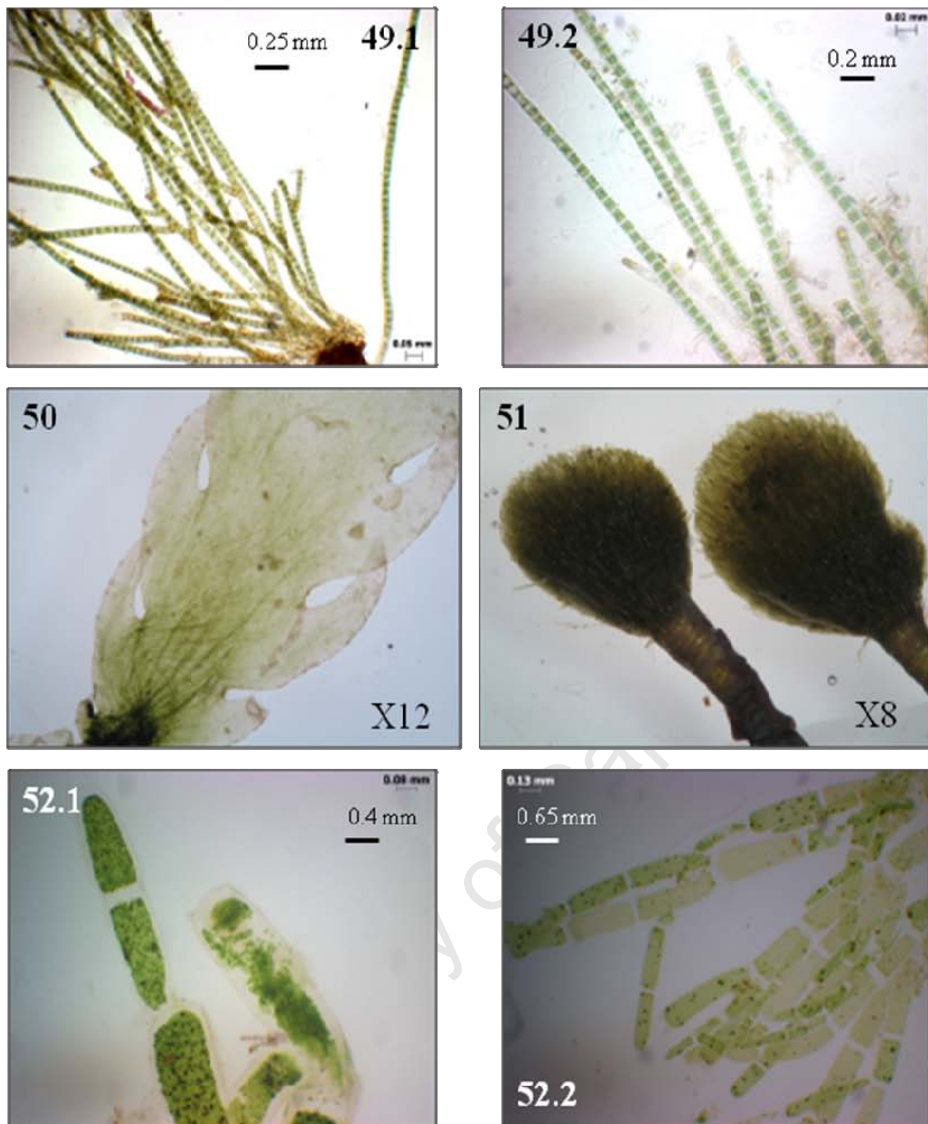
5 mm
 X8 _____
 X32 _____

Figure 45.1: *Asterocladon rhodochortonoides* (Børgesen) Uwai, Nagasato, Motomura & Kogame. Figure 45.2 shows spindle-shaped sporangia.

Figure 46.1 & 46.2: *Dictyopteris delicatula* J.V. Lamouroux. Strap-like blades with a distinct midrib.

Figure 47: *Dictyota ciliolata* Sonder ex Kützing

Figure 48: *Sphacelaria rigidula* Kützing



Approximate scales:

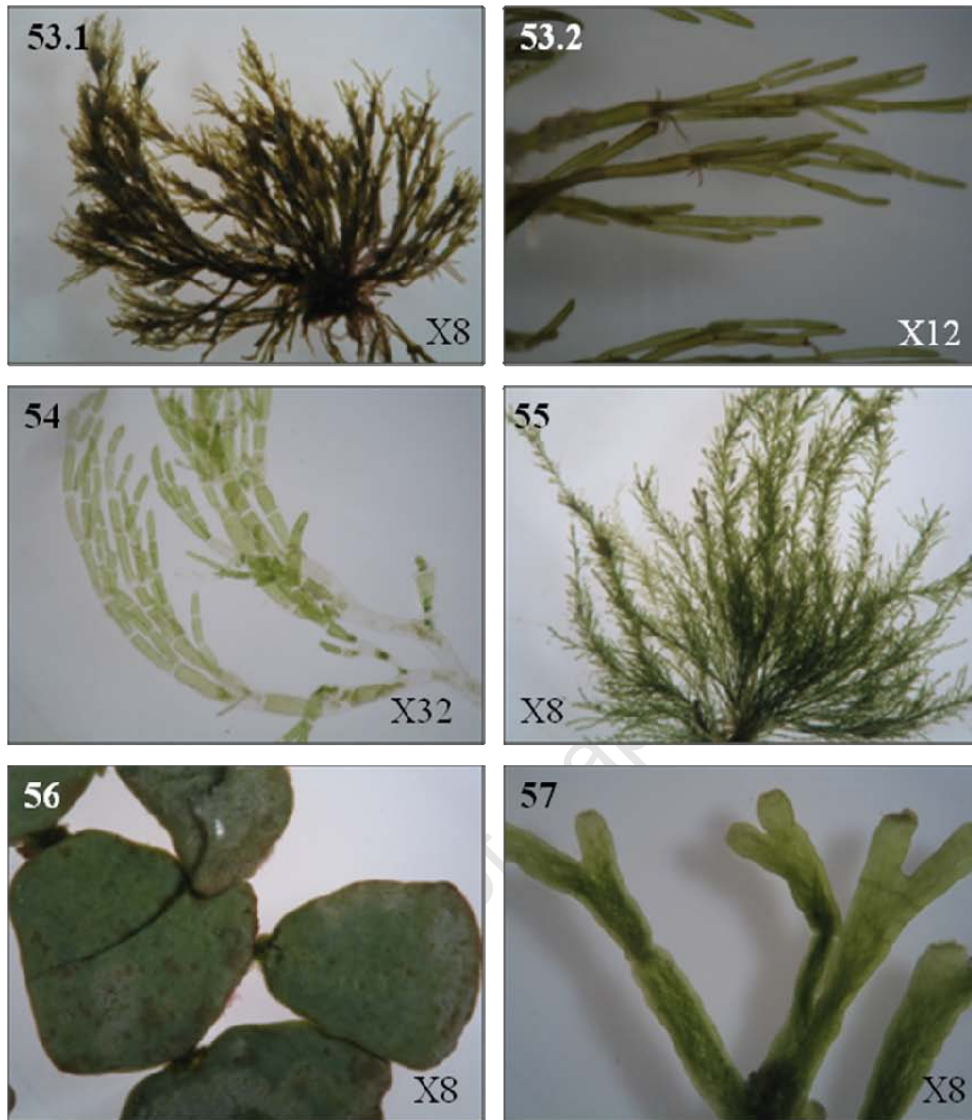
	5 mm
X8	_____
X12	_____

Figure 49: Ectocarpoid sp.1

Figure 50: *Caulerpa scalpelliformis* (R.Brown ex Turner) C.Agardh

Figure 51: *Chamaedoris delphinii* (Hariot) Feldman & Børgesen. Thallus dark green, forming erect stipitate capitula arising from stipe. Capitula penicillate ball-shaped and composed of branches, entangled filaments, formed without order at the apex of the stipe.

Figure 52.1 & 52.2: *Cladophora herpestica* (Montagne) Kützinger



Approximate scales:

	5 mm
X8	_____
X12	_____
X32	_____

Figure 53.1 & 53.2: *Cladophora prolifera* (Roth) Kützing

Figure 54: *Cladophora saviniana* Børgesen

Figure 55: *Cladophora sibogae* Reinbold

Figure 56: *Halimeda cuneata* Hering in Krauss. Flat, calcified segments, most often cuneate, longer than broad, with all segments more or less in a single plane. Each segment supported by a stalk as seen in photograph.

Figure 57: *Pseudocodium de-vriesii* Wever-van Bosse. Compressed or flattened distally.

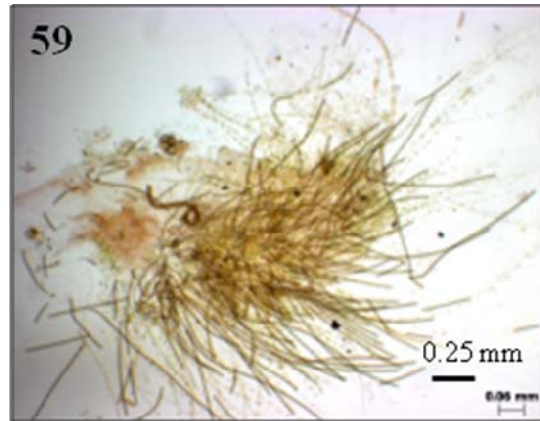
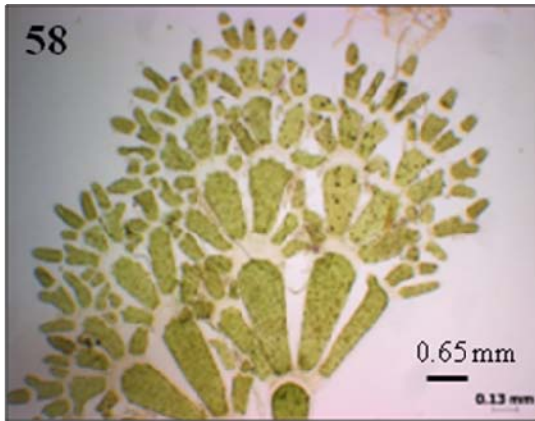


Figure 58: *Boodlea* sp.

Figure 59: Cyanobacteria cf. *Lyngbya* sp.

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