THE ABUNDANCE AND DIVERSITY PATTERNS OF SEAWEED COMMUNITIES ON NATURAL AND ARTIFICIAL SUBSTRATA IN A CORAL REEF SYSTEM AT SODWANA BAY, SOUTH AFRICA

By
Leanne Gersun

Dissertation Presented for the Degree of

MASTERS IN SCIENCE

In the

Faculty of Science

Department of Biological Sciences

UNIVERSITY OF CAPE TOWN

March 2014

Supervisors: Assoc. Prof. R.J. Anderson[1, 2] and Prof. J.J. Bolton[1]

[1]Department of Biological Sciences and Marine Research Institute, University of Cape Town, Rondebosch 7701, South Africa
[2] Fisheries Research, Department of Agriculture, Forestry and Fisheries, Private Bag X2, Roggebaai 8012, South Africa

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.

Department of Biological Sciences, University of Cape Town

March 2014

Table of Contents

Acknowledgements

First and foremost I would like to thank my supervisors, Prof. John J. Bolton and Associate Prof. Robert. J. Anderson, for their guidance, patience and support. Extended thanks go to Prof. Gavin Maneveldt for his time and assistance with crustose coralline identification and the lengthy use of his laboratory space at the University of the Western Cape (UWC). Thanks also to Elizabeth van der Merwe for her considerate help in the UWC laboratory and Chris Boothroyd for his general assistance in and out of the sea.

I am grateful to the National Research Foundation and the African Coelacanth Ecosystem Programme for their financial support of this research. I also thank the Oceanographic Research Institute in Durban for the opportunity to examine their experimental setup.

Sincere thanks are also due to Sandra Kay for her generous hospitality and her encouragement during trying periods.

Finally, I thank my parents, Phil and Jean, for allowing me to realize my own potential. All the support they have provided me over the years is immeasurable.

"The most incomprehensible thing about the world is that it is comprehensible"

-Albert Einstein

Abstract

The high latitude coral communities of southern Africa suffered minimal impacts during mass bleaching events in the recent past. However, during the 2005 warm-water anomaly in the southern Indian Ocean, coral bleaching reached unprecedented levels. There is surprisingly little known about the fate of bleached corals, which may either regain their zooxanthellae and recover, or may die, in which case they generally become overgrown by macroalgae. The nature and dynamics of this algal overgrowth are not well understood.

This study was done on Two-Mile Reef, Sodwana Bay, located in the iSimangaliso Wetland Park, a World Heritage Site. The first aim was to investigate the abundance and diversity of benthic algal communities colonising different hard substrata (comprising bleached digitate, brain and plate coral assemblages, and beach rock). The second was to compare the algal communities colonising various artificial hard substrata. The third was to document the species of non-geniculate coralline red algae found on the natural hard substrata during sampling. Fieldwork was carried out during the marine autumn (March) and spring (September) of 2010 using SCUBA. A total of 90 quadrats (10 cm x 10 cm) were sampled and the underlying substratum was recorded and classified. A Braun-Blanquet scale was used to assign cover-abundance values to each species within each quadrat. Additionally, the relative cover of different types of substrata was estimated using line-point intercept methods. Multivariate analysis (detrended correspondence analysis) and cluster analysis (complete linkage Bray-Curtis) were used to show how substrata and season relate with respect to their seaweed flora. Additionally, Kruskal-Wallis nonparametric tests with pairwise Mann-Whitney *U*-tests were used to examine differences in macroalgal assemblages among substratum types.

A total of 87 taxa representing 13 Chlorophyceae, 10 Phaeophyceae**,** 62 Rhodophyceae and one Cyanobacterium were identified. The resulting species list shows that the subtidal Sodwana Bay algal flora is typically tropical and most of the species occur across the Indo-West Pacific biogeographic province.

The most common species, occurring in 73% of quadrats, was the dictyotalean brown alga *Lobophora variegata*. Of the other macroalgae, non-geniculate crustose coralline algae were the next most common taxon, occurring in 63% of all quadrats.

Cluster analyses and ordination revealed no seasonal clustering or detectable clustering of substratum types according to the seaweed assemblages present. Significant differences were observed only among substratum types in *Pterocladiella caerulescens* and non-geniculate crustose coralline cover abundance.

The Oceanographic Research Institute afforded the opportunity to explore macroalgal colonisation of artificial settlement tiles. Ceramic, marble and pre-conditioned ceramic tiles were placed along Two-Mile Reef for a period of six months. Ceramic tiles were preconditioned for two months in an aquarium where *Mesophyllum funafutiense* was prolific. After retrieval, the Braun-Blanquet scale was used to assign a cover abundance value to the macroalgal (including non-geniculate coralline algae) recruits on the tiles.

There was no distinguishable clustering of tile types, and the ordination analysis did not display any major separation between tile types based on their algal assemblages. A total of 24 taxa were identified from the 145 settlement tiles. Attached algal floras on all tiles sampled were dominated by *Lobophora variegata* and non-geniculate crustose coralline algae, accounting for 80% of the overall algal cover. Other species with less cover, but relatively high

frequency (>10%) were: *Dictyota* sp., *Sphacelaria novae-hollandiae*, *Herposiphonia tenella*, *Hypnea spinella*, and *Chondria collinsiana*.

Recruitment of fleshy macroalgae was generally, but not always, higher on plates with rougher texture. Significant differences were detected in crustose coralline abundance between ceramic (2.50 [± 0.97]) and marble (3.58 [± 1.05]) tile types.

The most common species, occurring on both natural and artificial substrata, were *Lobophora variegata*, *Herposiphonia tenella* and *Hypnea spinella*.

This study also identified the non-geniculate coralline algae (Corallinales, Rhodophyta) found in samples on Two-Mile Reef. Species were identified using reproductive and vegetative anatomy as diagnostic features. Nine species were identified. Eight of the species were found on both algae and calcareous substrata, while the remaining one was exclusively epiphytic on *Valonia macrophysa*. One of the species is potentially new to science (*Pneophyllum* sp.), one is newly recorded for South Africa (*Lithophyllum cuneatum*) and five are newly recorded for the Maputaland region (*Lithophyllum acrocamptum*, *Hydrolithon farinosum*, *Hydrolithon pellire*, *Neogoniolithon brassica-florida* and *Lithothamnion muelleri*). This increased the known algal diversity in Sodwana Bay to 17 species. The reported species are compared to findings from other tropical reef systems.

Overall, this study is only a snapshot of the subtidal algal assemblages that occur at Sodwana Bay. However, the results presented here form a critical baseline for future long-term monitoring of this high latitude reef system.

Chapter 1: General Introduction

1.1 Coral-dominated reef systems

Coral reefs are among the most economically important and biologically diverse ecosystems on earth, forming heterogeneous environments that serve as vital sources of primary production within tropical marine waters (Odum and Odum 1955; Wilkinson and Buddemeier 1994). Coral reef systems have the greatest number of species of any marine ecosystem, including many uniquely specialised macroalgae that are significant members of reef communities. Macroalgae of a wide range of diversity, abundance, and form provide essential ecological functions such as development and stabilisation of reef structure, production of tropical sands, nutrient retention and recycling, primary productivity, and trophic support (Littler and Littler 1994). For example, the calcium carbonate (in the form of calcite) produced by crustose coralline algae provides the primary cement for the reef matrix and consolidates calcareous skeletons of coral and other debris which leads to reef formation (Littler and Littler 1988; Littler and Littler 1994). In addition, non-geniculate coralline algae form seaward intertidal ridges at the crest of reefs that buffer wave shock, and prevent erosion and damage to the more delicate corals and invertebrates of the backreef zone (Littler and Littler 1988). Another important source of carbonate in reef formation is calcified green algae, belonging to the orders of Bryopsidales and Dasycladales. This diverse group of algae deposit the aragonite form of calcium carbonate, which is responsible for much of the sandy sediments in backreefs and lagoons (Littler 1976; Littler and Littler 1988). For example, Macintyre *et al*. (1987) found

that the skeletal sand-sized components from the barrier reef sediment of a 9 km long emergent reef crest in Belize were composed of up to 40% *Halimeda* fragments.

Globally, degradation of coral reefs due to the impacts of human development is increasing, raising concerns for the future resilience of reefs and the ecosystem goods and services they provide, for example, fisheries, tourism, aesthetic and cultural values (Hughes 1994; Moberg and Folke 1999). Reefs around the world are facing a rising frequency of natural and anthropogenic stresses and disturbances including hurricanes/cyclones, crown-of-thorns starfish outbreaks, coral diseases, overexploitation, and climate change in particular (Hughes and Connell 1999; McCook 1999). Consequently, these events may lead to a partial or extensive phase shift in which abundant benthic algae replace abundant scleractinian corals because disturbed coral reefs are almost universally colonised and dominated by some form of benthic algae (Hughes 1994; McCook 1999; Diaz-Pulido and McCook 2002).

Benthic macroalgae play a fundamental role in the dynamics and functioning of tropical reefs (Steneck and Dethier 1994), and are one of the major competitors with corals, especially during periods when rates of herbivory are low and/or dissolved nutrient availability is high, as on many degraded reefs (McCook *et al*. 2001; McManus *et al*. 2000). Competition between macroalgae and larval and juvenile coral is a very important ecological force determining coral reef structure and composition (McCook *et al*. 2001; Birrell *et al*. 2008b). McCook *et al*. (2001) determined that competition between scleractinian corals and macroalgae occurs through a wide variety of mechanisms, including both chemical and physical processes that can impact all stages of the coral life cycle. Macroalgae are able to directly compete with hard corals for space or light, using seven major types of mechanisms (reviewed by McCook *et al*. 2001): basal encroachment, shading, abrasion (Lirman 2001; Box and Mumby 2007), sedimentation

due to reduced water flow (Nugues and Roberts 2003), allelopathy, space pre-emption by reducing available space for the successful settlement of coral larvae (Birrell *et al*. 2005; Box and Mumby 2007), and attraction of settling larvae to ephemeral algal surfaces (Littler and Littler 1997). The outcomes of coral-algal competition are likely to depend on the specific coral and algal taxa, and on extrinsic factors, such as herbivory rates, environmental disturbances, water quality, etc. (McCook *et al*. 2001). Previous studies have reported variable outcomes, including reduction in growth rates of both competitors (Jompa and McCook 2002), declines in coral fecundity (Tanner 1995), and even coral mortality (Lirman 2001).

Competitive interactions between corals and macroalgae vary widely among algal species (McCook *et al*. 2001; Birrell *et al*. 2008b). For example, in Roatán (Honduras) Box and Mumby (2007) investigated the mechanisms and outcomes of spatial competition between the brown algae *Lobophora variegata* and *Dictyota pulchella*, and the hard coral *Agaricia* spp. In particular, the effects on growth and mortality of juvenile corals by two forms of algal competition, shading and abrasion, were studied. They found that in the absence of grazing, shading by *Lobophora variegata* was lethal to juvenile *Agaricia* spp. In contrast, shading and peripheral contact (without shading) by *Dictyota pulchella* and inert algal mimics of *D. pulchella* retarded coral growth, suggesting the reduction in growth occurred because of physical mechanisms rather than allelochemical inhibition. Similarly, in an experimental study investigating competitive interactions between benthic algae and hard corals, Titlyanov *et al*. (2007) reported that individuals of *Dictyota dichotoma* reduce the photosynthetic efficiency and growth rates of the stony coral *Porites lutea* through abrasion of coral tissues. Furthermore, they found that the blue-green bacterium *Lyngbya bouillonii* had a toxic effect on *P. lutea*, inducing bleaching and severely damaging live coral tissue. However, the coral-

algal interaction is not one-sided; corals are also capable of inhibiting algal growth and overgrowing the colonising algae. For example, Jompa and McCook (2002) found that despite the ability of the creeping foliose brown alga *Lobophora variegata* to overgrow and induce tissue mortality of the branching coral *Porites cylindrica*, the coral was also able to inhibit the growth of the alga, although to a lesser degree, indicating mutual competitive inhibition.

1.2 Coral bleaching

Reef-building scleractinians are symbiotic with a diverse range of dinoflagellate algae of the genus *Symbiodinium*, commonly known as zooxanthellae because of their yellow-brown colour. Corals and their endosymbiotic algae form a mutualistic relationship, as both individuals derive benefit from the association (Littler and Littler 1988; Hoegh-Guldberg 1999). As a result of living within the coral's tissues, zooxanthellae gain protection from zooplankton predators and obtain a wide variety of essential nutrients, such as phosphate and ammonium, directly from the coral host's waste metabolism (Muscatine 1990). The dinoflagellate microalgae photosynthesize within their hosts and provide up to 95% of the corals' carbon requirements for growth, reproduction and maintenance (Hoegh-Guldberg 1999). The scleractinians acquire algal photosynthates in the form of glycerol and glucose, as well as oxygen (Littler and Littler 1988).

The most acute response of corals to environmental stress is to expel their zooxanthellae from their tissues into the environment during a phenomenon known as "coral bleaching." Coral bleaching results in the rapid whitening of the affected coral with varying levels of coral mortality depending on the severity of the thermal stress and is found to be due to the partial to total expulsion of the *Symbiodinium* population and/or degradation of the algal pigments

(Brown 1997; Buddemeier and Fautin 1993; Douglas 2003; Glynn 1993; Hoegh-Guldberg 1999; Baker *et al*. 2008).

While thermal stress is regarded as the primary cause of coral bleaching, other environmental factors can cause bleaching independently, and act synergistically by lowering the threshold temperature at which coral bleaching occurs (Lesser 2006). These other factors include physical stressors such as salinity changes, sedimentation, and exposure to ultraviolet radiation (Brown 1997; Hoegh-Guldeberg and Smith 1989), as well as chemical stressors such as copper ions, cyanide, herbicides, pesticides, and biological factors (e.g. bacteria; Brown 1997; Hoegh-Guldberg 1999; Jones 1997; Kushmaro *et al*. 1996).

Coral bleaching poses a major threat to the existence of coral reefs throughout their distributional range. Bleaching may occur at local (e.g. parts of reefs) or geographic scales that may involve entire reef systems and geographic regions. Severe bleaching events coincide with periods of high sea surface temperatures and are associated with the intensification of the El Niño Southern Oscillation phenomenon (ENSO; Hoegh-Guldberg 1999; Baker *et al*. 2008).

The mass coral bleaching event of 1998 is considered to be the most extensive on record with unprecedented bleaching affecting coral reefs in every region of the world (Hoegh-Guldberg 1999; Wilkinson *et al*. 1999; West and Salm 2003). Over 50 countries across the tropics experienced coral bleaching and mortality during the 1997-1998 ENSO (West and Salm 2003). Wilkinson *et* al. (1999) reported that the most severe bleaching occurred around the central Indian Ocean islands of the Maldives, the Seychelles, and Sri Lanka, and on the coasts and islands of India, Kenya, and Tanzania. This was the most significant bleaching event ever recorded for the western Indian Ocean, which resulted in the mortality of 90-95% of corals at

the most heavily impacted sites (Wilkinson *et al*. 1999; Wilkinson 2000). While the reefs in the northern regions of the western Indian Ocean suffered extensive losses of coral cover, bleaching and mortality decreased in a southerly direction until hardly evident in the coral communities of South Africa (Wilkinson 2002). Southern African coral reefs have, therefore, been considered as possible refugia in times of climate change (Riegl and Piller 2003).

Glynn (1996) hypothesized that reefs at high latitude sites, in a less usual setting than in clear, shallow, tropical water may have high refuge potential, and corals found there are more likely to survive environmental disturbances, such as raised global temperatures. The coral-inhabited reefs in South Africa are deeper than most tropical reefs (8-18 m) and are located in naturally turbid water. These environmental settings coupled with the high (cooler) latitude position of the reefs at Sodwana Bay had provided the coral communities there some protection up until the summer months of 2000, when bleached corals were first reported in April 2000 (Celliers and Schleyer 2002). This bleaching event was associated with increased sea surface temperatures with high seasonal peaks and increased radiation because of exceptionally clear water. The bleaching was limited to Two-Mile and Nine-Mile reefs in the central reef complex on the Maputaland coastline. Floros *et al*. (2004) reported that 26 coral genera were affected, among which the hard coral *Montipora* spp. was most susceptible to bleaching. Celliers and Schleyers' (2002) field measurements during this event showed that <12% of the total living coral cover (hard and soft coral) was affected on Two-Mile Reef.

Subsequently, in 2005, the southern Indian Ocean experienced a warm water anomaly resulting in extensive coral bleaching on Madagascar, Mozambique, and South African reefs (McClanahan *et al*. 2007). In Sodwana Bay, frequent small-scale upwelling events are common during the summer months and decrease seawater temperatures by 1-2°C (Roberts *et al*.

2006; Ruiz Sebastián *et al*. 2009). These events are believed to provide a cooling effect on surface waters, and thus keep temperatures below bleaching levels (Riegl 2003; Riegl and Piller 2003). However, in December 2004, two strong upwelling events occurred in Sodwana Bay lowering seawater temperatures by 5-6°C, reaching a summer minimum of 18.8°C that was followed by an acute rise that culminated in the summer's maximum temperature. Thus, cold stress, heat shock, and heat stress contributed to the accumulation of thermal stress resulting in unprecedented coral bleaching across Two-Mile and Nine-Mile reefs (Ruiz Sebastián *et al*. 2009). Ruiz Sebastián *et al*. (2009) found that the scleractinian corals *Stylophora pistillata* and *Montipora* were the most susceptible to bleaching during the 2005 event and thus confirmed previous reports that *Montipora* is the most bleaching-susceptible hard coral in Sodwana Bay (Celliers and Schleyer 2002; Floros *et al*. 2004).

1.3 Maputaland background

The Maputaland coral communities owe their existence to the clear, subtropical water carried southward by the Agulhas Current and the absence of silt- carrying rivers in the coastal surroundings (Ramsay and Mason 1990; Riegl *et al*. 1995). The most important large scale oceanographic feature on the northern KwaZulu-Natal coast is the Agulhas Current. This western boundary current is formed from the confluence of tropical surface waters in the Mozambique Channel and areas south of Madagascar (Schumann 1988; Ramsay 1994). The continental shelf in the area is characterised by submarine canyons and is very narrow, with the shelf break in many places only 2-4 km offshore (Ramsay 1996). As a consequence of the narrow shelf, the warm Agulhas Current flows close inshore and can attain speeds up to 3

m/s, generating the sub-tropical conditions in the region (Ramsay 1994). The mean sea-surface temperatures vary seasonally between 22°C in winter to 26°C in summer (Schleyer and Celliers 2000). The tidal range averages 2 m and the coast is therefore high microtidal or low mesotidal (Ramsay 1994). The coast is dominated by large swells from the south-east for 40% of the year, while smaller north-easterly to easterly swells prevail for another 40% of the time (Ramsay 1994).

The major coral-inhabited reefs in KwaZulu-Natal occur adjacent to the coast at 27°50ˈS (Riegl *et al*. 1995). They are the most southerly coral reefs in Africa, but are not considered 'true' coral reefs because there is no noticeable biogenic accretion, no typical geomorphological traits such as lagoons, reef crests or reef slopes, and the reefs have a uniform coral community structure (Ramsay and Mason 1990; Riegl *et al*. 1995). The reefs are formed by a thin veneer of Indo-Pacific type corals that have colonised late Pleistocene beachrock and aeolianite outcrops (at depths typically < 25 m), originating from the submersion and calcareous cementation of beach dunes that formed when sea levels were at least 100 m lower than present during the late Pleistocene glacial maximum, 18 000 BP (Ramsay 1994). Subsequent rises in sea level have left a series of rugged, linear shoals extending down most of the KZN coast, and a series of broad, marine intertidal beachrock platforms that are exposed at low tides (Ramsay 1994). Despite being at high latitude, the reef fauna is rich in species and is dominated by alcyonarian (soft) corals, which constitute 60-70% of the total coral fauna. Scleractinian (hard) corals dominate the deeper sandstone outcrops, and the deepest outcrops accessible by SCUBA are dominated by sponges (Riegl *et al*. 1995).

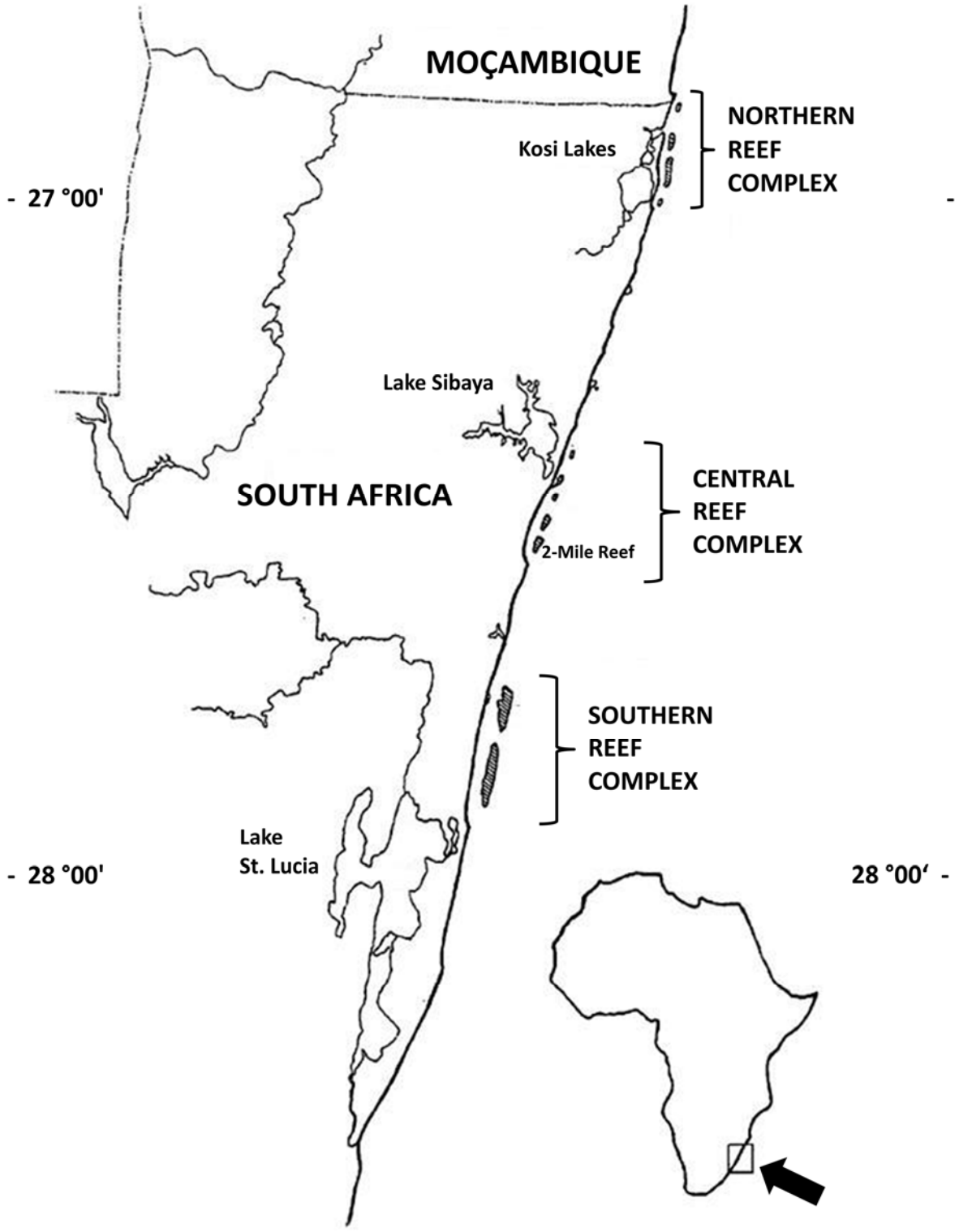


Figure 1.3.1: Location of the Maputaland reef complexes in northern KwaZulu-Natal, South Africa, showing position of Two-Mile Reef.

The KZN coral communities are grouped in what are known as the northern, central and southern reef complexes (Fig. 1.3.1, Riegl *et al*. 1995). The southern reefs fall within a sanctuary area (no take area) and the northern reefs are isolated from tourist activities. The central reefs are found in Sodwana Bay which is the hub of recreational diving in South Africa, where approximately 80 000 dives are conducted each year (Walters and Samways 2001).

Sodwana Bay is approximately 70 km south of Mozambique and 300 km north-northeast of Durban, South Africa (Fig. 1.3.2). Sodwana Bay falls within in a Marine Protected Area in the iSimangaliso Wetland Park (a World Heritage site) and is patrolled by Ezemvelo KwaZulu-Natal Wildlife staff. The bay is formed by Jesser Point, an aeolianite shelf that is exposed at low tide and creates a small bay that serves as the boat launch site from which dive charters and fishing vessels operate. Underwater, a series of submerged Pleistocene beachrock and aeolianite reefs runs parallel to the coastline at depths from 5 to 35 m. The major outcrops north-east from Jesser Point are known as Two-Mile, Four-Mile, Seven-Mile and Nine-Mile reefs, and are located between 27°23ˈS and 27°32ˈS. Their names describe their approximate distance, in nautical miles, from Jesser Point.

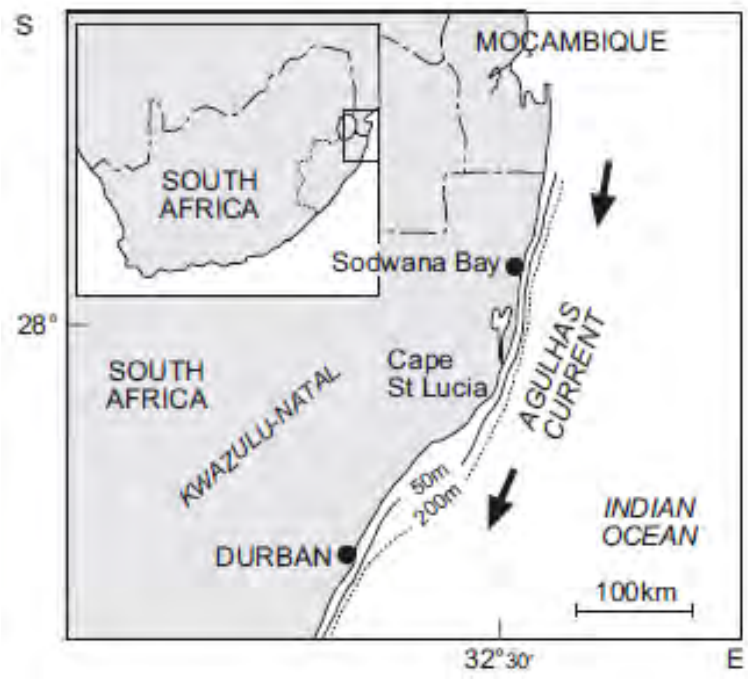


Figure 1.3.2: Map of the coastline of KwaZulu-Natal, South Africa, showing location of Sodwana Bay (Anderson *et al*. 2005).

1.4 Biogeography

Biogeographic studies aim to describe and usually to explain the geographic distribution of organisms. In the marine environment, sea temperature is the single most important explanatory factor controlling the geographical distribution of marine species (Tittensor *et al*. 2010).

The recent global marine biogeographic scheme of Spalding *et al*. (2007) places Sodwana Bay within the western edge of the tropical Western Indo-Pacific Realm, which extends from the Cape St. Lucia/ Cape Vidal area (80-90 km south of Sodwana) northwards up the African coast and across the Indian Ocean. In terms of seaweed biogeography, the Cape St Lucia area marks the boundary between the tropical Indo-West Pacific flora (in which Sodwana lies) and a

biogeographic overlap region between that extends down the central and southern KwaZulu-Natal coast into northern Transkei, where the Agulhas Marine Province begins (Bolton and Anderson 1997; Bolton *et al*. 2004). While some authors offer different interpretations of marine biogeographic patterns on these coasts (e.g. Sink *et al*. 2005; Porter *et al*. 2013), depending on the taxa under study or the criteria used to determine biogeographic regions, all agree that there is a biogeographic boundary around Cape St Lucia/Cape Vidal, and this is supported by a recent study of inshore sea temperatures around the South African coastline (Smit *et al*. 2013). Sodwana Bay thus falls within the tropical Indo-West Pacific province, which is the largest coastal biogeographic region on earth (Adey and Steneck 2001).

1.5 Aims and objectives

Background to this study

The subtidal seaweed communities of the KwaZulu-Natal (KZN) coast were until recently very poorly studied (Bolton and Anderson 1997; Anderson and Bolton 2005). In the early 2000's a South Africa/Flanders collaboration produced a number of taxonomic and biogeographic publications, including a KZN seaweed guide (De Clerck *et al*. 2005), and led to the initiation of ecological studies of KZN algal communities. However, there is only one published ecological report on subtidal macroalgae in Maputaland (Anderson *et al*. 2005). Their study of turf-forming communities was carried out by analysing 25 quadrats (25 cm x 25 cm) at 5 depths (1, 7, 10, 15, 26 m) at Sodwana Bay. They recorded 105 species of seaweeds, more than the recorded seaweed flora of many countries in tropical West Africa (Bolton *et al*. 2004). Although they found a remarkable diversity of seaweed species in these turfs, the total

sampled area was only 1.56 m^2. Their study was limited to algal turf communities (mainly near reef edges), and did not sample general macroalgal communities for which no ecological or community studies exist. However, previous observations by Anderson (pers.com) indicated some diversity of benthic macroalgae on the general substrata of the Sodwana Bay reefs, especially on seemingly bleached and dead coral, as well as beach-rock substratum.

There are various published studies focusing on the bleaching responses of coral assemblages on southern African reefs following mass bleaching events (Celliers and Schleyer 2002; Floros *et al*. 2004; McClanahan *et al*. 2007; Ruiz Sebastián *et al*. 2009). However, no data are available on the composition and type of reef macroalgae colonising these reefs after such acute disturbances.

Objectives of this study

This study was conducted under the auspices of the African Coelacanth Ecosystem Programme (ACEP), and is the first ecological reporting of general seaweed communities on the high latitude reefs of the tropical KZN coast. It explored the abundance and diversity of benthic algal communities colonising hard substrata (essentially comprising bleached coral assemblages and "beach rock") at Two-Mile Reef, Sodwana Bay, by testing several hypotheses (Chapter 2). Furthermore, the sampling method used allowed for a snapshot that reflects the current status of this reef in the context of past disturbances.

During the course of this study, the Oceanographic Research Institute (ORI) afforded the opportunity to investigate the algal colonisation of their artificial settlement plates (ceramic, marble and treated ceramic tiles) at the northern, central and southern areas of Two-Mile Reef. This was done to gain a broad overview of algal recruitment on empty (artificial)

substrata on Two-Mile Reef, and to determine whether algal colonisation differed between settlement plate types.

A further aim of the study was to provide an account of the non-geniculate coralline algae occurring on bleached and dead coral assemblages on Two-Mile Reef. Nine non-geniculate coralline species have been reported from Sodwana Bay (Maneveldt *et al*. 2008). However, most of these taxa were collected in the intertidal and shallow subtidal zones. Studies focusing on non-geniculate coralline algae below 5 m depth are lacking in Sodwana Bay, or in fact any part of the tropical KZN coast, despite the importance of this group of algae in coral reef systems.

Chapter 2: Seaweed communities on natural and artificial hard substrata on Two-Mile Reef, Sodwana Bay

2.1 Introduction

Coral reefs are among the most heterogeneous and economically important ecosystems on earth. However, reefs are rapidly degrading at a global scale due to a wide variety of anthropogenic factors, such as overfishing of herbivorous fishes, pollution, and sedimentation, as well as due to climate change and natural disturbances (Hughes 1994; Wilkinson 2002; Hughes *et al*. 2003; Pandolfi *et al*. 2005). For example, hurricanes and tropical storms are perhaps the most obvious and frequent natural disturbances affecting reef communities, causing extensive physical damage by powerful wave action, leading to possible widespread destruction of coral colonies (Glynn 1990). Heavy damage and colony loss can also be a consequence of a sharp increase in the population density of the coral-eating echinoid *Acanthaster* (Porter 1972).

Algae are rapid and efficient primary colonisers of newly available substrata on almost any area of coral reefs that has been opened by disturbances (Diaz-Pulido and McCook 2002). Hughes (1994) and Rogers *et al*. (1997) showed how hurricane damage on reefs can lead to dynamic macroalgal proliferation. Similarly, Fong and Lirman (1995) reported that within days of Hurricane Andrew, coral skeleton bared by hurricane damage was colonised by filamentous green algae that were succeeded by filamentous red algal turfs within a month. In severe cases, changes may lead to massive algal overgrowth of the newly available substratum, and thus amount to an extensive phase shift from coral-dominance to dominance by benthic algae

(McCook 1999; Hoegh-Guldberg *et al*. 2007), potentially contributing to long-term reef degradation (McCook 1999).

Rising ocean temperatures have triggered mass bleaching episodes that have resulted in catastrophic loss of coral cover around the world (Glynn 1993; Hoegh-Guldberg *et al*. 2007). Many studies on coral bleaching describe the physiological and climatological causes of bleaching, behaviour of zooxanthellae, and the recovery of zooxanthellae after damage (e.g. Hoegh-Guldberg 1999). However, there has been little work focussing on algal recruitment on damaged corals that fail to recover their zooxanthellae (Diaz-Pulido and McCook 2002). Diaz-Pulido and McCook (2002) addressed the fate of bleached colonies of *Porites* spp. on the Great Barrier Reef, Australia. Their study reported that dead coral tissue was colonised by diverse communities of macroalgae, which varied by reef location and season. Titlyanov *et al*. (2008) further showed that lesions occurring on artificially injured specimens of *Porites lutea* were occupied by 26 algal species after one month and 58 species three months after the experiment. These studies concluded that macroalgae do not colonise healthy coral tissue, and that algal colonisation was not the initial cause of coral tissue mortality, although some species may have contributed to the failure of zooxanthellae recovery after bleaching.

Successional patterns of tropical macroalgae rely upon vacant space, nutrient availability, and grazing pressure. Various studies have reported the recovery of coral reef systems after a catastrophic event, and the succession of algae during this process along with succession on experimental settlement plates. In general, turf algae are among the first to colonize available space, followed by a dominance of thin and finely branched filamentous seaweeds, which at a later stage are replaced by dense growths of thick canopy-forming seaweed (McManus and Polsenberg 2004; Mumby 2009). The 37-year history of the coral reef assemblages in Moorea,

French Polynesia, represents one of the longest kept records of coral reef dynamics. Between 1991 and 1994, disturbances caused declines in coral cover and accompanying colonisation by algal turfs. However, Adjeroud *et al*. (2009) did not observe a successional sequence of algal growth, but instead, the cover of turf algae decreased and returned to predisturbance levels within a decade. This result indicates that the availability of empty substratum is not sufficient to cause a persistent increase in algal cover, and that other factors, such as an increase in nutrients or a reduction in grazing pressure, may be pertinent for a phase shift to macroalgal dominance (McManus and Polsenberg 2004; Mumby *et al*. 2005). A similar pattern emerged from the extensive loss of coral cover on the Great Barrier Reef, Australia, following the massive bleaching event in 1998. Algal assemblages were initially dominated by blue-green algae, but rapidly shifted to an assemblage dominated by algal turfs, although fleshy macroalgae and crustose coralline algae overgrew the turfs during later stages of the succession, (Diaz-Pulido and McCook 2002).

Fluctuating weather conditions throughout the year have an acute effect on the abundance of macroalgae in tropical regions; particularly lower temperatures during the rainy season can cause a significant increase of algal biomass. Ateweberhan *et al*. (2006) carried out an extensive overview of seasonality of four major functional groups of coral reef macroalgae (canopy, foliose, turf, and crustose corallines) in the southern Red Sea. They observed strong seasonal shifts in macroalgal biomass, although seasonal variation differed among groups. Canopy and foliose macroalgae were highly seasonal, whereas turf and crustose coralline algae displayed much less seasonal variability.

The settlement and recruitment of algal propagules to reef communities requires suitable hard substrata and competition with organisms already present (Worm and Chapman 1998).

Surface texture, material, and chemical composition have been shown to strongly influence the settlement and survival of algal recruits. Diaz-Pulido and McCook (2002) reported that algal colonisation differed markedly on clay settlement tiles from that on dead coral skeleton, and their further study in 2004 (Diaz-Pulido and McCook 2004) found that natural substratum supported more mature assemblages than artificial substratum. Additionally, the species composition of algal assemblages differed according to the severity of bleaching damage to the corals: species composition on severely bleached corals was in a more developed successional stage than that on less bleached corals.

The inshore, high latitude coral communities of southern Africa suffered negligible impacts during the past mass bleaching events, but the most recent bleaching in southern Africa (in 2005), when a warm-water anomaly affected much of the southern Indian Ocean, caused severe and extensive bleaching of coral on South African reefs (McClanahan *et al*. 2007).

While some information on subtidal macroalgal turf communities in Sodwana Bay is available (Anderson *et al*. 2005), there is no information on the distribution of macroalgal assemblages on the different types of hard substrata, including dead corals. There is also no information on possible seasonal changes in algal community structure. Although anecdotal reports from divers suggested extensive seaweed colonisation of dead coral on Two-Mile Reef (pers. comm., RJ Anderson) this has never been formally investigated. This study aimed to fill some of the gaps in our knowledge by:

1. Investigating the different types of substratum (including types of dead coral) that are available for algal colonisation.

2. Testing the hypothesis that the different hard substrata support different algal communities.
3. Testing the hypothesis that algal communities differ between autumn and spring (seasonal differentiation).
4. Testing the hypothesis that communities colonising different types of artificial substrata (ceramic tiles, marble tiles, and pre-conditioned ceramic tiles) would differ.

2.2 Materials and Methods

2.2.1 *Study area*

The study was carried out on Two-Mile Reef (TMR: 27°31'29''S; 32°40'37''E), which is located in the central Maputaland reef complex at Sodwana Bay (KwaZulu-Natal, South Africa). Two-Mile Reef is highly rugose, with reef ridges, reef slopes and gullies and is considered to be a patch reef system (Ramsay and Mason 1990; Jordan and Samways 2001). The reef, lying 1 km offshore, is approximately 1.8 km long and 900 m wide and is always submerged (Ramsay and Mason 1990; Celliers and Schleyer 2008). The water depth on the reef varies between 6-10 m on its shallowest pinnacles, to 14-19 m on extensive deep subtidal reef flats and 24-27 m at the edge of the fore-reef (Celliers and Schleyer 2002). Study sites were scattered on the reef, at various depths ranging from 8 m to 19 m.

Seawater temperature was measured continuously with a Starmon Mini (Star-Oddi, Iceland) recorder at 12 m depth on Two-Mile Reef.

2.2.2 *Sampling*

All fieldwork was carried out between 1 and 4 March and 6 and 9 September 2010 by divers using SCUBA. Since algal communities were being studied, divers placed the quadrats subjectively (forty-five 10 cm x 10 cm wire quadrats per sampling period) on substrata bearing seaweeds, rather than randomly over the whole substratum. All the visible macroalgae within each quadrat, except highly adherent crustose forms, were scraped off the dead coral using a paint scraper and collected in fine-mesh bags. The substratum directly under each of the quadrats was then recorded and was visually classified into one of four categories: Digitate coral, plate coral, brain coral and “hard substratum”. In instances where it proved difficult or

impossible to effectively scrape the surface, chunks of the substratum were broken off using a chisel and hammer, and taken to the field laboratory.

In order to estimate the relative cover of different types of substrata, cover values were estimated using line-point intercept (LPI) methods along 20 m transect lines. A diver swam along the transect line and recorded the benthic category directly below the transect line at every 0.25 m interval (80 points/transect). Benthic categories used were live coral, dead coral, macroalgae (including non-geniculate coralline algae), sand, bare substratum and sponge. Dead coral was defined as a substratum that maintained the full structural integrity of coral, but had no live coral tissue, whilst bare consolidated surfaces on the reef that could not be recognised as dead coral were defined as “bare substratum”.

Upon returning to the field laboratory, each quadrat sample was placed in a sorting tray (45 x 30 x 10 cm) and covered with seawater. All macroalgae from each sample (quadrat) were sorted into separate species or genera (provisional identifications) and an initial visual estimate of cover-abundance was made. A modified Braun-Blanquet scale (Lepš and Hadincová 1992) was used to assign a cover-abundance value to each species within each quadrat: 0 = no cover; 1 – rare (less than 5% cover); 2 – occasional (5-25% cover); 3 – common (25-50% cover); 4 – abundant (50-75% cover); and 5 – dominant (greater than 75% cover). In cases where whole chunks of substratum were broken off, an initial estimate of cover was made, followed by subsequent sorting to species or generic level.

The seaweeds from each sample were preserved in 5% formalin in seawater for subsequent identification in the laboratory, to the level of species (where possible) or to the level of genus. Where necessary, specimens were stained with fast green and mounted in corn syrup on microscope slides for later identification and for cross-referencing during sorting of

subsequent samples. Seaweeds were identified using the morphological descriptions in *Guide to the Seaweeds of KwaZulu-Natal* (De Clerck *et al*. 2005), *Seaweeds of the South African west coast* (Stegenga *et al*. 1997), *Intertidal Seaweeds of Tanzania* (Jaasund, 1976), *Marine Plants of Tanzania: A Field Guide to the Seaweeds and Seagrasses* (Oliveira *et al*. 2005) and/or compared to appropriate material and published literature. Identification procedures for non-geniculate coralline algae are described in chapter 3.

2.2.3 *Artificial settlement surfaces*: *Experimental design*

To test the hypothesis that seaweed recruitment would differ on different artificial settlement surfaces we investigated the colonisation, by seaweed species, on a series of artificial tiles. These were placed on Two-Mile Reef by researchers from ORI to test for suitable artificial substrata for coral settlement, but were very close to the sampling study site and offered an opportunity to examine seaweed colonisation. At each of the three sites, three replicate concrete Y-frames were positioned 5–15 m apart from each other on flat reef areas. Each monitoring site differed marginally with regards to depth and topography, and was selected in a north-south direction on TMR. The northern site (15-17 m) was the deepest site characterised by flat topography with few gullies. The central (12-15 m) and southern site (9-12 m) were at shallower depths in an area of varied topography with sharp drop-offs into sand gullies.

Three types of artificial substratum were used: unglazed ceramic tiles, marble tiles, and ceramic tiles pre-conditioned with crustose coralline algae (ceramic tiles were pre-conditioned for two months in an aquarium where *Mesophyllum funafutiense* was prolific). All tile types were 9.7 x 9.7 x 1 cm and had a 6 mm hole drilled in their centre to enable horizontal attachment onto the frames. The weight of each frame (75 kg) and its flat, three-

armed shape provided sufficient anchorage and stability for the settlement tiles during major turbulence on the reef. Five replicates of each tile type were anchored onto each Y-frame, in a stratified sampling design (Fig. 2.2.1), resulting in 15 replicates of each tile type at each of the three monitoring sites.

The tiles were left on the reef for a period of six months (October 2009-April 2010), then retrieved and preserved in 4% formalin seawater solution for storage prior to examination in the laboratory. The upper surface of each tile was censused for fleshy and non-geniculate coralline algae using a Zeiss Stemi stereo dissection microscope at 10X magnification. The Braun-Blanquet scale was used to assign a cover-abundance value to the macroalgal (including non-geniculate coralline algae) recruits on the tiles: 0 = no cover; 1 – rare (less than 5% cover); 2 – occasional (5-25% cover); 3 – common (25-50% cover); 4 – abundant (50-75% cover); and 5 – dominant (greater than 75% cover). Subsequently, the macroalgae were scraped off the tile with a dull surgical blade; the algal material obtained was, wherever possible, identified to species level. Identification procedures are described in section 2.2.2.

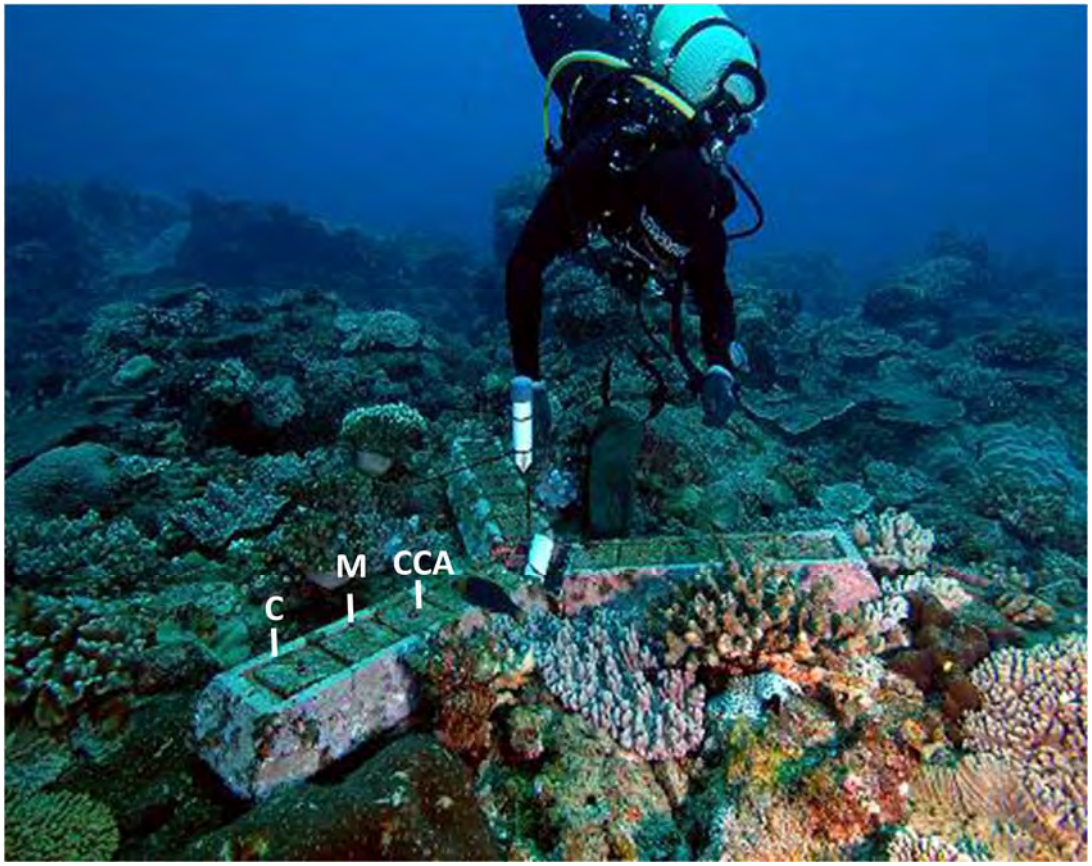


Figure 2.2.1: Stratified attachment of the three tile types (ceramic [C], marble [M], and pre-conditioned ceramic [CCA] tiles) onto a Y-frame. Photo credit: C. Floros.

2.2.4 *Analyses*

Data were analysed using Community Analysis Package 4.0 (Pisces Conservation Limited 2007). The seaweed community data were subjected to multivariate analysis (ordination by detrended correspondence analysis [DECORANA], using the option to downweight rare species) and cluster analysis (complete linkage, Bray-Curtis similarity coefficient), to show how substrata and season cluster with respect to their seaweed flora. To assess the adequacy of sampling, species accumulation curves were generated in PRIMER v6 (Clark and Gorley 2006), where a first-order jacknife (Jacknife 1), a species richness estimator, was calculated. Using Statistica (Release 11), a Kruskal-Wallis nonparametric test was used to detect significant

differences in macroalgal abundance among different natural substrata (digitate coral, brain coral, plate coral and hard substratum), and likewise between the tile treatments (marble, ceramic, and treated ceramic tiles). Differences amongst substrata/treatments were considered significant if $p < 0.05$. After statistically significant Kruskal-Wallis tests, pairwise Mann-Whitney tests between the substrata/treatments were performed with significance levels adjusted to account for multiple comparisons (Bonferroni correction, $\alpha = 0.017$).

2.3 Results

2.3.1 *Sea temperature*

Monthly mean sea water temperatures were between 22°C and 26°C, and the lowest temperature recorded was 20.2°C and the highest 27.8°C (Fig. 2.3.1). Minima occurred in winter and maxima in summer. The measurements indicate that monthly mean temperature reached a maximum of 26-27°C during the summer with a minimum monthly mean temperature of 21°C in winter (Fig. 2.3.1).

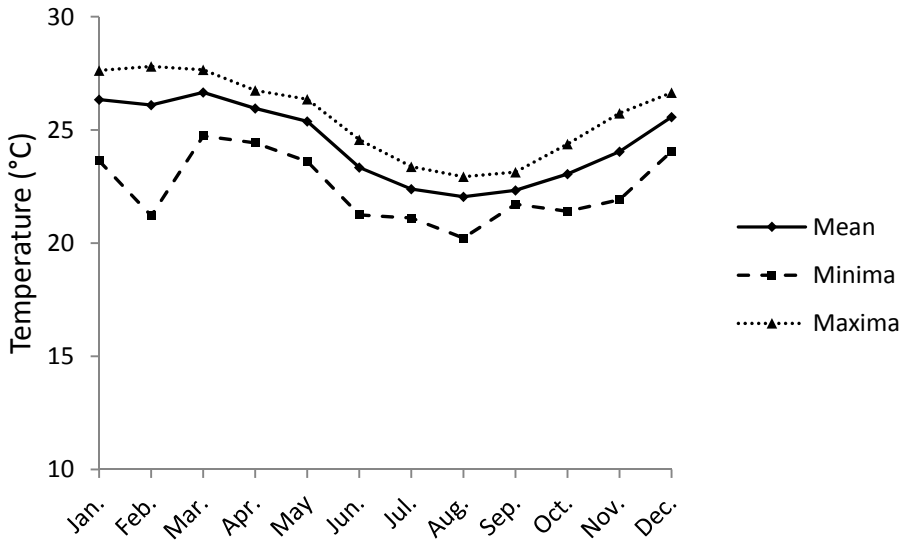


Figure 2.3.1: Sea water temperatures at Sodwana Bay, January to December 2010. Solid line shows monthly mean temperature, broken lines show the highest and lowest absolute temperatures measured during each month.

2.3.2 *Composition of hard substrata*

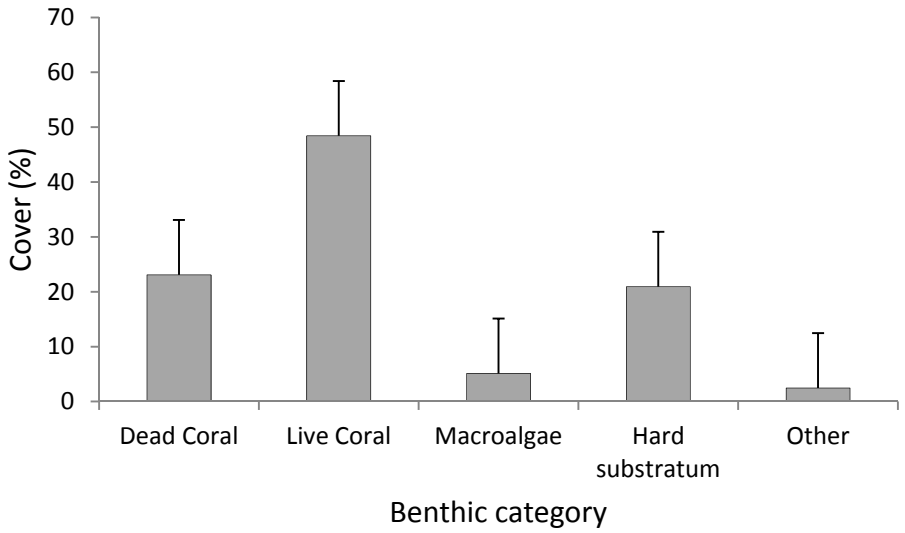


Figure 2.3.2: Benthic composition for March and September 2010 (combined) at Two-Mile Reef depicted as mean percent cover (± SE) of dominant benthic groups: corals indicate scleractinian corals only; "Other" is composed of sessile benthic invertebrates not included in previous groups (e.g. sponges, ascidians).

Benthic cover was dominated by live scleractinian corals, comprising 48.4% of the total cover (Fig. 2.3.2). Dead and bleached corals occupied much less space (23.1% of total benthic cover) followed by bare hard substratum (20.9%). Non-geniculate coralline and fleshy macroalgae (5%) exceeded sponges and other invertebrate groups, the latter comprising less than 3% of the cover (Fig. 2.3.2).

2.3.3 *Species accumulation curve*

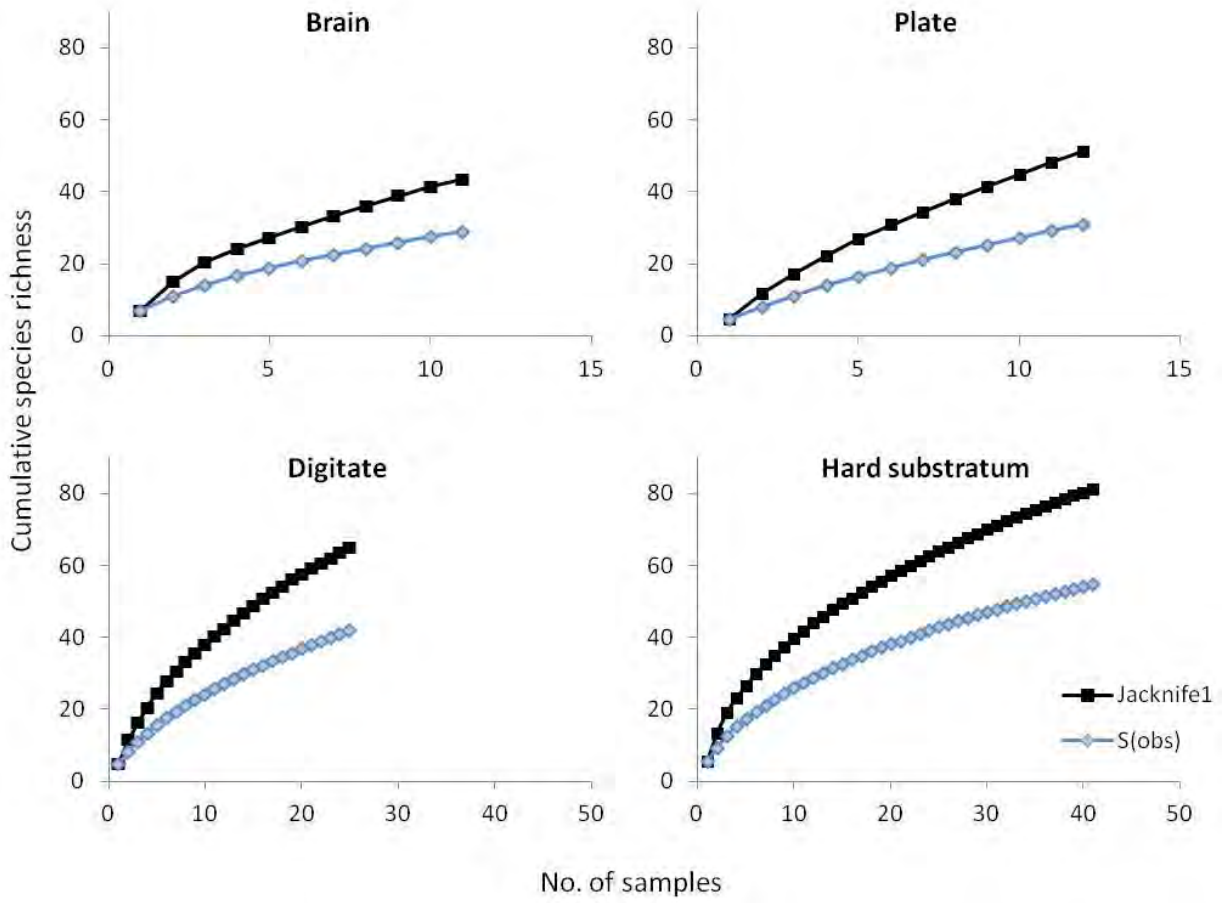


Figure 2.3.3: Species accumulation curves and Jacknife 1 estimate curves for macroalgae on each substratum type on Two-Mile Reef, Sodwana Bay. S(obs) is the observed species count. Scale of the *x* axis adjusted to accommodate the estimated curve.

On all four substratum types, species richness increased as a function of sampling effort (Fig. 2.3.3). Observed species accumulation and Jacknife 1 estimated curves did not plateau on any substratum type (Fig. 2.3.3), indicating that the macroalgal species identified comprise only a portion of the actual total biodiversity occurring on the different substrata. Based on Jacknife 1 estimates, the expected number of species was 43 on brain coral, 51 on plate coral, 65 on digitate coral and 81 on hard substrata.

A further species accumulation curve, based on the cumulative number of species plotted against the overall number of samples collected, is shown in Figure 2.3.4. This curve is approaching asymptote, indicating that the macroalgae found on Two-Mile Reef were sufficiently well-sampled to capture most of the species diversity. Overall, the number of samples collected represents a reasonable estimate of diversity on Two-Mile Reef: the estimate curve predicted 123 species while the observed curve recorded 85 species.

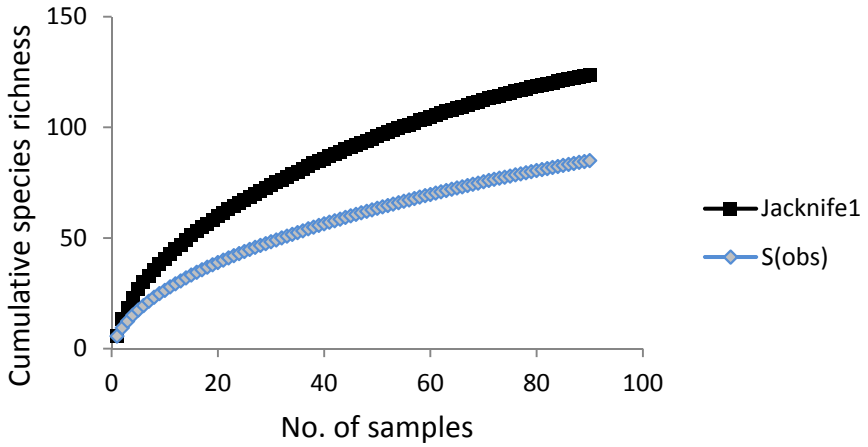


Figure 2.3.4: Species accumulation and Jacknife 1 estimate curves for benthic macroalgae on all substrata on Two-Mile Reef Sodwana Bay. S(obs) is the observed species count.

2.3.4 *Algal colonisation on natural substrata*

A total of 87 taxa of subtidal seaweeds were recorded in the 90 sample quadrats, including 13 Chlorophyceae, 10 Phaeophyceae, 62 Rhodophyceae and one Cyanobacteria (Table 1). In all quadrats, the greatest number of species belonged to the red algae (Table 1), and were mostly small turf-forming species. Rhodophyta that were present and relatively common in March and September were: *Hypnea spinella*, *Pterocladiella caerulescens*, and *Herposiphonia tenella*. The brown alga *Lobophora variegata* was found throughout the sampling periods (66 out of 89 quadrats) either as a low turf component or with larger conspicuous blades. Three species were recorded for the first time in South Africa: *Codium dwarkense* (Chlorophyceae, Codiaceae), *Lithophyllum cuneatum* and *Pneophyllum* sp. (both Rhodophyceae, Corallinaceae; see Chapter 3) (Table 1).

Table 1: Seaweeds (including non-geniculate coralline algae) collected at Two-Mile Reef, Sodwana Bay. Species marked with an asterisk are new records for South Africa.

Taxon	March	September	Tiles
CHLOROPHYCEAE			
Caulerpa serrulata (Forsskål) J.Agardh	1	0	0
Caulerpa nummularia Harvey ex J.Agardh	1	1	0
Cladophora coelothrix Kützing	0	1	0
Cladophora sp.	0	1	1
Codium acuminatum O.Schmidt	0	1	0
Codium arabicum Kützing	0	1	1
Codium dwarkense Børgesen *	1	1	1
Codium geppii O.C.Schmidt	0	1	0
Codium pocockiae P.C.Silva	1	0	0
Derbesia sp.	0	1	0
Neomeris sp.	0	1	0
Neomeris van-bosseae M.A.Howe	0	0	1
Ulva sp.	1	0	0
Valonia macrophysa Kützing	0	1	0
PHAEOPHYCEAE			
Dictyopteris delicatula J.V.Lamouroux	1	1	1
Dictyota cervicornis Kützing	1	1	1
Dictyota humifusa Hörnig, Schnetter and Coppejans	1	0	0
Dictyota sp. 1	0	1	0
Dictyota sp. 2	0	0	1
Lobophora variegata (J.V.Lamouroux) Womersley ex E.C.Oliveira	1	1	1
Sargassum sp. 1	1	0	0
Sargassum sp. 2	1	0	1
Sargassum sp. 3	0	1	0
Sphacelaria novae-hollandiae Sonder	0	1	1
Turbinaria ornata (Turner) J.Agardh	1	0	0
RHODOPHYCEAE			
Acrosorium ciliolatum (Harvey) Kylin	0	1	0
Acrosorium sp.	1	0	0
Amansia rhodantha (Harvey) J.Agardh	0	1	0
Amphiroa sp.	1	0	0
Amphisbetema indica (J.Agardh) Weber-van Bosse	0	0	0
Anotrichium sp.	0	1	0
Apoglossum spathulatum (Sonder) Womersley and Shepley	1	1	0
Botryocladia leptopoda (J.Agardh) Kylin	1	0	0
Botryocladia sp.	0	1	0
Callophycus condominius R.E.Norris	0	1	0
Centroceras clavulatum (C.Agardh) Montagne	0	0	1
Centroceras sp.	0	1	0
Ceramium centroceratiforme Simons	0	1	0
Ceramium sp.	1	1	1
Champia compressa Harvey	0	1	0
Champia parvula (C.Agardh) Harvey	0	1	1

Table 1 (cont.)

Taxon	March	September	Tiles
Champia sp.	1	0	0
Chondria collinsiana M.A.Howe	0	1	1
Chondria sp. 1	1	1	0
Chondria sp. 2	0	1	0
Crouania attenuata	0	1	0
Dasya baillouviana (S.G.Gmelin) Montagne	0	1	0
Dasya pedicellata (C.Agardh) C.Agardh	0	1	0
Dasya sp. 1	1	0	1
Dasya sp. 2	0	1	0
Dasya sp. 4	0	1	0
Dasya sp.3	0	0	0
Eucheuma sp.	0	0	1
Gelidiella myriocladia (Børgesen) Feldmann and G.Hamel	1	1	1
Gelidiopsis repens (Kützing) Weber-van Bosse	1	1	0
Gelidiopsis variabilis (Greville ex J.Agardh) F.Schmitz	0	1	0
Gelidium reptans (Suhr) Kylin	1	1	0
Gloiocladia iyoensis (Okamura) R.E.Norris	1	1	0
Griffithsia sp.	0	1	0
Griffithsia weber-vanbosseae Børgesen	0	1	0
Halichrysis coalescens (Farlow) R.E.Norris and A.J.K.Millar	1	1	0
Halymenia durvillei Bory de Saint-Vincent	0	1	1
Herposiphonia tenella (C.Agardh) Ambronn	1	1	1
Heterosiphonia wurdemannii (J.Bailey ex Harvey) Falkenberg	1	1	0
Hydrolithon farinosum (J.V.Lamouroux) D.Penrose and Y.M.Chamberlain	0	0	0
Hydrolithon pellire Y.M.Chamberlain and R.E.Norris	0	0	0
Hypnea sp. 1	1	0	0
Hypnea sp. 2	1	0	0
Hypnea spinella (C.Agardh) Kützing	1	1	1
Jania intermedia (Kützing) P.C.Silva	0	1	0
Jania pumila J.V.Lamouroux	0	1	1
Jania sp.	1	0	0
Laurencia sp. 1	1	1	1
Laurencia sp. 2	0	1	0
Lithophyllum acrocamptum Heydrich	0	0	0
Lithophyllum cuneatum Keats *	0	0	0
Lithothamnion muelleri Lenormand ex Rosanoff	0	0	0
Martensia elegans Hering	0	1	0
Neogoniolithon brassica-florida (Harvey) Setchell and L.R.Mason	0	0	0
Platysiphonia delicata (Clemente) Cremades	1	0	0
Plocamium beckeri F.Schmitz ex Simons	0	1	0
Plocamium sp.	0	1	0
Pneophyllum sp. *	0	0	0
Porolithon onkodes (Heydrich) D.Penrose and Woelkerling	0	0	0
Polysiphonia coacta C.K.Tseng	0	1	1
Polysiphonia ferulacea Suhr ex J.Agardh	0	1	0
Pterocladiella caerulescens (Kützing) Santelices and Hommersand	1	1	1
Ptilothamnion cladophorae (Yamada and T.Tanaka) G.Feldmann-Mazoyer	0	1	0
Rhodymenia sp.	0	1	0
Spongites yendoi (Foslie) Y.M.Chamberlain	0	0	0
Tiffaniella sp.	0	1	0
Tolypiocladia calodictyon (Harvey ex Kützing) P.C.Silva	1	0	0
Wrangelia penicillata (C.Agardh) C.Agardh	0	0	0
Wurdemannia miniata (Sprengel) Feldmann and G.Hamel	0	1	0
CYANOPHYCEAE			
Lyngbya sp.	1	0	1

2.3.4.1 *Seasonal variability*

Ordination of the species' Braun-Blanquet data in all 90 quadrats (correspondence analysis, not shown) produced a highly skewed pattern with Quadrat 43 (March) completely separate on the x-axis and forcing all 89 other quadrats into a small group. Quadrat 43 was very unusual in that it contained only one species of alga. It was therefore excluded from subsequent ordinations.

The cluster analysis (Fig. 2.3.5) of the 89 remaining quadrats revealed no seasonal clustering in the composition and abundance of algal communities. The results were similar for the ordination analysis where the DECORANA (Fig. 2.3.6) failed to display any distinct pattern that related to seasonal change. As a result, data for the two sampling periods were combined for many of the subsequent analyses.

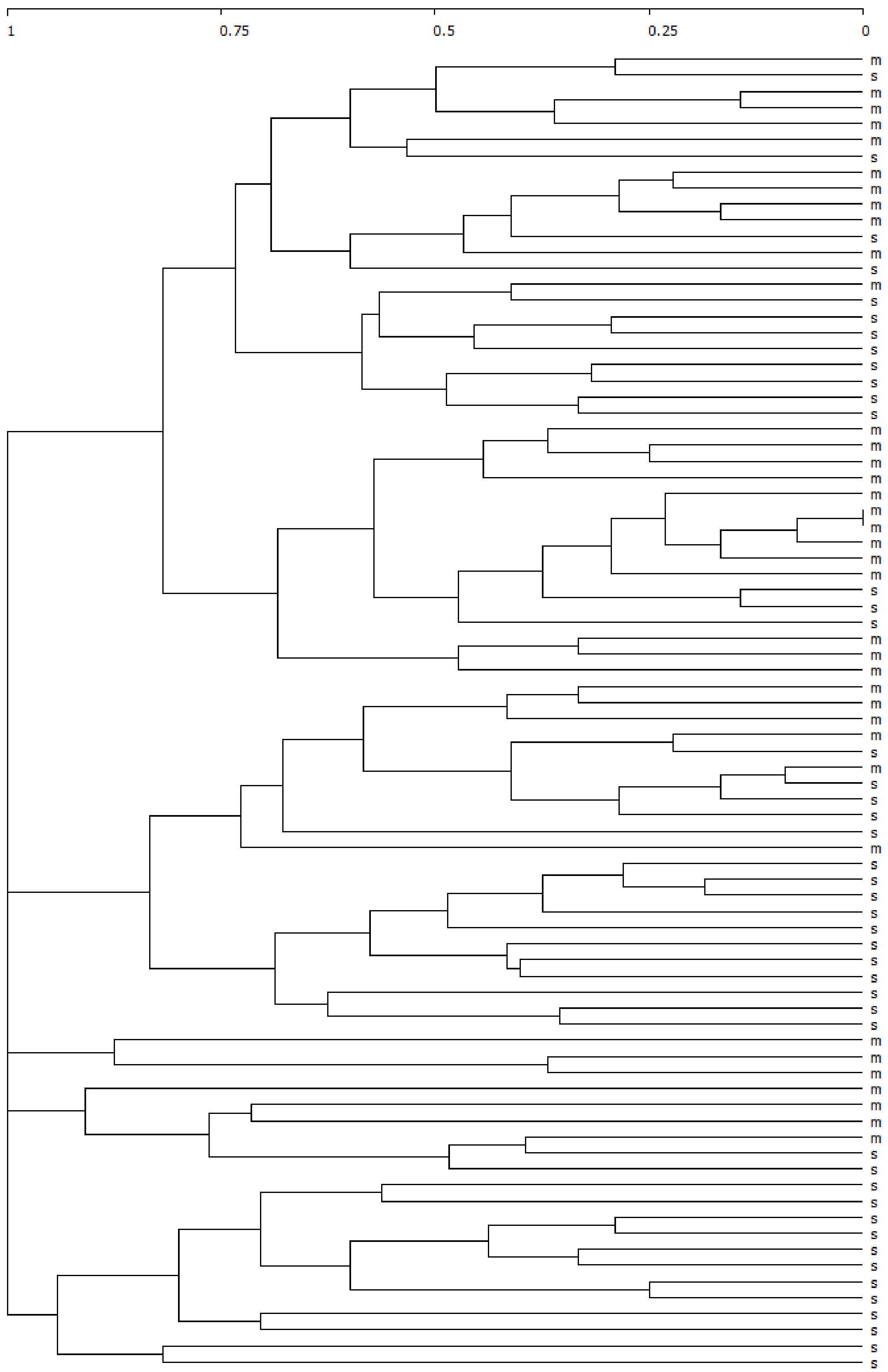


Figure 2.3.5: Dendrogram of hierarchical clustering of algal communities (Bray-Curtis, complete linkage) based on cover abundance data in March (m) and September (s) 2010 on Two-Mile Reef, Sodwana Bay.

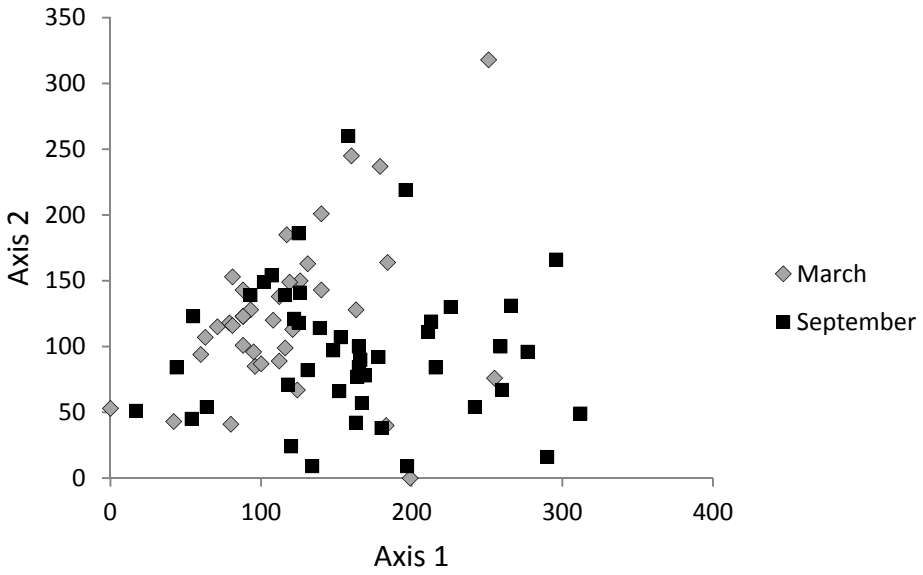


Figure 2.3.6: DECORANA **analysis** showing similarity between samples (quadrats), based on species' Braun-Blanquet cover values (excluding quadrat 43) in March and September 2010. Each point represents a single quadrat (Eigenvalues: Axis 1 = 0.344, Axis 2 = 0.294).

2.3.4.2 *Overall patterns of algal communities*

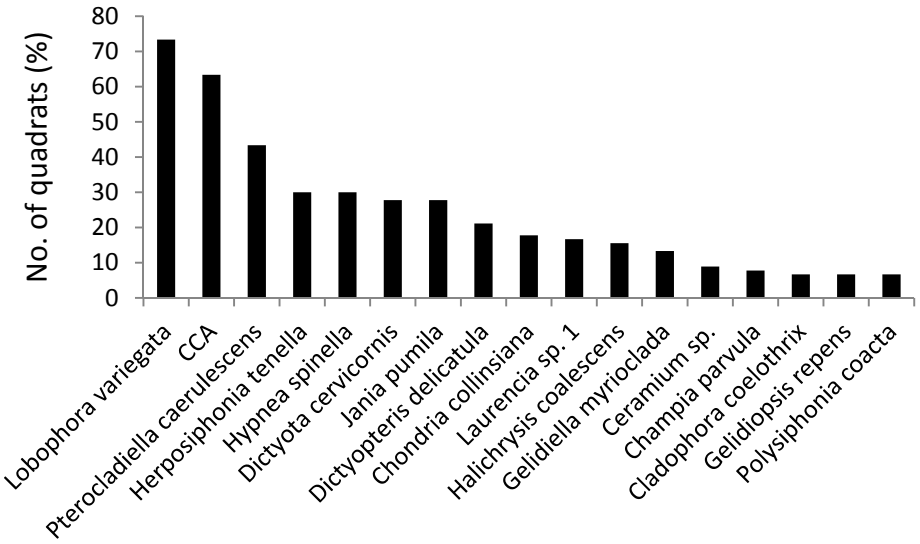


Figure 2.3.7: Overall percentage frequency patterns for dominant taxa (mean cover >6%) including crustose coralline algae (CCA) in March and September 2010.

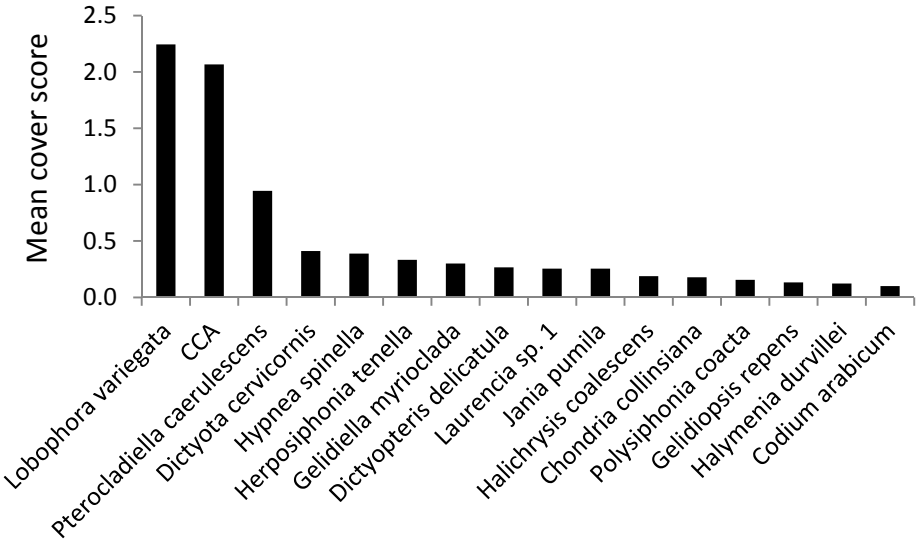


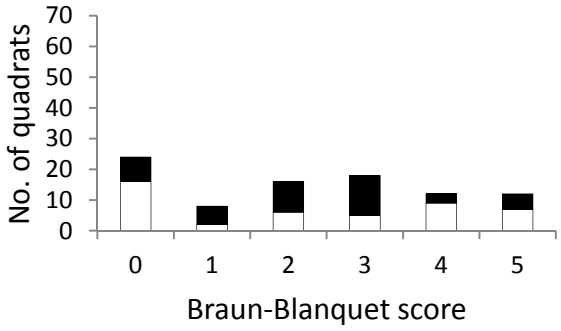
Figure 2.3.8: Overall mean Braun-Blanquet cover scores for dominant taxa (mean cover score >0.1) including crustose coralline algae (CCA) in March and September 2010.

Lobophora variegata was the most common macroalga encountered in the quadrat surveys, it was found in 73% of all the samples (Fig. 2.3.7) from Two-Mile Reef. It was usually abundant

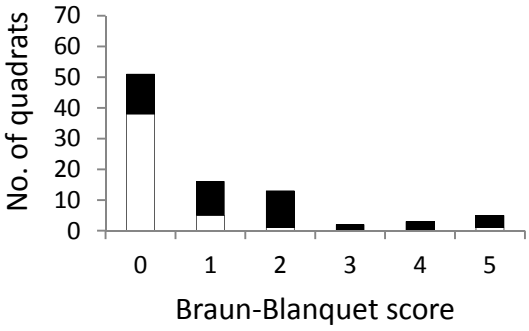
across all substratum types in March and September, and it had the highest mean Braun-Blanquet score of any of the taxa (Fig. 2.3.8). Of the other macroalgae, non-geniculate crustose coralline algae (as a combined form) were the next most common 'taxon', occurring in 63% of all quadrats with a mean Braun-Blanquet score of 2.07.

Six species were present at a frequency greater than 20%, and two species greater than 50%, while 67 species showed a frequency less than 5% (Fig. 2.3.7). Among the most common species were the Phaeophyta *Lobophora variegata*, *Dictyota cervicornis*, *Dictyopteris delicatula,* the Chlorophyta *Cladophora coelothrix*, the Rhodophyta *Pterocladiella caerulescens*, *Herposiphonia tenella*, *Hypnea spinella*, *Jania pumila, Halichrysis coalescens*, *Laurencia* sp. 1 and crustose coralline algae. Several species were considered 'rare' according to their Braun-Blanquet cover score, including *Halymenia durvillei*, *Jania intermedia*, *Platysiphonia delicata*, *Turbinaria ornata*, *Wurdemannia miniata* and *Codium acuminatum* (Figure 2.3.8).

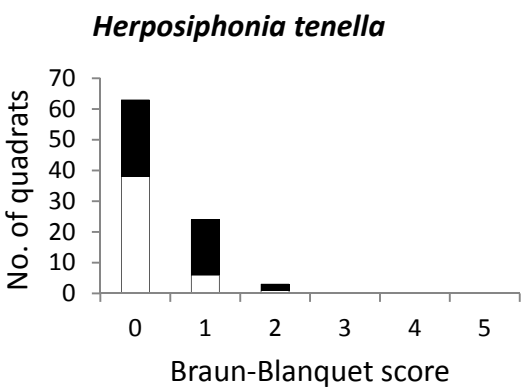
a)


Lobophora variegata
No. of quadrats
70
60
50
40
30
20
10
0
0 1 2 3 4 5
Braun-Blanquet score

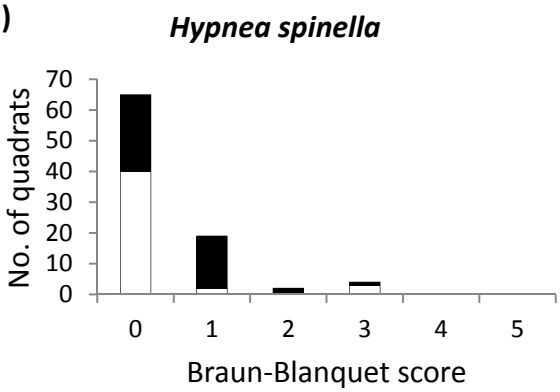
b)


Pterocladiella caerulescens
No. of quadrats
70
60
50
40
30
20
10
0
0 1 2 3 4 5
Braun-Blanquet score

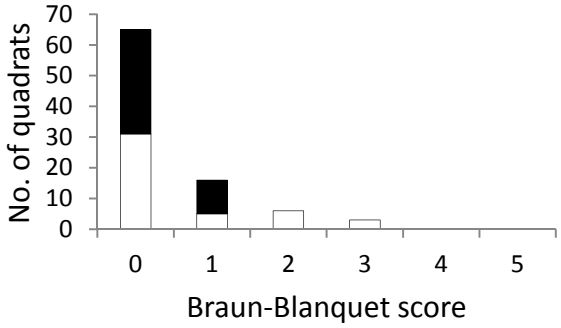
c)


Herposiphonia tenella
No. of quadrats
70
60
50
40
30
20
10
0
0 1 2 3 4 5
Braun-Blanquet score

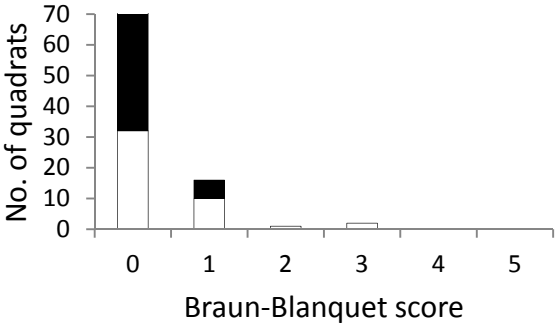
d)

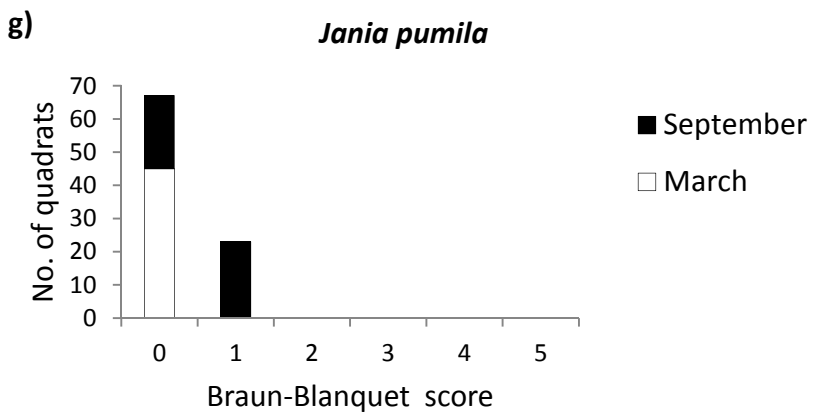

Hypnea spinella
No. of quadrats
70
60
50
40
30
20
10
0
0 1 2 3 4 5
Braun-Blanquet score

e)


Dictyota cervicornis
No. of quadrats
70
60
50
40
30
20
10
0
0 1 2 3 4 5
Braun-Blanquet score

f)


Dictyopteris delicatula
No. of quadrats
70
60
50
40
30
20
10
0
0 1 2 3 4 5
Braun-Blanquet score



Figures 2.3.9 a - g: Frequency of Braun-Blanquet cover scores of the seven macroalgae with the highest cover (> 19%) within the 10 x 10 cm quadrats (n = 89) in March and September 2010. .

The brown foliose macroalga *Lobophora variegata* was found to dominate the majority of quadrats during the reef survey. The Braun-Blanquet cover abundance scores showed that *L. variegata* was present from very low amounts to extremely abundant throughout the year (Fig. 2.3.9.a). The cover abundance of the red turf alga *Pterocladiella caerulescens* was generally low; however, it was relatively more abundant in September (Fig. 2.3.9.b). Turf red algae *Herposiphonia tenella* and *Hypnea spinella* were fairly common; both were present in March and September (Figs. 2.3.9.c-d). Foliose seaweeds *Dictyota cervicornis* and *Dictyopteris delicatula* occurred occasionally within quadrats in March, but were rarely encountered in September when they were present in only 11 and 6 quadrats respectively (Figs. 2.3.9.e-f). The geniculate coralline *Jania pumila* was rarely abundant in September, though present in 23 quadrats, but entirely absent in March (Fig. 2.3.9.g).

2.3.4.3 *Community variation on different substrata*

There was no detectable clustering of substratum types according to the community assemblages on them (Fig. 2.3.10). This result was supported by the DECORANA ordination analysis (Fig. 2.3.11) of the cover abundance of algal species. The ordination analysis produced a minor separation along the first axis (Eigenvalue 0.344), with digitate coral quadrats having low values.

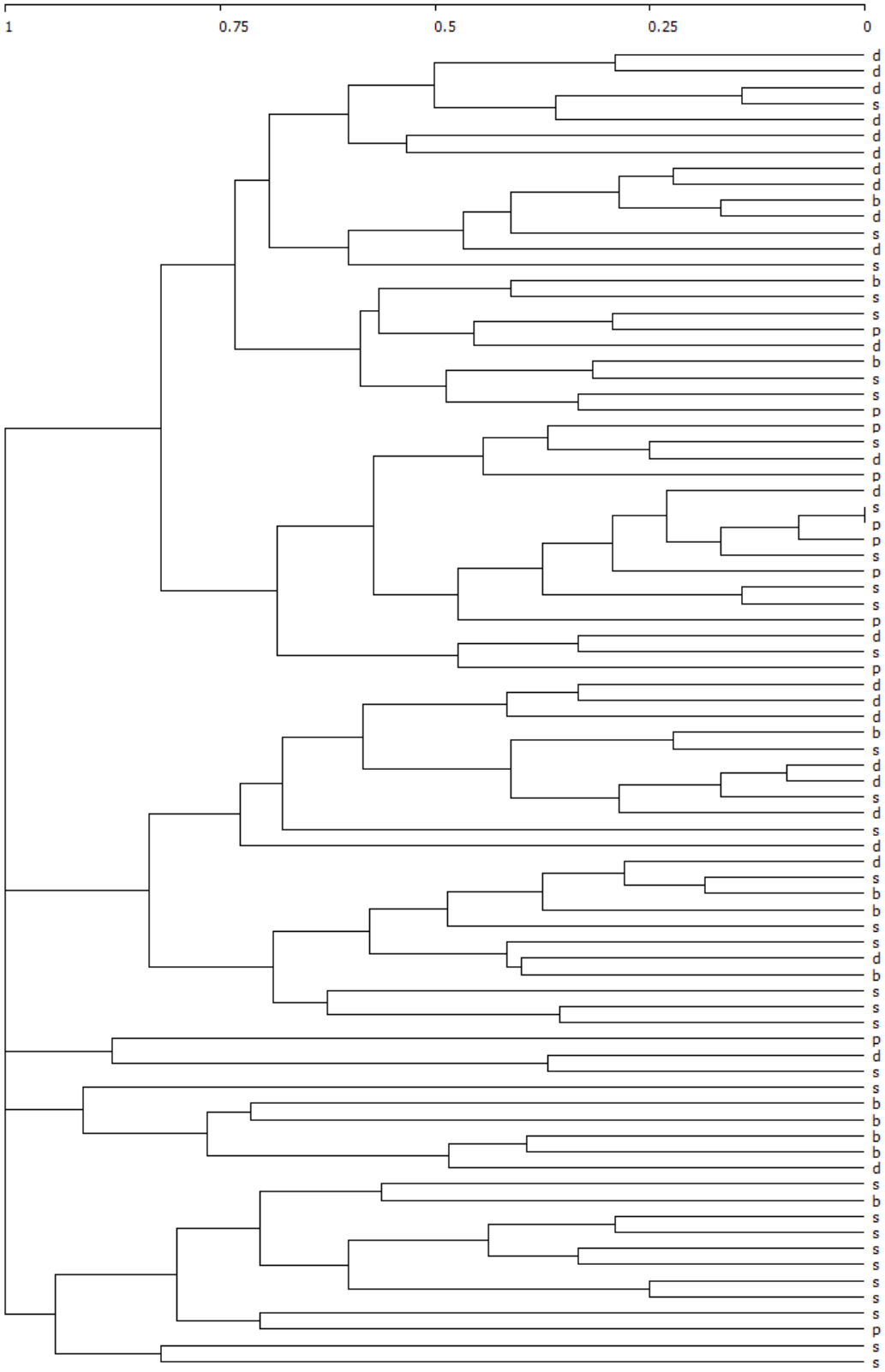


Figure 2.3.10: Dendrogram of hierarchical clustering of algal communities (Bray-Curtis, complete linkage) based on overall cover abundance data of assemblages on different substrata (B: brain coral; D: digitate coral; P: plate coral; S: hard substratum) on Two-Mile Reef.

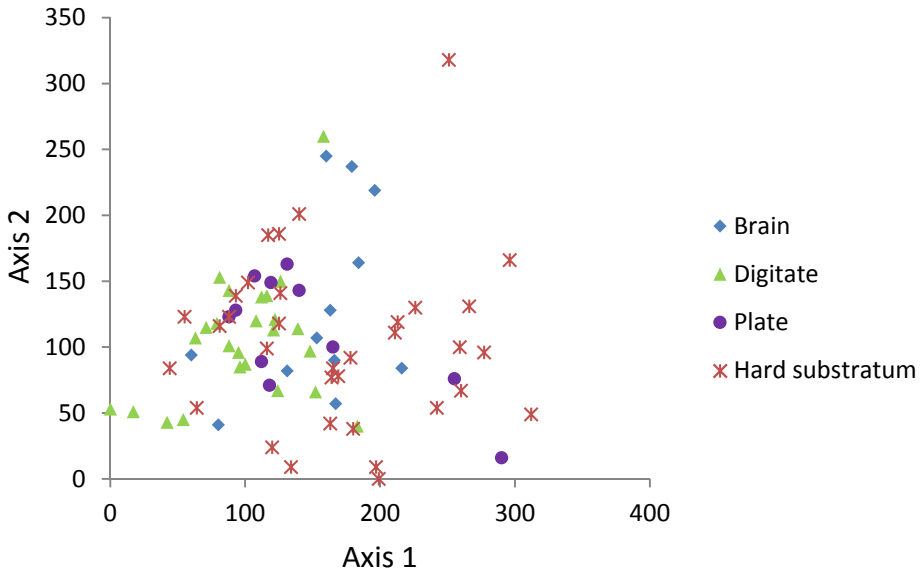


Figure 2.3.11: DECORANA analysis showing similarity between samples (quadrats) based on overall species' Braun-Blanquet cover values on different substrata (excluding quadrat 43). Each point represents a single quadrat (Eigenvalues: Axis 1 = 0.344, Axis 2 = 0.294).

Table 2: Percentage frequency of dominant macroalgal species collected on each substratum type (B: brain coral; D: digitate coral; P: plate coral; S: hard substratum) for March and September 2010 combined.

	%			
Algal taxon	B	D	P	S
Lobophora variegata	91.7	76.0	75.0	63.4
CCA	66.7	92.0	50.0	48.8
Pterocladiella caerulescens	66.7	24.0	25.0	56.1
Herposiphonia tenella	41.7	28.0	16.7	29.3
Hypnea spinella	41.7	16.0	25.0	31.7
Dictyota cervicornis	58.3	32.0	25.0	14.6
Jania pumila	33.3	12.0	8.3	36.6
Dictyopteris delicatula	16.7	36.0	16.7	14.6

Dead corals and consolidated hard substrata on Two-Mile Reef generally supported a high cover of *Lobophora variegata*, which was present in almost all the quadrats, and had the highest frequency value of all the fleshy macroalgae (91.7%; Table 2). However, cover

abundance of *L. variegata* showed no statistical difference among the substratum types (Kruskal-Wallis: $H_{(3,N = 90)} = 5.05$; NS).

Pterocladiella caerulescens, a common turf alga, displayed the highest frequency of all turf taxa found on consolidated substratum (Table 2). There was a slight significant difference in *P. caerulescens* abundance between brain and digitate coral (Kruskal-Wallis: $H_{(3,N = 90)} = 11.33$; $P = 0.01$; Post hoc Mann-Whitney *U*-test: $U = 74$; $P < 0.01$), and it was most often observed distributed in small patches across the different substrata.

Crustose coralline algae were by far the most abundant taxa encountered on digitate corals, being recorded on 92% of digitate corals during the study (Table 2). Significant differences in abundance cover were evident between digitate and plate corals (Kruskal-Wallis: $H_{(3,N = 90)} = 17.75$; $P < 0.001$; Post hoc Mann-Whitney *U*-test: $U = 43.5$; $P < 0.001$). Additionally, the abundance of crustose coralline algae significantly varied between digitate coral and hard substratum ((Kruskal-Wallis: $H_{(3,N = 90)} = 17.75$; $P < 0.001$; Post hoc Mann-Whitney *U*-test: $U = 242.5$; $P < 0.001$).

Table 3: Mean Braun-Blanquet cover scores (±SD) of dominant macroalgal species on each substratum type (B: brain coral; D: digitate coral; P: plate coral; S: hard substratum) for March and September 2010 combined and significance of the difference among substratum types.

Algal taxon					
	B	D	P	S	Significance
Lobophora variegata	2.33 (± 1.07)	2.44 (± 1.73)	3.08 (± 2.07)	1.88 (± 1.79)	ns
CCA	2.33 (±2.06)	3.28 (±1.51)	1.08 (±1.24)	1.54 (±1.80)	*
Pterocladiella caerulescens	1.58 (± 1.62)	0.32 (± 0.63)	0.50 (±1.00)	1.30 (± 1.65)	*
Herposiphonia tenella	0.58 (± 0.79)	0.28 (± 0.46)	0.17 (± 0.39)	0.33 (± 0.53)	ns
Hypnea spinella	0.50 (±0.67)	0.32 (± 0.85)	0.25 (± 0.45)	0.45 (± 0.78)	ns
Dictyota cervicornis	0.67 (± 0.65)	0.68 (± 1.11)	0.33 (± 0.65)	0.18 (± 0.45)	ns
Jania pumila	0.33 (±0.49)	0.12 (±0.33)	0.08 (±0.29)	0.38 (±0.49)	ns
Dictyopteris delicatula	0.17 (± 0.39)	0.48 (± 0.77)	0.17 (± 0.39)	0.20 (± 0.56)	ns

ns = non significant, * = $P < 0.001$

Macroalgae rarely had mean cover scores over 2, indicating they rarely covered more than 25% of a quadrat, but occasionally *Lobophora variegata* or crustose coralline algae were found to cover most of a quadrat. The high SD values indicate extreme patchiness in the distribution of almost all taxa.

Crustose coralline algae and *Lobophora variegata* comprised most of the macroalgal cover on each substratum type with other algae patchy, scattered, or rare.

2.3.5 *Algal colonisation on artificial substrata*

There was no detectable clustering of tile types according to the macroalgal communities studied, at any but the lowest levels of similarity (Fig. 2.3.12). The results were similar for the ordination analysis where the DECORANA (Fig.2.3.13) failed to display any major separation between tile types based on their algal assemblages.

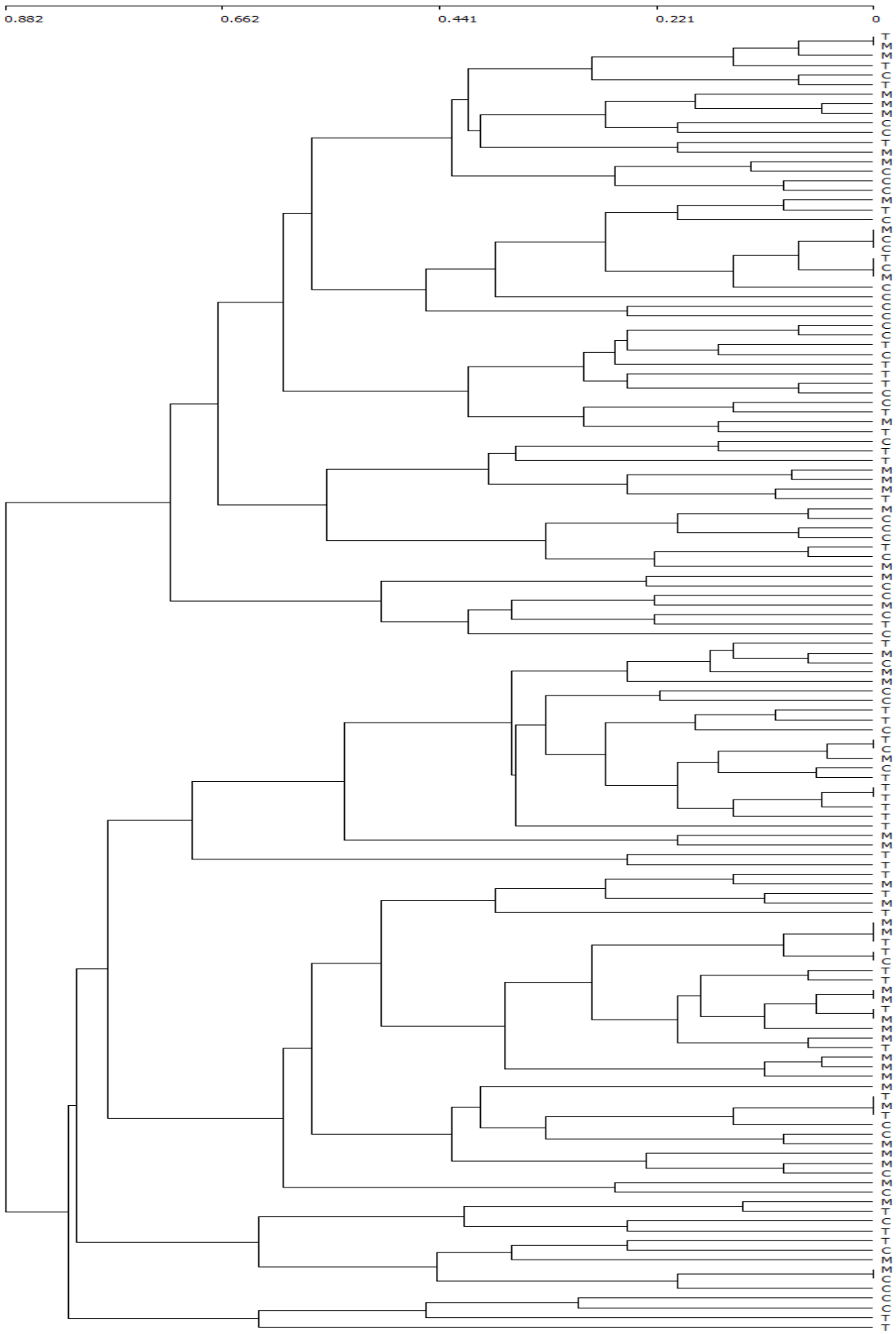


Figure 2.3.12: Dendrogram of hierarchical clustering of algal communities (Bray-Curtis, complete linkage) based on overall cover abundance data of assemblages on different tile types (T: treated ceramic; M: marble; C: ceramic).

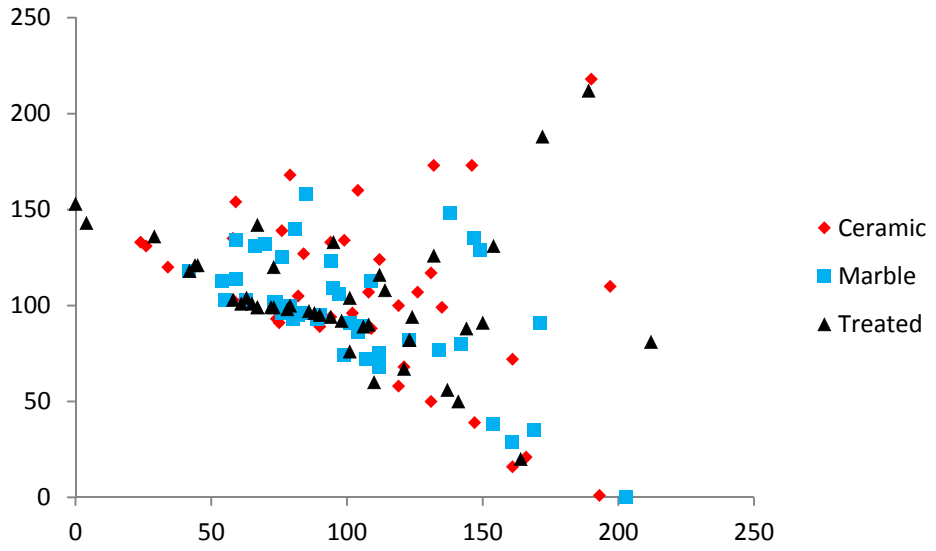


Figure 2.3.13: DECORANA analysis of tile types (treated, marble and ceramic), based on the macroalgae that occur on them (Eigenvalues: Axis 1 = 0.239, Axis 2 = 0.178).

A total of 24 taxa were identified growing on artificial settlement tiles, comprising 4 Chlorophyta, 6 Phaeophyceae and 14 Rhodophyta (Table 1).The macroalgal cover was floristically fairly homogeneous, with *Lobophora variegata* and crustose coralline algae (CCA) accounting for 80% of the overall algal cover (Fig. 2.3.14). Other species with less cover but with relatively high frequency (>10%) were: *Dictyota* sp. 1, *Sphacelaria novae-hollandiae*, *Herposiphonia tenella*, *Hypnea spinella* and *Chondria collinsiana* (Fig. 2.3.14).

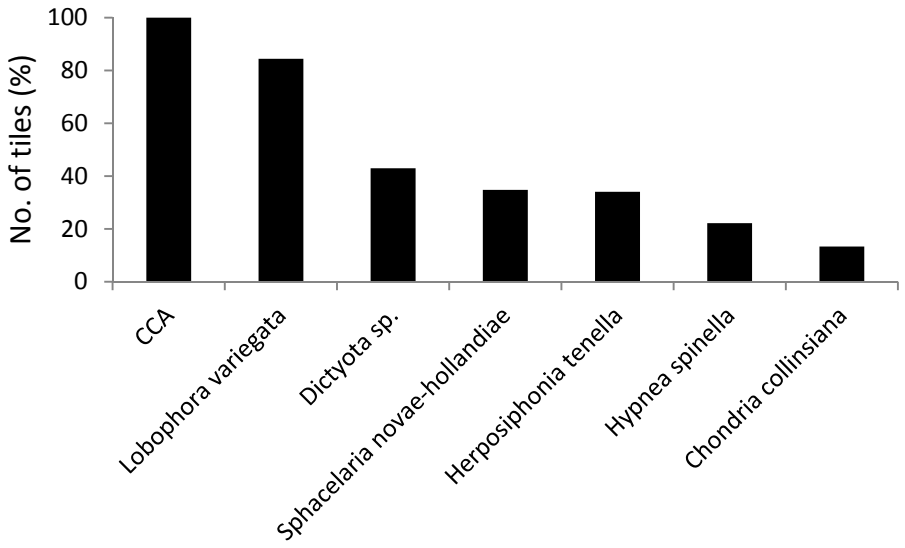


Figure 2.3.14: Overall percentage frequency patterns for the seven most common macroalgal taxa (mean cover >10%), including crustose coralline algae (CCA), on all tile types.

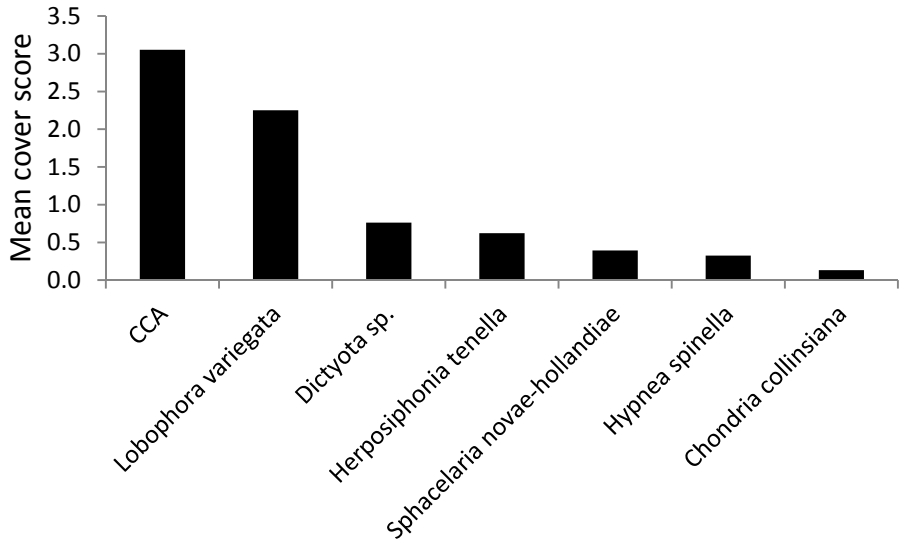
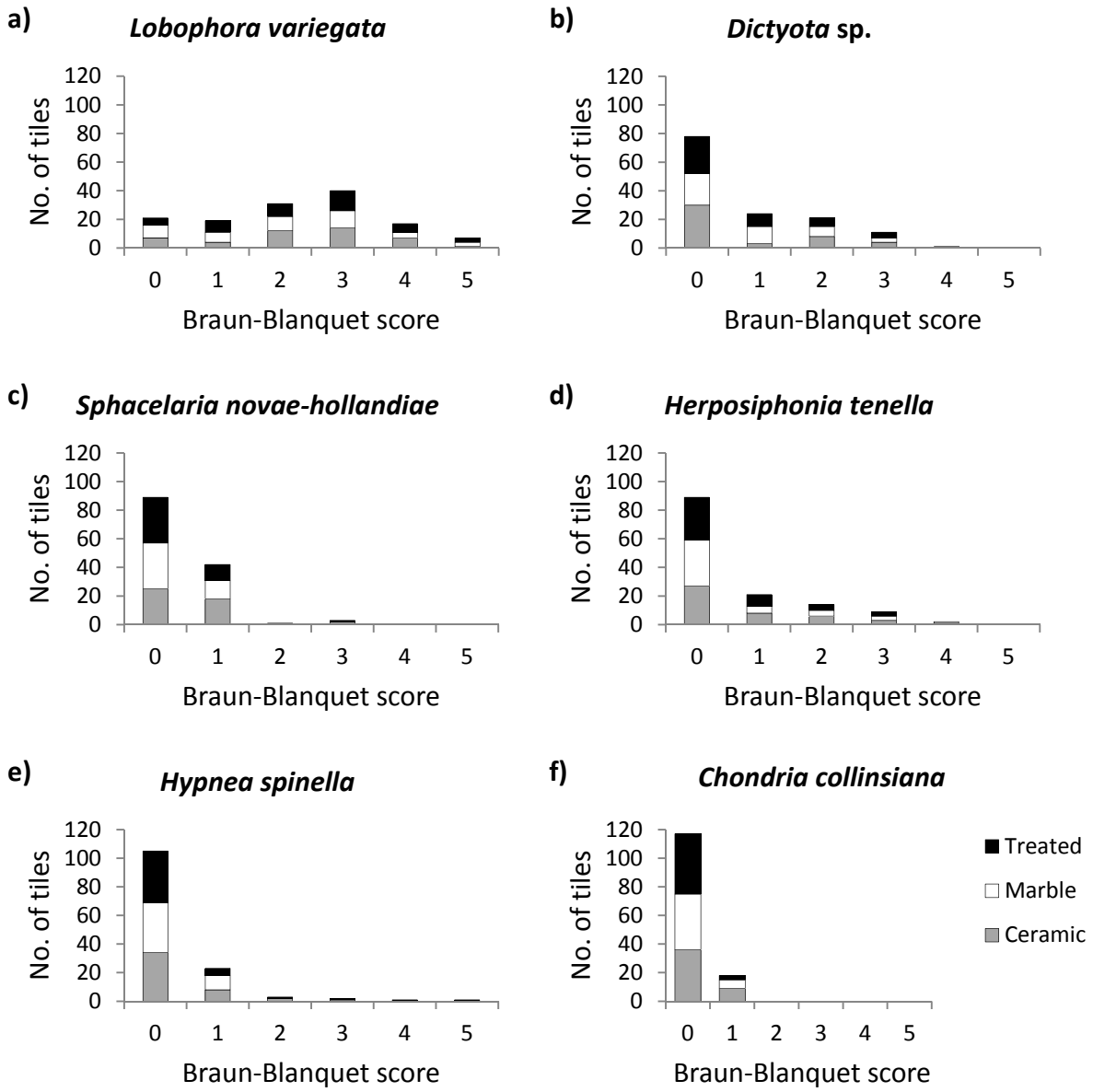


Figure 2.3.15: Overall mean Braun-Blanquet cover scores for the seven most common macroalgal taxa (mean cover score >0.1), including crustose coralline algae (CCA), on all tile types.

Crustose coralline algae were by far the most abundant macroalgae encountered during the tile surveys, with at least one species of CCA being recorded on 100% of the tiles (Fig. 2.3.14). These algae were frequently found with high abundance across all tile types with the highest mean Braun-Blanquet score (3.05) of any of the taxa (Fig. 2.3.15). Among the other taxa, brown foliose seaweeds were the next most common macroalgae found on the tiles.

Lobophora variegata occurred on 84% of the 135 tiles (Fig. 2.3.14) with a mean Braun-Blanquet score of 2.25 (Fig. 2.3.15), while both *Dictyota* sp. and the filamentous *Sphacelaria novae-hollandiae* occurred on >34% of the tiles (Fig. 2.3.14) but with lower mean covers scores of 0.76 and 0.393 respectively (Fig. 2.3.15). Of the remaining seaweed species, the turf algae *Herposiphonia tenella*, *Hypnea spinella* and *Chondria collinsiana* were the most common Rhodophyceae, with overall frequencies of 13-34 (Fig. 2.3.14). Most of the macroalgal species had low mean cover scores (seldom over 1; Fig. 2.3.15), indicating they rarely covered more than 5% of a tile, but frequently *L. variegata* and CCA were observed to cover the majority of a tile.



Figures 2.3.16 a – h: Braun-Blanquet cover score frequency for the six most common macroalgae (> 10% cover) growing on ceramic, marble and pre-conditioned ceramic tiles. The Braun-Blanquet coverage abundance is computed beginning at the zero point and is classified as follows: 0 = no cover; 1 = less than 5% cover; 2 = 5-25% cover; 3 = 25-50% cover; 4 = 50-75% cover; 5 = greater than 75% cover.

The overall macroalgal settlement on the tiles did not markedly differ between the three tile types. At the end of the six month experiment, crustose coralline algae were observed to have settled on every tile tested, regardless of treatment or material (Fig. 2.3.17). Additionally, all

three tile types supported a high frequency and abundance of *Lobophora variegata*, where frequency ranged between 88.9% on treated tiles to 80% on marble tiles (Fig. 2.3.17) and cover scores between 2.38 (± 1.40) on treated tiles to 2.09 (± 1.49) on marble tiles (Table 4). In contrast, *Herposiphonia tenella*, *Hypnea spinella* and *Chondria collinsiana* were most often distributed in small patches with low cover abundance scores (Table 4).

Cover values were compared among the pre-treated ceramic, marble, and ceramic tiles. These data did not have homogenous variances and were thus analysed using Kruskal-Wallis tests. The brown seaweed *Lobophora variegata* was observed overgrowing the majority of tiles during the study. There was no significant difference in the abundance cover of *L. variegata* among tiles types (Kruskal-Wallis: $H_{(2,N = 135)} = 1.05$; NS), although, abundance was slightly, but not significantly, higher in pre-conditioned tiles (Table 4). In contrast, there was a significant difference in crustose coralline abundance between ceramic and marble tile types (Kruskal-Wallis: $H_{(2,N = 135)} = 20.06$; $P < 0.001$; Post hoc Mann-Whitney *U*-test: $U = 494.5$; $P < 0.001$).

Table 4: Mean Braun-Blanquet cover scores (±SD) for the seven most common macroalgae taxa, including crustose coralline algae (CCA) for each tile type and significance of the difference between tile type.

Algal taxon				
	Treated	Marble	Ceramic	Significance
CCA	3.04 (± 0.98)	3.58 (± 1.05)	2.50 (± 0.97)	*
Lobophora variegata	2.38 (± 1.40)	2.09 (± 1.49)	2.29 (± 1.34)	ns
Dictyota sp.	0.73 (± 1.01)	0.87 (± 1.06)	0.69 (± 1.06)	ns
Sphacelaria novae-hollandiae	0.36 (± 0.65)	0.29 (± 0.46)	0.53 (± 0.73)	ns
Herposiphonia tenella	0.56 (± 0.92)	0.58 (± 1.06)	0.73 (± 1.07)	ns
Hypnea spinella	0.42 (± 1.08)	0.22 (± 0.42)	0.33 (± 0.67)	ns
Chondria collinsiana	0.07 (± 0.25)	0.13 (± 0.34)	0.20 (± 0.40)	ns

ns = non significant, * = $P < 0.001$

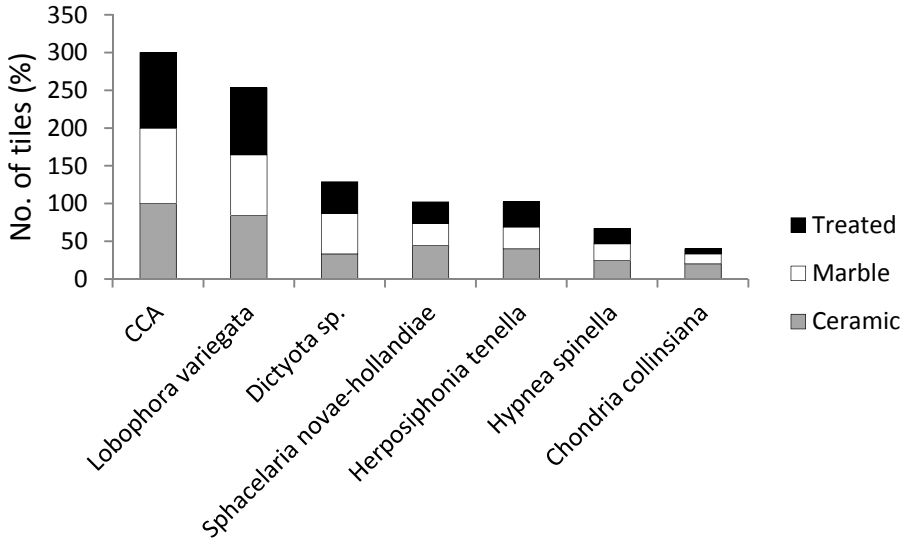


Figure 2.3.17: Percentage frequency for the seven most common macroalgae taxa (mean >6%), including crustose coralline algae (CCA) for each tile type.

2.4 Discussion

2.4.1 *Sea temperature*

The one year of measurements in this study gave a seasonal temperature curve almost identical in shape to that of Schleyer (1999) and Anderson *et al*. (2005), including an annual cold-spike that occurs in February during the height of marine summer, decreasing average maximum temperatures, which is attributed to small-scale localised upwelling (Riegl and Piller 2003; Roberts *et al*. 2006). In Sodwana Bay, Riegl and Piller (2003) suggest that such upwelling events play a role in protecting local reefs from bleaching by counteracting excessive heating of the sea water. Sodwana Bay coral reefs are therefore usually protected from extreme heat by the active water dynamics on the narrow shelf, generated mainly by the Agulhas current and periodic upwelling events in summer that, if they occur at the right time, reduce sea surface temperatures to well below bleaching levels (Ramsay 1989; Riegl and Piller 2003).

The minimum monthly mean sea water temperature is above the 20°C considered to indicate a tropical biogeographical region (Lüning 1990). The means of even the lowest temperatures recorded during each month never fell below 20°C, indicating that there are possibly very few instances when cooler water might inhibit the growth or reproduction of tropical species. Previous studies of seaweed communities at Sodwana and in northern Kwazulu-Natal confirm the dominance of tropical elements in the flora (e.g. Bolton *et al*. 2004; Anderson *et al*. 2005).

2.4.2 *Composition of hard substrata*

High latitude coral reefs are typically characterised by relatively low coral cover and high abundance of fleshy macroalgae (Harriott and Banks 2002; Vroom and Braun 2010). This study revealed that the live coral cover on Two-Mile Reef, one of Africa's southernmost coral communities, was higher (overall mean = 48.1%) than most other high latitude reefs (ca. 3.9-25.3%; Tribble and Randall 1986; Harriott and Banks 2002; Vroom and Braun 2010) and broadly comparable to lower latitude reefs of the Great Barrier Reef, where mean coral cover typically ranges from 18.3-27.0% and 30.7-33.6% on inshore and offshore reefs respectively (Wismer *et al*. 2009; Emslie *et al*. 2010). The estimates of coral cover from the present study are similar to previous records from Sodwana Bay (ca. 38.6-63.4%, Riegl *et al*. 1995; Riegl and Riegl 1996), suggesting that coral cover has changed little over the past two decades. This apparent stability of Sodwana Bays' coral communities may imply that they are relatively resilient, since these reefs have largely escaped the bleaching and disease that have caused marked declines in coral cover on other tropical Indo-Pacific reefs over the same period (Bellwood *et al*. 2004). However, the most recent bleaching event in southern Africa (2005) highlights that these high latitude reefs are not immune, with extensive bleaching (up to 39% of colonies) in localised areas of the Maputaland coastline caused by fluctuating sea temperatures and solar radiation (Ruiz Sebastián *et al*. 2009).

The results of the present study indicate that benthic cover on Two-Mile Reef was similar to the findings of Riegl *et al*. (1995) and Riegl and Riegl (1996). They found scleractinian corals occupied slightly more space than Alcyonaceans (soft corals), and both exceeded sponges and other invertebrates. Macroalgae were not mentioned in their studies. Riegl and Riegl (1996)

specifically reported that Two-Mile Reef was clearly dominated by soft corals and low growing massive hard corals.

During the 2005 warm-water anomaly in the southern Indian Ocean, coral bleaching reached unprecedented levels (McClanahan *et al*. 2007), and resulted in a significant shift in abundance of corals and benthic algae on the high latitude reefs. Coral mortality at our study site was high, which is unsurprising since *Stylophora* (digitate coral) and *Montipora* (plate coral) are considered to be the most bleaching-susceptible scleractinian coral genera in Sodwana Bay (Celliers and Schleyer 2002; Floros *et al*. 2004). Importantly, in the present study, all corals that died from bleaching or other injuries were colonised by macroalgae. Rapid colonisation by algae after environmental disturbances is a general phenomenon that has been documented following mechanical injuries (Glynn 1990) and bleaching events (Glynn 1993; Hoegh-Guldberg 1999).

2.4.3 Algal colonisation on natural substrata

This study provides the first quantitative description of the composition and abundance of species comprising the macroalgal community on digitate coral, brain coral, plate coral and hard substrata of Two-Mile Reef. The epilithic and epizoic algal communities were characterised by a high incidence of 'rare' species, as is common of tropical systems elsewhere. Stuercke and McDermid (2004) found that 60% of the Hawaiian shallow subtidal turfs were 'rare' taxa, based on methods that fundamentally measured cover. Scott and Russ (1987) considered 63% of the epilithic algal community of the central Great Barrier Reef to be 'rare' species, individually comprising <7% of the canopy cover. On Two-Mile Reef, 91% of the species individually comprised <7% of the percentage cover. A considerable number of algal

genera observed on Two-Mile Reef are common components of algal communities in other tropical parts of the world. Of the 16 macroalgal genera described by Scott and Russ (1987) as being widespread across several coral reef areas, such as the Caribbean, the Great Barrier Reef, Hawaii, and Guam, 12 were common at Two-Mile Reef. These include *Centroceras*, *Ceramium*, *Gelidiella*, *Herposiphonia*, *Hypnea*, *Jania*, *Laurencia*, *Polysiphonia* (Rhodophyta), *Cladophora* (Chlorophyta), *Dictyota*, *Sphacelaria* (Phaeophyta) and *Lyngbya* (Cyanobacteria). Only six of the 86 macroalgae (including crustose coralline algae) were classed as common, abundant or dominant in terms of occurrence (Fig. 2.3.5); two of these, the dictyotalean *Lobophora variegata* and the non-geniculate corallines, accounted for most of the algal cover on all the different substrata.

2.4.3.1 *Seasonal variability*

The macroalgal communities of Two-Mile Reef showed no marked seasonal dynamics. Lüning (1990) and Ateweberhan *et al*. (2006) described temperature as one of the primary factors controlling macroalgal growth in high latitude reefs, because algal growth was stimulated during low water temperatures in winter. Yet, the present study could not identify significant seasonal changes in macroalgal communities on natural substrata.

Finding that seasonality had no significant influence on the abundance of macroalgae is inconsistent with previous studies. For example, studies on tropical Atlantic and Caribbean macroalgae have found that different algal groups dominated their respective communities at distinct times of the year (Lirman and Biber 2000; Diaz-Pulido and Garzón-Ferreira 2002; Ferrari *et al*. 2012). Studies investigating the seasonality of Caribbean seaweeds reported that *Dictyota* spp. and *Lobophora variegata* were susceptible to seasonal fluctuations and found that *Dictyota* spp. was positively correlated with water temperature, exhibiting the highest

abundance during the summer (Lirman and Biber 2000; Ferrari *et al*. 2012) while *Lobophora variegata* was negatively influenced by water temperature, being more abundant during winter (Ferrari *et al*. 2012). Similar seasonal changes in *L. variegata* have been observed on the Great Barrier Reef by Diaz-Pulido *et al*. (2009).

2.4.3.2 Community variation on different substrata

The findings of the current study indicate that *Lobophora variegata* is the dominant macroalgal low-growing species in the subtidal of Sodwana Bay, as it is in other tropical to warm-temperate areas around the world (Womersley 1967; Littler and Littler 2000). The abundance of *L. variegata* along Two-Mile Reef is concurrent with the expected pattern of dominance of dictyotalean assemblages along the Maputaland region of northern Kwazulu-Natal (Bolton *et al*. 2004). The fact that *L. variegata* exhibits dominance may be partly explained by the defence mechanisms adopted by algal species that allow their survival against herbivory. Two common macroalgal defence mechanisms are escape and deterrence (Hay and Fenical 1988). For *L. variegata*, it is likely that these two strategies allow its survival under herbivore pressure. *Lobophora variegata* was frequently observed growing between the branches of most digitate coral colonies in the area. However, previous work on *L. variegata* (Diaz-Pulido *et al*. 2009) reported that under normal or undisturbed conditions it is not able to grow beyond the base of the branches, due to competitive inhibition by the corals. The high abundance of *L. variegata* in branching environments suggests that it was released from space competition with the corals due to the bleaching mortality on Two-Mile Reef. Additionally, the high cover of *L. variegata* further suggests it is provided with an 'escape' from herbivores within the branching coral framework.

The second mode of defence that may have contributed to the high cover of *Lobophora variegata* is deterrence. The deterrence of herbivores by *L. variegata* is achieved primarily through the use of allelochemicals (Targett and Arnold 1998), and its exhibition of different morphological forms (ruffled, decumbent, and encrusting; Coen and Tanner 1989). In the present study, encrusting and decumbent forms of *L. variegata* were commonly found along Two-Mile Reef. Coen and Tanner (1989) suggest that the decumbent form may be among the least palatable tropical algae for both crabs and fish, while the encrusting form appears to be less susceptible to grazing due to its tightly adhering (encrusting) habit.

There are no previous observations of such extensive growths of *Lobophora variegata*, or indeed any single species of fleshy macroalga, on Two-Mile Reef. Our data support the observations of Coen and Tanner (1989), Bennett *et al*. (2010), and Sangil *et al*. (2011) showing that *Lobophora variegata* forms a dynamic component of many coral reef communities.

The lack of virtually any differences in seaweed species on the different types of substrata, including the types of coral, indicates that seaweeds will apparently recruit onto any hard substratum on these reefs. In a system like this, where there are many species present and scattered throughout the reef, with few dominants, this is perhaps not surprising, and this patchy distribution pattern with numerous “rare” species (as found on Hawaiian reefs by Stuercke and McDermid 2004) suggests that opportunistic recruitment is the main determinant of community composition. There do not appear to be any other studies that have looked at algal growth on different morphological types of dead coral.

2.4.4 *Algal colonisation of artificial substrata*

The most important outcome of this study was that the nature of the artificial substratum had little influence on the recruitment success of coral reef macroalgae on Two-Mile Reef. In general, variations in the abundance of non-crustose macroalgal recruits among tile types were not significant, notwithstanding significant differences in crustose coralline abundance between ceramic and marble tiles.

Previous researchers have generally found that some crustose coralline algae inhibit the recruitment of algal propagules either by epithallial shedding or enhanced grazing on the surface of the crustose corallines (Keats *et al*. 1997; Littler and Littler 1997). These processes could explain the weak negative relationship between non-crustose macroalgal recruits and pre-treated ceramic tiles. However, this contrasts markedly with the relatively high cover of *Lobophora variegata* on the conditioned tiles. Santelices and Varela (1994) found that calcium carbonate facilitated rhizoidal attachment in fleshy macroalgae, perhaps explaining an apparent association between *L. variegata* and crustose coralline algae.

At the end of the experiment, bare tile surfaces had developed epilithic algal communities dominated by filamentous algal turfs, non-geniculate (crustose) corallines, and canopy-forming brown algae. The algal colonisation on the settlement tiles described in this study shows a similar structure to those of previous studies in the western Indian Ocean (Uku *et al*. 2000) and Great Barrier Reef (McClanahan 1997). McClanahan (1997) reported that within 150 days following tile placement, algal turf and coralline algae were dominant on all plates. McClanahan described that the succession of algae was from algal turf to coralline algae, followed by an increase in calcareous algae, and climaxing with an abundance of large canopy-forming brown algae genera, such as *Sargassum* and *Turbinaria*. The results of the present

study suggest that the sequence of succession was similar except that calcareous algae never developed greatly on most tiles, in the six month period.

Relatively large brown algae, such as *Lobophora variegata* would appear to be the most abundant space-occupying species at the climax of succession. Fleshy algae, although common on Two-Mile Reef (personal observation), did not develop greatly on the experimental tiles. This may be due to insufficient time, but is more likely due to the flat shape of the tiles. Flat tiles may not provide the rugosity and associated refuge that is necessary for the development of these species (McClanahan 1997). Rugose ceramic tiles have been suggested to protect algal recruits from dislodgement by herbivore activity and wave action, and to increase the tile surface area available for settlement and recruitment (Amsler *et al*. 1992; Anderson and Underwood 1994). Diaz-Pulido and McCook (2004) found that ceramic tiles with rougher surfaces had significantly more algal recruits than those with smoother surfaces. Among the ceramic and pre-conditioned ceramic tiles in the present study, there was a higher (not significant) cover abundance of *L. variegata* compared to the smoother marble tiles. Contrastingly, it is interesting that marble tiles had significantly higher cover of non-geniculate coralline algae. This may reflect competition with other macroalgae, the recruitment of which may have been weakened by the smooth texture.

Although it is not possible to directly compare recruitment on natural substrata and artificial tiles in a factorial analysis, it is worth noting that cover abundance of non-geniculate coralline algae was lower on natural substrata than on artificial substrata. Whether this is due to physical or chemical differences in the substrata is unclear, although flat surfaces provide little refuge and are therefore more susceptible to grazing disturbance. Consequently, roaming

herbivorous fish, like some surgeonfish and parrotfish, promote corallines by cropping the easily accessible nutritious turfs.

In order to fully understand the consequences of coral death, it is necessary to develop a better understanding of the algal successional process as influenced by the type of substratum, organisms already present, the species involved, and the life history processes (attachment, survival and growth).

Chapter 3: Diversity of Non-Geniculate Coralline Red Algae (Corallinales, Rhodophyta) on Two-Mile Reef, Sodwana Bay

3.1 Introduction

Non-geniculate coralline red algae (Corallinales, Rhodophyta), also referred to as encrusting coralline algae, are both abundant and diverse worldwide (Johansen 1981; Woelkerling and Lamy 1998). No other group of marine algae inhabits such an extensive range of environments (Steneck 1986). They are reported to dominate intertidal and subtidal hard substrata across polar, temperate and tropical regions of the world's oceans, and are reported to be the deepest known benthic photosynthetic organisms on earth, occurring to depths of over 200 m (Littler *et al*. 1991). These algae are ecologically important components of benthic hard-bottomed environments where they play a fundamental role in the construction and maintenance of coral reefs (Littler and Littler 1988; Littler and Littler 1994), provide food for many herbivores (Steneck and Dethier 1994), induce settlement and metamorphosis of a variety of marine invertebrate larvae (Hadfield and Paul 2001), and are important sources of primary production (Lewis 1977; Littler *et al*. 1991).

South Africa's extensive rocky shoreline is rich in abundance and diversity of non-geniculate coralline algae (Maneveldt *et al*. 2008). Despite their ubiquity, however, they are not easily identified due to strong similarities in appearance of phylogenetically distant taxa, and thus they have been a relatively poorly understood group of marine organisms.

No useful accounts of non-geniculate coralline algae from Sodwana Bay (KwaZulu-Natal) existed before 1993. Between 1993 and 1997, however, a series of detailed descriptive

studies of South African non-geniculate coralline algae were published (e.g. Keats and Chamberlain 1993, 1994a, 1994b; Keats and Maneveldt 1997). More recently, Maneveldt *et al*. (2008) published a catalogue with keys to the South African non-geniculate coralline algae. In this latter report, 43 species of non-geniculate coralline algae were catalogued, representing 17 genera and four subfamilies. Since then, more species have been described for South Africa (e.g. Maneveldt and van der Merwe 2012), and it appears that the South African flora has been underestimated (see van der Merwe *et al*. 2014). Most of these reports have focused on intertidal rocky shores and shallow subtidal reefs of the South African west and south coasts; current records from the northeastern, tropical coast are limited. Ten species have thus far been reported from Sodwana Bay (Table 5), and not all of these have been described in detail. There is thus a general lack of information on the taxonomy of the tropical non-geniculate coralline species, including those growing on the subtidal reefs of Sodwana Bay.

The aim of this part of the present study was to identify the non-geniculate corallines found on natural substrata in order to build a more complete record of taxa present on these southernmost tropical Indo-West Pacific coral reefs.

Table 5: List of species of non-geniculate coralline red algae (Corallinales) previously reported from Sodwana Bay.

Species	References
***Hydrolithon onkodes* (Heydrich) Penrose et Woelkerling**	Keats and Chamberlain 1994a
***Hydrolithon samoënse* (Foslie) Keats et Chamberlain**	Keats and Chamberlain 1994a
***Hydrolithon superficiale* Keats et Chamberlain**	Keats and Chamberlain 1994a
***Mesophyllum erubescens* (Foslie) Lemoine**	Keats and Chamberlain 1994b
***Mesophyllum funafutiense* (Foslie) Verheij**	Keats and Chamberlain 1994b
Pneophyllum amplexifrons (Harvey) Chamberlain et Norris	Browne *et al*. 2013
***Spongites yendoi* (Foslie) Chamberlain**	Chamberlain 1993
***Synarthrophyton patena* (Hooker et Harvey) Townsend**	Seagrief 1980, Browne *et al*. 2013
***Sporolithon episporum* (Howe) Dawson**	Keats and Chamberlain 1993
***Sporolithon ptychoides* Heydrich**	Keats and Chamberlain 1993

3.2 Materials and Methods

Study area

In situ collections were made during March and September 2010 from dead reef coral or from adjacent primary rock. All material was collected by SCUBA diving at 10-16 m depth at Two-Mile Reef, Sodwana Bay (27°31'29''S 32°40'37''E), KwaZulu-Natal, South Africa. Refer to chapter 2 for further site and collection details. Specimens were preserved in 5% formalin seawater solution for storage prior to examination.

Identification

Histological methods follow Maneveldt and van der Merwe (2012) and are summarized as follows. Formalin preserved specimens were first decalcified in 10% nitric acid. Thereafter, specimens were immersed in 70 %, 90 % and 100 % ethanol solutions respectively for a minimum of 60 mins each in order to displace any water and acid in the specimens. Following this procedure, each specimen was removed from the 100 % ethanol and allowed to air dry for no more than a few seconds. Specimens were then immersed in Leica Historesin filtration medium for several hours (3-6) until completely infiltrated. A hardening solution was then added to the infiltration medium and the specimens orientated in this final solution until set. Gelling of the hardener usually occurred within 30-45 mins; for more rapid hardening, specimens were placed immediately in an oven at 60 °C for approximately 10-20 mins.

Specimens were then sectioned at 6-12 µm thickness using a Bright 5030 microtome. Individual cut sections were removed from the microtome blade using a fine sable hair brush and transferred to a slide covered with distilled water. In this way, multiple sections were orientated on a single slide. Slides were then left to air dry for at least 24 hrs. Once dried, slides bearing sections were stained with toluidine blue (0.25 g borax/100 ml and 0.06 g toluidine blue/100 ml) that was previously filtered

to prevent dye crystal formation, again left to air dry, and later covered with cover slips using DPX Mountant for microscopy (BDH Laboratory Supplies, England).

In cell measurements, length denotes the distance between primary pit connections, and diameter the maximum width of the cell lumen at right angles to this. Conceptacle measurements follow Adey and Adey (1973). Thallus anatomical terminology follows Chamberlain (1990). Morphological (growth form) terminology follows Woelkerling *et al*. (1993). Typification data follow Woelkerling (1993). Coralline identification was achieved using the online electronic identification tool developed by Maneveldt *et al.* (2013). Herbarium codes are those used in *Index Herbariorum*, previously in print (Holmgren *et al*. 1990) and now electronically online (Thiers 2013, continuously updated).

3.3 Results

Nine species representing six genera and three subfamilies of non-geniculate coralline red algae were positively identified from the material collected. Two of these species, *Lithophyllum cuneatum* and *Pneophyllum* sp. are new records for South Africa, and five (*Lithophyllum acrocamptum*, *Hydrolithon farinosum*, *Hydrolithon pellire*, *Neogoniolithon brassica-florida* and *Lithothamnion muelleri*) are new records for Sodwana Bay and the Maputaland region. *Hydrolithon farinosum* was epiphytic exclusively on *Valonia macrophysa*, while the remaining eight species grew on both algae and calcareous substrata.

Subfamily Lithophylloideae Setchell

Lithophyllum acrocamptum Heydrich

BASIONYM: *Lithophyllum acrocamptum* Heydrich, 1902: 474

HETEROTYPIC SYNONYMS:

Lithophyllum incrustans f. *incrassatum* Foslie, 1900: 28

Lithophyllum incrassatum (Foslie) Foslie, 1909: 18-20

Lithothamnion incrassatum (Foslie) Jadin, 1935: 171

HOLOTYPE: M. Ferlus; date not indicated; PC unnumbered, General Herbarium box collection, includes one unnumbered slide (Woelkerling 1998: 299). Holotype fragments in TRH (see Woelkerling 1993: 16).

TYPE LOCALITY: Fort-Dauphin (Taolanaro), Madagascar (Silva *et al*. 1996: 246).

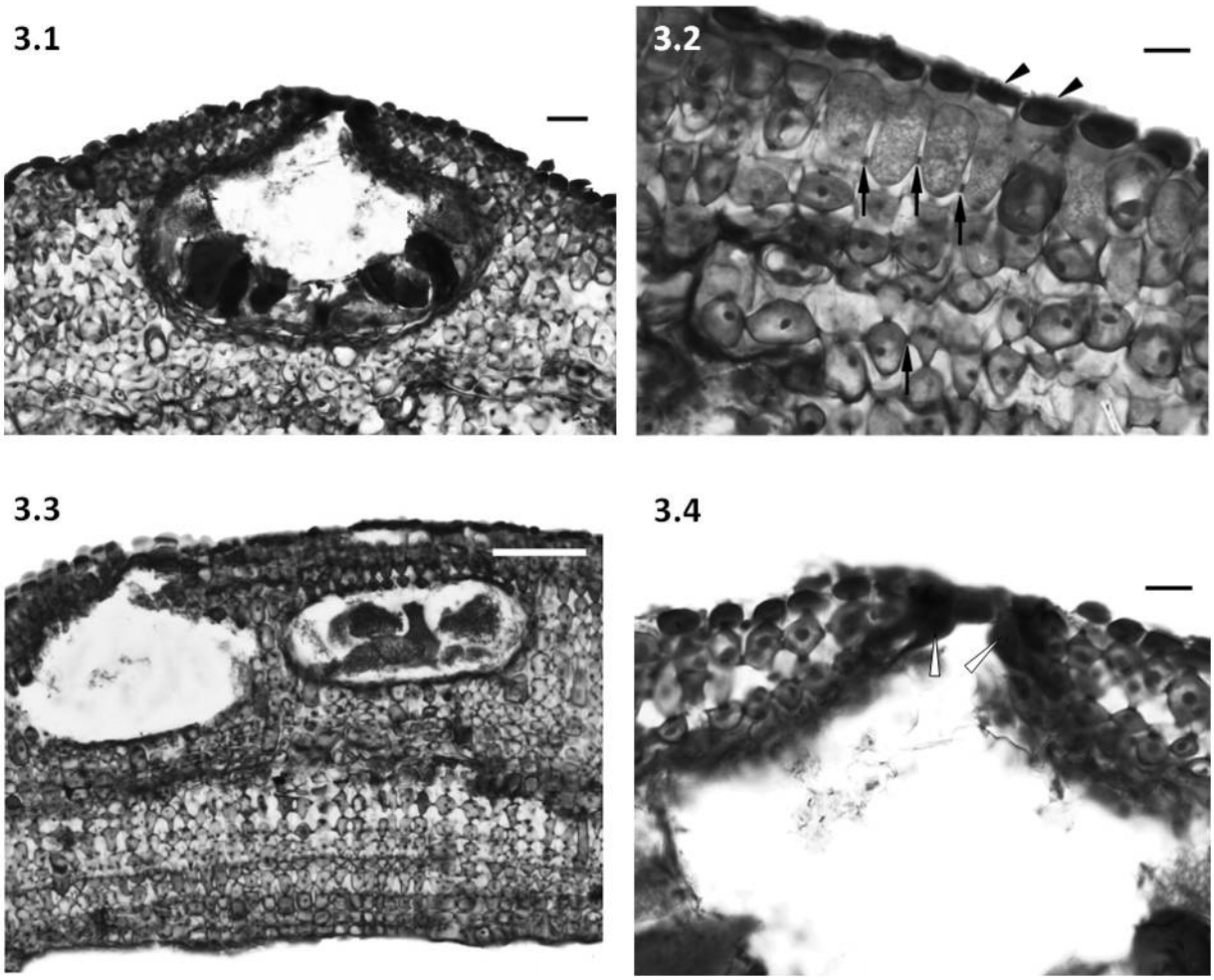
ETYMOLOGY: Derived from the Greek words *acros* meaning at the tip or summit, and *camptos* meaning bent. Heydrich (1902) did not explain the etymology, but presumably it refers to the bent or curved branch tips that Heydrich thought were characteristic of the species.

REPRESENTATIVE SPECIMEN EXAMINED: Only one specimen was examined.
South Africa. KwaZulu-Natal: Two-Mile Reef, Sodwana Bay (27°31'29''S 32°40'37''E), epizoic on dead coral, 16 m depth (08.ix.2010, *L. Gersun and R.J. Anderson*, UCT SD3).

DISTRIBUTION (South Africa): Seaview (Port Elizabeth) to Sodwana Bay (Maneveldt *et al*. 2008; this study).
DISTRIBUTION (elsewhere): Kenya, Madagascar, Mauritius, Saudi Arabia, Sri Lanka (Guiry and Guiry 2014).

DESCRIPTION:
Lithophyllum acrocamptum is characterised by the following combination of characters: 1) tetra/bisporangia are zonately divided and borne in uniporate conceptacles that lack apical pore plugs (Fig. 3.1); 2) cells of adjacent filaments joined primarily by secondary pit connections (Fig. 3.2) with cell fusions absent or comparatively rare; 3) thalli non-geniculate and lacking haustoria; 4) thalli lacking bead-like protuberant branches; and 5) thalli dorsiventral and mostly dimerous (Fig. 3.3) (but may also be secondarily monomerous), possessing a basal layer of cells that are either predominantly non-palisade, predominantly palisade or both.

Character 1 places the taxon within the order Corallinales and family Corallinaceae, character 2 within the subfamily Lithophylloideae, and the remaining three characters collectively within the genus *Lithophyllum*. Within the genus *Lithophyllum*, South African specimens ascribed to *L. acrocamptum* are described by the following combination of features: 1) tetra/bisporangial conceptacle pore canal lined by papillate cells that are orientated more or less parallel to the roof surface (Fig. 3.4); and 2) tetra/bisporangial conceptacle roofs 3-5 cells thick, with short pore canals that taper markedly towards the pore (Maneveldt *et al*. 2008).



Figs 3.1-3.4: *Lithophyllum acrocamptum*

Fig. 3.1: Vertical section of the thallus showing a uniporate tetrasporangial conceptacle (scale is 20 µm).

Fig. 3.2: Vertical section of the vegetative thallus showing a single layer of epithallial cells (arrowheads) and secondary pit connections (arrows) between adjacent filaments (scale is 10 µm).

Fig. 3.3: Vertical section of the thallus showing a dimerous thallus construction and buried tetrasporangial conceptacles (scale is 60 µm).

Fig. 3.4: Vertical section of a uniporate conceptacle showing a short pore canal and the pore canal lined with papillate cells (arrowheads) (scale is 10 µm).

Lithophyllum cuneatum Keats

BASIONYM: *Lithophyllum cuneatum* Keats, 1995: 151

HOLOTYPE: UWC 94/1135, D.W. Keats; 19 June 1994. Specimen deposited in L.

TYPE LOCALITY: Makuluva Island, Suva Barrier Reef, Fiji.

ETYMOLOGY: *cuneatum* from the Latin *cuneatus* meaning wedge-shaped (Stearn 1973), making reference to the wedge-like thallus that is commonly partially buried in the thallus of the host coralline *Hydrolithon onkodes*.

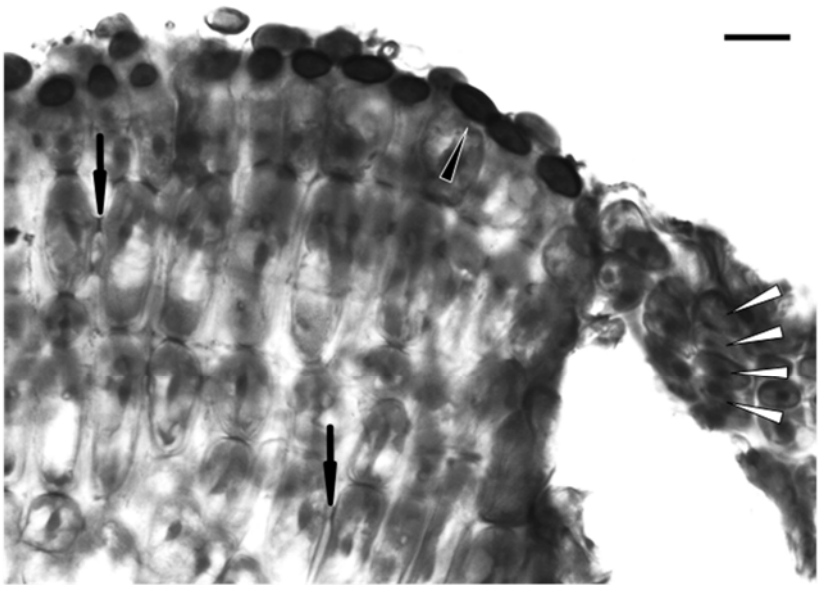
REPRESENTATIVE SPECIMENS EXAMINED: Only two specimens were examined.
South Africa. KwaZulu-Natal: Two-Mile Reef, Sodwana Bay (27°31'29''S 32°40'37''E), semi-endophytic in *Hydrolithon onkodes,* 10-16m depth (03.iii.2010, *L. Gersun and R.J. Anderson*, UCT M22B; 08.ix.2010, *L. Gersun and R.J. Anderson*, UCT SE2).

DISTRIBUTION (South Africa): Thus far only known from Sodwana Bay, KwaZulu-Natal (this study).
DISTRIBUTION (elsewhere): Australia, Fiji, Tahiti (Guiry and Guiry 2014).

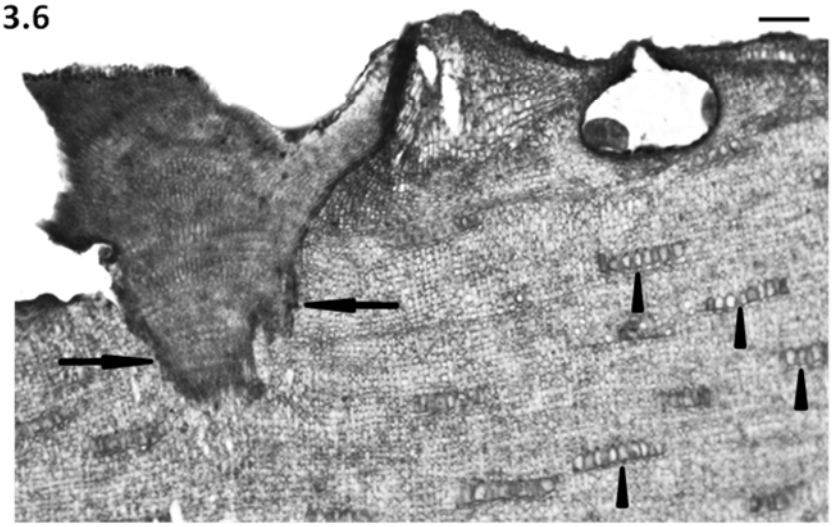
DESCRIPTION:
Lithophyllum cuneatum is characterised by the following combination of characters: 1) tetra/bisporangia are zonately divided and borne in uniporate conceptacles that lack apical pore plugs; 2) cells of adjacent filaments joined primarily by secondary pit connections (Fig. 3.5) with cell fusions absent or comparatively rare; 3) thallus semi-endophytic and found parasitizing other non-geniculate coralline algae.

Character 1 places the taxon within the order Corallinales and family Corallinaceae, character 2 within the subfamily Lithophylloideae. *Lithophyllum cuneatum* is currently the only known species within the Lithophylloideae that is known to be semi-endophytic and commonly found parasitizing *Hydrolithon onkodes* (Keats 1995). Furthermore, *L. cuneatum* is characterised by a wedge-like thallus that is partially buried in the thallus of the host coralline (Fig. 3.6).

3.5



3.6



Figs. 3.5-3.6: *Lithophyllum cuneatum*

Fig. 3.5: Vertical section through the thallus showing a single layer of epithallallial cells (black arrowhead) and secondary pit connections (arrows). Note multi-layered epithallus of *P. onkodes* (white arrowheads) (scale is 10 µm).

Fig. 3.6: Vertical section of the thallus showing the wedge-shaped *Lithophyllum cuneatum* (between arrows) embedded in *Porolithon onkodes*. Note the buried trichocyte fields in *H. onkodes* (arrowheads) (scale is 70 µm).

Subfamily Mastophoroideae Setchell

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

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

HOMOTYPIC SYNONYMS:

Fosliella farinosa (J.V.Lamouroux) M.A.Howe, 1920: 587

HETEROTYPIC SYNONYM:

Melobesia granulata (Meneghini) Zanardini, 1843: 44

LECTOTYPE: on *Sargassum linifolium*. CN Herb. Lamouroux (Chamberlain 1994: 123). See Penrose and Chamberlain (1993) for more information on the lectotype.

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

ETYMOLOGY: *farinosum* from the Latin *farina* meaning flour-like powdery covering (Stearn 1973), making reference to the thin, epiphytic, powdery appearance of the plants on the thalli of macroalgae.

REPRESENTATIVE SPECIMENS EXAMINED: In total, three specimens were examined.

South Africa. KwaZulu-Natal: Two-Mile Reef, Sodwana Bay (27°31'29''S 32°40'37''E), epiphytic on *Valonia macrophysa*, 10-16 m depth (06.ix.2010, *L. Gersun and R.J. Anderson*, UCT S23A, UCT S23B; 08.ix.2010, *L .Gersun and R.J. Anderson*, UCT S38).

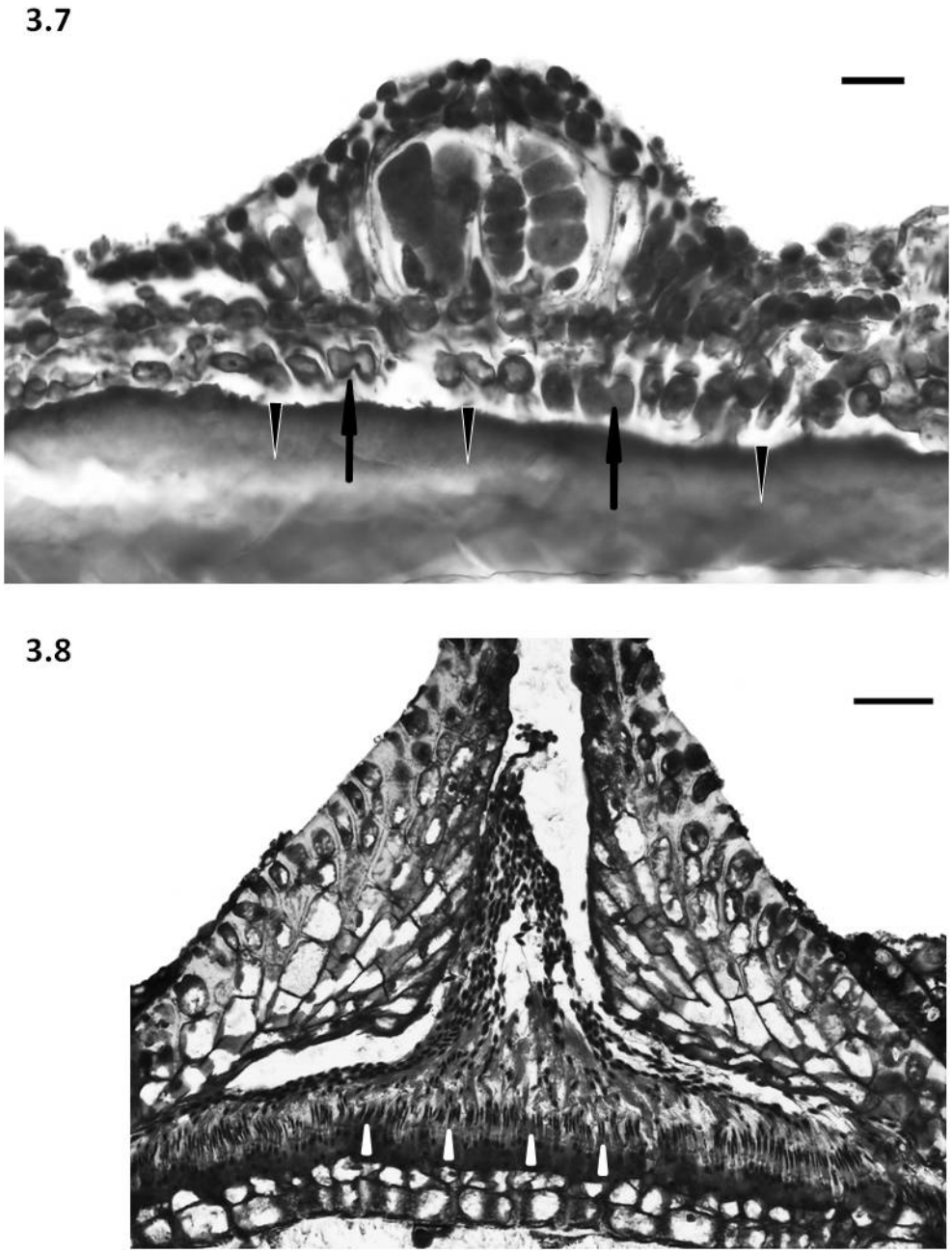
DISTRIBUTION (South Africa): Maphelane (approximately 100 km south of Sodwana Bay) to Sodwana Bay (Maneveldt *et al*. 2008, Browne *et al*. 2013, this study), KwaZulu-Natal.
DISTRIBUTION (elsewhere): Widespread globally: Antarctic and the subantarctic islands, Atlantic Islands, Australia, Brazil, Caribbean Islands, Chile, Colombia, Israel, Japan, Mediterranean Sea, Pacific Ocean Islands, Venezuela, Vietnam, Western Indian Ocean and Eastern Atlantic Ocean (Guiry and Guiry 2014).

DESCRIPTION:

Hydrolithon farinosum is characterised by the following combination of characters: 1) tetra/bisporangia are zonately divided and borne in uniporate conceptacles that lack apical pore plugs (Fig. 3.7); 2) cells of contiguous (adjacent) vegetative filaments joined primarily by cell fusions; secondary pit connections absent or comparatively rare (Fig. 3.7); 3) thalli are non-geniculate; 4) thallus non-endophytic and lacking haustoria; 5) epithallial cells present on vegetative thallus filaments; 6) thallus lacking a basal layer of predominantly palisade cells throughout; 7) trichocytes not occurring in large, tightly packed horizontal fields; 8) pore canals of tetra/bisporangial conceptacles lined by a ring of conspicuously enlarged cells that arise from filaments interspersed among and peripheral to the developing sporangia; 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 (Fig. 3.8); and

10) gonimoblast filaments borne from the margin 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 seven features collectively within the genus *Hydrolithon*. Within the genus *Hydrolithon*, South African specimens ascribed to *H. farinosum* are described by the following combination of features: 1) dimerous internal construction (Fig. 3.8); 2) thalli entirely epiphytic (Fig. 3.7); 3) thalli up to 150 µm thick with reproductively mature thalli no more than 2-5 cells thick; and trichocytes occurring singly and not in large, tightly packed horizontal fields (Maneveldt *et al.* 2008).



Figs. 3.7-3.8: *Hydrolithon farinosum*

Fig. 3.7: Section through thallus showing a uniporate tetrasporangial conceptacle and cell fusions (arrows) (scale is 20 µm). Note *Hydrolithon farinosum* is epiphytic on *Valonia* sp. (arrowheads).

Fig. 3.8: Section through a male conceptacle (scale is 60 µm). Note the dimerous basal layer and the simple spermatangia confined to the floor of the conceptacle chamber (arrowheads).

Hydrolithon pellire Y.M.Chamberlain and R.E.Norris

BASIONYM: *Hydrolithon pellire* Y.M.Chamberlain and R.E.Norris, 1994: 291

HOLOTYPE: YMC and REN (YMC 89/125), 16 October 1989; Intertidal, on *Gelidium pteridifolium*. Specimen deposited in L (L 993.052-341).

TYPE LOCALITY: Umdloti, Natal (KwaZulu-Natal), South Africa (Chamberlain and Norris 1994: 291).

ETYMOLOGY: *pellire* from the Latin word *pellis* meaning skin (Stearn 1973), referring to the delicately membranous-looking nature of this species (Chamberlain and Norris 1994).

REPRESENTATIVE SPECIMENS EXAMINED: In total, 3 specimens were examined.

South Africa. KwaZulu-Natal: Two-Mile Reef, Sodwana Bay (27°31'29''S 32°40'37''E), epizoic on dead coral, 10-16m depth (01.iii.2010, *L. Gersun and R.J. Anderson*, UCT M7E; 02.iii.2010, *L. Gersun and R.J. Anderson*, UCT M18D; 03.iii.2010, *L. Gersun and R.J. Anderson*, UCT M28).

DISTRIBUTION (South Africa): Port Alfred (Eastern Cape) to Sodwana Bay, KwaZulu-Natal (Maneveldt *et al*. 2008, this study).

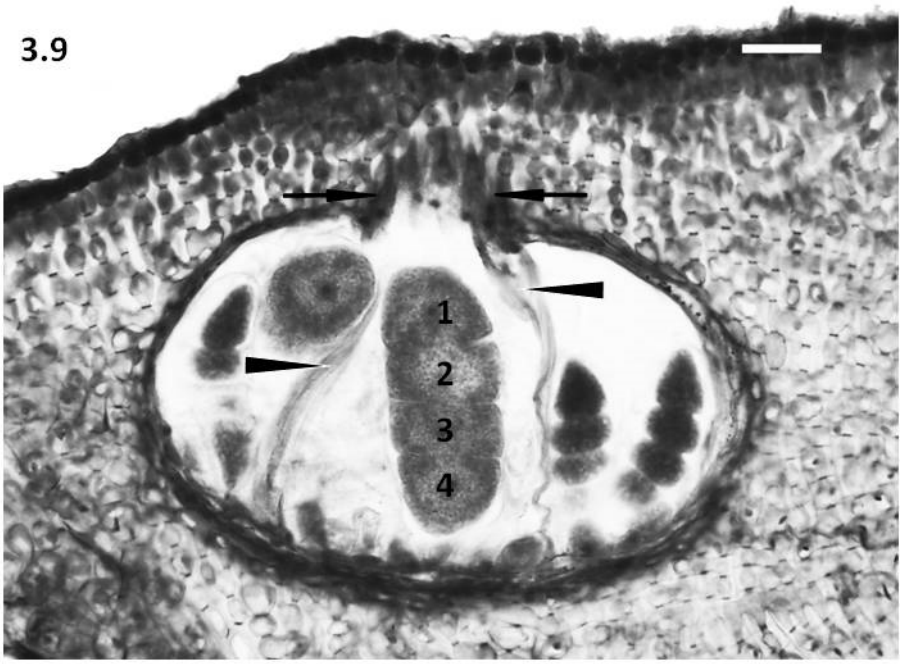
DISTRIBUTION (elsewhere): A South African endemic.

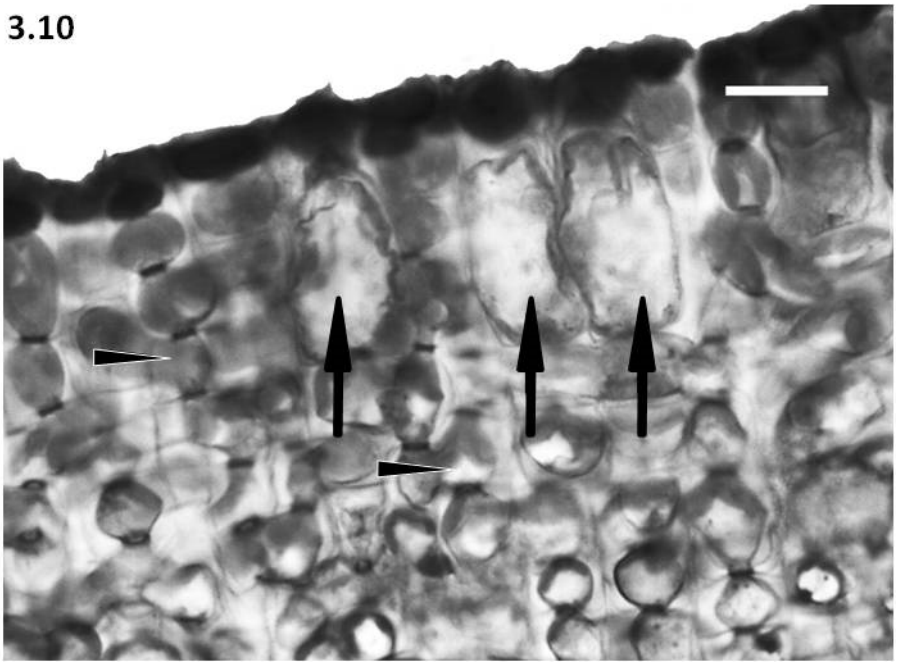
DESCRIPTION:

Hydrolithon pellire is characterised by the following combination of characters: 1) tetra/bisporangia are zonately divided and borne in uniporate conceptacles that lack apical pore plugs (Fig. 3.9); 2) cells of contiguous (adjacent) vegetative filaments joined primarily by cell fusions (Fig. 3.10); secondary pit connections absent or comparatively rare 3) all thalli

non-geniculate; 4) thallus non-endophytic and lacking haustoria; 5) epithallial cells present on vegetative thallus filaments; 6) thallus lacking a basal layer of predominantly palisade cells throughout; 7) trichocytes not occurring in large, tightly packed horizontal fields; 8) pore canals of tetra/bisporangial conceptacles lined by a ring of conspicuously enlarged cells (Fig. 3.9) that arise from filaments interspersed among and peripheral to the developing sporangia; 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; and 10) gonimoblast filaments borne from the margin 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 seven features collectively within the genus *Hydrolithon*. Within the genus *Hydrolithon*, South African plants ascribed to *H. pellire* are described by the following combination of features: 1) epiphytic with dimerous internal construction; 2) vegetative thalli no more than 370 µm thick; 3) reproductively mature thalli more than 5 cells thick; and trichocytes occurring singly and/or paired and not in large, tightly packed horizontal fields (Fig.3.10) (Maneveldt *et al*. 2008).





Figs. 3.9-3.10: *Hydrolithon pellire*

Fig. 3.9: Vertical section of a uniporate conceptacle bearing zonately divided tetrasporangia (1-4). Note the filaments (arrowheads) that gave rise to the enlarged cells at the base of the pore canal (arrows) (scale is 20 µm).

Fig. 3.10: Vertical section of the thallus showing cell fusions (arrowheads) and solitary and paired trichocytes (arrows) (scale is 10 µm).

Neogoniolithon brassica-florida (Harvey) Setchell and L.R.Mason

BASIONYM: *Melobesia brassica-florida* Harvey, 1849: 110

HOMOTYPIC SYNONYMS:

Lithothamnion brassica-florida (Harvey) Areschoug, 1852: 523

Goniolithon brassica-florida (Harvey) Foslie, 1898: 9

HETEROTYPIC SYNONYMS:

See Guiry and Guiry (2014) for an extensive list of heterotypic synonyms.

LECTOTYPE: Bowerbank; BM algal box collection no. 78, designated by Penrose and Chamberlain (in Woelkerling 1993: 43).

TYPE LOCALITY: Algoa Bay, Cape Province (Eastern Cape), South Africa (Silva *et al*. 1996: 261).

ETYMOLOGY: *brassica* from the Latin meaning cabbage and *florida* from the Latin word *floridus* meaning flowering profusely (Stearn 1973), making reference to the fruticose appearance of the alga on rock.

REPRESENTATIVE SPECIMENS EXAMINED: In total, 7 specimens were examined.

South Africa. KwaZulu-Natal: Two-Mile Reef, Sodwana Bay (27°31'29''S 32°40'37''E), epizoic on dead coral, 10-16m depth (01.iii.2010, *L. Gersun and R.J. Anderson*, UCT M3B, UCT M7C; 02.iii.2010, *L. Gersun and R.J. Anderson*, UCT M18D, UCT M18E, UCT M19B; 08.ix.2010, *L. Gersun and R.J. Anderson*, UCT S42, UCT S43).

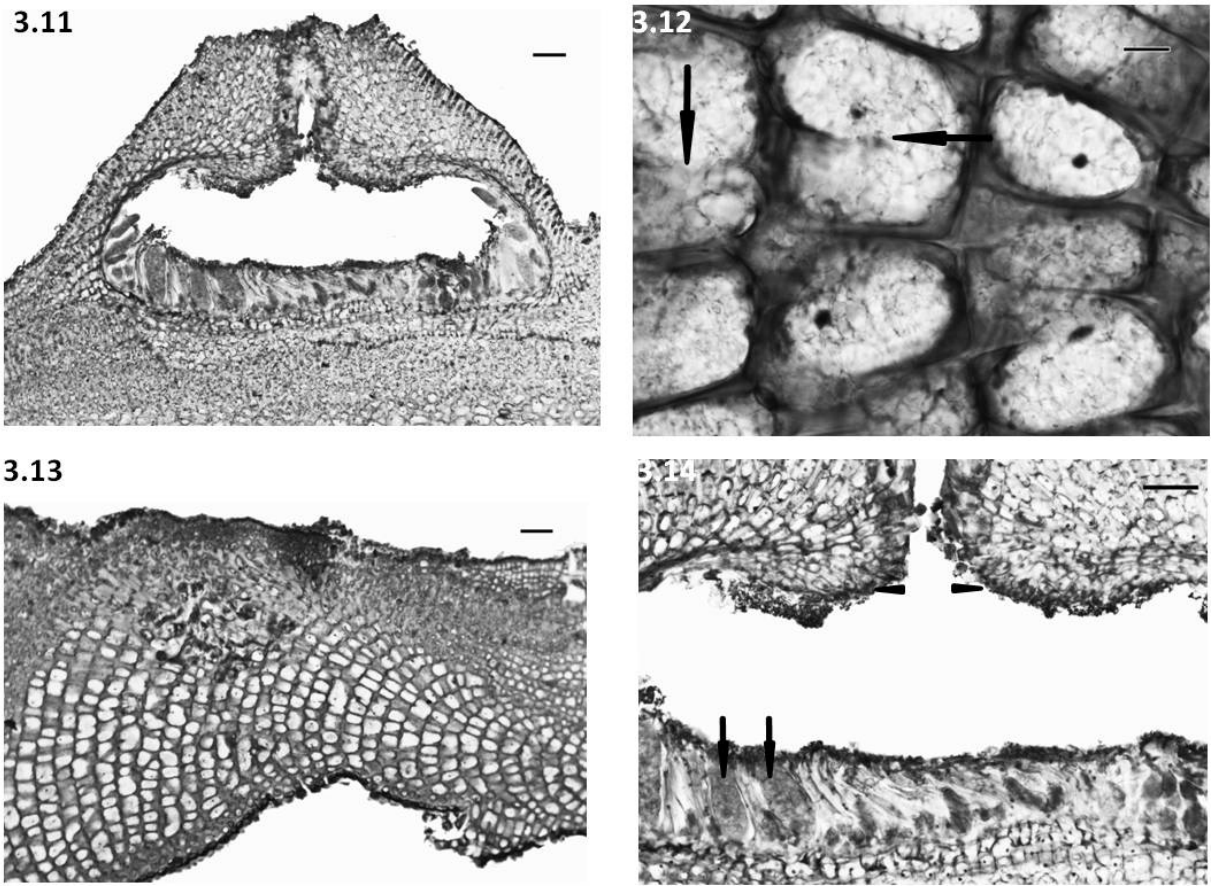
DISTRIBUTION (South Africa): Algoa Bay (Eastern Cape) to Sodwana Bay, KwaZulu-Natal (Maneveldt *et al*. 2008, this study).

DISTRIBUTION (elsewhere): Widespread in all of the world's oceans. See Guiry and Guiry (2014) for an extensive list of localities.

DESCRIPTION:

Neogoniolithon brassica-florida is characterised by the following combination of characters: 1) tetra/bisporangia are zonately divided and borne in uniporate conceptacles that lack apical pore plugs (Fig. 3.11); 2) cells of contiguous (adjacent) vegetative filaments joined primarily by cell fusions (Figs. 3.12); secondary pit connections absent or comparatively rare; 3) thalli non-geniculate; 4) thallus non-endophytic and lacking haustoria; 5) thallus monomerous (Fig. 3.13), lacking a basal layer of palisade cells throughout; 6) pore canals of tetra/bisporangial conceptacles lined by cells that arise from peripheral roof filaments (Fig. 3.14); these cells protrude into the pore canal as papillae and are oriented more or less parallel or at a sharp angle to conceptacle roof surface; 7) spermatangial (male) conceptacles containing simple (unbranched) spermatangial systems that are arranged on the floor, walls and roof of the conceptacle chamber; and 8) gonimoblast filaments arising dorsally (across) from the central fusion cells.

Character 1 places the taxon within the order Corallinales and family Corallinaceae, characters 2 and 3 within the subfamily Mastophoroideae, and the remaining five features collectively within the genus *Neogoniolithon*. Within the genus *Neogoniolithon*, *N. brassica-florida* is, at present, the only species recorded for South Africa (Maneveldt *et al*. 2008). The relatively large dimensions of the conceptacles also indicate that the specimens reported here belong to *N. brassica-florida* (Woelkerling *et al*. 1993).



Figs. 3.11-3.14: *Neogoniolithon brassica-florida*

Fig. 3.11: Vertical section through a uniporate conceptacle containing tetrasporangia that have arisen from initials formed across the chamber floor (scale is 70 µm).

Fig. 3.12: Vertical section through the thallus showing adjoining cell fusions (arrows) (scale is 10 µm).

Fig. 3.13: Vertical section through the thallus showing a monomerous and coaxial construction (scale is 70 µm).

Fig. 3.14: Vertical section of a uniporate conceptacle showing zonately divided tetrasporangia distributed across the conceptacle floor (arrows) (scale is 60 µm). Note the pore canal is lined by cells that arise from peripheral roof filaments (arrowheads).

Pneophyllum sp.

Pneophyllum Kützing, 1843: 385

ETYMOLOGY: Kützing (1843) did not explain the etymology, but *Pneophyllum*, presumably from the Greek verb *pneo* (to breath) and the latinized Greek word *phyllon* (leaf) (Maneveldt *et al*. 2013).

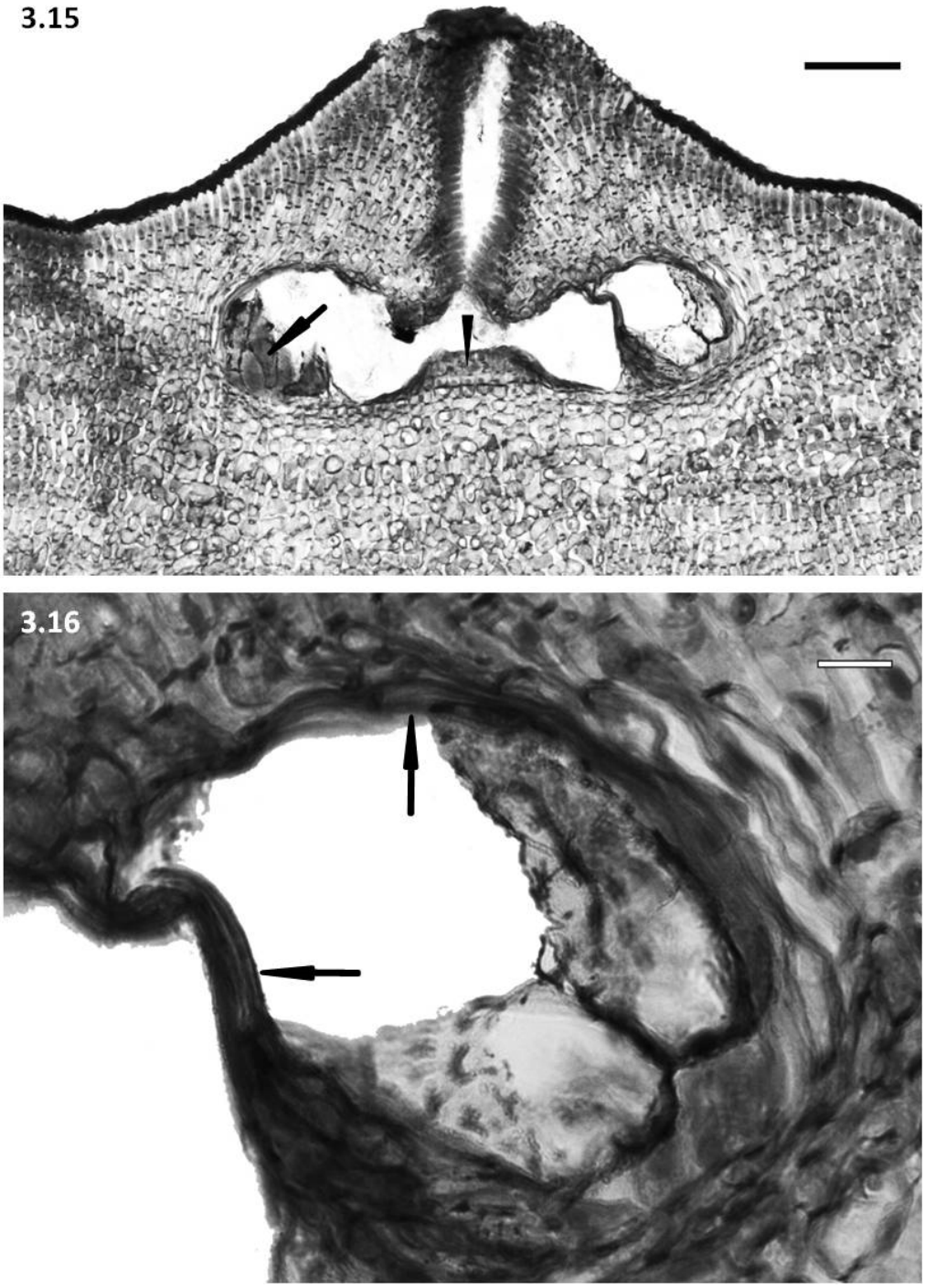
REPRESENTATIVE SPECIMENS EXAMINED: In total, 6 specimens were examined.
South Africa. KwaZulu-Natal: Two-Mile Reef, Sodwana Bay (27°31'29''S 32°40'37''E), epizoic on dead coral, 10-16m depth (06.ix.2010, *L. Gersun and R.J. Anderson*, UCT S2, UCT S3, UCT S6, UCT S17A, UCT S17B, UCT S24).

DISTRIBUTION (South Africa): The species is as yet undescribed and so can only be reported from Sodwana Bay, KwaZulu-Natal (this study).

DESCRIPTION:
Pneophyllum sp. is characterised by the following combination of characters: 1) tetra/bisporangia are zonately divided and borne in uniporate conceptacles that lack apical pore plugs (Fig. 3.15); 2) cells of contiguous (adjacent) vegetative filaments joined primarily by cell fusions; secondary pit connections absent or comparatively rare; 3) thalli are non-geniculate; 4) thallus non-endophytic and lacking haustoria; 5) epithallial cells present on vegetative thallus filaments; 6) thallus dimerous, but lacking a basal layer of palisade cells throughout; 7) tetra/bisporangial conceptacle roof developing from filaments interspersed among, as well as from filaments surrounding the sporangial initials (Fig. 3.16); and 8) pore

canals of tetra/bisporangial conceptacles lined by cells that protrude into the pore canal as papillae and are orientated more or less parallel or at a sharp angle to the conceptacle roof surface.

Character 1 places the taxon within the order Corallinales and family Corallinaceae, characters 2 and 3 within the subfamily Mastophoroideae, and the remaining five features collectively within the genus *Pneophyllum*. Four species of *Pneophyllum* have thus far been described from South Africa, but unlike *Pneophyllum* sp. reported here, the currently known species are all epiphytic. *Pneophyllum amplexifrons* forms thick, trumpet-shaped adjoining thalli encircling seagrass and green algal stalks. *Pneophyllum coronatum* and *P. keatsii* are known to form thin thalli only on the stipes and holdfasts of the kelp *Ecklonia maxima* (Osbeck) Papenfuss. *Pneophyllum fragile* forms thin thalli on *E. maxima*, on red algal hosts, and on seagrasses (Maneveldt *et al.* 2008, Browne *et al*. 2013). The species of *Pneophyllum* reported from Two-Mile Reef is smooth and featureless, is epizoic, and not nearly as thin as either *P. keatsii* or *P. fragile*. Thus it is a new record for South Africa and may be a species new to science. However, there was insufficient material to make an informed decision about the specific placement of the species.



Figs. 3.15-3.16: *Pneophyllum* sp.

Fig. 3.15: Section through a uniporate tetrasporangial conceptacle containing incompletely divided zonately arranged tetrasporangia (arrow) arranged peripherally in the chamber. Note the central columella (arrowhead) (scale is 60 µm).

Fig. 3.16: Section through a tetrasporangial conceptacle chamber showing the remains of the filaments (arrows) that gave rise to the conceptacle roof (scale is 10 µm).

Spongites yendoi (Foslie) Y.M.Chamberlain

BASIONYM: *Goniolithon yendoi* Foslie, 1900: 25

HOMOTYPIC SYNONYMS:

Lithophyllum yendoi (Foslie) Foslie, 1900: 20

Lithothamnion yendoi (Foslie) Lemoine, 1965: 10

Pseudolithophyllum yendoi (Foslie) Adey, 1970: 14

HETEROTYPIC SYNONYMS:

Lithophyllum yendoi f. *mahëicum* Foslie, 1906: 19

Lithophyllum yendoi f. *malaysicum* Foslie, 1906: 19

Lithophyllum natalense Foslie, 1907: 24

Pseudolithophyllum natalense (Foslie) Adey, 1970: 13

LECTOTYPE: K. Yendo; April 1899; TRH Yendo No. 66, designated by Foslie (1904a: expl. Pl. XI).

TYPE LOCALITY: Shimoda, Shizuoka Prefecture, Japan (Silva *et al*. 1996: 272). Chamberlain (1993: 102) cites Shimodo Harbour, Izul, Japan as the type locality.

ETYMOLOGY: *yendoi* in honour of the Japanese phycologist Kichisaburo Yendo.

REPRESENTATIVE SPECIMENS EXAMINED: In total, 11 specimens were examined.

South Africa. KwaZulu-Natal: Two-Mile Reef, Sodwana Bay (27°31'29''S 32°40'37''E), epizoic on dead coral, 10-16m depth (01.iii.2010, *L. Gersun and R.J. Anderson*, UCT M7B, UCT M7D1, UCT M7D2; 03.iii.2010, *L. Gersun and R.J. Anderson*, UCT M22C, UCT M26A; 06.ix.2010, *L. Gersun and R.J. Anderson*, UCT S9, UCT S25; 08.ix.2010, *L. Gersun and R.J. Anderson*, UCT S44, UCT SA, UCT SE1, UCT SH).

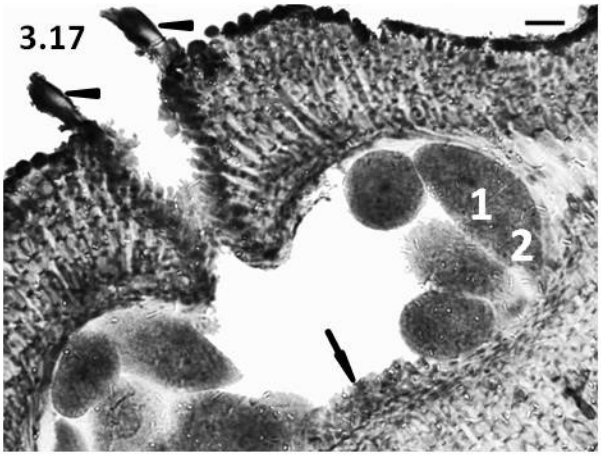
DISTRIBUTION (South Africa): Throughout South Africa (Namibia to the Mozambican border), being most abundant along the southern west and south coasts, becoming less common toward the east (Maneveldt *et al*. 2008).

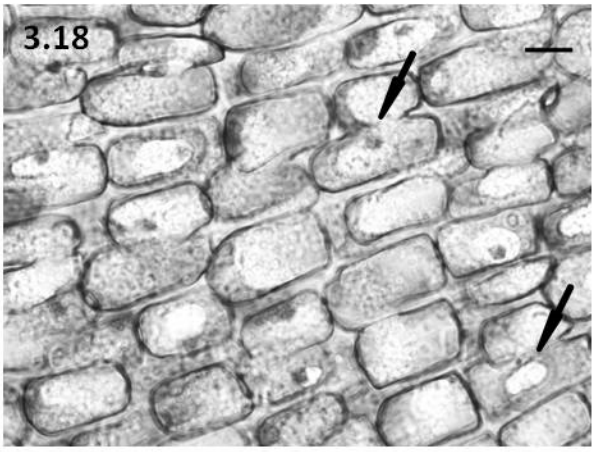
DISTRIBUTION (elsewhere): Alaska, Australia, China, Comoros, Indonesia, Japan, Korea, Mauritius, Mayotte, New Zealand, Réunion, Saudi Arabia, Seychelles, Tropical and subtropical Western Atlantic Ocean (Guiry and Guiry 2014).

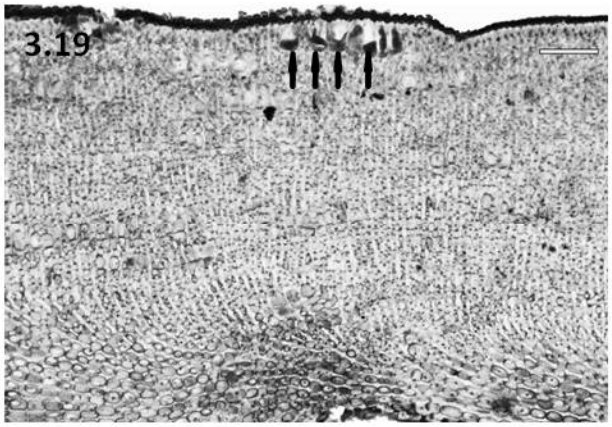
DESCRIPTION:

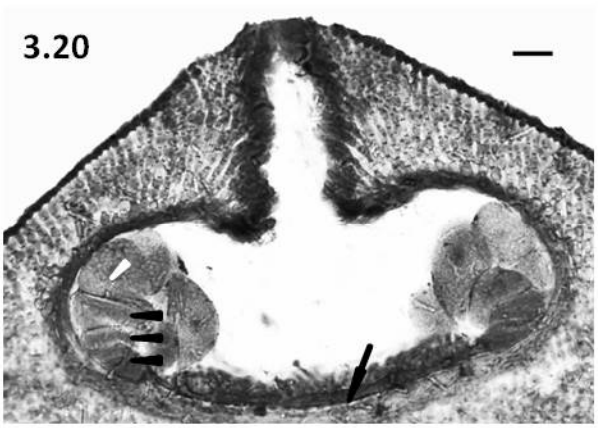
Spongites yendoi is characterised by the following combination of characters: 1) tetra/bisporangia are zonately divided and borne in uniporate conceptacles that lack apical pore plugs (Fig. 3.17); 2) cells of contiguous (adjacent) vegetative filaments joined primarily by cell fusions (Fig. 3.18); secondary pit connections absent or comparatively rare; 3) thalli non-geniculate; 4) thallus non-endophytic and lacking haustoria; 5) epithallial cells present on vegetative thallus filaments; 6) thallus either monomerous only or both monomerous and dimerous, but lacking a basal layer of palisade cells throughout (Fig. 3.19); 7) pore canals of tetra/bisporangial conceptacles lined by cells that arise from peripheral roof filaments; these cells protrude into the pore canal as papillae and are oriented more or less parallel or at a sharp angle to conceptacle roof surface; 8) spermatangial (male) conceptacles containing simple (unbranched) spermatangial systems confined to the conceptacle floor; and 9) gonimoblast filaments borne from the margin of the central fusion cell (they are arranged peripherally) (Fig. 3.20).

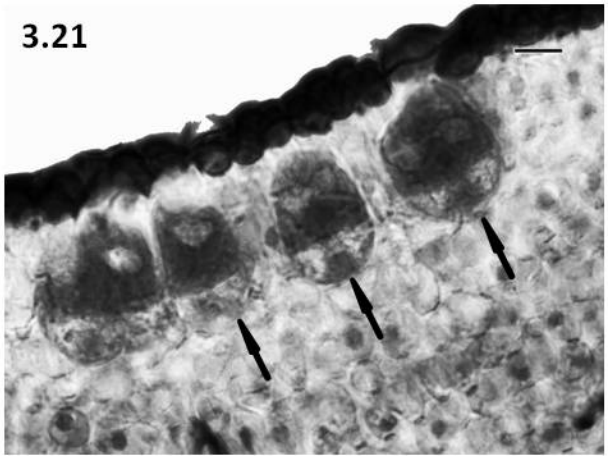
Character 1 places the taxon within the order Corallinales and family Corallinaceae, characters 2 and 3 within the subfamily Mastophoroideae, and the remaining six features collectively within the genus *Spongites*. Within the genus *Spongites*, South African plants ascribed to *S. yendoi* are described by the following combination of features: 1) thalli thin and flat to protuberant; and 2) crusts greyish to beige-ish to blueish mauve (Maneveldt *et al*. 2008).

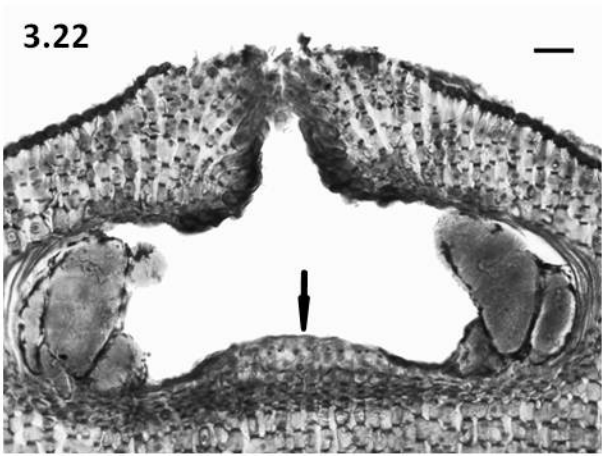












Figs: 3.17-3.22: *Spongites yendoi*

Fig. 3.17: Section through a uniporate conceptacle showing incompletely divided zonately arranged tetrasporangia (1-2). Note the central columella (arrow) and a corona of filaments surrounding the pore canal (arrowheads) (scale is 20 µm).

Fig. 3.18: Vertical section of the thallus showing cell fusions (arrows) between adjacent filaments (scale is 10 µm).

Fig. 3.19: Vertical section of the thallus showing a monomerous construction and a horizontal row of individual trichocytes (arrows), separated from each other by regular vegetative cells (scale is 60 µm).

Fig. 3.20: Section through a carposporangial conceptacle showing gonimoblast filaments (black arrowheads), terminated by carpospores (white arrowhead), borne from the margins of a central fusion cell (arrow) (scale is 20 µm).

Fig. 3.21: Vertical section of the thallus showing a horizontal trichocyte field with individual trichocytes (arrows) separated by normal vegetative filaments (scale is 10 µm).

Fig. 3.22: Section through an immature tetrasporangial conceptacle containing peripherally arranged tetrasporangia with a low-mounded central columella (arrow) (scale is 20 µm).

Subfamily Melobesioideae Bizzozero

Lithothamnion muelleri Lenormand ex Rosanoff

BASIONYM: *Lithothamnion muelleri* Lenormand ex Rosanoff, 1866: 101

HETEROTYPIC SYNONYMS:

Archaeolithothamnion mirabile Foslie, 1899: 3

Lithothamnion muelleri f. *cingens* Foslie, 1900: 69

Lithothamnion gabrieli Foslie, 1905: 3

Lithothamnion mirabile (Foslie) Foslie, 1909: 4

Mesophyllum gabrielii (Foslie) W.H.Adey, 1970: 24

LECTOTYPE: W.H. Harvey (communicated by F. Mueller); 1851; CN (Herb. Lenormand), designated by Woelkerling (1983: 193). Isolectotypes exist in MEL (588439) and L (941.149-249) (communicated by Lenormand).

TYPE LOCALITY: Western Port Bay, Victoria, Australia (Wilks and Woelkerling 1995: 555).

ETYMOLOGY: *muelleri* in honour of Ferdinand Jacob Heinrich von Mueller (F. Mueller).

REPRESENTATIVE SPECIMENS EXAMINED: Only 2 specimens were examined.

South Africa. KwaZulu-Natal: Two-Mile Reef, Sodwana Bay (27°31'29''S 32°40'37''E), epizoic on dead coral, 10-16m depth (02.iii.2010, *L. Gersun and R.J. Anderson*, UCT M19A; 03.iii.2010, *L. Gersun and R.J. Anderson*, UCT M27).

DISTRIBUTION (South Africa): Robben Island (off the Cape Peninsula, Western Cape) to Sodwana Bay, KwaZulu-Natal (Maneveldt *et al*. 2008, this study).

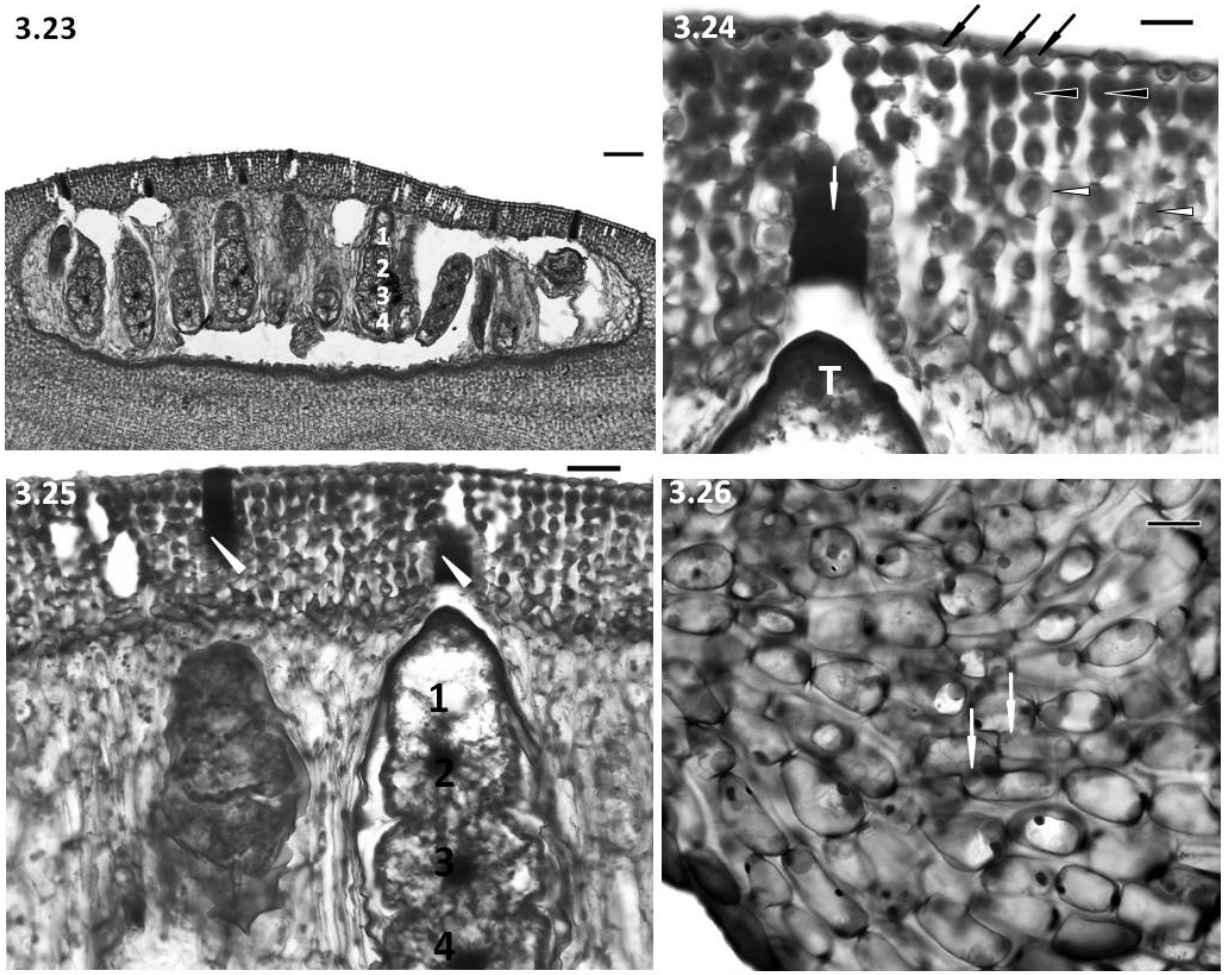
DISTRIBUTION (elsewhere): Australia, Chile, Fuegia, Korea, New Zealand, Tropical and subtropical Western Atlantic Ocean (Guiry and Guiry 2014).

DESCRIPTION:

Lithothamnion muelleri is characterised by the following combination of characters: 1) tetra/bisporangia are zonately divided and borne in multiporate conceptacles that bear apical

pore plugs (Figs. 3.23, 3.24 and 3.25); 2) tetra/bisporangial conceptacle pore plate of cellular construction; 3) cells of contiguous (adjacent) vegetative filaments joined predominantly by cell fusions (Figs. 3.24 and 3.26); secondary pit connections absent or rare; 4) thallus non-geniculate and lacking haustoria; 5) growth form not arborescent (tree-like) and flabelliform (fan-shaped); 6) thallus construction monomerous throughout (Fig. 3.26); 7) outermost walls of terminal epithallial cells flattened and flared at their corners (Fig. 3.24); 8) subepithallial initials usually as long as, or longer than cells immediately subtending them (Fig.3.24) ; 9) spermatangial (male) conceptacle roofs formed centripetally from groups of peripheral filaments; 10) spermatangial systems distributed across the floor, walls and roof of the male conceptacle chambers; 11) spermatangial systems on the conceptacle floor are dendroid (branched); and 12) gonimoblast filaments arising dorsally (across) from the central fusion cells.

Character 1 places the taxon within the order Corallinales and family Hapalidiaceae, characters 2 and 3 within the subfamily Melobesioideae, and the remaining nine features collectively within the genus *Lithothamnion*. Within the genus *Lithothamnion*, South African plants ascribed to *L. muelleri* are described by the following combination of features: 1) cortex lacking areas of large angular cells; and 2) tetra/bisporangial conceptacle pore plate with a smooth (not spiny) surface (Maneveldt *et al*. 2008).



Figs: 3.23-3.26: *Lithothamnion muelleri*

Fig. 3.23: Section through a mature multiporate tetrasporangial conceptacle bearing zonately divided tetrasporangia (1-4) scattered across the chamber floor (scale is 70 µm).

Fig. 3.24: Section though a tetrasporangial conceptacle roof showing a single layer of flared epithallial cells (black arrows), subepithallial initials (black arrowheads), cell fusions (white arrowheads) and an apical pore plug (white arrow) located above a tetrasporangium (T) (scale is 10 µm).

Fig. 3.25: Section through a conceptacle roof showing zonately arranged tetrasporangia (1-4) and apical pore plugs (arrowheads) (scale is 20 µm).

Fig. 3.26: Section of a monomerous thallus showing cell fusions (arrows) between adjacent filaments (scale is 10 µm).

Subfamily Porolithoideae A.Kato and Baba

Porolithon onkodes (Heydrich) Foslie

BASIONYM: *Lithothamnion onkodes* Heydrich, 1897: 6

HOMOTYPIC SYNONYMS:

Goniolithon onkodes (Heydrich) Foslie, 1898: 8

Hydrolithon onkodes (Heydrich) D.Penrose and Woelkerling, 1992: 83 (see also Bittner *et al*. 2011, Kato *et al*. 2011)

Lithophyllum onkodes (Heydrich) Heydrich, 1901: 553

Spongites onkodes (Heydrich) D.Penrose and Woelkerling, 1988: 173

HETEROTYPIC SYNONYMS:

Lithophyllum onkodes f. *subramosum* Foslie, 1907: 29

Lithophyllum funduense Pilger, 1908: 42

Lithophyllum onkodes f. funduense (Pilger) Foslie, 1909: 38, 40

Porolithon hanzawai Ishijima, 1954: 52

LECTOTYPE: TRH Heydrich no. 97, designated by Adey *et al.*, 1982: 9 (Woelkerling 1998: 357).

ISOLECTOTYPE: PC, unnumbered. General Herbarium box collection (non-fossil; filed in non-geniculate coralline type collections cabinet under basionym) (Guiry and Guiry 2014).

TYPE LOCALITY: Tami Island, Gulf of Huon, Papua New Guinea (Woelkerling 1998: 357).

ETYMOLOGY: *onkodes* from the Greek *onco* meaning swollen, puffed out, bulky (Stearn 1973). Heydrich (1897) did not explain the origin of the epithet. It presumably makes reference to the granular texture of the thallus surface owing to the presence of abundant pustulate trichocyte fields. This may have given the surface a swollen, puffed out appearance.

Alternatively, Heydrich (1897) may simply have referred to the slightly warty appearance of the coralline growing over lumpy coral (Maneveldt 2005).

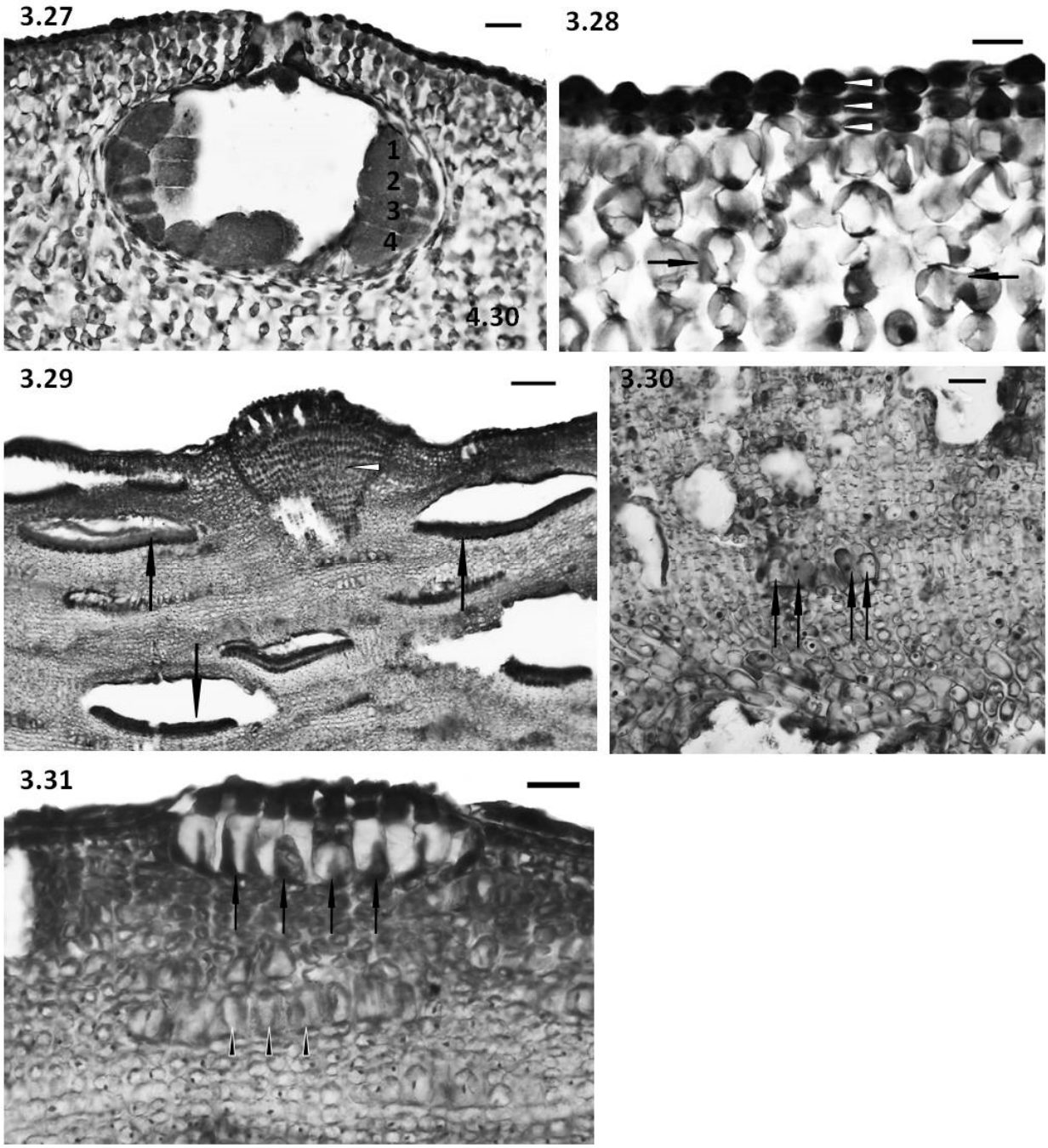
REPRESENTATIVE SPECIMENS EXAMINED: In total, 17 specimens were examined.
South Africa. KwaZulu-Natal: Two-Mile Reef, Sodwana Bay (27°31'29''S 32°40'37''E), epizoic on dead coral, 10-16 m depth (01.iii.2010, *L Gersun and R.J. Anderson*, UCT M1A, UCT M3A; 02.iii.2010, *L. Gersun and R.J. Anderson*, UCT M14A, UCT M14B, UCT M16A, UCT M16B, UCT M18A1, UCT M18A2, UCT M18C; 03.iii.2010, *L. Gersun and R.J. Anderson*, UCT M22A, UCT M22B; 06.ix.2010, *L. Gersun and R.J. Anderson*, UCT S20A, UCT S27, UCT S28; 08.ix.2010, *L. Gersun and R.J. Anderson*, UCT SC2, UCT SE2, UCT SI).

DISTRIBUTION (South Africa): Sodwana Bay, KwaZulu-Natal (Maneveldt *et al*. 2008, this study).
DISTRIBUTION (elsewhere): Widely distributed throughout subtropical and tropical localities in the Indian Ocean, Pacific Ocean, and western Atlantic (Guiry and Guiry 2014).

DESCRIPTION:
Porolithon onkodes is characterised by the following combination of characters: 1) tetra/bisporangia are zonately divided and borne in uniporate conceptacles that lack apical pore plugs (Fig. 3.27); 2) cells of contiguous (adjacent) vegetative filaments joined primarily by cell fusions (Fig. 3.28); secondary pit connections absent or comparatively rare; 3) thalli are non-geniculate; 4) thallus non-endophytic and lacking haustoria; 5) epithallial cells present on vegetative thallus filaments; 6) thallus lacking a basal layer of predominantly palisade cells throughout; 7) trichocytes occurring in large, tightly packed horizontal fields that lack any

regular vegetative cells between them; 8) pore canals of tetra/bisporangial conceptacles lined by a ring of conspicuously enlarged cells that arise from filaments interspersed among and peripheral to the developing sporangia; 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 (Fig. 3.29); and 10) gonimoblast filaments borne from the margin 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 seven features collectively within the genus *Porolithon*. Within the genus *Porolithon*, South African plants ascribed to *P. onkodes* are described by the following combination of features: 1) predominantly monomerous internal construction (Fig. 3.30); and 2) presence of abundant, large, horizontally arranged pustulate trichocyte fields that lack any regular vegetative cells between them and that become buried in the thallus (Figs. 3.30 - 3.31) (Maneveldt *et al*. 2008; Bittner *et al*. 2011; Kato *et al*. 2011).



Figs: 3.27-3.31: *Porolithon onkodes*

Fig. 3.27: Uniporate tetrasporangial conceptacle bearing zonately divided tetrasporangia (1-4) (scale is 20 µm).

Fig. 3.28: Vertical section of the outer thallus showing multiple epithallial cells (arrowheads) and cell fusions (arrows) (scale is 10 µm).

Fig. 3.29: Vertical section of thallus showing buried male conceptacles containing spermatangia confined to their floors (arrows) (scale is 70 µm). Note the endophyte (arrowhead) buried in the thallus.

Fig. 3.30: Vertical section of the thallus showing a monomerous construction (scale is 20 µm). Note the horizontal rows of trichocyte fields buried in the thallus (arrows).

Fig. 3.31: Thallus containing a horizontally arranged pustulate trichocyte field at the surface (arrows) and a trichocyte field buried in the thallus (arrowheads) (scale is 20 µm).

3.4 Discussion

The present study provides the most recent account of non-geniculate coralline species occurring on Two-Mile Reef, Sodwana Bay, and the first modern account for the Maputaland region. Most species occurring on Two-Mile Reef were found throughout the study site with varying abundances. Nine species representing six genera were encountered on Two-Mile Reef during this study. Two of these species (*Lithophyllum cuneatum*, *Pneophyllum* sp.) represent new records for South Africa and five (*Lithophyllum acrocamptum*, *Hydrolithon farinosum*, *Hydrolithon pellire*, *Neogoniolithon brassica-florida* and *Lithothamnion muelleri*) are newly recorded for Sodwana Bay. The two remaining species, *Porolithon onkodes* and *Spongites yendoi*, had previously been reported from Sodwana Bay by Keats and Chamberlain (1994a) and Chamberlain (1993) respectively.

Although South African records of non-geniculate coralline algae are increasing (e.g. Maneveldt and van der Merwe 2012), the results from this study illustrate that there are still gaps in our knowledge of this group as a whole. Maneveldt *et al*. (2008) gathered all the information on non-geniculate red algae from recent references and earlier records from South Africa and published a taxonomic list of 43 species occurring in South African waters, nine of which were reported from Sodwana Bay.

The total number of species found on Two-Mile Reef in the present study was similar to regions where comparable research has taken place, even though the current study may have been slightly biased towards collecting epizoic species (on dead coral). Ballesteros and Afonso-Carrillo (1995) identified seven species from the eastern coast of Mauritius and one of these species (*Hydrolithon onkodes*) was also collected on Two-Mile Reef. Barry and

Woelkerling (1995) reported 10 non-geniculate coralline species on the reefs of Shark Bay, Western Australia, and three of these species (*Hydrolithon farinosum*, *Neogoniolithon brassica-florida* and *Porolithon onkodes*) were also found on Two-Mile Reef. Similarly, Ringeltaube and Harvey (2000) identified 11 species in the first comprehensive account of non-geniculate coralline algae occurring on the Great Barrier Reef (Heron Reef) and three of these species (*Hydrolithon farinosum*, *Hydrolithon onkodes* and *Neogoniolithon brassica-florida*) were also found on Two-Mile Reef.

The seven species newly recorded for Sodwana Bay are known both from Northern and Southern Hemisphere locations. *Lithophyllum acrocamptum* is known from the western and south-western Indian Ocean and has, up to now, only been reported from Kenya, Madagascar, Mauritius and Sri Lanka (Silva *et al*. 1996), and by Papenfuss (1968) from Saudi Arabia. *Neogoniolithon brassica-florida* and *Lithothamnion muelleri* are generally common tropical species, and so it was not surprising to find these two species in South African tropical waters. Similarly, *Hydrolithon farinosum* is a cosmopolitan epiphytic species, widespread across both cool temperate and warm tropical waters.

The worldwide distribution of species of non-geniculate coralline algae present in Sodwana Bay is uncertain due, to some extent, to the predominance of unverified records. Of the species (excluding *Pneophyllum* sp.) dealt with during this study, only *Hydrolithon pellire* has not been reported outside South Africa nor been reported previously from Sodwana Bay, but is known from various localities further south on the east coast of KwaZulu-Natal and from Port Alfred on the south east coast of the Eastern Cape (Chamberlain and Norris 1994).

Of the total number of species recorded in this study, two species are believed to be new records for the South African marine flora. The record of *Lithophyllum cuneatum* is the most unusual, as this species has only been previously reported from the Pacific Islands of Fiji (Keats 1995; South and Skelton 2003) and Tahiti (Woelkerling *et al*. 2013), and Australia (Harvey *et al*. 2009).

Prior to this study only 10 species of non-geniculate coralline algae were known to occur in Sodwana Bay (Maneveldt *et al*. 2008). Seven of the species recorded in the current study represent new records for Sodwana Bay, bringing the total number of coralline red algal species to 17. It is likely that further, more intensive, sampling may reveal that other species of non-geniculate Corallinales occur in Sodwana Bay, and thus the present study should not be regarded as a monographic account for the area.

Chapter 4: General discussion and conclusions

This study provides the first quantitative description of the composition and abundance of species comprising the epilithic macro-algal community on different types of hard substrata on South African coral communities, and showed that substratum type has little or no effect on community composition. In addition, there were no substantial differences in macroalgal communities that settled on three types of artificial substrata.

Although a biogeographic investigation of the macroalgae found here was beyond the scope of this study, it is clear that tropical species and genera are overwhelmingly represented, supporting the contention of Bolton *et al*. (2004) that the algal flora of northern Maputaland lies within the Indo-West Pacific biogeographic region (or Indo-West Pacific Realm of Spalding *et al*. 2007).

It was not always possible to identify these tropical taxa to species level, and 33 out of the 86 specimens collected (Table 1) could only be identified to genus. In some cases this was a result of poor or non-reproductive material, but identifications were hindered by our generally limited knowledge of the subtidal flora of this region (northern Maputaland extending into Mozambique). There is clearly a need for more collections, taxonomic studies, and ultimately for a comprehensive guide to the seaweeds of this region.

The experimental element of this study afforded the opportunity to investigate algal recruitment on bare artificial surfaces, a process that may occur when substratum becomes available as corals die. The tiles on Two-Mile Reef experienced various stages of algal succession from algal turf, to non-geniculate coralline algae and signs of perhaps a climax vegetation of space-occupying brown algae that may even form a very low canopy.

This recruitment of algae is a critical process during coral reef degradation, and here, as in other areas, it usually comprises the replacement of hard corals by benthic algae.

Marine protected areas (MPA) are documented as protecting and improving the diversity of reef macroalgae in various parts of the world, including Hawaii and East Africa (McClanahan 1997; Uku *et* al. 2002; Vroom and Braun 2010). However, no comparisons of reef macroalgal abundance in protected versus fished areas have been investigated for the southern coral communities of south-eastern Africa, and the Maputaland complex may offer such an opportunity. South Africa's high latitude coral reefs are located within the boundaries of two longstanding, contiguous MPAs. Two types of conservation strategies are implemented in the MPAs: no-take sanctuary areas and multiple-use zones.

In order to further our understanding of algal succession on southern Africa's high latitude coral reefs it might be possible to do a long-term experiment that will allow us to distinguish the specific mechanisms that control algal communities among reefs overseen by contrasting management strategies, at least with respect to fish-related effects.

I suggest a future study comparing algal assemblages among reefs regarded as (1) 'sanctuaries' that receive total protection against any human activities (Leadsman Shoal, southern reef complex); (2) partially protected areas that are exposed to SCUBA diving and boat-based capture of pelagic gamefish, but exclude fishing of reef fish (Two-Mile Reef); and (3) 'open' reefs that are subject to all forms of extractive and non-extractive activities, provided they fall within national regulations (Malongane, southern Mozambique). However, although all these reefs are all essentially Indo-West Pacific in nature, they lie along a biogeographic gradient and this may confound the results. In that case, a series of graded, fish-exclusion experiments would have to be done at a fully protected site such as Leadsman

Shoal. Similar experiments in other tropical systems have demonstrated that on protected reefs dominated by herbivorous fishes, macroalgal assemblages pass through more successional stages, and have a great diversity of functional groups. Herbivory is thus an important process controlling macroalgal and turf abundance (McClanahan 1997; Uku *et al*. 2000; Ferrari *et al*. 2012).

Overall, it is clear that the present study is only a snapshot of the algal assemblages that occur on Two-Mile Reef, and assumptions cannot be made that they are representative of all existent depths and environments. However, the results presented here offer a quantitative glimpse of the most common seaweeds and non-geniculate coralline algae present on Two-Mile Reef and form a critical baseline for future monitoring. Seaweeds are very useful organisms for biogeographic studies and for monitoring the health of shallow marine ecosystems. As pointed out by Bolton *et al*. (2004), they are ubiquitous, sessile (non-motile), easy to collect, and comprise three phyla with different evolutionary origins, but often similar functional forms. They have been used to study the effects of changing marine climates (e.g. Beardall *et al*. 1998). For these reasons, long-term monitoring of seaweed communities and broader studies of the Sodwana and other Maputaland reefs (e.g. Leadsman Shoal) would both continue to improve our understanding of macroalgal communities, and might well be useful for alerting MPA managers to any changes on these reefs resulting from climate change or any other environmental perturbations.

References

Adey, W.H. 1970. A revision of the Foslie crustose herbarium. *Det Kongelige Norske Videnskabers Selskabs Skrifter* 1: 1-46.

Adey, W.H. and Adey, P.J. 1973. Studies on the biosystematics and ecology of the epilithic crustose Corallinaceae of the British Isles. *British Phycological Journal* 8: 343-407.

Adey, W.H. and Steneck, R.S. 2001. Thermogeography over time creates biogeographic regions: a temperature/space/time-integrated model and an abundance-weighted test for benthic marine algae. *Journal of Phycology* 37: 677-698.

Adjeroud, M., Michonneau, F., Edmunds, P.J., Chancerelle, Y., Lison de Loma, T., Penin. L., Thibaut, L., Vidal-Dupiol, J., Salvat, B. and Galzin, R. 2009. Recurrent disturbances, recovery trajectories and resilience of coral assembleages on a South Central Pacific reef. *Coral Reefs* 28: 775-780.

Amsler, C.D., Reed, D.C. and Neushul, M. 1992. The microclimate inhabited by macroalgal propagules. *British Journal of Phycology* 27: 253-270.

Anderson, M.J. and Underwood, A.J. 1994. Effects of substratum on the recruitment and development of an intertidal estuarine fouling assemblage. *Journal of Experimental Marine Biology and Ecology* 184: 217-236.

Anderson, R.J., McKune, C., Bolton, J.J., Declerck, O. and Tronchin, E. 2005. Patterns in subtidal seaweed communities on coral-dominated reefs at Sodwana Bay on the KwaZulu-Natal coast, South Africa. *African Journal of Marine Science* 27: 529-537.

Anderson, R.J. and Bolton, J.J. 2005. Introduction. In: *Guide to the seaweeds of KwaZulu-Natal*. De Clerck, O., Bolton, J.J., Anderson, R.J. and Coppejans, E. (Eds). Scripta Botanica Belgica, pp 21-25.

Aterweberhan, M., Bruggemann, J.H. and Breeman, A.M. 2006. Effects of extreme seasonality on community structure and functional group dynamics of coral reef algae in the southern Red Sea (Eritrea). *Coral Reefs* 25: 391-406.

Baker, A.C., Glynn, P.W. and Riegl, B. 2008. Climate change and coral reef bleaching: An ecological assessment of long-term impacts, recovery trends and future outlook. *Estuarine, Coastal and Shelf Science* 80: 435-471.

Ballesteros, E. andand Afonso-Carrillo, J. 1995. Species records and distribution of shallow-water coralline algae in a Western Indian Ocean coral reef (Trou d'Eau Douce, Mauritius). *Botanica Marina* 38: 203-213.

Barry, G.C. and Woelkerling, W. J. 1995. Non-geniculate species of Corallinaceae (Corallinales, Rhodophyta) in Shark Bay, Western Australia: Biodiversity, salinity tolerances and biogeographic affinities. *Botanica Marina* 38: 135-149.

Beardall, J., Beer, S. and Raven, J.A. 1998. Biodiversity of marine plants in an era of climate change: some predictions based on physiological performance. *Botanica Marina* 41: 113-123.

Bellwood, D.R., Hughes, T.P., Folke, C. and Nyström, M. 2004. Confronting the coral reef crisis. *Nature* 429: 827-833.

Bennett, S., Vergés, A., and Bellwood, D.R. 2010. Branching coral as a macroalgal refuge in a marginal coral reef system. *Coral Reefs* 29: 471-480.

Birrell, C.L., McCook, L.J. and Willis, B.L. 2005. Effects of algal turfs and sediment on coral settlement. *Marine Pollution Bulletin* 51: 408-414.

Birrell, C.L., McCook, L.J., Willis, B.L. and Harrington, L. 2008a. Chemical effects of macroalgae on larval settlement of the broadcast spawning coral *Acropora millepora*. *Marine Ecology Progress Series* 362: 129-137.

Birrell, C.L., McCook, L.J., Willis, B.L. and Diaz-Pulido G.A. 2008b. Effects of benthic algae on the replenishment of corals and the implication for the resilience of coral reefs. *Oceanography and Marine Biology: An Annual Review* 46: 25-63.

Bittner L., Payri, C.E., Maneveldt, G.W., Couloux, A., Cruaud, C., de Reviers, B. and Le Gall, L. 2011. Evolutionary history of the Corallinales (Corallinophycidae, Rhodophyta) inferred from nuclear, plastidial and mitochondrial genomes. *Molecular Phylogenetics and Evolution* 61: 697-713.

Bolton, J.J. and Anderson, R.J. 1997. Marine vegetation. In *Vegetation of Southern Africa*. Cowling, R.M., Richardson, D.M. and Pierce, S.M. (Eds). Cambridge University Press, Cambridge: 348-370.

Bolton, J.J., Leliaert, F., De Clerck, O., Anderson, R.J., Stegenga, H., Engledow, H.E. and Coppejans, E. 2004. Where is the western limit of the tropical Indian Ocean seaweed flora? An analysis of intertidal seaweed biogeography on the east coast of South Africa. *Marine Biology*. 144: 51-59.

Box, S.J. and Mumby, P.J. 2007. Effect of macroalgal competition on growth and survival of juvenile Caribbean corals. *Marine Ecology Progress Series* 342: 139-149.

Brown, B.E. 1997. Coral bleaching: causes and consequences. *Coral Reefs* 16: 129-138.

Browne, C.M., Maneveldt, G.W., Bolton, J.J. and Anderson, R.J. 2013. Abundance and species composition of non-geniculate coralline red algae epiphytic on the South African populations of the rocky shore seagrass *Thalassodendron leptocaule* M.C. Duarte, Bandeira and Romeiras. *South African Journal of Botany* 86: 101-110.

Buddemeier, R.W. and Fautin, D.G. 1993. Coral bleaching as an adaptive mechanism. *Bioscience* 43: 320-326.

Celliers, L. and Schleyer, M.H. 2002. Coral bleaching on high latitude marginal reefs at Sodwana Bay, South Africa. *Marine Pollution Bulletin* 44: 1380-1387.

Celliers, L. and Schleyer, M.H. 2008. Coral community structure and risk assessment of high latitude reefs at Sodwana Bay, South Africa. *Biodiversity and Conservation* 17: 3097-3117.

Chamberlain, Y.M. 1990. The genus *Leptophytum* (Rhodophyta, Corallinales) in the British Isles with descriptions of *Leptophytum bornetii*, *L. elatum* sp. nov., and *L. laevae*. *British Phycological Journal* 25: 179-199.

Chamberlain, Y.M. 1993. Observations on the crustose coralline red alga *Spongites yendoi* (Foslie) comb. nov. in South-Africa and its relationship to *S. decipiens* (Foslie) comb. nov. and *Lithophyllum natalense* Foslie. *Phycologia* 32: 100-115.

Chamberlain, Y.M. 1994. Mastophoroideae Setchell. In: *Seaweeds of the British Isles. Volume 1. Rhodophyta. Part 2B. Corallinales, Hildenbrandiales*. (Irvine, L.M. and Chamberlain, Y.M. Eds), pp. 113-158. London: HMSO.

Chamberlain, Y.M. and Norris, R.E. 1994. *Hydrolithon pellire* sp. nov., a mastophoroid crustose coralline red algal epiphyte from South Africa. *Phycologia* 33: 291-297.

Clark, K.R. and Gorley, R.N. 2006. PRIMER v6. *User manual/tutorial*. Plymouth routine in multivariate ecological research. Plymouth Marine Laboratory.

Coen, L.D. and Tanner, C.E. 1989. Morphological variation and differential susceptibility to herbivory in the tropical brown alga *Lobophora variegata*. *Marine Ecology Progress Series* 54: 287-298.

De Clerck, O., Bolton, J.J., Anderson, R.J. and Coppejans, E. 2005. *Guide to the seaweeds of KwaZulu-Natal*. Scripta Botanica Belgica.

Diaz-Pulido, G. and Garzón-Ferreira, J. 2002. Seasonality of algal assemblages on upwelling-influenced coral reefs in the Colombian Caribbean. *Botanica Marina* 45: 284-292.

Diaz-Pulido, G. and McCook, L.J. 2002. The fate of bleached corals: patterns and dynamics of algal recruitment. *Marine Ecology Progress Series* 232: 115-128.

Diaz-Pulido, G. and McCook, L.J. 2004. Effects of live coral, epilithic algal communities and substrate type on algal recruitment. *Coral Reefs* 23: 225-233.

Diaz-Pulido, G., McCook, L.J., Dove, S., Berkelmans, R., Roff, G., Kline, D.I., Weeks, S., Evans, R.D., Williamson, D.H. and Hoegh-Guldberg, O. 2009. Doom and boom on a resilient reef:

Climate change, algal overgrowth and coral recovery. *PLoS ONE* DOI: 10.1371/journal.pone.0005239

Douglas, A.E. 2003. Coral bleaching - how and why? *Marine Pollution Bulletin* 46: 385-392.

Emslie, M.J., Pratcherr, M.S., Cheal, A.J. and Osborne, K. 2010. Great Barrier Reef butterflyfish community structure: the role of shelf position and benthic community type. *Coral Reefs* 29: 705-715.

Ferrari, R., Gonzalez-Rivero, M., Ortiz, J.C. and Mumby P.J. 2012. Interaction of herbivory and seasonality on the dynamics of Caribbean macroalgae. *Coral Reefs* 31: 683-692.

Floros, C.D., Samways, M.J. and Armstrong, B. 2004. Taxonomic patterns of bleaching within a South African coral assemblage. *Biodiversity and Conservation* 13: 1175-1194.

Fong, P. and Lirman D. 1995. Hurricanes cause population expansion of the branching coral *Acropora palmata*. *Marine Ecology* 16: 317-335.

Foslie, M. 1898. List of species of Lithothamnia. Det Kongelige Norske Videnskabers Selskabs Skrifter 1898 (3), 1-11.

Foslie, M. 1900. New or critical calcareous algae. Det Kongelige Norske Videnskabers Selskabs Skrifter 1899 (5), 1-34.

Foslie, M. 1907. Algologiske notiser II. Det Kongelige Norske Videnskabers Selskabs Skrifter 1907 (8), 1-34.

Foslie, M. 1909. Algologiske notiser. VI. Det Kongelige Norske Videnskabers Selskabs Skrifter 1909 (2), 1-63.

Glynn, P.W. 1990. Coral mortality and disturbances to coral reefs in the tropical eastern Pacific. In P.W. Glynn (Ed) *Global consequences of the 1982-83 El Niño southern oscillation. Elsevier Oceanography Series Volume 52.* Elsevier, Amsterdam 55-126.

Glynn, P.W. 1993. Coral reef bleaching: ecological perspectives. *Coral Reefs* 12: 1-17.

Glynn, P.W. 1996. Coral reef bleaching: facts, hypotheses and implications. *Global Change Biology* 2: 495-509.

Guiry, M.D. and Guiry, G.M. 2014. *AlgaeBase*. World-wide electronic publication, National University of Ireland, Galway. http://www.algaebase.org; searched on 08 August 2012.

Hadfield, M.G. and Paul, V.J. 2001. Natural chemical cues for settlement and metamorphosis of marine-invertebrate larvae. In: McClintock, J. and Baker, B. (eds) Marine chemical ecology. CRC Press, Boca Raton pp 431-462.

Harriott, V.J. and Banks, S.A. 2002. Latitudinal variation in coral communities in eastern Australia: a qualitative biophysical model of factors regulating coral reefs. *Coral Reefs* 21: 83-94.

Harvey, W.H. 1849. *Nereis australis,* or algae of the southern ocean: being figures and descriptions of marine plants, collected on the shores of the Cape of Good Hope, the extra-tropical Australian colonies, Tasmania, New Zealand, and the Antarctic regions; deposited in the Herbarium of the Dublin University. Part 2. pp. 65-124, pls XXVI-L. London: Reeve Brothers.

Harvey, A.S., Woelkerling, W.J. and Millar, A.J.K. 2009. The genus *Lithophyllum* (Lithophylloideae, Corallinaceae, Rhodophyta) in south-eastern Australia, with the description of *L. riosmenae*, sp. nov. *Australian Systematic Botany* 22: 296-317.

Hay, M.E. and Fenical, W. 1988. Marine plant-herbivore interactions: the ecology of chemical defence. *Annual Review of Ecology, Evolution and Systematics* 19: 111-145.

Heydrich, F. 1897. Corallinaceae, inbesondere Melobesieae. Berichte der Deutschen Botanischen Gesellschaft 15, 34-71 pl. 3.

Heydrich, F. 1901. Die Lithothamnien des Muséum d'Histoire Naturelle in Paris. Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie 28, 529-545 p. 11.

Heydrich, F. 1902. Quelques nouvelles Mélobésiées due Muséum d'histoire naturelles de Paris. *Bulletin du Muséum National d'Histoire Naturelle, Paris* 8: 473-476.

Hoegh-Guldberg, O. and Smith, G.J. 1989. The effect of sudden changes in temperature, irradiance and salinity on the population density and export of zooxanthellae from the reef corals *Stylophora pistillata* (Esper 1797) and *Seriatopora hystrix* (Dana 1846). *Journal of Experimental Marine Biology and Ecology* 129: 279-303.

Hoegh-Guldberg, O. 1999. Climate change, coral bleaching and the future of the world's coral reefs. *Marine Freshwater Research* 50: 839-866.

Hoegh-Guldberg, O., Mumby, P.J., Hooten, A.J., Steneck, R.S., Greenfield, P. 2007. Coral reefs under rapid climate change and ocean acidification. *Science* 318: 1737-1742.

Holmgren, P., Holmgren, N.H. and Bartlett, L.C. 1990. *Index herbariorum, Pt.1. The herbaria of the world.* 8. Koeltz Scientific Books, Königstein. 693 pp.

Hughes, T.P. 1994. Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. *Science* 265: 1547-1551.

Hughes, T.P. and Connell J.H. 1999. Multiple stressors on coral reefs: a long term perspective. *Limnology and Oceanography* 44: 932-940.

Hughes, T.P., Baird, A.H., Bellwood, D.R., Card, M., Connolly, S.R., Folke, C., Grosberg, R., Hoegh-Guldberg, O., Jackson, J.B.C., Kleypas, J., Lough, J.M., Marshall, P., Nyström, M., Palumbi, S.R., Pandolfi, J.M., Rosen, B. and Roughgarden, J. 2003. Climate change, human impacts, and the resilience of coral reefs. *Science* 301: 929-933.

Jaasund, E. 1976. *Intertidal Seaweeds in Tanzania: A Field Guide*. University of Tromsø, Tromsø.

Johansen, H.W. 1981. *Coralline algae, a first synthesis*. CRC Press, Boca Raton, Florida, pp. 239.

Jompa, J. and McCook L.J. 2002. Effects of competition and herbivory on interactions between a hard coral and a brown alga. *Journal of Experimental Marine Biology and Ecology* 271: 25-39.

Jompa, J. and McCook L.J. 2002. The effects of nutrients and herbivory on competition between a hard coral (*Porites cylindrica*) and a brown alga (*Lobophora variegata*). *Limnol*. *Oceanogr*. 47: 527-534.

Jones, R.J. 1997. Zooxanthellae loss as a bioassay for assessing stress in corals. *Marine Ecology Progress Series* 149: 163-171.

Jordan, I.E. and Samways, M.J. 2001. Recent changes in coral assemblages of a South African coral reef, with recommendations for long-term monitoring. *Biodiversity and Conservation* 10: 1027-1037.

Kato, A., Baba, M. and Suda, S. 2011. Revision of the Mastophoroideae (Corallinales, Rhodophyta) and polyphyly in nongeniculate species widely distributed on Pacific coral reefs. *Journal of Phycology* 47: 662-672.

Keats, D.W. and Chamberlain, Y.M. 1993. *Sporolithon ptychoides* Heydrich and *S. episporum* (Howe) Dawson: two crustose coralline red algae (Corallinales, Sporolithaceae) in South Africa. *South African Journal of Botany* 59: 541-550.

Keats, D.W. and Chamberlain, Y.M. 1994a. Three species of *Hydrolithon* (Rhodophyta, Corallinaceae): *Hydrolithon onkodes* (Heydrich) Penrose and Woelkerling, *Hydrolithon superficiale* sp. nov., and *H. samoënse* (Foslie) comb. nov. from South Africa. *South African Journal of Botany* 60: 8-21.

Keats, D.W. and Chamberlain, Y.M. 1994b. Two melobesioid coralline algae (Rhodophyta, Corallinales), *Mesophyllum erubescens* (Foslie) Lemoine and *Mesophyllum funafutiense* (Foslie) Verheij from Sodwana Bay, South Africa. *South African Journal of Botany* 60: 175-190.

Keats, D.W. 1995. *Lithophyllum cuneatum* sp. nov. (Corallinaceae, Rhodophyta), a new species of non-genicultae coralline alga semi-endophytic in *Hydrolithon onkodes* and *Neogoniolithon* sp. from Fiji, South Pacific. *Phycological Research* 43: 151-160.

Keats, D.W., Knight, M.A. and Pueschel, C.M. 1997. Antifouling effects of epithallial shedding in three crustose coralline algae (Rhodophyta, Corallinales) on a coral reef. *Journal of Experimental Marine Biology and Ecology* 213: 281-293.

Keats, D.W. and Maneveldt, G. 1997. Two new melobesioid algae (Corallinales, Rhodophyta) *Synarthrophyton robbenense* sp. nov. and *S. munimentum* sp. nov., in South Africa and Namibia. *Phycologia* 36: 447-467.

Kushmaro, A., Loya, Y., Fine, M. and Rosenberg, M. 1996. Bacterial infection and coral bleaching. *Nature* 380: 396.

Kützing, F.T. 1843. Phycologia gerneralis oder Anatomie, Physiologie und Systemkunde der Tange. Leipzig pp 458.

Lepš, J. and Hadincová, V. 1992. How reliable are our vegetation analyses? *Journal of Vegetation Science* 3: 119-124.

Lesser M.P. 2006. Oxidative stress in marine environments: biochemistry and physiological ecology. *Annual Review of Physiology* 68: 253-278

Lewis, J.B. 1977. Processes of organic production on coral reefs. *Biological Reviews* 52: 305-347.

Lirman, D. 2001. Competition between macroalgae and corals: effects of herbivore exclusion and increased algal biomass on coral survivorship and growth. *Coral Reefs* 19: 392-399.

Lirman, D. and Biber, P. 2000. Seasonal dynamic of macroalgal communities of the northern Florida reef tract. *Botanica Marina* 43: 305-314.

Littler, M.M. 1976. Calcification and its role among the macroalgae. *Micronesica* 12: 27-41.

Littler, M.M. and Littler, D.S. 1988. Structure and role of algae in tropical reef communities. In: Lembi, C.A. and Waaland, J.R. (Eds). *Algae and human affairs*. Cambridge University Press, Cambridge, pp 29-56.

Littler, M.M., Littler, D.S. and Hanisak, M.D. 1991. Deep-water rhodolith distribution, productivity, and growth history at sites of formation and subsequent degradation. *Journal of Experimental Marine Biology and Ecology* 150: 163-182.

Littler, M.M. and Littler, D.S. 1994. Tropical reefs as complex habitats for diverse macroalgae. In: Lobban, C.S. and Harrison, P.J. (Eds). *Seaweed ecology and physiology*. Cambridge University Press, New York, pp 72-75.

Littler, M.M. and Littler, D.S. 1997. Disease induced mass mortality of crustose coralline algae on coral reefs provides rationale for the conservation of herbivorous fish stocks. *Proc 8th Int Coral Reef Symposium* 1: 719-724.

Littler, D.S. and Littler, M.M. 2000. *Caribbean reef plants*. *An identification guide to the reef plants of the Caribbean, Bahamas, Florida and Gulf of Mexico*. Offshore Graphics, Washington, 542 pp.

Lüning, K. 1990. *Seaweeds. Their environment, biogeography, and ecophysiology*. Wiley, New York, 527pp.

Macintyre, I.G., Graus R.R., Reinthal, P.N., Littler, M.M. and Littler D.S. 1987. The barrier reef sediments apron: Tobacco Reef, Belize. *Coral Reefs* 6: 1-12.

Maneveldt, G.W. 2005. A global revision of the non-geniculate coralline algal genera *Porolithon* Foslie (defunct) and *Hydrolithon* Foslie (Corallinales, Rhodophyta). Ph.D Thesis. Department of Biodiversity and Conservation Biology, University of the Western Cape.

Maneveldt, G.W., Chamberlain, Y.M. and Keats, D.W. 2008. A catalogue with keys to the non-geniculate coralline algae (Corallinales, Rhodophyta) of South Africa. *South African Journal of Botany* 74: 555-566.

Maneveldt, G.W., Keats D.W. and Woelkerling, Wm J. 2013. An Introduction to the Coralline Red Algae. World-wide electronic publication, University of the Western Cape, Bellville. http://www.bcb.uwc.ac.za/clines; searched on 17 August 2013.

Maneveldt, G.W. and Van Der Merwe, E. 2012. *Heydrichia cerasina* sp. nov. (Sporolithales, Corallinophycidae, Rhodophyta) from the southern-most tip of Africa. *Phycologia* 51: 11-21.

McClanahan, T.R. 1997. Primary succession of coral-reef algae: Differing patterns on fished versus unfished reefs. *Journal of Experimental Marine Biology and Ecology* 218: 77-102.

McClanahan, T.R., Ateweberhan, M., Graham, N.A.J., Wilson, S.K., Ruiz Sebastián C., Guillaume, M.M.M. and Bruggemann, J.H. 2007. Western Indian Ocean coral communities: bleaching responses and susceptibility to extinction. *Marine Ecology Progress Series* 337: 1-13.

McCook, L.J. 1999. Macroalgae, nutrients and phase shifts on coral reefs: scientific issues and management consequences for the Great Barrier Reef. *Coral Reefs*. 18: 357-367.

McCook, L.J., Jompa, J. and Diaz-Pulido, G. 2001. Competition between corals and algae on coral reefs: a review of evidence of mechanisms. *Coral Reefs*. 19: 400-417.

McManus, J.W., Meñez, L.A.B., Reyes, K.N.K., Vergara, S.G. and Ablan, M.C. 2000. Coral reef fishing and coral-algal phase shifts: Implications for global reef status. *ICES Journal of Marine Science* 57: 572-578.

McManus, J.W. and Polsenberg, J.F. 2004. Coral-algal phase shifts on coral reefs: ecological and environmental aspects. *Progress in Oceanography* 60: 263-279.

Moberg, F. and Folke, C. 1999. Ecological goods and services of coral reef ecosystems. *Ecological Economics* 29: 215-233.

Mumby, P.J. 2009. Phase shifts and the stability of macroalgal communities on Caribbean coral reefs. *Coral Reefs* 28: 761-773.

Mumby, P.J., Foster, N.L. and Fahy, E.A.G 2005. Patch dynamics of coral reef macroalgae under chronic and acute disturbance. *Coral Reefs* 24: 681-692.

Muscatine, L. 1990. The role of symbiotic algae in carbon and energy flux in reef corals. *Coral Reefs* 25: 1-29. In: *Ecosystems of the world vol 25: Coral Reefs*, Z. Dubinsky ed. Elsevier, Amsterdam, pp 75-87.

Nugues, M.M. and Roberts C.M. 2003. Coral mortality and interaction with algae in relation to sedimentation. *Coral Reefs* 22: 507-516.

Odum, H.T. and Odum, E.P. 1995. Trophic structure and productivity of a windward coral reef community on Eniwetok Atoll. *Ecological Monographs* 25: 291-320.

Oliveira, E.C., Österland, K. and Mtolera, M.S.P. 2005. *Marine plants of Tanzania: A field guide to the seaweeds and seagrasses*. Botany Department, Stockholm University, Stockholm.

Pandolfi, J.M., Jackson, J.B.C., Baron, N., Bradbury, R.H., Guzmán, H.M., Hughes, T.P., Kappel, C.V., Micheli, F., Ogden, J.C., Possingham, H.P. and Sala, E. 2005. Are U.S. coral reefs on the slippery slope to slime? *Science* 307: 1725-1726.

Papenfuss G.F. 1968. A history, catalogue, and bibliography of the Red Sea benthic algae. *Israel Journal of Botany* 17: 1-118.

Penrose, D. and Chamberlain, Y.M. 1993. *Hydrolithon farinosum* (Lamouroux) comb. nov.: implications for generic concepts in the Mastophoroideae (Corallinaceae, Rhodophyta). *Phycologia* 32: 295-303.

Porter, J.W. 1972. Predation by *Acanthaster* and its effect on coral species diversity. *The American Naturalist* 106: 487-492.

Porter, S.N., Branch, G.M. and Sink, K.J. 2013. Biogeographic patterns on shallow subtidal reefs in the western Indian Ocean. *Marine Biology* 160: 1271-1283.

Ramsay, P.J. 1989. The occurrence and formation of ladderback ripples in subtidal, shallow-marine sands, Zululand, South Africa. *Marine Geology* 86: 229-235.

Ramsay, P.J. 1994. Marine geology of the Sodwana Bay shelf, southeast Africa. *Marine Geology* 120: 225-247.

Ramsay, P.J. 1996. Quaternary marine geology of the Sodwana Bay continental shelf northern KwaZulu-Natal. *Bulletin of the Geological Survey of Southern Africa* 117: 1-85.

Ramsay, P.J. and Mason, T.R. 1990. Development of a type zoning model for Zululand coral reefs, Sodwana Bay, South Africa. *Journal of Coastal Research* 6: 829-852

Riegl, B. 2003. Climate changes and coral reefs: different effects in two high latitude areas (Arabian Gulf, South Africa). *Coral Reefs* 22: 433-446.

Riegl, B., Schleyer, M.H., Cook, P.J. and Branch, G.M. 1995. Structure of Africa's southernmost coral communities. *Bulletin of Marine Science* 56: 679-691.

Riegl, B. and Riegl, A. 1996. Studies on coral community structure and damage as a basis for zoning marine reserves. *Biological Conservation* 77: 269-277.

Riegl, B. and Piller, W.E. 2003. Possible refugia for reefs in times of environmental stress. *International Journal of Earth Sciences* 92: 520-531

Ringeltaube, P. and Harvey, A. 2000. Non-geniculate coralline algae (Corallinales, Rhodophyta) on Heron Reef, Great Barrier Reef (Australia). *Botanica Marina* 43: 431-454.

Roberts, M.J., Ribbink A.J., Morris, T., van den Berg, M.A., Engelbrecht, D.C. and Harding, R.T. 2006. Oceanographic environment of the Sodwana Bay coelacanths (*Latimeria chalumnae*), South Africa. *South African Journal of Science* 102: 435-443.

Rogers, C.S., Garrison, V. and Grober-Dunsmore, R. 1997. A fishy story about hurricanes and herbivory, seven years of research on a reef in St. John, U.S. Virgin Islands. *Proc 8th International Coral Reef Symposium* 1: 555-560.

Rosanoff, S. 1866. Recherches anatomiques sur les Mélobésiées (*Hapalidium*, *Melobesia*, *Lithophyllum* et *Lithothamnion*). Mémoires de la Société Impériale des Sciences Naturelles de Cherbourg 12: 5-112.

Ruiz Sebastián, C., Sink, K.J., McClanahan, T.R. and Cowan, D.A. 2009. Bleaching response of corals and the *Symbiodinium* communities in southern Africa. *Marine Biology* 156: 2049-2062.

Sangil, C., Sansón, M. and Afonso-Carrillo, J. 2011. Spatial variation patterns of subtidal seaweed assemblages along a subtropical oceanic archipelago: Thermal gradient vs. herbivore pressure. *Estuarine, Coastal and Shelf Science* 94: 322-333.

Santelices, B. and Varela, D. 1994. Abiotic control of reattachment in *Gelidium chilense* (Montagne) Santelices and Montalva (Gelidiales; Rhodophyta). *Journal of Experimental Marine Biology and Ecology* 177: 145-155.

Schleyer, M.H. 1999. A synthesis of KwaZulu-Natal coral research. *South African Association of Marine Biological Research Special Publication* 5:36.

Schleyer, M.H. and Celliers, L. 2000. The status of South African coral reefs. In: Souter, D., Obura, D., Linden, O. (Eds.), *Coral Reef Degradation in the Indian Ocean: Status Report 2000*. CORDIO, Stockholm, pp 49-50.

Schumann, E.H. 1988. Physical oceanography off Natal. In: *Coastal ocean studies off Natal, South Africa*. Schumann, E.H. (Ed). Berlin; Springer: 101-130 (Lecture Notes on Coastal and Estuarine Studies 26).

Scott, F.J. and Russ, G.R. 1987. Effects of grazing on species composition of the epilithic algal community on coral reefs of the central Great Barrier Reef. *Mar. Ecol. Prog. Ser.* 39: 293-304.

Seagrief, S.C. 1980. Seaweeds of Maputaland. In: Bruton, M.N., Hooper, K.H. (Eds.), *Studies on the ecology of Maputaland*. Rhodes University and the Natal Branch of the Wildlife Society of Southern Africa, Durban pp. 18-41.

Silva, P.C., Basson, P.W. and Moe, R.L. 1996. Catalogue of the benthic marine algae of the Indian Ocean. *University of California Publications in Botany* 79: 1-1259.

Sink, K.J., Branch, G.M. and Harris, J.M. 2005. Biogeographic patterns in rocky intertidal communities in KwaZulu-Natal, South Africa. *African Journal of Marine Science* 27: 81-96.

Smit, A.J., Roberts, M., Anderson, R.J., Dufois, F., Dudley, S.F.J., Bornman, T.G., Olbers, J. and Bolton, J.J. 2013. A coastal seawater temperature dataset for biogeographical studies: Large biases between *in situ* and remotely-sensed data sets around the coast of South Africa. PLoS ONE 8: e81944.

South, G.R. and Skelton, P.A. 2003. Catalogue of the marine benthic macroalgae of the Fiji Islands, South Pacific. *Australian Systematic Botany* 16: 699-758.

Spalding, M.D., Fox, H.E., Allen, G.R., Davidson, N., Ferdaña, Z.A., Finlayson, M., Halpern, B.S., Jorge, M.A., Lombana, A., Lourie, S.A., Martin, K.D., McManus, E., Molnar, J., Recchia, C.A. and Robertson, J. 2007. Marine ecoregions of the world: A bioregionalization of coastal and shelf areas. *BioScience* 57: 573-583.

Stearn, W.T. 1973. *Botanical Latin*. David and Charles, Newton Abbot. 566 pp.

Stegenga, H., Bolton, J.J. and Anderson, R.J. 1997. *Seaweeds of the South African west coast*. Bolus Herbarium, University of Cape Town, Cape Town.

Steneck, R.S. 1986. The ecology of coralline crusts: Convergent patterns and adaptive strategies. *Annual Review of Ecology and Systematics 1*7: 273-303.

Steneck, R.S. and Dethier, M.N. 1994. A functional group approach to the structure of algal-dominated communities. *Oikos* 69: 476-498.

Stuercke, B. And McDermid, K.J. 2004. Variation in algal turf species composition and abundance on two Hawaiian shallow subtidal reefs. *Cryptogamie Algologie* 25: 353-365.

South, G.R. and Skelton, P.A. 2003. Catalogue of the marine benthic macroalgae of the Fiji Pacific. *Australian Systematic Botany* 16: 699-758.

Tanner, J.E. 1995. Competition between scleractinian corals and macroalgae: an experimental investigation of coral growth, survival and reproduction. *Journal of Experimental Marine Biology and Ecology* 190: 151-168.

Targett, M.N. and Arnold, T.M. 1998. Predicting the effects of brown algal phlorotannins on marine herbivores in tropical and temperate oceans. *Journal of Phycology* 34: 195-205.

Thiers, B.M. 2013 [Continuously updated electronic resource]. *Index herbariorum: A global directory of public herbaria and associated staff.* New York Botanical Garden's Virtual Herbarium, New York. http://sweetgum.nybg.org/ih/

Titlyanov, E.A., Yakovleva, I.M. and Titlyanova, T.V. 2007. Interaction between benthic algae (*Lyngbya bouillonii*, *Dictyota dichotoma*) and scleractinian coral *Porites lutea* in direct contact. *Journal of Experimental Marine Biology and Ecolgy* 342: 282-291.

Titlyanov, E.A., Titlyanova, T.V. and Chapman, D.J. 2008. Dynamics and patterns of algal colonization on mechanically damaged and dead colonies of the coral *Porites lutea*. *Botanica Marina* 51: 285-296.

Tittensor, D.P., Mora, C., Jetz, W. Lotze, H.K., Ricard, D., Vanden Berghe, E. and Worm, B. 2010. Global patterns and predictors of marine biodiversity across taxa. *Nature* 466: 1098-1101.

Tribble, G.W. and Randall, R.H. 1986. A description of the high latitude shallow water coral communities of Miyake-jima, Japan. *Coral Reefs* 4: 151-159.

Uku, J., Ndirangu, S. and Muthama, C. 2002. Trends in the distribution of macroalgae in a bleached Kenyan reef ecosystem. In: Lindén, O., Souter, D., Wilhelmsson, D. and Obura, D. (Eds) *Coral Reef Degradation in the Indian Ocean* CORDIO pp. 61-69

van der Merwe, E., Miklasz, K., Channing, A., Maneveldt, G.W. and Gabrielson, P.W. (under review) DNA sequencing confirms two historically confused *Spongites* (Corallinaceae, Corallinales, Rhodophyta) species, *Spongites decipiens* and South African *Spongites yendoi*, reveals a new species, *Spongites agulhensis* sp. nov., from South Africa, and recognises *Spongites neofarlowii* comb. nov. from the Northeast Pacific. *Phycologia*.

Vroom, P.S. and Braun, C.L. 2010. Benthic composition of a healthy subtropical reef: baseline species-level cover, with an emphasis on algae, in the Northwestern Hawaiian Islands. PLoS ONE 5: e9733.

Walters, R.D.M and Samways, M.J. 2001. Sustainable dive ecotourism on a South African coral reef. *Biodiversity and Conservation* 10: 2167-2179.

West, J.M. and Salm, R.V. 2003. Resistance and resilience to coral bleaching: Implications for coral reef conservation and management. *Conservation Biology* 17: 956-967.

Wilkinson, C.R. 2000. Status of Coral Reefs of the World: 2000. Global Coral Reef Monitoring Network and Australian Institute of Marine Science, Townsville, Australia. Wilkinson, C. 2002. Status of Coral Reefs of the World: 2002. Australian Institute of Marine Science, Townsville, Australia.

Wilkinson, C.R. and Buddemeier, R.W. 1994. *Global Climate Change and Coral Reefs: Implications for People and Reefs. Report of the UNEP-IOC-ASPEI-IUCN Global Task Team on the implications of climate change on coral reefs.* IUCN, Switzerland 124pp.

Wilkinson, C., Linden, O., Cesar, H., Hodgson, G., Rubens, J. and Strong, A. 1999. Ecological and socioeconomic impacts of 1998 coral mortality in the Indian Ocean: An ENSO impact and a warning of future change? *Ambio* 28: 188-196.

Wilks, K.M. and Woelkerling, W.J. 1995. An account of southern Australian species of *Lithothamnion* (Corallinaceae, Rhodophyta). *Australian Systematic Botany* 8: 549-583.

Wismer, S., Hoey, A.S. and Bellwood, D.T. 2009. Cross-shelf benthic community structure on the Great Barrier Reef: relationships between macroalgal cover and herbivore biomass. *Marine Ecological Progress Series* 376: 45-54.

Woelkerling, W.J. 1993. Type collections of Corallinales (Rhodophyta) in the Foslie Herbarium (TRH). *Gunneria* 67: 1-289.

Woelkerling, W.J. 1998. Lamarck's nullipores. In: Woelkerling, Wm J., Lamy, D. (Eds), *Non-geniculate Coralline Red Algae and the Paris Muséum: Systematics and Scientific History*. Publications Scientifiques du Muséum/A.D.A.C., Paris, pp. 101-104.

Woelkerling, W.J., Penrose, D. and Chamberlain, Y.M. 1993. A reassessment of type collections of non-geniculate Corallinaceae (Corallinales, Rhodophyta) described by C. Montagne and L. Dufour, and of *Melobesia brassica-florida* Harvey. *Phycologia* 32: 323-331.

Woelkerling, W.J. and Lamy, D. 1998. *Non-geniculate coralline red algae and the Paris Muséum: Systematics and scientific history*, Paris, Publications scientifique du Muséum/A.D.A.C.: i-viii, 1-767. Paris.

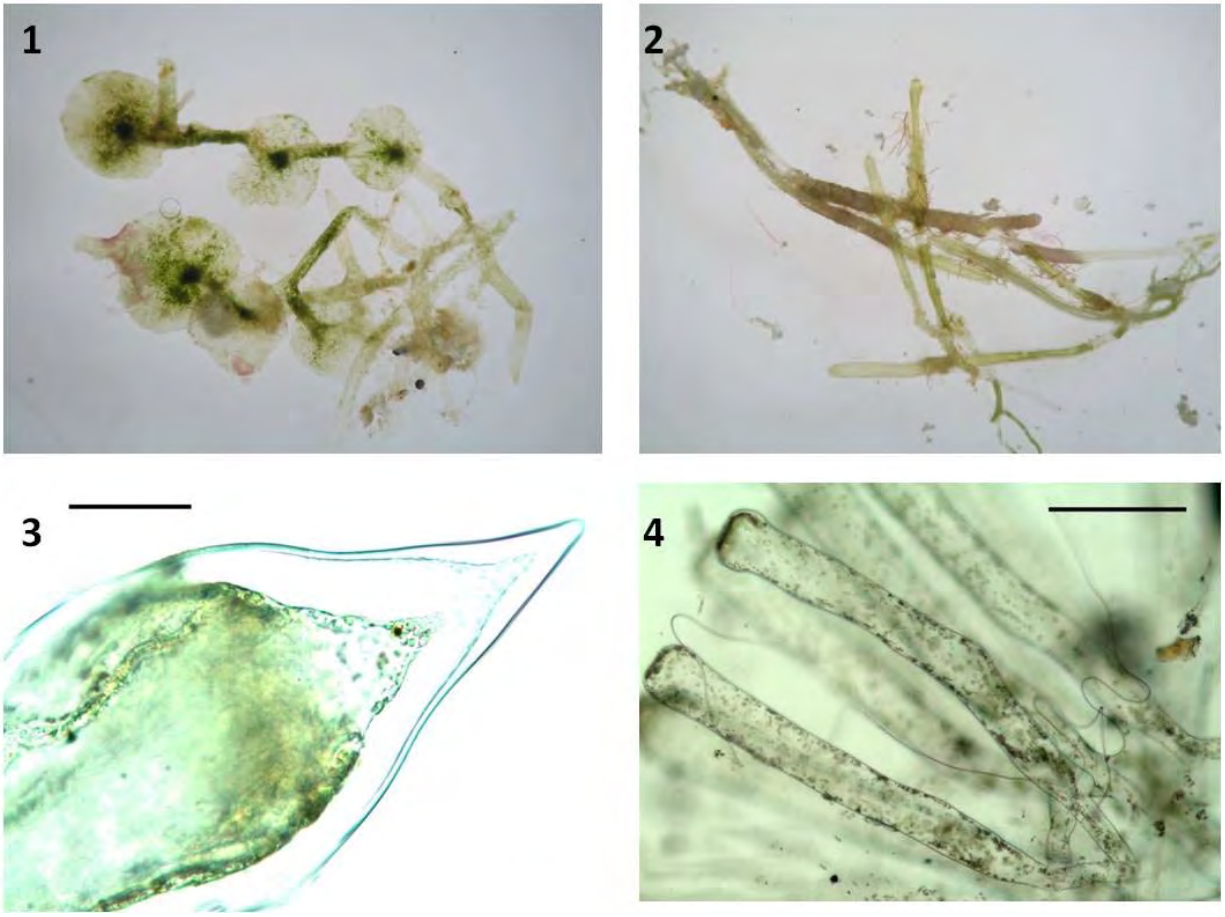
Woelkerling, W.J., Iryu, Y. and Bassi, D. 2013. Fossil semi-endophytic species of *Lithophyllum* (Corallinaceae, Rhodophyta) from Tahiti, including *L. kenjikonishii* sp. nov., and their taphonomic signatures. *Phycologia* 52: 397-397.

Womersley, H.B.S. 1967. A critical survey of the marine algae of southern Australia. II. Phaeophyta. *Australian Journal of Botany* 15: 189-279.

Worm, B. and Chapman, A.R.O. 1998. Relative effects of elevated grazing pressure and competition from a red algal turf on two post-settlement stages of *Fucus evanescens* C. Ag. *Journal of Experimental Marine Biology and Ecology* 220: 247-268.

Appendix

Photographs have been taken of various specimens. They are not comprehensive but include those which are clean enough to assist with future identifications.



Figures 1-28: Seaweeds collected at Two-Mile Reef, Sodwana Bay. Figures 1-4 include Chlorophyceae, Figures 5-28 Rhodophyceae and Figure 29 Cyanobacteria.

Fig. 1: *Caulerpa nummularia* Harvey ex J.Agardh (X20).

Fig. 2: *Cladophora* sp. (X12)

Fig. 3: *Codium acuminatum* O.Schmidt (scale is 50 µm).

Fig. 4: *Codium arabicum* Kützing (scale is 200 µm).

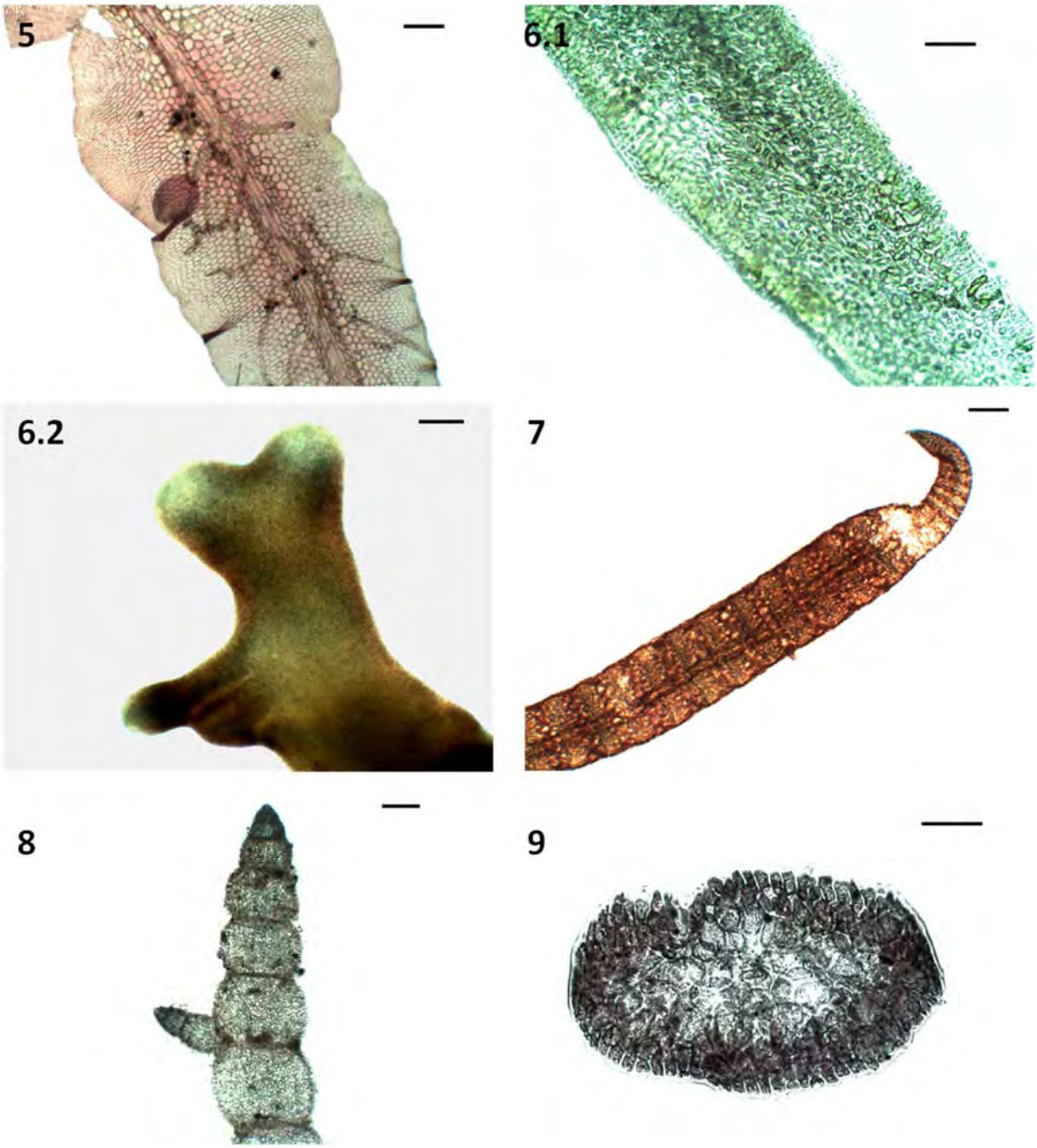


Fig. 5: *Apoglossum spathulatum* (Sonder) Womersley and Shepley (scale is 200 µm).

Figs. 6.1 and 6.2: *Callophycus condominius* R.E.Norris (scales are 50 µm and 200 µm respectively).

Fig. 7: *Ceramium centroceratiforme* Simons (scale is 200 µm).

Fig. 8: *Champia parvula* (C.Agardh) Harvey (scale is 200 µm).

Fig. 9: *Chondria* sp. (scale is 100 µm).

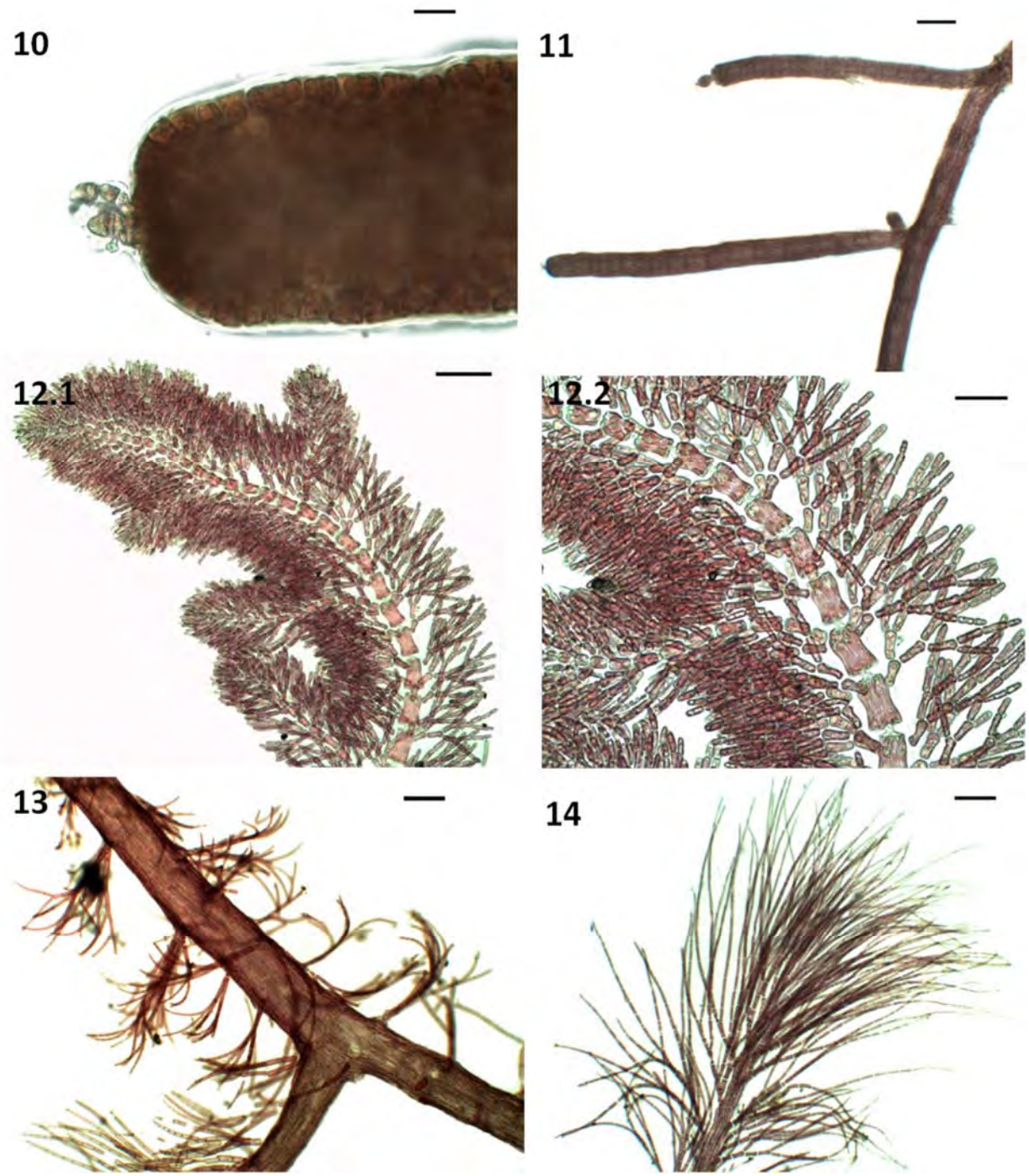


Fig. 10: *Chondria* sp. 2 (scale is 20 µm).

Fig. 11: *Chondria* sp. 2 (scale is 200 µm).

Figs. 12.1 and 12.2: *Crouania attenuata* (scales are 100 µm and 200 µm respectively).

Fig. 13: *Dasya baillouviana* (S.G.Gmelin) Montagne (scale is 200 µm).

Fig. 14: *Dasya pedicellata* (C.Agardh) C.Agardh (scale is 200 µm).

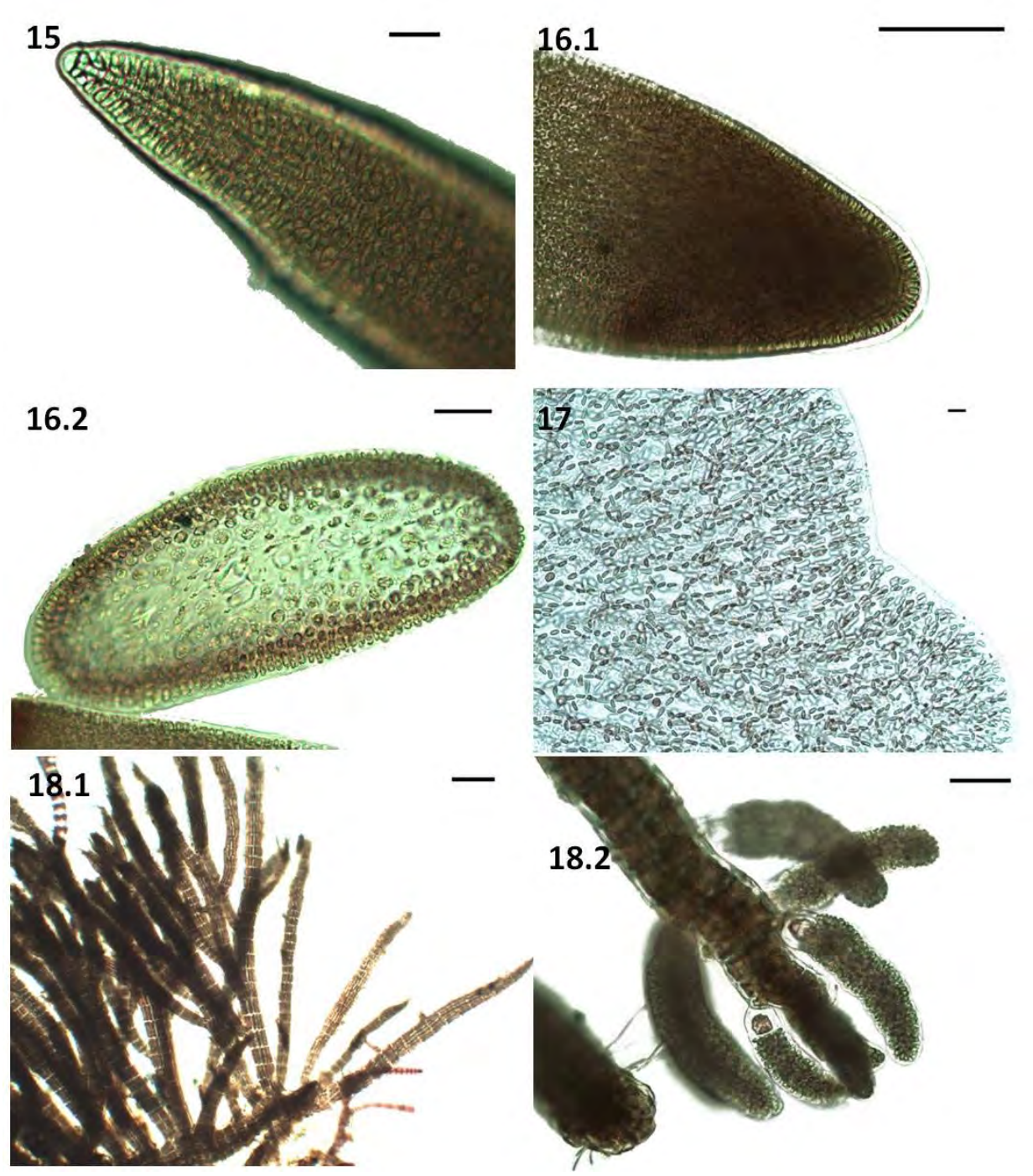
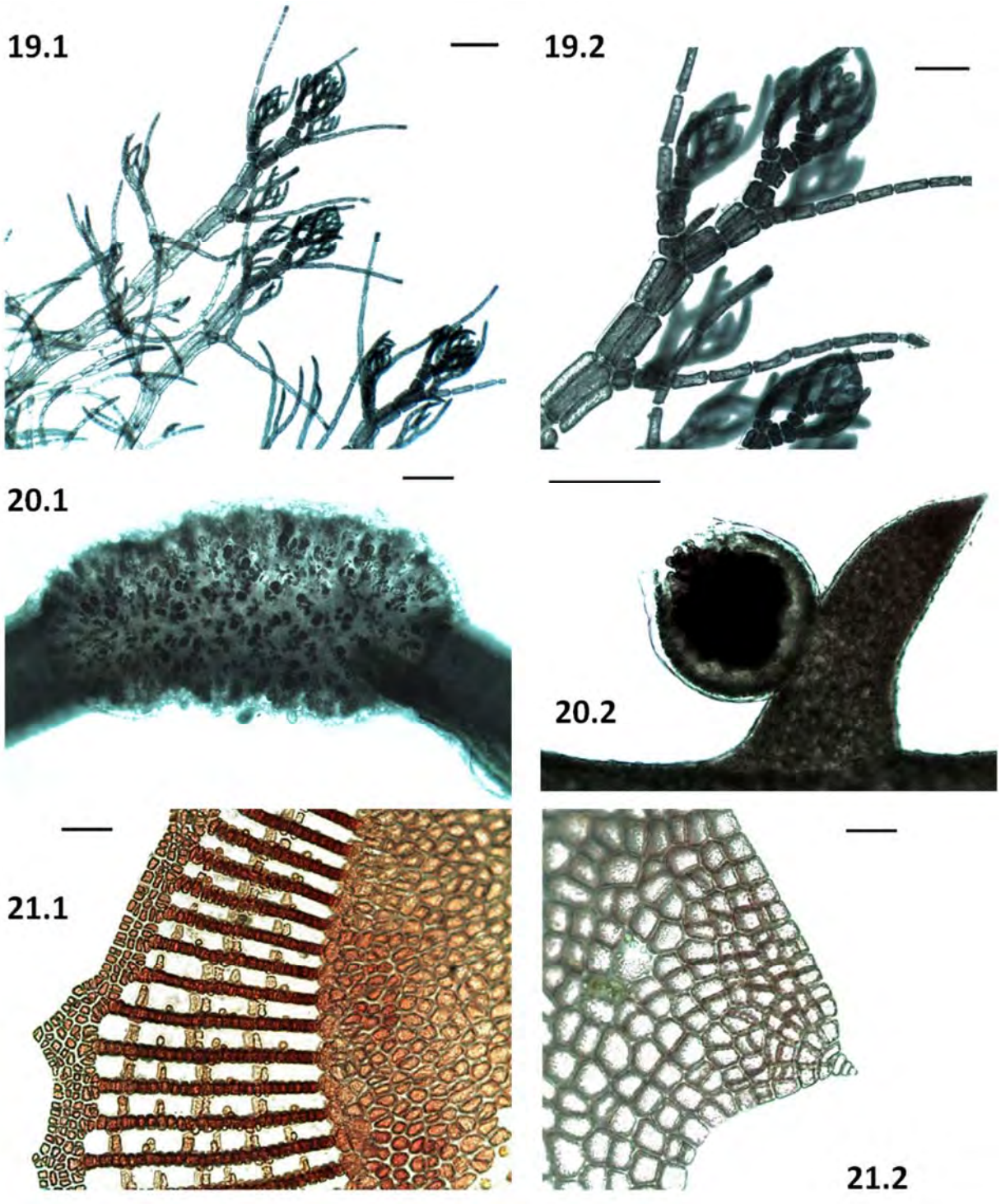


Fig. 15: *Gelidiella myriocladia* (Børgesen) Feldmann and G.Hamel (scale is 20 µm).

Figs. 16.1 and 16.2(XS): *Gelidiopsis variabilis* (Greville ex J.Agardh) F.Schmitz (scales are 100 µm and 50µm respectively).

Fig. 17: *Gloiocladia iyoensis* (Okamura) R.E.Norris (scale is 20 µm).

Figs. 18.1 and 18.2 (male): *Herposiphonia tenella* (C.Agardh) Ambronn (scales are 200 µm and 50µm respectively).



Figs. 19.1 and 19.2: *Heterosiphonia wurdemannii* (J.Bailey ex Harvey) Falkenberg (scales are 200 µm and 100µm respectively).

Figs. 20.1 and20.2: *Hypnea spinella* (C.Agardh) Kützing (scales are 100 µm and 200µm respectively).

Figs. 21.1 and 21.2: *Martensia elegans* Hering (scales are 100 µm and 50µm respectively).

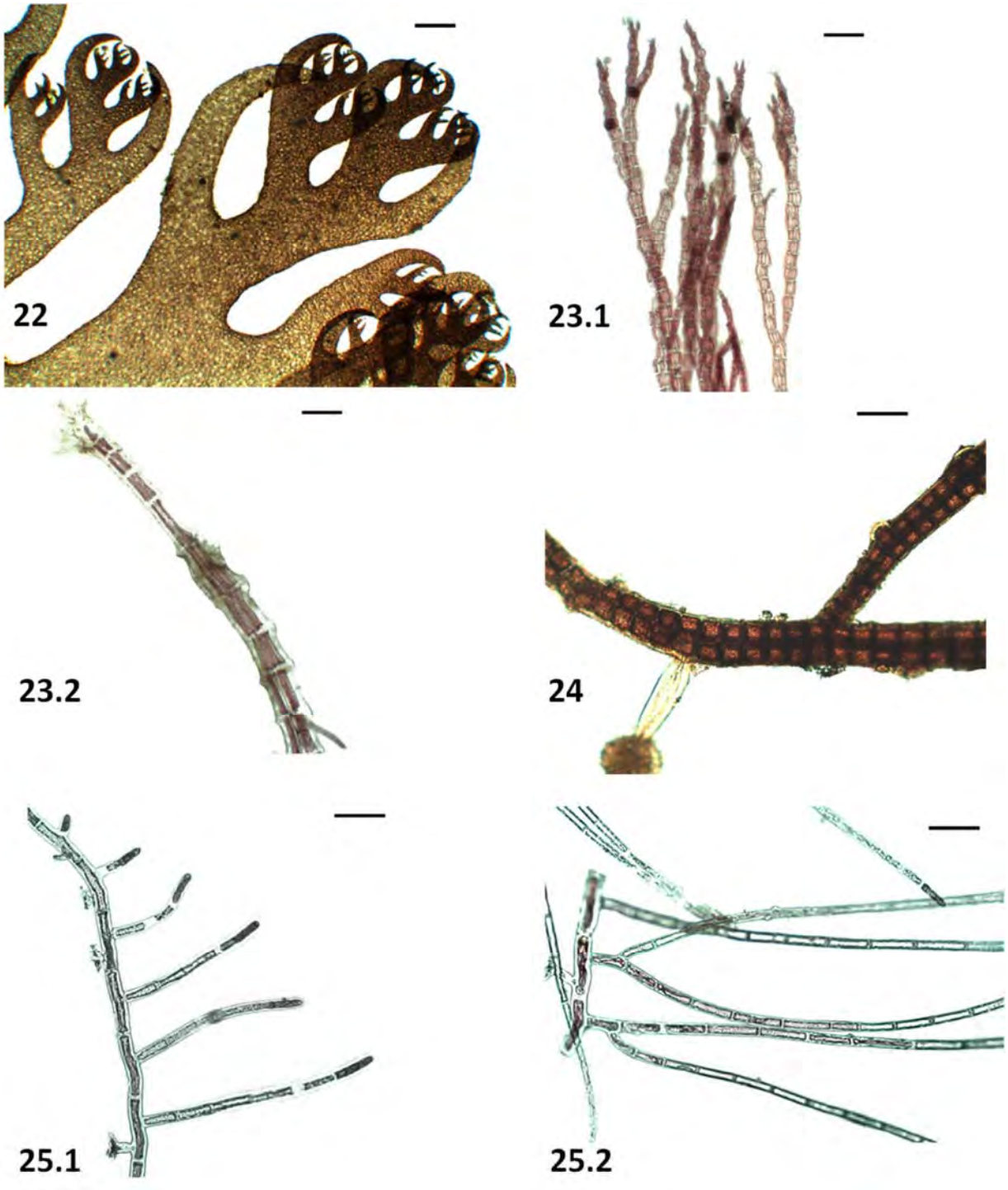
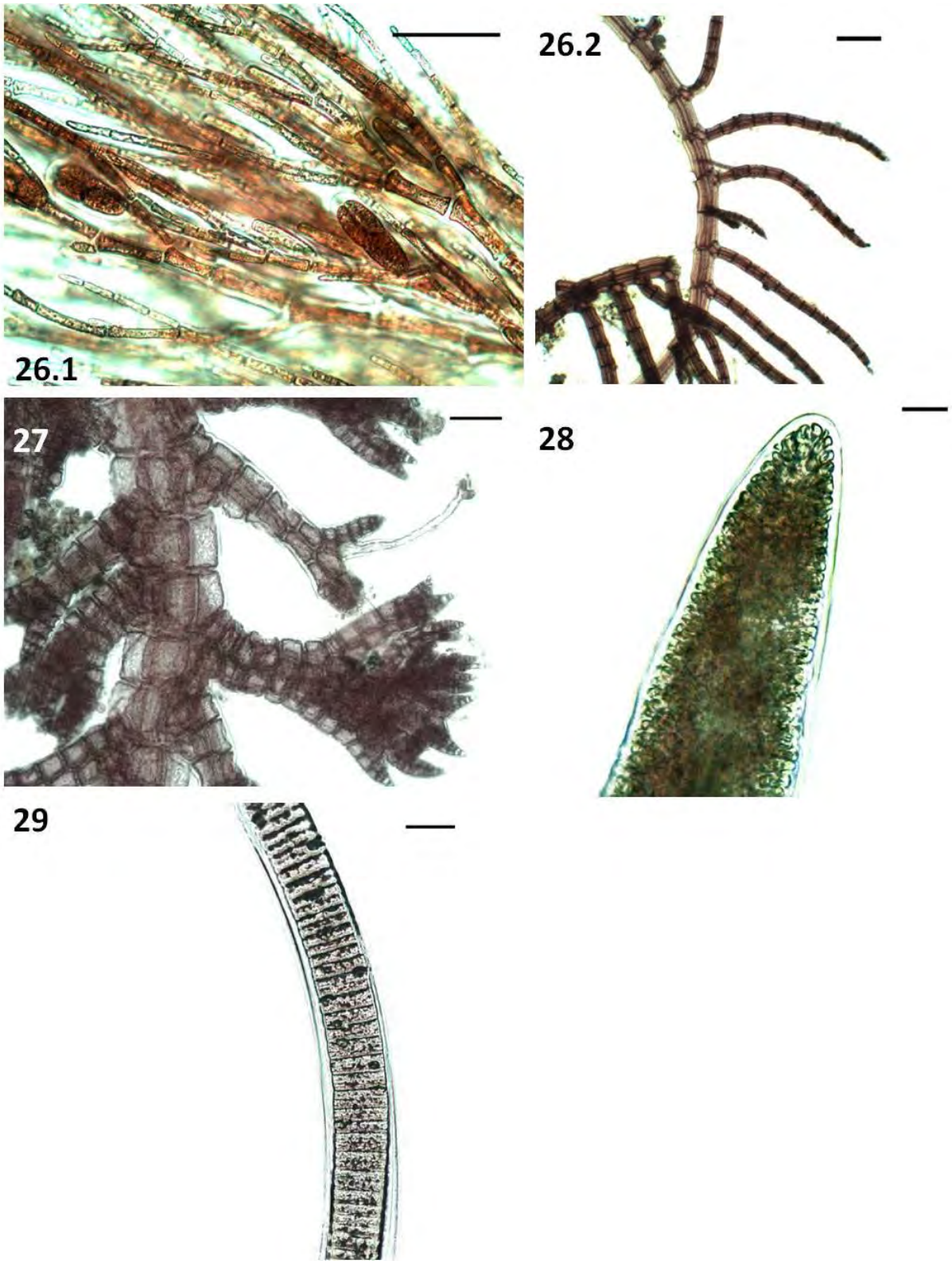


Fig. 22: *Plocamium beckeri* F.Schmitz ex Simons (scale is 200 µm).

Figs. 23.1 and 23.2: *Polysiphonia coacta* C.K.Tseng (scales are 200 µm).

Fig. 24: *Polysiphonia ferulacea* Suhr ex J.Agardh (scale is 100 µm).

Figs. 25.1 and 25.2: *Ptilothamnion cladophorae* (Yamada and T.Tanaka) G.Feldmann-Mazoyer (scales are 100 µm).



Figs. 26.1 and 26.2: *Tiffaniella* sp. (scales are 100 µm).

Fig. 27: *Tolypiocladia calodictyon* (Harvey ex Kützing) P.C.Silva (scale is 100 µm).

Fig. 28: *Wurdemannia miniata* (Sprengel) Feldmann and G.Hamel (scale is 20 µm).

Fig. 29: *Lyngbya* sp.