Sponge bioerosion and habitat degradation on Indonesian coral reefs

by

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Abstract

Coral reefs are among the most diverse ecosystems on the planet, yet they are also sensitive to anthropogenic disturbances that can degrade these systems. On many degraded reefs, large increases in bioeroding sponge abundance have occurred. On healthy reefs these sponges contribute to species diversity and habitat complexity, however there is growing concern that their proliferation on degraded reefs could lead to a state of net-erosion. In the Southeast Asian Indo-Pacific, the ecology of bioeroding sponges in relation to coral degradation has been poorly studied compared to other coral reef regions. This thesis aims to increase our understanding of the ecology of these sponges in the Wakatobi region of Indonesia, and their likely trajectory if reefs continue to degrade in the region.

My first research chapter aimed to identify the common bioeroding sponge species of the Wakatobi. This was achieved through in-water surveys, and subsequent spicule and phylogenetic analysis. This resulted in the identification of eight commonly occurring Wakatobi bioeroding sponge species, two of which are described for the first time. The assemblage composition was distinctly different from the only other bioeroding sponge study in Indonesian waters (Calcinai et al. 2005), highlighting the need for more clonaid taxonomic information from the region.

Having identified the common bioeroding sponge species in the region, my second chapter assessed the major environmental drivers of the abundance and assemblage composition of these sponges. Abundance surveys were conducted at 11 reef sites characterised by different environmental conditions and states of reef health. Bioeroding sponges occupied 8.9% of suitable substrate, and differences in abundance and assemblage composition were primarily attributed to differences in the availability of dead substrate. However, abundance was lowest at a sedimented and turbid reef, despite abundant dead substrate availability. This indicates a limited resilience in some species to conditions associated with terrestrial run-off and that not all forms of reef degradation are beneficial for bioeroding sponges. The capacity to increase spatial occupation of degraded reefs is also dependent upon larval recruitment and my third chapter was a two year recruitment study using *in situ* experimental calcareous blocks. Recruitment occurred rapidly and consistently with bioeroding sponges recruiting to approximately 70% of experimental blocks and exhibiting a preference for settlement on uncolonised dead calcareous substrates. The importance of substrate settlement cues and extent of larval dispersal appeared to

differ between species, indicative of different recruitment mechanisms. Any significant increase in the availability of exposed calcareous substrate (e.g. following a mass coral bleaching event) is therefore likely to result in widespread increases in bioeroding sponge recruitment.

Surveys conducted in my second research chapter revealed that two of the three locally abundant zooxanthellate bioeroding species were absent from a highly turbid reef, Sampela. My fourth research chapter investigated whether this was due to light limitation by examining the photoacclimatory capabilities of the *Symbiodinium* photosymbionts of *Cliona* aff. *viridis* n. sp. A. PAM chlorophyll fluorometry was employed in a 25 day shading experiment and *Symbiodinium* of *C. aff. viridis* n. sp. A demonstrated an ability to photoacclimate to extreme light reduction and recover quickly when conditions returned to normal. My results demonstrate that the absence of this species at Sampela is not due to light limitation but possibly due to other stressors associated with turbidity, e.g. suspended sediment.

My final chapter was an assessment of the environmental drivers of rates of bioerosion in *Spheciospongia* cf. *vagabunda*, a common species in the Wakatobi. Erosion rates were determined from changes in dry-weight of calcareous substrates with attached grafts of *S. cf. vagabunda* after a year deployment across seven reef sites. The average bioerosion rate was 12.0 kg m² sponge tissue yr⁻¹ ($\pm$ 0.87 SE), but differed between sites and was negatively correlated with settled sediment depth. Bioerosion by this species can play a significant part in the carbonate budget on reefs where it is abundant (up to 20% of available substrate on some reefs in the Wakatobi) but is likely reduced on highly sedimented reefs.

In summary, the Wakatobi bioeroding sponge assemblage is diverse and overall, both adult abundance and recruitment are primarily driven by the availability of dead calcareous substrates. Therefore, further coral mortality and a subsequent rise in the availability of dead substrate in the region is likely to result in increased abundance of bioeroding sponges. However, not all forms of reef degradation will benefit these sponges; turbid and sedimented reefs will likely constitute stressful habitats for some bioeroding sponge species and assemblages in these environments will be comprised of fewer more resilient species.

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Chapter contributions and chapter manuscripts

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Chapter 2

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Chapter 3

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Chapter 5

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Chapter 6

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Chapter 1: Introduction

1.1. Coral reefs

1.1.1. Diversity and importance

Coral reefs are among the most biodiverse and resilient ecosystems on earth; they are host to an estimated 600,000 to 9 million species and have persisted for over 240 million years (Small et al. 1998; Bouchet & Duarte 2006; Veron et al. 2009). They are the ubiquitous ecosystem in shallow tropical coastal environments across the globe and none more so than in the Indo-Pacific region, which harbours approximately 75% of the world's coral reefs (Roberts et al. 2002). This region is also home to the global centre of coral reef biodiversity, the Coral Triangle; this triangular area of tropical waters stretching from the Philippines in the north to Indonesia in the south and Papua New Guinea in the east, encompasses more species of corals, fish and other reef taxa than anywhere else on the planet (Briggs 2005; Veron et al. 2009). The benefits of healthy coral reefs extends far beyond merely the preservation of high levels of biodiversity and endemism, as coral reefs provide critical ecosystem goods and services for hundreds of millions of people (Moberg & Folke 1999). More than 275 million people live within 30 km of a coral reef (Burke et al. 2011) and due to the equatorial distribution of coral reefs a significant proportion of these people live in developing nations where dependence on reef fish as a protein source (and also income) is high. For many tropical countries, in addition to the financial income from fishing, coral reefs are vital source of income through tourism activities such as diving. The non-market use value of diving in Indonesia, Malaysia and Thailand alone has been valued at US\$4.5 billion a year (Pascoe et al. 2014). As physical structures, the ability of coral reefs to dissipate wave energy also provide coastal countries with coastal protection (Villanoy et al. 2012).

1.1.2. Threats and regime shifts

Despite the well-known benefits that are derived from healthy functioning coral reefs, reefs worldwide have suffered from substantial anthropological induced declines in coral cover, habitat complexity, fish abundance and biodiversity (Gardner et al. 2003; Bruno & Selig 2007; Burke et al. 2011). Human activities are negatively affecting coral reefs on a global scale; there are currently no reefs left on the planet that could be considered pristine; 19% of reefs have been lost permanently and 35% are at a high risk of being lost in the next 40 years (Wilkinson 2008).

It is unfortunate that the region with the highest biodiversity, the Indo-Pacific, is also highly threatened; the region has seen coral-cover declines of 20% since historical reference points (Bruno & Selig 2007) and 95% of reefs in the region are at risk from local threats (Burke et al. 2011). At the local scale reefs are over-fished, often with destructive fishing methods and dense coastal populations with poor coastal development management has led to increased watershed-based pollution, turbidity and sedimentation (Burke et al. 2011). On the global scale, anthropogenically introduced increases in atmospheric carbon dioxide are affecting reefs through two mechanisms – rising sea temperatures (global warming) and ocean acidification (Hoegh-Guldberg et al. 2007). Rising water temperatures are increasingly causing the disintegration of scleractinia coral/symbiont endosymbiosis (bleaching), which often leads to permanent coral mortality (Hoegh-Guldberg 1999; Donner et al. 2005), and can occur across large geographic areas (Goreau et al. 2000; Normile 2016). Ocean acidification and the consequent increased disassociation of carbonic acid reduces the availability of carbonate to calcium carbonate accreting organisms such as scleractinian corals and is predicted to result in decreased growth rates and skeletal density of these critical reef builders (Hoegh-Guldberg et al. 2007).

With the current and predicted declines in hard coral cover on tropical reefs, a lot of research has focused on those resilient benthic taxa that might benefit from increased substrate availability in what has traditionally been considered a spatially competitive system dominated by scleractinian corals. The majority of the literature has focused on shifts to macroalgal-dominated communities (e.g. Hughes 1994; Szmant 2002; McManus & Polsenberg 2004; Cheal et al. 2010) and shifts in the Caribbean (e.g. Hughes 1994; Mumby 2009). Despite region wide declines in coral cover in the Indo-Pacific (Bruno & Selig 2007), a subsequent shift to macroalgal dominance is not common; Bruno et al. (2009) found that amongst 963 sites across the Indo-Pacific region only 1% of sites were considered macroalgal-dominated (>50% cover) and that the regional average was 9-12% algal cover. Shifts to states dominated by other (non-algal) benthic taxa, have been reported to a lesser degree and help to highlight how other organisms may benefit from declines in coral cover. In their 2009 review, Norström et al. revealed a wide variety (taxonomically and geographically) of these incidences including soft corals (e.g. Fox et al. 2003; Stobart et al. 2005), corallimorphians (e.g. Kuguru et al. 2004; Loya 2004), ascidians (e.g. Bak et al. 1996) and sponges (e.g. Aronson et al. 2002; Rützler 2002a; Ward-Paige et al. 2005). Interestingly, the majority of literature on increases in sponge abundance on degraded reefs has shown increases of

bioeroding sponges of the Clionaidae family (e.g. Ward-Paige et al. 2005; Schönberg & Ortiz 2009; Carballo et al. 2013).

1.2. Sponges on coral reefs

Sponges are ancient organisms that have existed on reefs for millennia. During the Upper Carboniferous period (~ 310 MYA) they were the major frame-building organisms on reefs (West 1988), and were responsible for other significant reef building events throughout the geological record (Brunton & Dixon 1994; Wood 1999; Bell et al. 2013). The persistence of this group for over 500 million years has resulted in wide diversification of species and today sponges are among the most prominent groups of taxa on coral reefs with species diversity that equals and often exceeds that of corals in the same region. For example, over 420 species of sponges have been recorded from Indonesia and it is thought that there is probably up to 830 species (van Soest 1989; 1994) whereas the highest number of coral species recorded in the Indonesia (and the world) is 456 (McKenna et al. 2002). Similarly sponge abundance is often exceedingly high, occupying up to 24% of substrate on some Caribbean reefs (Diaz & Rützler 2001) and up to 30% on some Indo-Pacific reefs (Bell & Smith 2004).

Sponges are not only species diverse, but also functionally diverse and are a critical functional component of modern coral reefs. As obligate filter feeders, all sponges must pump water through their tissues in order to obtain food and nutrients, which can result in extremely high volumes of water exchange, for example *Verongia lacunosa* can pump up to 6l/h per 500 ml volume of sponge (Gerrodette & Flechsig 1979). By removing carbon, nitrogen and other nutrients from the water column, sponges are a significant link between the pelagic environment and the benthos. The transfer of this dissolved organic matter to higher trophic levels can take place through activities such as predation (Wulff 2006) or by rapidly recycling and expelling filter cells as detritus. It has been hypothesised that this “sponge-loop” is critical for the existence of coral reef in oligotrophic seas (de Goeij et al. 2013). Sponges can also contain very high densities of photosynthetically active organisms such as cyanobacteria or the dinoflagellate *Symbiodinium* (Rützler 1990) and are important contributors to reef primary production (Wilkinson 1987).

It is sponge impacts on the substrate that probably constitutes their most important functional roles on tropical reefs. These functional roles can be broadly broken down into the coral-accretion facilitating processes (consolidation and stabilisation) and the destructive process of bioerosion. In the Caribbean (Wulff 1984; 2001) some sponges are able to bind coral rubble together after disturbance events, which in turn creates a more stable platform for successive coral settlement (Biggs 2013). The antagonistic process to stabilisation and consolidation is bioerosion, where sponges are often the dominant agents of on coral reefs (Risk et al. 1995).

1.3. Reef bioerosion

Bioerosion is biological mediated erosion (rather than physical or due to oceanic chemistry) and on reefs includes any of the activities that cause the erosion or weakening of calcareous structures by a reef species (Neumann 1966). Bioerosion is the primary source of erosion on coral reefs as physical erosion is temporary and localised (e.g. storms and hurricanes) and chemical erosion is negligible due to the composition of ocean chemistry (Scoffin et al. 1980; Tribollet & Golubic 2011). Bioerosion plays an important role in producing reef sediments (Hutchings 1986), in increasing reef biodiversity by creating microhabitats (Hutchings 1986; Moran & Reaka 1988) and in reef biochemistry by recycling dissolved Ca^{2+} and C (Tribollet & Golubic 2011). As the primary source of erosion on coral reefs, bioerosion is the key antagonistic process to calcium carbonate accretion by scleractinian corals and coralline algae, and hence an integral part of the reef carbonate budget. Coral reefs must maintain a positive balance between calcification and erosion if net reef growth is to occur (Glynn 1997; Perry et al. 2008) although this carbonate budget is often evenly balanced (Scoffin et al. 1980; Glynn 1988).

The organisms that are responsible for bioerosion are termed bioeroders and are comprised of a diverse range of taxa. These organisms can be broadly divided into two groups: 1) external bioeroders, which graze on benthic organisms and consequently abrade the substrate: and 2) internal bioeroders, which excavate carbonate substrates for shelter or nutritional purposes (Tribollet & Golubic 2011). External bioeroders are a diverse group and range from small gastropods such as limpets (Radtko & Campion-Alsumard 1996) to echinoderms (Herrera-Escalante et al. 2005) and large fish species, such as *Bolbometopon muricatum*, (Bellwood et al. 2003). Internal bioeroders can be classed as either microborers (<100 μm) or macroborers (>100 μm) and are present in both live and dead carbonate substrates (Tribollet & Golubic 2011).

Microborers are either organotrophic (e.g. fungi and foraminifera) or phototrophic (e.g. prokaryotic cyanobacteria and eukaryotic chlorophytes) microorganisms and penetrate carbonate substrates by dissolution (Tribollet 2008; Tribollet & Golubic 2011). Macroborers are also a diverse group ranging from bryozoans (e.g. Smyth 1988) to polychaetes (e.g. Wielgus et al. 2006) and sponges (e.g. Rützler 2002b).

The extent to which these different bioeroders contribute towards bioerosion on different reefs is dependent on a range of biotic and abiotic conditions, including eutrophication (Sammarco & Risk 1990; Risk et al. 1995; Tribollet & Golubic 2005), grazing pressure (Golubic & Schneider 1979; Kiene & Hutchings 1994), substrate exposure time (Tribollet & Golubic 2005; Kiene & Hutchings 1994) and light availability (Magnusson et al. 2007). Whilst the complement of bioeroders may differ with environmental and abiotic conditions, the majority of internal coral reef bioerosion is consistently attributed to demosponges, which frequently represent 60 to 90% of macroborer activity (Risk et al. 1995).

1.4. Bioeroding sponges

1.4.1. Taxonomy and morphology

Bioeroding sponges have been found in the geological record for a very long time, they were first documented in the lower Cambrian (~525 MYA) (Kobluk & Risk 1977) and with time increased in abundance in diversity so that by the Devonian (~420 MYA) many were very similar to modern representatives (Wilson 2007). Today there are over 200 described and accepted bioeroding sponge species from around the world, the majority of which belong to eight genera within the Clionaidae Family (Rützler 2002b), although they are not all restricted to this family or even the Hadromerida order (Rosell & Uriz 1997).

Bioeroding sponges are unique amongst Porifera due to their endolithic life histories, the degree of which can vary and has been categorised as either papillate α -form, encrusting β -form or free-living Y-form. The α -form is proportionally the most endolithic, with the majority of the sponge occupying the interior of the substrate and only separate inhalent ostial and exhalent oscular papillae penetrating the substrate surface. The β -form is encrusting, with a continuous tissue covering at the surface and an even penetration of the substrate below. The Y-form is restricted to a few species (e.g. *Cliona celata*) and is entirely free living. These growth forms have

previously been described as growth “phases”, primarily due to the presence of all three stages in *C. celata* in the Atlantic (Xavier et al. 2010) and the postulation that this might also occur for some species within the *Cliona viridis* complex (Rosell & Uriz 1991). Whilst Xavier et al. (2010) used phylogenetic reconstructions of mitochondrial and nuclear gene fragments to prove that this is indeed the case for *C. celata*, the case is not so clear for other species as often not all growth forms can be found in all habitats (e.g. Schönberg 2000a) and most bioeroding sponge species retain the α -form (e.g. Hartman 1958).

Identification of species is primarily achieved through spicule analysis; comparisons of the size, shape and composition of the microscopic siliceous spicules that constitute the sponge skeleton (e.g. Schönberg 2000a; Rosell & Uriz 2002; Calcinaï et al. 2005). In the Clionidae identification focuses on megascleres which are predominately composed of tylostyles, but may include oxeas and microscleres which, where present, include spirasters, amphiasters, microxeas, microrhabds, or raphides (Rützler 2002b). Spicule analysis has its drawbacks; spicule morphology can vary depending on environmental conditions, resulting in intraspecific variation that can outweigh interspecific variation in some closely related species (Rosell & Uriz 1991; Bavestrello et al. 1993). Although molecular tools have only been applied in a handful of studies, phylogenetics is increasingly being incorporated into identification publications (e.g. Barucca et al. 2007; Escobar et al. 2012; Leal et al. 2016). Unfortunately there has been little overlap in terms of the regions of DNA used in the respective studies and consequently new studies are limited in their phylogenetic comparisons.

1.4.2. *Sponge bioerosion*

The reason these sponges have evolved to become obligate endoliths has been widely debated; bioerosion is metabolically costly activity and the benefits are not entirely understood. Ward & Risk (1977) proposed that sponges may obtain some nutritional benefit from the eroded substrate, however Schönberg & Wisshak (2012) point out that the sponges are efficient filter feeders and those of the *C. viridis* complex harbour symbiotic dinoflagellate zooxanthellae (Sammarco et al. 1987; Schönberg 2002), which would also compliment their energy intake. Other authors have hypothesised that an endolithic habitat provides a better refuge from grazers and predators (e.g. González-Rivero et al. 2011), which would support observations that these sponges have far lower spicule:tissue ratios than free living sponges (Schönberg & Wisshak

2012). An endolithic habitat may also allow the sponges to grow whilst minimizing competition with other benthic taxa, however many encrusting clionoids are extremely efficient spatial competitors (Rützler 2002b).

The process by which bioeroding sponges excavate the substrate is both mechanical and chemical and still not fully understood. The chemical component of erosion is accomplished by specialised etching cells that chemically carve out small chips (15-100 μm diameter), which are then mechanically transported out of the sponge through the aquiferous system (Cobb 1969; Rützler & Rieger 1973; Pomponi 1980). Several etching cells are involved in etching out each chip, combining to produce a web of filopods that form a basket around the chip (Rützler & Rieger 1973). The exact chemical agent that is used to remove the chips remains elusive; Cobb (1969) reasoned that the process of dissolving calcium carbonate would necessarily involve acid and an additional enzyme but few studies have made progress beyond this hypothesis. Pomponi (1980) demonstrated that carbonic anhydrase activity was associated with etching cells. Sullivan & Faulkner (1990) described a calcium chelator pathway in *Aka coralliphaga* in which the chelator molecule releases H^+ at the sponge-substrate interface and receives calcium ions in return. Schönberg (2008) used microsensors to measure pH and calcium concentrations within *C. celata* and found weak evidence that acid plays a role in chemical bioerosion. By measuring the width of sponge chips, Rützler and Rieger (1973) gauged the chemical component to be 2-3% and the mechanical component 97-98%. However, more recent studies suggest that chemical dissolution is a greater contributor than previously thought. Zundelovich et al. (2007) determined the chemical boring rates in *Pione vastifica* by measuring the changes in total alkalinity in sponge-containing chambers and concluded that 75% of erosion in *P. vastifica* was due to chemical dissolution. This same methodology was used by Nava and Carballo (2008) who also concluded that the amount of erosion due to chemical dissolution in *Cliona vermifera* and *Cliona flavifodina* was significant (27 and 10.2%, respectively).

Rates of erosion are often measured in terms of mass of calcium carbonate per m^2 of sponge tissue per year and can vary significantly between species e.g. 0.34 $\text{kg m}^{-2} \text{ sponge yr}^{-1}$ for *P. vastifica* and 23.8 $\text{kg m}^{-2} \text{ sponge yr}^{-1}$ for *Cliona orientalis* (Schönberg 2002; Zundelovich et al. 2007). However, this variability has to be considered in the context of the wide range of factors that can affect sponge erosion rates, which are not always controlled for in studies. Most studies

that evaluate the influence of abiotic and environmental factors on sponge erosion do so by inferring differences in bioerosion rates from differences in *in situ* measurements of abundance and sponge size (e.g. Holmes et al. 2000). Due to the long experimental time periods required, fewer studies actually directly measure *in situ* rates of bioerosion in specific species. This is normally achieved by deploying experimental calcareous substrates with attached grafts of the target species and the additional deployment of control substrates (e.g. Holmes et al. 2009). Bioerosion rates are measured in terms of substrate weight loss over the period of the deployment and standardized using the control substrates to any other forms of weight change due to calcification or grazing etc.

One of the most studied variables to effect sponge erosion rates is differences in mineralogy and substrate density (e.g. Rose & Risk 1985; Sammarco et al. 1987; Edinger & Risk 1996; Schönberg 2002). Numerous studies have shown that erosion rates increase with substrate density (e.g. Neumann 1966; Schönberg 2002; Calcinai et al. 2008); it is proposed that sponges first occupy any porous material before beginning excavation, hence the lower erosion rates in less dense porous substrates (Schönberg 2002; Calcinai et al. 2008).

As filter feeders any mechanism that provides these sponges with increased food availability is also likely to result in increases in bioerosion rates. Most studies addressing this link have either focused on the relationship between erosion rates with eutrophication or with currents that deliver suspended matter (e.g. Hallock 1998). Numerous studies have demonstrated that sponge bioerosion rates correlate with natural or anthropogenic eutrophication gradients (e.g. Rose & Risk 1985; Carballo et al. 1996; Ward-Paige et al. 2005; López-Victoria & Zea 2005). For example, Holmes et al. (2000) found sponge bioerosion to be significantly higher on polluted reefs than control reefs in Indonesia, with the most dramatic differences occurring on Javan reefs with high concentrations of chlorophyll α .

Sponges of the *C. viridis* complex harbour photosynthetic *Symbiodinium* symbionts that have been shown to enhance sponge bioerosion. Schönberg (2006) demonstrated that *C. orientalis* was able to erode through experimental substrate blocks 4.5 to 11 times faster in ambient light than when shaded and Hill (1996) found that *Cliona varians* erosion rates were 50% higher under ambient conditions than when shaded. However, not all species appear to rely as heavily on their

symbionts as Zundeleovich et al. (2007) found that the rates of chemical erosion by *P. vastifica* were constant during a diurnal cycle.

Recent research has focused on the effects of climate change on sponge erosion rates. It is believed that as a result of projected increases in atmospheric carbon dioxide, ocean acidification will facilitate bioerosion by weakening existing carbonate structures and reducing any pH gradient that needs to be overcome to enable chemical erosion (Duckworth & Peterson 2013; Fang et al. 2013; Wisshak et al. 2012; 2013; Stubler et al. 2014). Experimental manipulations of $p\text{CO}_2$ and temperature with various sponge species have shown that increasing $p\text{CO}_2$ amplifies a sponges bioerosion capacity but increasing temperature can have neutral to negative effects. Stubler et al. (2014) observed significant increases in the erosion efficiency of *C. varians* and *Pione furcata* when treated under $p\text{CO}_2$ conditions replicating an end of the century scenario (SRES A2 scenario (IPCC 2007)). Increases in temperature do not have the same effect. Wisshak et al. (2013) found a 17% increase in bioerosion rates of *C. orientalis* at moderately elevated levels of $p\text{CO}_2$ and a 61% increase at strongly elevated levels but bioerosion rates actually slightly dropped at elevated temperatures.

1.4.3. Symbiodinium

Amongst Porifera, a significant number of bioeroding sponge species have associations with dinoflagellate *Symbiodinium*, the “zooxanthellae” that are usually associated with Cnidarian hosts. This association was first observed in *C. viridis* (Sarà & Liaci 1964), but has since been observed in many other clionaid species (Schönberg 2000b; Schönberg & Loh 2005; Calcinaï et al. 2005; Granados et al. 2008; Cruz-Barraza et al. 2011; Zea & López-Victoria 2016), which appear to be closely related and are grouped together in the *C. viridis* species complex (Rosell & Uriz 1991, Schönberg 2000b). Similar to Cnidarian hosts, it is believed the members of the complex receive nutrients from the symbionts in the form of photosynthates (Rosell & Uriz 1992; Hill 1996; Weisz et al. 2010) or by direct ingestion of the symbionts themselves (Sarà 1971). The benefits to the host have been observed in shading experiments where lateral growth and bioerosion rates were greater in ambient light conditions than shaded for *C. orientalis* (Schönberg 2006) and *C. varians* (Hill 1996). Members of this complex are also among the most efficient spatial competitors, often living adjacent to live coral colonies, some of which they are capable of overgrowing and eventually killing (Hill 1999; Schönberg & Wilkinson 2001). The

symbiotic relationship appears to be mutualistic with the symbionts receiving shelter from environmental stressors and predation (Schönberg & Wilkinson 2001). However, it has been suggested that the nature of this relationship is flexible and under extreme light-limited conditions, *Symbiodinium* could survive through parasitism of the host sponge (Fang et al. 2017a). The three-dimensional nature of sponges also means that the symbionts are less susceptible to heat and light stress than in corals as the host is able to auto-shade them within deeper tissue layers. Evidence suggests that this shading effect might not be just passive. Schönberg & Suwa (2007) observed a shifting of zooxanthellae to deeper tissues in *C. orientalis* after exposure to light stress, suggesting that the species is capable of mitigating potential bleaching events. This evidence supports observations that bleaching rarely occurs in *C. viridis* spp., even during disturbance events that have caused large scale bleaching in corals (Vicente 1990; Hill & Wilcox 1998). However, recent evidence from the Caribbean demonstrates that elevated water temperature can cause large-scale bleaching in these sponges (Hill et al. 2016). Three studies have used phylogenetics to identify the *Symbiodinium* associated with *C. viridis* spp. (Schönberg & Loh 2005; Granados et al. 2008; Hill et al. 2011). Identification of *Symbiodinium* is based upon lineages (Clades A-H) and to date symbionts of clades A,B,C and G have been detected in associations with clionaid sponges. The Clade G *Symbiodinium* found in many clionaid sponges appear to be from a sponge-specialist G2 sub-clade (Hill et al. 2011), which is evolutionary much older than many common Cnidarian associated clades (Pochon et al. 2006) and is believed to be more tolerant to external stressors. The mechanism of acquisition and transmission of symbionts is not still fully understood. Mariani et al. (2000; 2001) observed vertical transmission (i.e. via gametes) in *C. viridis* in the Mediterranean and Schönberg & Loh (2005) concluded the same type of transmission was occurring in *C. orientalis* in the Great Barrier Reef (GBR). However, the observation of different clade associations within different individuals of the same species of *Cliona laticavicola*, *Cliona aprica* and *Cliona caribbaea* (Granados et al. 2008) suggest that horizontal transmission (environmentally acquired) is also possible.

Currently there is very little information on the ability of *Symbiodinium* hosting sponges to photoacclimate to naturally or anthropogenically induced changes in light availability. Photoacclimation is the process by which either the photosymbiont or the host or both (the holobiont) change their photophysiological apparatus in order to maintain photosynthetic

efficiency with changing light availability. In scleractinian corals this has been studied extensively and a high photoacclimatory capacity allows certain coral species to thrive in highly turbid conditions or occupy a broad depth range (e.g. Anthony & Fabricius 2000; Hennige et al. 2010). The confinement of some zooxanthellate bioeroding sponge species to certain depth categories (e.g. López-Victoria & Zea 2005) suggests that potentially these species are unable to photoacclimate to less ideal light conditions. However the only *in situ* study for bioeroding sponges (Steindler et al. 2001) found that the usually deep and cryptic sponge, *P. vastifica*, was capable of photoacclimating to conditions of significantly increased light availability, suggesting that its depth preference is not a function of light availability. The effects of extreme reductions in light availability have been investigated in *ex situ* experiments on *C. orientalis*; prolonged exposure to complete darkness, caused a marked reduction in *Symbiodinium* density, maximum quantum yield and no change in heterotrophic uptake (Pineda et al. 2016; Fang et al. 2017a). Nevertheless, recovery was observed in sponges when ambient light conditions returned (Pineda et al. 2016)

1.5. Bioeroding sponge abundance & distribution

1.5.1. Reproductive output & recruitment

Sponges are capable of sexual and asexual reproduction. Sexual reproduction can be either gonochoristic or hermaphroditic and either oviparous or viviparous (Maldonado & Riesgo 2008) and all these strategies have been observed in bioeroding sponges (e.g. Mariani et al. 2000; Maldonado & Riesgo 2008; Piscitelli et al. 2011; González-Rivero et al. 2013; Bautista-Guerrero et al. 2014) although the majority of clonoid species are oviparous and gonochoristic. Gametogenesis is usually environmentally dependent and correlates with changes in water temperature; in most species (both temperate and tropical) oogenesis and fertilization occur during the warmer summer months (Mariani et al. 2000; Piscitelli et al. 2011; Bautista-Guerrero et al. 2014) although in the Caribbean species *Cliona tenuis* and *C. caribbaea*, reproduction is during the cooler winter months (Rützler 1974; González-Rivero et al. 2013). In tropical species, the reproduction appears to be iteroparous where the reproductive period often encompasses multiple pulses of reproductive output (González-Rivero et al. 2013; Bautista-Guerrero et al. 2014). As these sponges are not brooders, a lot of energy is invested in mass production of eggs

(Piscitelli et al. 2011). Once the gametes are released, fertilization and embryogenesis of the negatively buoyant eggs usually occurs on the substrate (Maldonado 2006) and larval settlement occurs within days (Nassonov 1883; Mariani et al. 2001). In general sponge larvae are poor swimmers but clionaid larvae appear to be particularly poor; *C. viridis* displays crawling rather than swimming behaviour and as a result dispersal distance is extremely low (Mariani et al. 2000). Generally sponge population maintenance (not specifically bioeroders) is dependent upon sexual reproduction but asexual reproduction through gemmulation, budding or fragmentation can also play an important role (Maldonado & Riesgo 2008). Transplantation experiments with *C. tenuis* and *C. orientalis* have shown that stable fragments of bioeroding sponges and sponge-bearing-rubble are able to colonise adjacent substrate and hard coral with very high rates of survival (Schönberg & Wilkinson 2001; López-Victoria & Zea 2004).

1.5.2. Adult distribution

Like any sessile benthic organism, the availability of suitable substrate for colonisation and growth is an important driving factor for bioeroding sponge abundance. This appears to be especially important for bioeroding sponges due to their obligate endolithic life history and inability to occupy non-calcareous substrates. Recent work by Schönberg (2015a) has found that the most important determinant of bioeroding sponge abundance in the GBR is the availability of suitable substrate and suggests that abundance monitoring should be standardised for substrate availability. Similar results were found at the Columbian island of Islas del Rosario in the Caribbean (López-Victoria & Zea 2005), where *C. aprica*, *C. caribbaea* and *C. tenuis* were most abundant at sites with the greater availability of calcareous rock. The substratum occupation/availability ratios of these sponges were more positively associated with recently dead coral skeletons than older incrustated substratum. This tendency towards preferential establishments on “cleaner” substrates would explain observed increases in bioeroding sponge abundance following bleaching events e.g. an 81% increase in the Indian Ocean following the 1998 El Nino event (Sheppard et al. 2002) and up to 150% increase after two bleaching events in the GBR (Schönberg & Ortiz 2009). Substrate preference is species-specific and not all bioeroding sponge species show a preference for recently dead coral skeletons. Carballo et al. (2008a) found that in the Mexican Pacific, *C. vermifera* and *Cliona mucronata* showed a preference for coral rubble whilst *Aka cryptica* and *Cliothosa hancocki* were commonly found in

the vicinity of living coral. Substrate complexity can also be a limiting factor for the abundance of these species; in the same study at Islas de Rosario, López-Victoria & Zea (2005) found that on reefs with high rugosity, the sponges were unable to spread laterally and therefore smaller in size than on the low relief reef terraces.

Whilst substrate availability is a crucial driver of bioeroding sponge abundance it may not always be the most important factor. Nava et al. (2014) found that on the Mexican Pacific coast, the preferred substrate type for bioeroding sponges was dead coral framework and coral rubble, but sites with the highest coverage of these substrates did not necessarily have highest sponge abundance. The highest abundances and diversity were actually found on reefs closest to tourist developments where the highest concentrations of $\delta^{15}\text{N}$, $\delta^{13}\text{C}$ and chlorophyll existed, but not the highest substrate availability. Similar abundance patterns have been observed in the Caribbean where Ward-Paige et al. (2005) found the highest abundances of sponges at sites with the highest levels of total nitrogen, ammonium and $\delta^{15}\text{N}$. This relationship between abundance and eutrophication is due to the exact same mechanism, which results in higher erosion rates in these environments – increased food availability. However, the indirect effects of high nutrient input can also limit sponge abundance; an assessment of the abundance of *Cliona delitrix* and *Cliona lampa* along the Florida Reef Tract by Chaves-Fonnegra et al. (2007) found that the abundance of *C. delitrix* increased with proximity to sewage sources on a reef in the Colombian Caribbean, but dropped off adjacent to the sewage outlet presumably due to excessive sedimentation and turbidity. Nava and Carballo (2013) came to a similar conclusion when they found no relationship between the distribution of boring sponge assemblages and chlorophyll α concentrations on Pacific Mexican reefs.

Sedimentation can be another important regulator of bioeroding sponge abundance and there are large inter-specific differences in sedimentation tolerance. Some species, such as *Siphonodictyon mucosum*, have adapted to live in highly sedimented habitats; on the GBR *S. mucosum* is often found buried beneath sediment with only fistules protruding into the water column (Schönberg 2000a). Other important bioeroding sponge species such as *C. celata* and *C. viridis* have been shown to withstand very high sedimentation rates (Muricy 1991; Carballo et al. 1994) and this tolerance has allowed them to dominate some highly impacted sites (Carballo et al. 1996). However, many species are not so resilient to the adverse effects of sedimentation (smothering,

turbidity, abrasion and clogging). Another study, also in the Mexican Pacific, found sediment disposition and water movement negatively correlated with bioeroding sponge abundance (Nava & Carballo 2013). The combined effect of high water flow and high sediment loads is thought to limit sponge abundance through either clogging or abrasion (Nava & Carballo 2013) or possibly through prevention of larval settlement (Bell & Barnes 2000). Other studies have found similar negative impacts; an assessment of the bioeroding community in Discovery Bay, Jamaica, by Macdonald and Perry (2003) found that the community structure shifted from being dominated by sponges at clear water sites to being dominated by worms and bivalves and highly sedimented sites.

For those zooxanthellate species that comprise the *C. viridis* species complex, light availability appears to play an important role in determining their distribution. Light availability may be influenced by depth, turbidity and reef complexity (and interactions among these factors) and influence different species in different ways. For example in the Columbian Caribbean, three species in the *C. viridis* complex, *C. aprica*, *C. caribbaea* and *C. tenuis*, are all most abundant on well-lit surfaces, but restricted to different depth categories (López-Victoria & Zea 2005). This depth distribution could be related to different tolerances for wave exposure but could also be a reflection of different photosynthetic requirements for each species. The zooxanthellate *C. orientalis* is most abundant in the very shallow waters just below the low tide mark around the Orpheus Island in the GBR (Schönberg 2001), however at Davies Reef (also in the GBR) the same species is most abundant between 3 and 8 m depth (Bergman 1983). This difference in distribution is attributed to the higher turbidity levels at Orpheus Island, forcing the sponge to seek shallower more optimal light conditions (Schönberg 2001). However as discussed earlier, the distribution of photosynthetic bioeroding sponges isn't always dependent upon light availability. When Steindler et al. (2001) showed that *P. vastifica* could photoacclimate to light levels far higher than in its natural habitat, the authors concluded that the distribution of *P. vastifica* was likely driven by factors controlling larval settlement or competition rather than photosynthetic requirements.

1.5.3. Competition

Space is at a premium on coral reefs; suitable substrata is a limiting resource for the settlement, growth and reproduction of benthic organisms and competition is a major process that can govern distribution of abundance and diversity (Connell et al. 2004; Foster et al. 2008; Chadwick & Morrow 2011). The competitive abilities of bioeroding sponges are therefore an important biotic factor that can regulate the distribution of these organisms independently of environmental conditions. Reef sponges are important spatial competitors and are able to outcompete adjacent sessile invertebrates through a variety of means from physical overgrowth to producing an array of allelopathic chemicals (Porter & Targett 1988; Aerts & van Soest 1997; de Voogd et al. 2004). Encrusting bioeroding sponges (β form) are particularly aggressive spatial competitors. Their ability to erode the substrate beneath adjacent coral competitors allows them to avoid many of their defensive mechanisms and eventually displace it (Rützler 2002a; López-Victoria et al. 2003). Erosion beneath the coral polyps is accomplished by pioneering excavating tissue filaments, which precede the front of the sponge tissue (Schönberg & Wilkinson 2001; López-Victoria et al. 2003). This competitiveness allows species such as *C. caribbaea* to advance at rates of up to 9.2 cm yr⁻¹ into adjacent corals (Acker & Risk 1984) and form large encrusting sheets (e.g. Calcinaï et al. 2005; López-Victoria & Zea 2005). Of course the outcome in any competitive interaction is also jointly determined by the competitive abilities of the sponges neighbor, Vicente (1978) found that *C. varians* on Puerto Rican reefs was competitively superior to 13 coral species but was unable to overgrow *Mycetophyllia lamarckiana*, one of the most aggressive Caribbean coral species (Lang 1973). Fang et al. (2017b) found similar competitive dominance by the *Porites* over *C. orientalis* using an *ex situ* experiment with sponge and coral cores. Competitive interactions are not limited to scleractinian corals, in the Caribbean there have been large increases in macroalgae abundance which are significant spatial competitors for bioeroding sponges. González-Rivero et al. (2011) found that the macroalgae *Lobophora variegata* was able to outcompete *C. tenuis* through a combination of allelopathy and physical shading.

1.6. The Wakatobi

The Wakatobi Marine National Park (Wakatobi) in south-east Sulawesi, Indonesia, is an area of 1.4 million hectares encompassing the four major islands of the Tukang Besi Archipelago and the surrounding waters. It was gazetted a marine park in 1996 and a UNESCO Biosphere Reserve in 2012 due to its extremely high marine biodiversity; over 390 species of coral and 590 species of fish (Pet-Soede & Erdmann 2003). The park is the third largest in Indonesia and while it includes approximately 50,000 hectares of coral reefs (Clifton et al. 2010), it is also home to over 90,000 local people who depend heavily on the local reefs for their protein intake and income (Cullen et al. 2007). The combination of heavy local reliance on the reefs, a history of poor resource management in the park (Cullen 2010) and regional/global stressors has resulted in declines in coral cover and fish abundance (Curtis-Quick 2013). As reef degradation within the Wakatobi is patchy (Powell et al. 2010), it represents a microcosm of the Southeast Asian Indo-Pacific region; some reefs are severely degraded while others have been less influenced by anthropogenic disturbance, and some are in near pristine condition. A classic example of a degraded reef is the fringing reef adjacent to the Bajo village of Sampela off the island of Kaledupa (Figure 1.1); the reef is heavily overfished, has experienced an 83% reduction in coral cover to below 10% in the last decade (Curtis-Quick 2013) and sedimentation levels are approximately four times higher than neighbouring reefs (Crabbe & Smith 2005). The sediment is comprised of fine particles, which settle on the substrate, smothering benthic organisms, but also acts in suspension to dramatically increase turbidity (Crabbe & Smith 2005). Healthier sites include an exposed part of the Hoga fringing reef called “Ridge 1”, which has experienced a 51% decline in coral cover over the last decade and currently still has over 25% cover (Curtis-Quick 2013; Fig 1.1). Some reefs around the lesser populated islands such as Tomia appear to be in near pristine condition with greater than 65% coral cover (J. Marlow pers obs.) which is comparative with historical baselines for the region (Bruno & Selig 2007).

Figure 1.1. Map of the main study sites within the Wakatobi. Sites Buoy 1 & 3, Kaledupa 1 and Kaledupa Double Spur, Pak Kasim's, Ridge 1 and Sampela 1 are abbreviated as B1, B3, K1, KDS, PK, R1 and S1 respectively.

The ecology of the sponge assemblages within the Wakatobi is relatively well studied for the Indo-Pacific region (e.g. Bell et al. 2010; Powell et al. 2014) and to date over 100 species have been reported in the area (Bell & Smith 2004). Bell & Smith (2004) found sponge species richness to increase with depth and a significant difference in the sponge assemblage composition between the impacted site Sampela and another healthier site on the Hoga fringing reef. To date there has been no research into bioeroding sponges in the Wakatobi, although Bell & Smith (2004) did report one unidentified clionaid sponge species in their assessment of the Hoga sponge assemblage. Within Indonesia there are only four published studies specifically addressing these organisms; two studies into erosion rates and eutrophication (Edinger et al. 2000; Holmes et al. 2000), one study identifying species of the bioeroding sponge community in North Sulawesi (Calcinai et al. 2005) and another addressing erosion rates and substrate composition (Calcinai et al. 2008).

Anthropogenic disturbances that have caused declines in coral cover in the Wakatobi have coincided with significant increases in abiotic substratum (Curtis-Quick, 2013). This increase in available substrate, potentially creates an opportunity for clionaid sponges to increase in

abundance. It is therefore critical to understand the factors that control bioeroding sponge abundance and understand how the factors that constitute disturbance for corals, will affect the functioning and abundance of these sponges within the context of the reef system.

1.7. Thesis aims

The overall aim of this thesis is:

To obtain a greater understanding of how habitat degradation will affect the ecology and function of bioeroding sponges on Indonesian coral reefs

1.7.1. Thesis objectives

1. To use spicule characteristics and phylogenetics to identify the common bioeroding sponge species in the Wakatobi.
2. To assess current trends in the abundance, distribution and assemblage composition of bioeroding sponges in the Wakatobi and relating these trends to local environmental and abiotic conditions. Consequently, gaining a greater understanding of how changes in these factors, particularly those which co-vary with reef degradation, might drive abundance and assemblage composition on degraded reefs.
3. To assess the rates of bioeroding sponge recruitment and determine the relative importance of the abundance of local adult population and substrate settlement cues for this recruitment
4. To measure the capacity for zooxanthellate sponges to photoacclimate to conditions of reduced light availability associated highly turbid reefs.
5. To measure the bioerosion rates of *Spherospongia* cf. *vagabunda* and determine how these vary in relation to environmental variables.

Chapter 2: Bioeroding Sponges from Wakatobi National Park, Southeast Sulawesi, Indonesia

2.1. Abstract

Sponges that excavate and inhabit calcareous substrate, predominantly of the Clionaidae family, have a cosmopolitan distribution but are particularly diverse and abundant on coral reefs.

Unfortunately, their cryptic habitat and difficult identification means their taxonomy is poorly understood and therefore they are rarely included in reef surveys. This is particularly true of the Southeast Asian Indo-Pacific, where compared to other coral reef regions, they are understudied.

I conducted *in situ* surveys of the common bioeroding sponges in the Wakatobi region of Southeast Sulawesi, Indonesia, and samples were retained for spicule and molecular analysis.

The Wakatobi bioeroding sponge fauna comprised 8 common species including two putative new species. Three species, *Cliona orientalis*, *Spheciospongia* cf. *vagabunda* and *Cliothosa* cf. *aurivilli*, have been previously described in Indonesian waters, while three species, *Cliona* cf. *schmidtii*, *Cliothosa hancocki* and *Zyzzya criceta* were new descriptions for Indonesia. Finally, two sponges belonging to the *Cliona viridis* species complex, *Cliona* aff. *viridis* n. sp. A & B, were morphologically distinct from other species within the complex. A maximum likelihood analysis of ITS1 rDNA for these sponges found both to be monophyletic clades, phylogenetically closer to *C. orientalis* and *Cliona varians* than other species within the complex. Both species are described here for the first time.

2.2. Introduction

Sponges are globally ubiquitous coral reef organisms that through a variety of mechanisms are major contributors to the functioning of reef ecosystems (Wulff 2001; Bell 2008). While some sponge species indirectly contribute towards reef building (Wulff & Buss 1979), bioeroding sponges actively erode calcium carbonate. These sponges make a considerable contribution to reef bioerosion, frequently representing 60 to 90% of macroborer activity on coral reefs (Risk et al. 1995). Bioerosion influences coral reef structural complexity (Scott & Risk 1988), produces significant amounts of sediment for framework accretion (Hubbard et al. 1990) and by counterbalancing calcification processes, affects the reef carbonate cycle (Perry et al. 2008). Bioeroding sponges have recently become the focus of numerous studies following reports of their apparent proliferation on many degraded reefs across the globe (e.g. Ward-Paige et al. 2005; Schönberg & Ortiz 2009; Carballo et al. 2013). This rise in abundance is attributed to: 1) bioeroding sponge resilience to the anthropogenic disturbances that are stressors for hard corals (e.g. López-Victoria & Zea 2004; Schönberg & Suwa 2007; Schönberg & Ortiz 2009; Wisshak et al. 2012); and 2) their close association with carbonate substrate which increases as a consequence of coral mortality (Chaves-Fonnegra et al. 2007; Nava & Carballo 2013; Schönberg 2015a). Stressor resilience, endolithic dependency and bioerosion rates vary among species (e.g. Schönberg 2001; Murphy et al. 2016) and bioeroding sponge assemblages on degraded reefs are often dominated by a few resilient species (e.g. Schönberg & Ortiz 2009). Therefore, to better understand the trajectories of these sponges on future degraded reefs, relevant studies need to be undertaken at the species level. Regrettably this is often hampered by the lack of taxonomic knowledge.

Taxonomically, Mediterranean and Caribbean bioeroding sponges have traditionally been very well studied (e.g. Schmidt 1862; Carter 1882; Pang 1973; Vicente 1978; Carballo et al. 1994; Hill 1996; Rosell et al. 1999; Zea & Weil 2003; Escobar et al. 2012; González-Rivero et al. 2013), and in the wider Caribbean bioeroding sponges are the subject of long-term monitoring programs (e.g. Atlantic and Gulf Rapid Reef Assessment (Lang et al. 2010) and Southeast Florida Coral Reef Evaluation and Monitoring Project (Gilliam 2010)). The situation is different for Indo-Pacific reefs and although bioeroding sponges in some areas such as the Great Barrier Reef (GBR) and the Mexican Pacific have received recent attention (e.g. Schönberg 2000a;

Schönberg & Ortiz 2009; Nava & Carballo 2008; 2013; Cruz-Barraza et al. 2011), other important areas remained unstudied or only superficially studied. One such location is Indonesia; the 17,000 island archipelago nation is located centrally within the coral-triangle, the global epicentre of reef biodiversity (Briggs 2005; Veron et al. 2009), and is considered the largest and most important coral reef nation in the world (Spalding et al. 2001). To date, 314 sponge species have been recorded in Indonesian waters (World Porifera Database, (WPD; van Soest et al. 2017)) and it is estimated that the Indonesian sponge fauna could be comprised of up to 830 species (Van Soest 1989; 1994). However, very little is known about the Indonesian bioeroding sponge assemblage composition and only nine species are officially listed within the WPD. Despite this, Tomascik et al. (1997) tentatively reported the Indonesian bioeroding sponge fauna to consist of 33 species, of which 19 were provisionally identified to the species level; 17 species belonging to Clionaidae and 2 to Phloeodictyidae (van Soest, pers. comm.). Nevertheless, the only detailed assessment from this region is by Calcinaï et al. (2005) who identified six clionaid species around the island of Bunaken in Northern Sulawesi.

Due to the lack of taxonomic information on Indonesian bioeroding sponges (and their cryptic habit), they are mostly excluded from surveys and monitoring work (e.g. de Voogd et al. 2006). Consequently, very little information exists on the status of these organisms on degraded Indonesian reefs (see Edinger et al. 2000; Holmes et al. 2000). The current gap in our knowledge of the Indonesian bioeroding sponge fauna needs to be addressed given the significant anthropogenic threats to these important reefs (Spalding 2001; Burke et al. 2011) and considerable potential negative impacts of proliferation of these sponges (e.g. Carballo et al. 2013). In this context, this chapter is an assessment and description of the eight most common bioeroding sponge species in the Wakatobi region of Southeast Sulawesi, Indonesia.

2.3. Methods

2.3.1. Sampling and morphological analysis

Surveys were carried out at seven reef sites in the UNESCO Wakatobi Biosphere Reserve (here; Wakatobi) (Fig. 2.1) between the depths of 3 and 20 m during March-April and June-August 2014. Specimens were collected using a hammer and chisel or by rubble collection and preserved in 70 or 96% ethanol. In addition to the collection of specimen samples, comprehensive field notes and photographs were taken *in situ* detailing live colour, organism size, inhalant and exhalant structures and macroscopic characteristics of erosion. In addition, application of Pulse Amplitude Modulated Fluorometry (RED DIVING-PAM, Walz, Iffeltrich) to detect fluorescence yield in *in situ* light-adapted sponges, and subsequent tissue examination (using light microscopy) identified the presence of symbiotic *Symbiodinium*.

Spicule arrangement and composition within papillae/ecotosome and choanosome tissue was investigated using light microscopy (Leica DMLB, Wetzlar). Cross sections of papillae or ecotosome tissue were cut using a scalpel and choanosome tissue was removed from erosion chambers using forceps (pluck preparation; Schönberg 2000a). Tissue samples were fully dehydrated in 100% ethanol, cleared in Xylene and mounted on microscopy slides with DPX (Sigma-Aldrich, St Louis).

Spicule dimensions were studied with both light microscopy (Leica DMLB, Wetzlar) and scanning electron microscopy (SEM; Hitachi TM3000, Tokyo). For spicule preparation, portions of tissue from the choanosome and surface tissue were selected from each sample and separately heat dissolved in nitric acid, rinsed in distilled water and dehydrated in ethanol (procedure after Schönberg 2000a). Spicules were mounted on microscopy slides with DPX for light microscopy and placed on stubs before sputtering with gold for SEM. Spicule dimensions were measured using a micrometre eyepiece for light microscopy and the software package ImageJ for SEM images. Measurements were carried out along haphazardly selected transects across the slide or stub, disregarding broken, malformed and newly recruited spicules and using a minimum sample size of $n = 25$ per spicule type. Megasclere dimensions were measured in terms of total length, shaft width (widest part) and tyle width, and microscleres were measured in terms of total length

(including spines and branches), shaft width (widest part without spines) and number of bends for spirasters (see Schönberg 2000a).

Figure 2.1. Map of sponge sampling locations within the Wakatobi National Park. Sites Buoy 1 & 3, Kaledupa 1 and Kaledupa Double Spur, Pak Kasim's, Ridge 1 and Sampela 1 are abbreviated as B1, B3, K1, KDS, PK, R1 and S1 respectively.

2.3.2. Molecular analysis

DNA was extracted from two specimens of two 96% ethanol preserved zooxanthellate species, *Cliona* aff. *viridis* n. sp. A & B (see below) using a Qiagen extraction kit. PCR amplifications of the ITS1 region were carried out according to the methodology outlined by Escobar et al. (2012), using the primers D-ITS1-F and D-ITS1-R and sequenced in both directions by a third party service (Macrogen, South Korea). Sequence alignment and phylogenetic tree construction were conducted in the software package MEGA v.7. Searches through the NCBI BLAST algorithm identified potential homologues for the sponges in question and were used with the Wakatobi sequences to generate a multiple sequence alignment using the MUSCLE method. The phylogenetic tree was constructed using the maximum likelihood method with the Kimura 2-

parameter model (the best model selected by MEGA) and rapid bootstrap analysis with 1000 replicates.

Homologous sponges selected for the phylogenetic tree were *Cliona aprica* (JN011557.1, JN011558.1 & JN011501.1), *Cliona caribbaea* (JN011500.1, JN011497.1 & JN011555.1), *Cliona tenuis* (JN011499.1, JN011496.1, JN01149.1), *Cliona orientalis* (JN011482.1) and *Cliona varians* (JN011469.1, JN011474.1 & JN011473.1). As per Escobar et al. (2012), *Spirastrella coccinea* (JN011577.1, JN011578.1 & JN011579.1) was used as an outgroup.

2.4. Results

Order Clionaida Morrow & Cárdenas 2015

Family Clionaidae d'Orbigny 1851

Genus *Cliona* Grant 1826

Diagnosis

Heteroscleromorph clionaid genus with sponges in endolithic-papillate (alpha), endolithic-encrusting (beta), free-living (gamma) and intermediate morphologies and with ability to erode calcareous materials. Silicate skeleton - monaxon megascleres, tylostyles, oxeas or modifications. If present, secondary or microscleres spirasterose spicules, amphiasters, oxeas, raphides and microrhabds. Arrangement of papillar tylostyles in palisade or as bouquets, tyles anchored in sponge tissue, points above tissue surface. Erosion traces largely camerate and small, but some species with large-camerate to cavernous erosion chambers. Symbiosis with *Symbiodinium* spp. common in sponges with tylostyles and spirasters.

2.4.1. *Cliona* cf. *schmidtii* (Ridley 1881)

Synonymised names

Thoosa istriaca Müller 1979

Vioa schmidtii Ridley 1881 (genus transfer)

Material examined

Wakatobi Material: B1-PA-01, B1-PA-02, B3-PA-01

Morphology and erosion

Exclusively in alpha form (Fig. 2.2A). Papillae and choanosome vivid purple *in situ*, and colour maintained after preservation in ethanol. Numerous circular papillae visible on substrate surface, usually up to 5 mm in diameter, but occasionally merging to form single papillae up to 10 mm in

diameter (Fig. 2.2B). Inhalants level, fleshy patches with several small pores, while exhalants of similar or larger diameter slightly conical, with single oscular hole (Fig. 2.2B). Short papillar channels (2-5 mm) penetrate substrate and connect to small ($1.2 \text{ mm}^2 \pm 0.6 \text{ SD}$) densely packed erosion chambers separated by irregularly shaped contiguous islands of substrate. Erosion overall shallow and rarely exceeding beyond 15 mm in depth (Fig. 2.2C).

Tissue characteristics and Symbiodinium presence

Papillae tylostyles densely packed in palisade form with tips pointing to the exterior. Tylostyles and abundant spirasters irregularly dispersed in papillar channels and choanosome. Low levels of fluorescence measured with DIVE-PAM but no *Symbiodinium* observed within tissue.

Spicules

Megascleres – Straight to slightly curved tylostyles (Fig. 2.2D), predominantly with spherical, but occasionally subterminal tyles or stylar modifications. Dimensions (min-max and mean): length 218 - 345 μm ($307.7 \mu\text{m} \pm 27.2 \text{ SD}$); shaft width 5 - 9 μm ($6.5 \mu\text{m} \pm 1.3 \text{ SD}$); and tyle width 5 - 12 μm ($8.4 \mu\text{m} \pm 2.0 \text{ SD}$).

Microscleres - Spirasters morphologically very varied but broadly falling into two groups: 1) long and spindly spirasters with a maximum of 7 slight bends with fine, discrete spines in regular spiral distribution on convex side of shaft (Fig. 2.2E & F); and 2) shorter, stout spirasters with up to three bends and large conical spines mostly concentrated at the ends of shafts (Fig. 2.2E & F). Dimensions of spindly variety (min-max and mean): length 17.5 - 75 μm ($46.3 \mu\text{m} \pm 15.6 \text{ SD}$); and width 1- 4 μm ($2.3 \mu\text{m} \pm 0.6 \text{ SD}$). Dimensions of stout variety (min-max and mean): length 20 - 38 μm ($28.8 \pm 4.9 \text{ SD}$); and width 3 - 10 μm ($5.4 \mu\text{m} \pm 1.5 \text{ SD}$).

Habitat and occurrence

Common; most frequently found in crevices on steep reef walls and often associated with crustose coralline algae (Fig. 2.2A).

Figure 2.2. *Cliona cf. schmidtii*. (A) Field image of papillae; (B) field image of merged papillae; (C) exposed erosion of carbonate rock; (D) tylostyle; (E & F) “spindly” & “stout” spirasters.

Remarks

Purple clionaid sponges stand out in the field and have been sampled from a wide range of sites, including

- the Mediterranean (*C. schmidtii*; Rosell and Uriz 2002),
- the Atlantic (*C. schmidtii*; Jamaica, Pang 1973)
- the Indo-Pacific (*Cliona jullieni*; Reunion, Kelly-Borges & Vacelet 1998; *C. schmidtii*; Polynesia, Kirkpatrick 1900; Maldives, Calcinaï et al. 2000; Indonesia, Hooper et al. 2000; Great Barrier Reef, Schönberg et al. 2006. *Cliona tinctoria*; Great Barrier Reef, Schönberg 2000a. *Spheciospongia purpurea*; East coast of Australia, Lamarck 1814).

Consequently, there are presently only four recognised species of purple clionoids, and due to their comparatively distinct spicule characters and growth form their identification is not generally considered difficult. Based on spicule dimensions *C. jullieni* and *C. tinctoria* were readily determined as not being conspecific with the Wakatobi material, even though these species have been described from the Indo-Pacific. Mean tylostyle dimensions of both *C. jullieni* (750 x 12 x 15 µm; Topsent 1891) and *C. tinctoria* (380 x 14 x 17 µm; Schönberg 2000a) are considerably larger than those sampled from the Wakatobi sponge specimens. The spirasters of both *C. jullieni* and *C. tinctoria* species are also characteristically smaller (17 x 4 µm and 30 x 1.5 µm, respectively) than *C. schmidtii*. *S. purpurea* was equally readily ruled out due to its massive morphology which contrasts with the Wakatobi material that was exclusively found in papillae form.

The spicules of the purple clionaid in my study appear characteristic of *C. schmidtii*. Megasclere size is highly comparable to megascleres of other accounts (e.g. Ridley 1884; Carballo et al. 1994), and the size spectrum and appearance of microscleres are also in accordance with earlier publications, and within the typical size spectrum (e.g. Schmidt 1870). However, it should be noted that other published descriptions of the species report significantly larger spirasters, e.g. Ridley (1881) found two size classes 75 x 2 and 50 x 6 µm.

The World Porifera Database (van Soest et al. 2017) currently does not accept other distributional areas than the Mediterranean and Eastern Atlantic as valid for *C. schmidtii* despite published records of occurrences listed above, which include Indonesia. The cautious approach

by van Soest et al. (2017) is due to the attempt to separate *Cliona carteri* (Ridley, 1881) from *C. schmidtii*; the same publication by Ridley contains the full description of *C. carteri* and the first correct, but somewhat hidden, account of *C. schmidtii*. This is now accepted as the original description, but has led to the confusion of the two species that have occasionally been placed in synonymy (Schönberg pers. comm.). However, if it is accepted that *C. schmidtii* is a brightly purple sponge in alpha form with tylostyles and spirasters that display a continuum of lengths and widths, then based on the samples and accounts listed above its distribution is more widespread than stated by van Soest et al. (2017). Moreover, molecular phylogenetic work by Barucca et al. (2007) sequenced *C. schmidtii* specimens from the Mediterranean and the Celebes Sea (Indonesia) and found no evolutionary distance between the specimens, confirming the occurrence of *C. schmidtii* in Indonesia and providing good support for species identification of the Wakatobi material. Nevertheless, further molecular studies are required to fully confirm whether *C. schmidtii* is a circum-global species that can be found in temperate to tropical waters. Given this, this ambiguity is acknowledged and the identification of the Wakatobi material is limited to *C. cf. schmidtii*.

2.4.2. *Cliona orientalis* Thiele 1900

Synonymised names

Anthosigmella orientalis (Thiele 1900) (reverted genus transfer)

Material examined

Wakatobi Material: KDS-BeA-01, KDS-BeA-02, PK-BeA-01

Morphology and erosion

Exclusively in alpha form (Fig. 2.3A). Circular to irregular-shaped papillae which frequently merge, 1-15 mm in diameter, dark brown with pale grey oscular rings that protrude 1 mm into water column (Fig. 2.3B). Short (2-6 mm) papillar canals leading to shallow, densely packed irregular-shaped erosion chambers ($0.8 \text{ mm}^2 \pm 0.2 \text{ SD}$), separated by irregularly shaped contiguous islands of substrate (Fig. 2.3C). Choanosome yellow.

Tissue characteristics and Symbiodinium presence

Papillae tylostyles densely packed in palisade form with tips pointing to the exterior. Abundant spirasters irregularly dispersed beneath the palisade layer, in papillar channels and choanosome. Tylostyles irregularly dispersed and becoming rarer in the choanosome. High fluorescence measured with DIVE-PAM and *Symbiodinium* observed within ectosome tissue under light microscope.

Spicules

Megascleres – Straight to slightly curved, slender tylostyles with pronounced tyles (Fig. 2.3D). Dimensions (min-max and mean): length 250 - 385 μm ($316.7 \mu\text{m} \pm 28.8 \text{ SD}$); shaft width 4 - 7 μm ($5.4 \pm 0.6 \text{ SD}$) and tyle width 5 - 10 μm ($8.3 \pm 1.2 \text{ SD}$).

Microscleres – Spirasters (abundant), either straight, c-shaped or more often helical with three to four bends. Spines arranged in bouquets along both sides of spicule shaft and in terminal clusters (Fig. 2.3E & F). Spiraster dimensions (min-max and mean): length 15 - 27 μm ($22.5 \mu\text{m} \pm 3.2 \text{ SD}$) and shaft width 0.7 - 1.5 μm ($1.0 \mu\text{m} \pm 0.2 \text{ SD}$).

Habitat and occurrence

Very rare, found on bare substrate, CCA and oyster shells in shallow waters (max 7 m depth) at low turbidity sites.

Figure 2.3. *Cliona orientalis*. (A) Field image of sponge; (B) close-up field image of exhalant papillae; (C) cross-section of erosion zone; (D) tylostyle; (E & F) spirasters.

Remarks

The spicule composition of tylostyles and delicate spirasters in combination with the presence of symbiotic *Symbiodinium* places the Wakatobi specimens within the “*Cliona viridis* species complex” (see Schönberg 2000b). Species within this complex found within the Indo-Pacific are *C. orientalis* (Thiele 1900), *Cliona albimarginata* (Calcinai et al. 2005), *Cliona caesia* (Schönberg 2000a) and in the east Pacific *Cliona acephala* (Zea & López-Victoria 2016) and *Cliona tropicalis* (Cruz-Barraza et al. 2011). Based on the comparisons made below this species was identified as *C. orientalis*.

Wakatobi *C. orientalis* was only found in the alpha form, which distinguishes it from *C. albimarginata* and *C. acephala* which have only been found in the beta form. *C. albimarginata* tylostyle dimensions are similar (288.1 x 4.6 µm), but the tyloses are only subtly developed, the spirasters are smaller (12.8 x 1 µm), and microscleres are comprised of both amphistyles and spirasters (Calcinai et al. 2005). The differences for *C. acephala* also go beyond morphology as this species lacks spirasters altogether (Zea & López-Victoria 2016).

The two exclusively papillate species in the region are *C. caesia* and *C. tropicalis*. *C. caesia* shares a similar raised central conical portion of the papillae, however the papillae are much smaller (0.5-2mm; Schönberg 2000a). Smaller tylostyles, oxeas and the absence of spirasters further differentiate *C. caesia* from the Wakatobi specimens. Similarities between the Wakatobi specimens and *C. tropicalis* are limited to tylostyles, which are of a similar shape and size (193 x 5 µm in *C. tropicalis*; Cruz-Barraza et al. 2011). However, *C. tropicalis* spirasters are predominantly straight and the sponge is morphologically quite dissimilar to the Wakatobi specimens; externally the papillae are yellow in colour and erosion chambers are large and well-spaced (Cruz-Barraza et al. 2011).

C. orientalis was originally described in both the alpha and beta form from Ternate, Indonesia (Thiele 1900) and has since been described in Western Australia (Fromont et al. 2005), the Great Barrier Reef (Schönberg 2000a) and New Caledonia (Kelly-Borges & Vacelet 1998). Schönberg (2000a) described the sponge surface as “beige-brown to mottled dark grayish brown” with oscula that are “slight elevated rings”, which is very similar to the description by Fromont et al. (2005). Kelly-Borges & Vacelet (1998) describe a broadly similar sponge but with distinctly

large and raised yellow oscula. Although only found in the alpha form in the Wakatobi, the description fits, specifically the raised yellow oscules. Erosion characteristics are also similar; shallow erosion, small and irregularly shaped chambers, and rich-yellow choanosome colour.

Skeletal features of *C. orientalis* vary between descriptions. Tylostyles are generally described as straight/slightly curved with pronounced round to drop-shaped tyles but average sizes can range from 230 x 9 µm (Thiele 1900) through 270 x 7 x 10 µm (Schönberg, 2000a) and 336 x 9 µm (Kelly-Borges & Vacelet 1998) to 344 x 9 µm (Fromont et al. 2005). The tylostyles of the Wakatobi specimens are therefore similar in form and length but slightly narrower than previous descriptions. Microsclera composition of *C. orientalis* is similar between published descriptions; delicate spirasters with variable curvature width and length but averaging 23-25 x 1-2 µm, 3-4 bends and bouquet spination on convex side of shaft (Thiele 1900; Borges & Vacelet 1998; Schönberg, 2000a; Fromont et al. 2005).

Despite only occurring in alpha form, the external morphology, erosion characteristics and skeletal composition supports the identification Wakatobi specimens as *C. orientalis*.

2.4.3. *Cliona* aff. *viridis* n. sp. A

Material examined

Wakatobi Material: PK-LBB-01, PK-LBB-02, KDS-LBB-01

Morphology and erosion

Sponge predominantly in beta form (Fig. 2.4A), but occasionally in alpha form (possibly only in recruits; Fig. 2.4B). Light brown or tan ectosome, yellow choanosome. Individual organisms usually small ($\sim 10 \text{ cm}^2$), but capable of reaching 75 cm^2 . Regularly distributed oscular openings 2-4 mm diameter and obvious small ostia. Surface tissue layer coating substrate 1 mm thick, and sponge evenly and densely pervading substrate beneath, to a depth of 5-7 mm (Fig. 2.4C). Erosion removing roughly 50% of material leaving irregularly shaped islands of substrate behind (visual assessment) and contiguous. Chambers with irregular outline and mean area of 2.0 mm^2 ($\pm 1.1 \text{ SD}$) are densely crowded, with well-delineated erosion and not leaving a solid frame of substrate on the surface.

Tissue characteristics and Symbiodinium presence

Tylostyles in ectosome arranged in palisade pattern with tips pointing to the exterior. Choanosomal tissue comprised of irregularly dispersed tylostyles and numerous spirasters. Spirasters not visible in ectosome. High fluorescence yield measured with DIVE-PAM and *Symbiodinium* observed within ectosome tissue.

Spicules

Megascleres delicate straight tylostyles with considerable variation in tyle morphology and occasional subtylostyles (Fig. 2.4D). Dimensions (min-max and mean): length 225 - 375 μm ($310 \mu\text{m} \pm 34.7 \text{ SD}$); shaft width 3 - 7 μm ($4.9 \mu\text{m} \pm 0.9 \text{ SD}$); and tyle width 4 -10 μm ($7.4 \pm 1.4 \text{ SD}$).

Microscleres slender spirasters with sparse supination along convex side of shafts, spines multisplit, ending in bouquets; additional bushy, amphiaster-like, terminal crowding of spines. Spirasters C-shaped with spines on convex side, or straight with no spines on central shaft or

with two-three bends and spines along convex sides of shaft (Fig. 2.4E & F). Dimensions (min-max and mean): length 13 - 23.8 μm (19.1 ± 2.8 SD) and shaft width 0.7 - 1.7 μm (1.1 ± 0.2 SD).

Molecular analysis

C. aff. viridis sp. A appears to be a monophyletic clade with high bootstrap values and a sister taxon to *Cliona varians*, *C. orientalis* and *C. aff. viridis* n. sp. B (Fig. 2.5).

Habitat and occurrence

Common in Wakatobi, most abundant at clear water sites and absent from highly sedimented sites. Spreading across bare substrate or massive coral colonies and often seen neighbouring live coral.

Figure 2.4. *Cliona* aff. *viridis* n. sp. A. (A) Field images of adult specimen; (B) field image of recruits/papillae; (C) field cross-section image showing sponge ectosome and extent of sponge erosion; (D) tylostyle; (E) c-shaped spiraster; (F) three-bend spiraster.

Figure 2.5. Phylogenetic tree analysis by Maximum Likelihood method based on the Kimura 2-parameter model. The tree with the highest log likelihood is shown (-1018.61). The percentage of trees in which the associated taxa clustered together is shown next to the branches. Sequences are listed by GenBank accession number and taxon. *S. coccinea* is rooted as an outgroup.

Remarks

The spicule composition of tylostyles and delicate spirasters in combination with the presence of symbiotic *Symbiodinium* and position within the phylogenetic tree places the Wakatobi specimens within the “*C. viridis* species complex” (see Schönberg 2000b). Wakatobi specimens were compared to other species within the species complex that are either known to occur (or possibly occur) in the Indo-Pacific region or that bare close resemblance. The material reviewed below highlights the subtle yet important differences between the Wakatobi specimens and these species and leads to the conclusion that the Wakatobi specimens are likely a novel species.

C. albmarginata which is found in North Sulawesi is highly comparable with the Wakatobi specimens on the macro-morphological scale; dark-olive brown ectosome, yellow choanosome and irregular to spherical erosion chambers (Calcinai et al. 2005). However, these features are largely characteristic of all beta form *C. viridis* spp. and are not suitable for species comparison. Spicule composition does differ in two important ways: 1) while *C. albmarginata* tylostyle length is similar (322-337µm), subtylostyles are described as the norm rather than the exception as in the Wakatobi; and 2) *C. albmarginata* possesses spirasters (although smaller) but also small amphiasters that are absent in the Wakatobi material.

The molecular analysis inferred that *C. aff. viridis* n. sp. A was monophyletic clade distinct from the Caribbean species of *C. caribbaea*, *C. aprica* and *C. tenuis* and potentially a sister taxon to *C. varians* and *C. orientalis*. This inference is borne out by spicule similarities between the Wakatobi material and both *C. varians* and *C. orientalis*.

The distribution for *C. varians* is accepted for the Caribbean and West Atlantic (van Soest et al. 2017), and Pang (1973) suggested that it is endemic to the area, but the species has also been reported from the Indian and Pacific Oceans (e.g. Thomas 1979; Calcinai et al. 2000). The species displays high phenotypic plasticity with reported growth forms similar to the Wakatobi specimens; an endolithic papillate alpha form (Calcinai et al. 2000) and an endolithic encrusting beta form (Hill 1999). Tylostyle morphology is similar but often larger in *C. varians*, which can reach up to 465 µm in length (Pang 1973; Thomas 1972; 1979) and 16 µm in width (Pang 1973; Thomas 1972; 1979). However, it is the microscleres composition of *C. varians* that is diagnostic of the species as it is overwhelmingly dominated by C-shaped spiraster and other forms are rare

(e.g. Thomas 1972; Pang 1973; Calcinai et al. 2000). Conversely, while C-shaped spirasters are common in the Wakatobi specimens, they not overwhelmingly so and are half the width of those found in *C. varians* (Pang 1973, Hofman & Kielman 1992; Calcinai et al. 2000).

Another comparable sponge within the species complex is *C. orientalis*, which is described previously. In the beta form, it's a similar brown sponge with yellow choanosome, shallow erosion and spicule composition of tylostyles of delicate spirasters (Schönberg 2000a) and has previously been confused with *C. varians* (e.g. Thomas 1972; 1979). The most distinct difference between the Wakatobi specimens and *C. orientalis* is the shape of the spirasters, which despite similar spination and size are considerably more “curvy” in *C. orientalis* where an average of four bends is the norm.

2.4.4. *Cliona* aff. *viridis* n. sp. B

Wakatobi Material: PK-BIA-01, PK-BIA-02, B3-BIA-01

Morphology and erosion

Exclusively in alpha form (Fig. 2.6A). Circular to irregular shaped papillae with brown outer edge and pale grey inner region. Papillae 2-13 mm diameter, frequently merged, and with obvious differences between inhalant and exhalant papillae. Exhalant papillae with slightly raised pale oscular ring (often closed in sampled material) and inhalant papillae dominated by sieve-like structure. Short papillar canals leading to shallow erosion zone (< 20 mm depth), comprised of very small ($0.7 \text{ mm}^2 \pm 0.2 \text{ SD}$) irregularly shaped erosion chambers separated by small islands of substrate Fig. 2.6B. Choanosome yellow in colour.

Tissue characteristics and Symbiodinium presence

Papillae tylostyles in ectosome arranged in dense palisade pattern with tips pointing to the exterior. Choanosomal tissue comprised of sparse and irregularly dispersed tylostyles and spirasters. High fluorescence measured with DIVE-PAM and *Symbiodinium* observed within ectosome tissue.

Spicules

Megascleres – Stout tylostyles; shaft shape can vary from straight to extensively bent, tyles predominantly spherical but occasionally elongated (Fig. 2.6C & D). Dimensions (min-max and mean): length 290 - 376 μm ($340.0 \mu\text{m} \pm 21.2 \text{ SD}$), shaft width 6 - 11.5 μm ($9.2 \mu\text{m} \pm 1.3 \text{ SD}$) and tyle width 10 - 14.5 μm ($11.8 \mu\text{m} \pm 1.1 \text{ SD}$).

Microscleres – Very rare, long, slender spirasters with long thin spines projecting from convex side of spicule shaft. Spiraster curvature varied, ranging from straight to up 7 bends (average 4; Fig. 2.6E & F). Spiraster dimensions (min-max and mean): length 18 - 41 μm ($24.3 \mu\text{m} \pm 7.2 \text{ SD}$), shaft width 0.5 - 1 μm ($0.9 \mu\text{m} \pm 0.1 \text{ SD}$).

Molecular analysis

The phylogenetic tree (Fig. 2.5) infers that the specimens identified as *C. aff. viridis* n. sp. B occupied a monophyletic clade that is closely related to *C. orientalis* and relatively distantly related to *C. caribbaea*, *C. aprica* and *C. tenuis* (referred to as the *Ct*-complex by Escobar et al. (2012)).

Habitat and occurrence

Very common at all Wakatobi sites; usually on bare substrate or dead massive coral, but also on consolidated rubble. Most abundant between 7-12 m depth, except at highly turbid sites where absent below 7m.

Figure 2.6. *Cliona* aff. *viridis* n. sp. B. (A) Field images of inhalant and exhalant papillae (top right); (B) exposed erosion of carbonate rock; (C) straight tylostyle (spiraster also visible); (D) bent tylostyle; (E & F) spirasters.

Remarks

The spicule composition of tylostyles and delicate spirasters in combination with symbiotic *Symbiodinium* and positioning within the phylogenetic tree places the Wakatobi specimens within the “*C. viridis* species complex” (see Schönberg 2000b). Nevertheless distinct elements of the sponge’s morphology and spicule characteristics, as discussed below, appear unique to the Wakatobi samples and thus *C. aff. viridis* n. sp. B likely constitutes a new species.

Despite appearing to share a recent common ancestor with *C. orientalis*, two important characteristics of *C. viridis* sp. B are markedly different. The sieve-like inhalent papillae on the Wakatobi specimens are distinctive and quite different from *C. orientalis* where no such features have been described (Thiele 1900; Schönberg 2000a). Additionally, the spination of the spirasters is discrete and thorn-like, quite dissimilar to the multi-split, bouquet-like form found in *C. orientalis* (Thiele 1900; Schönberg 2000a).

The distinctive papillae and spirasters also excludes identification as *C. albimarginata*, *C. caesia*, *C. acephala*, *C. varians* or *C. tropicalis*. The only species within the complex to poses similar spiraster characteristics are the Caribbean sponges *C. caribbaea* and *Cliona flavidona* (Pang 1973; Rützler 1974; Zea & Weil 2003). *C. flavidona* can be readily ruled out due to it’s ovoid or droplet shaped tylostyle heads and the presence of amphiasters (Rützler 1974). *C. caribbaea* is considered a papillate or encrusting zooxanthellate sponge with tylostyles of rounded heads, spirasters with mostly unbranched spines and comparable spicule sizes to the Wakatobi specimens (Zea & Weil 2003). However, papillate *C. caribbaea* are rare, considered juvenile and quickly fuse into the encrusting form (Zea & Weil 2003), in contrast to *C. aff. viridis* sp. B, which is only encountered in papillae form and usually with less than twenty papillae. Phylogenetically the two are also quite distinct, with *C. caribbaea* grouped with other Caribbean species.

Genus *Sphaciospongia* Marshall 1892

2.4.5. *Sphaciospongia* cf. *vagabunda* (Ridley 1884)

Synonymised names

Anthosigmella vagabunda (Ridley 1884) (genus transfer)

Spirastrella cylindrica Kieschnick 1896 (genus transfer and junior synonym)

Spirastrella vagabunda Ridley 1884 (genus transfer)

Spirastrella vagabunda var. *fungoides* Dendy 1905 (genus transfer and junior synonym)

Spirastrella vagabunda var. *gallensis* Dendy 1905 (genus transfer and junior synonym)

Spirastrella vagabunda var. *tubulodigitata* Dendy 1905 (genus transfer and junior synonym)

Material examined

Wakatobi Material: B3-OB-01, B3-OB-02, B1-OB-01

Morphology and erosion

Occurs in beta and gamma form. Ectosome tissue predominantly dark olive green in colour but occasionally brown and choanosome light brown or light olive green (Fig. 2.7A) Individual organisms large, with average surface area of 30 cm², but occasionally up to 1.5 m². Large oscular openings 2-7 cm diameter, dispersed across sponge surface, often merging and in larger individuals rising as conical projections up to 10 cm above sponge surface. Surface generally smooth, however forms lamello-digitate projections in more sedimented environments. No obvious ostia visible with unaided eye. High erosion activity; average erosion depth 5 cm into substrate, but occasionally penetrating down to 7 cm (Fig. 2.7B). Erosion chambers circular, small (1.1 mm² ± 0.7 SD) and distributed in honeycomb orientation with little calcareous material between chambers.

Tissue characteristics and Symbiodinium Presence

Tylostyles organised bunched in palisade form in ecotosome with tips pointing towards exterior and abundant but irregularly dispersed in choanosome. Spirasters restricted to ectosome tissue. No evidence for photosymbionts, neither by surface fluorescence measured by PAM, nor through histology.

Spicules

Megascleres – Stout tylostyles (Fig. 2.7C), straight to slightly curved, highly variable in size and generally larger in the choanosome than in the ecotosome. Large variability in tyle development; generally subtylar and only subtly developed, with occasional styler modifications. Ectosome tylostyle dimensions (min-max and mean): length 254 - 665 μm ($451.6 \mu\text{m} \pm 116.3 \text{ SD}$), shaft width 7 - 11 μm ($6.8 \mu\text{m} \pm 1.4 \text{ SD}$) and tyle width 5 - 9 μm ($7.1 \mu\text{m} \pm 1.3 \text{ SD}$). Choanosome tylostyle dimensions (min-max and mean): length 304 - 703 μm ($541.7 \mu\text{m} \pm 113.0 \text{ SD}$), shaft width 5 - 10 μm ($7.4 \mu\text{m} \pm 1.4 \text{ SD}$) and tyle width 6 - 11 μm ($8.3 \mu\text{m} \pm 1.4 \text{ SD}$).

Microscleres – Spirasters, very variable in morphology, but broadly falling into two categories: 1) short amphiaster-like spirasters (common) and; 2) more slender, contorted spirasters (very rare). Amphiaster-like spirasters with only terminal clusters of spines (Fig. 2.7D), or with spine bouquets aligned along convex side of spicule (Fig. 2.7E), or combinations thereof. Amphiaster-like spiraster dimensions (min-max and mean): length 7 - 11.4 μm ($9.0 \mu\text{m} \pm 1.2 \text{ SD}$), central shaft width 1 - 3 μm ($2.1 \mu\text{m} \pm 0.4 \text{ SD}$). Slender, helical spirasters with average of three bends and short spines in bouquets on convex side of spicule (Fig. 2.7F). Slender, helical spiraster dimensions (min-max and mean): length 10 - 22.5 μm ($12 \pm 6.0 \text{ SD}$), central shaft width 2 - 2.5 μm ($2.1 \pm 0.3 \text{ SD}$).

Habitat and occurrence

Very common sponge; most abundant on steep drop-offs and overhangs, less abundant at high rugosity sites dominated by complex corals, and absent from highly sedimented site. Growing across bare substrate and often in apparent competition with live corals and other benthic taxa.

Figure 2.7. *Spheciospongia* cf. *vagabunda*. (A) Field images of adult specimen; (B) incision into sponge tissue revealing erosion zone; (C) tylostyle; (D & E) amphiaster-like spirasters; (F) slender spiraster.

Remarks

The spicule compliment of robust tylostyles, slender spirasters and amphiasterose derivatives is diagnostic of sponges belonging to the genus *Sphaciospongia* (Rützler 2002b) and the present samples were identified as *S. cf. vagabunda* (Ridley 1884), which has a wide distribution across the Indo-Pacific.

The WPD lists five other *Sphaciospongia* species in Indonesian waters; *S. carnosa* (Topsent 1897), *S. lacunosa* (Kieschnick 1898), *S. semilunaris* (Lindgren 1897), *S. solida* (Ridley & Dendy 1886) and *S. spiculifera* (Kieschnick 1898). These were eliminated as possible conspecifics with Wakatobi material due to morphological, colour or spicular differences: *S. carnosa* is described as “cauliflower-shaped, expanding upwards from a narrow base” (Kirkpatrick 1900); *S. lacunose* has a blue-grey ectosome covered in many fine pores; *S. semilunaris* has a yellow ectosome with no obvious oscula; *S. solida* is yellow and lobate with pronounced tylostyle tyles; and *S. spiculifera* is tall and club-like, grey, and with no oscula but abundant ostia.

When looking at the wider Indo-Pacific region, this list expands to include six other *Sphaciospongia* species: *S. alcyonoides* (Hallmann 1912), *S. congenera* (Ridley 1884), *S. inconstans* (Dendy 1887), *S. montiformis* (Hallman 1912), *S. poculoides* (Hallmann 1912), *S. purpurea* (Lamarck 1814). All of which are sufficiently dissimilar in either morphology (e.g. *S. poculoides*), colour (e.g. *S. purpurea*) and or spicule composition (e.g. *S. solida* & *S. congenera*) to be ruled out as concordant with the Wakatobi specimens.

The original description of *S. vagabunda* by Ridley (1884) is similar to those found in the Wakatobi; “massive, attached by broad base” and “tending to grow up into large nodular elevations, which may bear one or more vents” and olive greenish in colour. However other publications demonstrate a far more varied morphology (see Table 2.1). For example Kelly-Borges & Bergquist (1988) describe coral encrusting individuals following the contours of corals, juveniles and endopsammic individuals forming steep sided conical projections and individuals on dead substrate forming mounds. Unlike previous studies (see Table 2.1) endopsammic (sediment buried) individuals were not observed in the Wakatobi, but those

located in more sedimented environments formed lamello-digitate projections as described by Kelly-Borges & Bergquist (1988).

Spicule complement and size in *S. vagabunda* appears very varied, with early authors (e.g. Ridley 1884; Dendy 1905) describing tylostyles with well-developed tyles and later authors (de Laubenfels 1954 onwards) describing tyle variation and subtylar tylostyles. Wakatobi tylostyles are more comparable to the latter forms and are of comparable length but generally smaller in shaft width (see Table 2.1). The existence of two tylostyle size classes also concurs with the most recent work by Kelly-Borges & Bergquist (1988) and Sutcliffe et al. (2010). Two classes of ectosome restricted spirasters also concurs with previous studies and although the extent to which these size classes dominate varies from study to study, dominance by amphiaster-like spirasters (as in the Wakatobi) has been found in most. It should be noted that the Wakatobi spirasters are a little smaller than in previous descriptions but well within the variation seen between descriptions.

The allocation of this species as *S. cf. vagabunda* acknowledges that there are some morphological and skeletal differences between the Wakatobi specimens and some other descriptions of the species. However, previous descriptions are unusually varied and it is probable that *S. vagabunda* represents a species complex, to which the Wakatobi specimens belongs. Clarification on this point will likely only come from further phylogenetic research.

Table 2.1. Character list from previous descriptions of *Spheciospongia vagabunda* from around the Indo-Pacific. N/A indicates information not available.

Characters	Publication					
	<i>Riddley 1884</i>	<i>Dendy 1905</i>	<i>de Laubenfels 1954</i>	<i>Bergquist 1965</i>	<i>Kelly-Borges & Bergquist 1988</i>	<i>Sutcliffe et al. 2010</i>
Location	Torres Strait, Australia	Sri Lanka & Java, Indonesia	West-Central Pacific	Palau	Papua New Guinea	GBR, Australia
Habitat	N/A	Deep water & lagoon. Sand & rubble.	Lagoons & seagrass. Sand and rubble. ≤ 35 m depth	Sand	Shallow lagoons and seagrass	Sandy substrate 14 - 92 m depth
Morphology	Massive with large nodular elevations.	Four growth forms: Massive base & digitate projections; fistular; massive; cylindrical	Basal “ramifying mass”. Endopsammic & fistular.	Massive & digitate with prominent oscules	Varied: encrusting & excavating; endopsammic & fistular; massive	Massive and fistular with apical oscules
<i>In situ</i> Colour	Olive green	N/A	Brown	N/A	Dark olive; olive brown; dark reddish brown	N/A

Characters	Publication					
	<i>Riddley 1884</i>	<i>Dendy 1905</i>	<i>de Laubenfels 1954</i>	<i>Bergquist 1965</i>	<i>Kelly-Borges & Bergquist 1988</i>	<i>Sutcliffe et al. 2010</i>
Spicules (average (unless max stated) size in µm)						
Megascleres	Tylostyles:	Tylostyles:	Tylostyles;	Tylostyles:	Tylostyles:	Tylostyles:
	strong, slight curved shaft and oblong to oval head	curved, stout fusiform shafts with well developed heads.	some morph. variation & occasional style	large morph. variation from styles to tylostyles. Smaller variety in cortex	slightly curved with subterminal head	large morph. variation. Straight to slightly curved shafts. Tyles: subtylar to well rounded.
	One size class:	One size class:	One size class:	One size class:	Two size classes:	Two size classes:
	600 x 20 (max)	500-600 x 9-19	500-600 x 8-27	454 x 12.5	551 x 13 316 x 11	483 x 10 268 x 6
Microscleres	Spirasters:	Spirasters:	Spirasters:	Spirasters:	Spirasters:	Spirasters:
	delicate with three bends and 4 – 8 blunt spines.	not numerous and varied from only blunt c-shape to only slender spiral form.	not numerous, most “typical” i.e. spiral. Many c-shaped with blunt projections	found in “dermal crust” and only of one type – lacking slender spiral form	abundant in cortex. Pred. c-shaped with 5-7 spined tufts. Less common long spiral spirasters	pred. thick curved shafts + spination on curved side. Less common thin spiraster ≤ 4 bends
	32 x 16 (max)	Two size classes: 12 x N/A ≤ 48 x ≤ 2	13-20 x N/A	16 x N/A	Two size classes: 10 x 5 26 x 4	Two size classes: 11 x 5 14 x 2

Genus *Cliothosa* Topsent 1905

Diagnosis

Heteroscleromorph clionaid genus with sponges in endolithic-papillate (alpha) morphology and only one species reported to have free-living forms (gamma). With ability to erode calcareous materials. Silicate skeleton. Monaxon megascleres, robust tylostyles with round tyles. Microscleres spirasterose to amphiasterose forms with spines that commonly have multisplit tips. Arrangement of papillar tylostyles in palisade or as bouquets, tyles anchored in sponge tissue, points above tissue surface. Erosion traces commonly large-camerate or even single, cavernous erosion chambers.

2.4.6. *Cliothosa hancocki* (Topsent 1888)

Synonymised names

Cliona seurati (Topsent 1905) (genus transfer and junior synonym)

Cliothosa ramosa (Lendenfeld 1898) (junior synonym)

Cliothosa seurati Topsent 1905 (junior synonym)

Papillella quadrata (Hancock 1849)

Thoosa hancocci Topsent 1888 (genus transfer and spelling correction)

Thoosa hancocki Topsent 1888 (genus transfer)

Vioa ramosa Lendenfeld 1898 (genus transfer and junior synonym)

Material examined

Wakatobi Material: R1-OA-01, B1-OA-01, PK-OA-01

Morphology and erosion

Exclusively in alpha form (Fig. 2.8A). Papillae light orange to dark yellow, circular and 1-5 mm in diameter. Choanosomal tissue of slightly darker yellow-orange colour than papillae. Inhalant and exhalant papillae noticeably different; inhalant papillae more or less flush with substrate

surface, with villar papillar wall slightly extending as ring above, and central, meshed area covering papillar lumen slightly below substrate surface. Exhalant papillae rising as stubby, conical projections 2-5 mm above substrate, becoming more delicate towards minutely scalloped apical edge. Papillar canals lead to sub-ovoid large irregular erosion chambers ($5.1 \text{ cm}^2 \pm 6.5 \text{ SD}$; Fig. 2.8B) up to 5 cm depth, with multiple canals often merging into one chamber, creating a bagpipe appearance.

Tissue characteristics and Symbiodinium presence

Papillar tissue consists of tylostyles densely packed in a palisade orientation with no microscleres present. Tylostyles and amphiasters are irregularly diffused throughout the choanosome with amphiasters often clustered around tylostyles (Fig. 2.8C). No evidence for photosymbionts, neither by surface fluorescence measured by PAM nor through histology.

Spicules

Megascleres – Straight to slightly curved, stout tylostyles predominantly with pronounced spherical tyles (Fig. 2.8D). Dimensions (min-max and mean): length 300 - 481 μm ($368.4 \mu\text{m} \pm 48.6 \text{ SD}$), shaft width 7 - 14 μm ($11.1 \mu\text{m} \pm 2.0 \text{ SD}$) and tyle width 8 - 16 μm ($12.2 \mu\text{m} \pm 1.9 \text{ SD}$).

Microscleres – Characteristic, very abundant amphiasters, with 3-4 branches at either end of central shaft (Fig. 2.8E). Branches terminating in groups of curved spines. Amphiaster dimensions (min-max and mean): length 18 - 28 μm ($22.3 \mu\text{m} \pm 3.2 \text{ SD}$) and central shaft width 1.5 - 3.7 μm ($2.4 \mu\text{m} \pm 0.6 \text{ SD}$).

Habitat and occurrence

Found in low abundances in shallow water (<7 m depth) at most sites in the Wakatobi. Occurs on bare calcareous substrate and often found in dead massive *Porites* coral skeletons.

Figure 2.8. *Cliothosa hancocki*. (A) field image of exhalant (left & centre) and inhalant papillae; (B) field image of erosion chamber; (C) cluster of amphiasters around tyle; (D) tylostyle; (E) amphiaster.

Remarks

This genus has caused some confusion over time and Van Soest et al. (2017) presently accept six *Cliothisa* species as valid. They are yellow or orange to red or even dull pink, are not known for photosynthetic symbioses and occur in papillate alpha form without papillar fusion, with the exception of *Cliothisa aurivillii*. *Cliothisa* erosion chambers are often considerably larger than in *Cliona* and where respective observations are available, the endolithic tissue in *Cliothisa* spp. is exceedingly soft and fragile (Annandale 1915 for *Cliothisa investigatoris*; Cruz-Barraza et al. 2011 for *Cliothisa tylostrongylata*). The tylostyles are comparatively robust, and have been described as ensiform for a number of species (e.g. Calcinai et al. 2000 for *Cliothisa dichotoma*). Tyles are spherical as a rule and usually clearly set off from the shaft by a sharp edge, however, they can be subterminal (Annandale 1915; Rützler & Stone 1986; Cruz-Barraza et al. 2011). Importantly, finding amphiasters resembling “matchstick men” is a clear indicator for *Cliothisa*. These amphiasters can be less characteristic in some species, but the pattern is displayed in form of a short central axis with terminal branches that can in some species branch again into spines that recurve in the typical form. This pattern is again interrupted in *Cl. aurivillii*, in which long spirasters occur, but even these have terminally split spines. Nodulous forms of amphiasters exist, but cannot be found in every specimen, and Annandale (1915) published an observation that these stubby microscleres are patchily distributed.

In the regard to the Wakatobi material, the shape and dimensions of the tylostyles, as well as amphiasterose microscleres readily led to the conclusion that the material belonged into the genus *Cliothisa*. Of the presently six accepted *Cliothisa* spp. (van Soest et al. 2017), four have similar amphiasters: *Cl. dichotoma* (Calcinai et al. 2000), *Cl. investigatoris* (Annandale 1915), *Cl. quadrata* (Hancock 1849) and *Cl. tylostrongylata* (Cruz-Barraza et al. 2011). *Cl. dichotoma* from the Maldives has significantly shorter tylostyles than the Wakatobi specimens, and they have ensiform shafts, which are also not analogous (Calcinai et al. 2000). *Cl. dichotoma* amphiasters have conical branches with rare and irregular branching, while the Wakatobi specimens have amphiasters with slender branches that apically split into a few spines. Moreover, unlike the large chambers in the Wakatobi material, erosion traces of *Cl. dichotoma* were described as small-porous (Calcinai et al. 2000).

Identification of *Cl. hancocki* is usually largely determined by the presence of two distinctive groups of amphiasters; the ramose amphiasters described above & smaller nodulose amphiasters with bulbous branches (e.g. Rosell and Uriz 1997). The latter group of amphiasters were not identified in the studied specimens, however this is not unusual as they are significantly less abundant and can occur in clusters, which can be missed in sampling (Schönberg 2000a). All other skeletal characteristics of the Wakatobi specimens correspond with published descriptions (e.g. Rützler 1973; Schönberg 2000a) as is the cavernous erosion and the presence of little villi on the edges of the inhalant papillae (Schönberg 2000a).

The species has a cosmopolitan distribution spanning from the Mediterranean (e.g. Pulitzer-Finali 1983), to the East African Coast (Thomas 1979), to Vietnam (Calcinai et al. 2006) and the Australian Great Barrier Reef (Schönberg 2000a).

2.4.7. *Cliothosa cf. aurivillii* (Lindgren 1897)

Synonymised Names

Spirastrella aurivillii Lindgren 1897

Spirastrella aurivillii excavans Lindgren 1897

Material examined

Wakatobi Material: B1-RA-01, K1-RA-01, K1-RA-02

Morphology and erosion

Exclusively in alpha form (Fig. 2.9A). Papillae vivid red/orange, circular, 2 (inhalants) to 10 mm in diameter (exhalants). Inhalant and exhalant papillae of noticeably different shape when extended. Inhalant papillae shallow rings of villar tissue not extending far above substrate surface and centrally covered by horizontal sieve-like mesh. Exhalant papillae smooth chimney-like, wide open conical projections, rising 2-7 mm above substrate, with finely scalloped, more translucent apical edge. Long papillar canals leading to large ($4.5 \text{ cm}^2 \pm 3.2 \text{ SD}$), irregularly shaped erosion chambers, with multiple canals often merging into one chamber, creating “bagpipe” appearance (Fig. 2.9B). Choanosomal tissue paler than papillae and yellow/orange.

Tissue characteristics and Symbiodinium presence

Papillae tissue consisting of tylostyles in dense palisade with tips pointing to the exterior. Choanosome tissue comprised of irregularly dispersed tylostyles and very rare spirasters. No evidence for photosymbionts, neither by surface fluorescence measured by PAM, nor through histology.

Spicules

Megascleres – Straight to slightly curved tylostyles with large variability in shaft width, but overall appearing comparatively robust (Fig. 2.9C), predominantly with pronounced spherical tyles and clear crease between tyle and shaft, occasional subterminal tyles. Two size classes. Larger class dimensions (min-max and mean): length 280 - 515 μm ($451.2 \mu\text{m} \pm 33.8 \text{ SD}$), shaft width 9 - 16 μm ($11.4 \mu\text{m} \pm 1.7 \text{ SD}$) and tyle width 12 - 20 μm ($16.1 \mu\text{m} \pm 2.1 \text{ SD}$). Small class

dimensions (min-max and mean): length 250 - 390 μm ($331 \mu\text{m} \pm 34.4 \text{ SD}$), shaft width 6 - 13 μm ($9.4 \mu\text{m} \pm 2.0 \text{ SD}$) and tyle width 7 - 15 μm ($11.4 \mu\text{m} \pm 2.6 \text{ SD}$).

Microscleres – Helical slender spirasters (rare) with average of 2.5 bends (Fig. 2.9D & E). Conical spines radiate out along the spiraster length often ending in branched tips. Spiraster dimensions (min-max and mean): length 45 - 80 μm ($64.8 \mu\text{m} \pm 9.4 \text{ SD}$) and shaft width 2 - 2.5 μm ($2.2 \mu\text{m} \pm 0.3 \text{ SD}$).

Habitat and occurrence

Very common sponge found at all sites and depths studied in the Wakatobi. Highest abundances in shallower water (~ 5 m depth) on bare calcareous rock, dead coral or CCA.

Figure 2.9. *Cliothisa* cf. *aurivillii*. (A) field image of papillae, single exhalant papillae centre left; (B) field image of “bagpipe-like” erosion chamber; (C) tylostyles (smaller size class); (D & E) spirasters.

Remarks

The present samples were identified as *Cl. cf. aurivillii*. The villi on the inhalant papillae, the shape of the tylostyles, the split tips of the spines on the spirasters and the erosion traces all very much resembled characteristics of *Cliothosa* (see above). *Cl. aurivillii*, and its original description is based on material from the Java Sea (Lindgren 1897) and thus close to the present sample site, and is known from other places in the Pacific (Bergquist 1965; Calcinai et al. 2006; Schönberg & Wisshak 2014).

Nevertheless, the identification of this sponge as *Cl. cf. aurivillii* acknowledges some room for identification error, as there are some differences between the measured spicule dimensions and those in published literature. The original description by Lindgren (1897) describes two size classes of tylostyles (672 x 36 µm & 540 x 12 µm), which is similar to descriptions by other authors (e.g. Topsent 1928; Rosell & Uriz 1997). While two apparent size classes of tylostyles were found in this study, the tylostyles from these specimens are significantly shorter and thinner than previous descriptions. The spirasters are also slightly larger than those previously described (e.g. 40 x 4 µm, Lindgren 1897), although in this original description there appears to be some variation in spiraster shape and size (Lindgren 1897, Fig. 22c.). Despite the size differences, the helical axis of the spirasters and the conical spines, which often end in branched tips is characteristic of *Cl. aurivillii* (Lindgren 1897; Bergquist 1965; Rosell & Uriz 1997; Calcinai et al. 2006).

Family Acarnidae Dendy 1922

Genus Zyzzya de Laubenfels 1936

Diagnosis

Heteroscleromorph poecilosclerid genus with sponges in endolithic-papillate (alpha) morphology and one species known to have free-living forms (gamma). Silicate skeleton. Monaxon megascleres, robust tylostyles with round tyles. Microscleres spirasterose to amphiasterose forms with spines that commonly have multisplit tips. Arrangement of papillar tylostyles in palisade or as bouquets, tyles anchored in sponge tissue, points above tissue surface. Erosion traces commonly large-camerate or even single, cavernous erosion chambers.

2.4.8. *Zyzzya criceta* Schönberg 2000a

Material examined

Wakatobi Material: KDS-BF-01, KDS-BF-02, K1-BF-01

Morphology and erosion

Very dark green (appear black underwater) fistules, 1 mm in diameter and rising 2-4 mm above coral rubble surface (Fig. 2.10A). Erosion in form of numerous small and irregularly sized ($4.2 \text{ mm}^2 \pm 2.3 \text{ SD}$) chambers, interconnected to often occupy entirety of rubble interior (Fig. 2.10B). Choanosomal tissue dark green/grey.

Tissue characteristics and Symbiodinium presence

Fistular tyloes arranged criss-crossing parallel to surface in ectosome, irregularly in choanosome and acanthostrongyles rarely and irregularly dispersed throughout fistule. Acanthostrongyles far more abundant in erosion chamber choanosome, outnumbering tyloes and dispersed irregularly as per tyloes. No evidence for photosymbionts, neither by surface fluorescence measured by PAM, nor through histology.

Spicules

Megascleres – Comprised of numerous acanthostrongyles and terminally microspined tylotes. Acanthostrongyles softly curved, with regularly spaced spines orientated towards the middle of the spicule. Spine distribution varied from covering the entire spicule (Fig. 2.10C) to concentrated at the peripheries (Fig. 2.10D). Acanthostrongyle dimensions (min-max and mean): length 181 - 250 μm ($222.2 \mu\text{m} \pm 13.4 \text{ SD}$) and shaft width 8 - 16 μm ($13.1 \mu\text{m} \pm 2.0 \text{ SD}$). Tylotes long and slender, with microspined heads (Fig. 2.10E & F). Predominantly straight but occasionally slightly bent (Fig. 2.10E). Tylote dimensions (min-max and mean): length 182 - 262 ($221.8 \mu\text{m} \pm 22.5 \text{ SD}$), shaft width 4 - 7 μm ($5.0 \mu\text{m} \pm 0.8 \text{ SD}$) and head width 4 - 8 μm ($5.5 \mu\text{m} \pm 1.1 \text{ SD}$).

No microscleres found.

Habitat and occurrence

Very rare in the Wakatobi; only found in rubble at shallow depth (5-7 m) at two low turbidity/high flow sites.

Figure 2.10. *Zyzzya criceta*. (A) field image of fistules protruding from coral rubble; (B) field image of erosion cavity; (C & D) acanthostrongyles; (E) tylote; (F) microspined tylote head.

Remarks

The World Porifera Database presently accepts five valid species of *Zyzzya* (van Soest et al. 2017): *Z. coriacea* (Lundbeck 1910), *Z. criceta* (Schönberg 2000a), *Z. fuliginosa* (Carter 1879), *Z. invemar* (van Soest et al. 1994), and *Z. papillata* (Thomas 1968). Comparing these to my samples, four species were discounted as not analogous and the Wakatobi material was identified as *Z. criceta*.

Judging from the morphology and older synonyms, Lundbeck's North Atlantic *Z. coriacea* appears to be an endopsammic species, not an endolithic one. Unlike the Wakatobi material, alcohol-preserved specimens of *Z. coriacea* are pale-violet, and the acanthotylotes are considerably longer than in the Wakatobi samples and strongly size variable. The Thomas (1968) species *Z. papillata* is endolithic-fistulate, but yellow, while the Wakatobi specimens were blackish green. In *Z. papillata* the acanthostrongyles are only about half as long as the microspined tylotes, while they are of similar length in the Wakatobi samples. *Z. invemar* is similar to the Wakatobi material in fistule size however it can be excluded due to spicule differences. The Wakatobi material does not have the regular verticils of spination on the acanthostrongyles nor the large size difference between acanthostrongyles and tylotes or the microscleres found in *Z. invemar*. Microspined tylotes that are significantly longer than acanthostrongyles is also a feature of *Z. fuliginosa*. Spicule dimensions provided for *Z. fuliginosa* spicules vary widely in the literature (Carter 1879; Dendy 1922; Hooper & Krasochin 1989; Schönberg 2000a), but the size difference between the two spicule types has been uniformly reported, and precludes the identification of Wakatobi sponges as *Z. fuliginosa*.

Z. criceta is a Pacific sponge, with characteristic dark green (almost black) fistules (Schönberg 2000a), but unlike the Wakatobi material they are bulbous rather than small-fistulate. As in the present samples, the two megascleres in *Z. criceta* are of similar length, but those in the Wakatobi sponges are about 30 μm shorter. Acanthostrongyles in *Z. criceta* are straight or slightly curved and spines are alike in shape and distribution as in the Wakatobi material. Tylotes are also similar in form in *Z. criceta*, they are predominantly straight (or occasionally slightly bent) with microspined heads.

2.5. Discussion

This study provides information on the bioeroding sponge fauna in the Wakatobi Marine National Park and advances our knowledge of the species composition of this critical functional group in Indonesian waters. Of the known species, the distribution of *C. schmidtii*, *Cl. hancocki* and *Z. criceta* is currently not listed as extending to Indonesian waters (WPD), although Hooper et al. (2000) suggest that *C. schmidtii* and *Cl. hancocki* could be. Regardless, this study provides the first description of *Z. criceta* outside of the GBR and describes two potential new species belonging to the *C. viridis* species complex.

The only other study to specifically address Indonesian bioeroding sponge taxonomy was by Calcinai et al. (2005) who focused on the reefs around the Island of Bunaken, in North Sulawesi, a site that is comparatively near the Wakatobi. Interestingly, the present study found no species in common with those identified by Calcinai et al. (2005) and both studies identified novel species. High variability in sponge assemblage composition between different geographic locations has been observed before in Indonesia (e.g. Amir 1992) and is likely to be due to a combination of environmental factors and dispersal ability (Zea 1993; Mariani et al. 2000). Larval dispersal ability is generally limited in sponges, dependent on a combination of larval behaviour, larval life-span and hydrographic regimes (Maldonado 2006; Mariani et al. 2006), and in the case of bioeroding sponges is highly limited (Mariani et al. 2000). Therefore differences in dispersal capacity may structure Wakatobi species diversity between a combination of more region-wide distributed species (e.g. *Cl. hancocki* and *S. cf. vagabunda*) and locally endemic species with limited dispersal capabilities.

The systematics of bioeroding sponges is particularly obscure and has had several recent revisions (Rosell & Uriz 1997; Rützler & Hooper 2000; Rützler 2002b). Many original descriptions are based on a single microscope slide, however spicule types (and sponge colour/morphology) can vary intraspecifically depending on environmental conditions (Rosell & Uriz 1991; Bavestrello et al. 1993). This plasticity means that intraspecific variation can sometimes outweigh interspecific variation, making some species particularly hard to identify. Indeed some authors have for example merely classified them as in the *C. viridis* spp. complex (e.g. Sammarco et al. 1987; Sammarco 1996). The difficulty in relying on observable morphological and spicule characteristics for identification purposes has led to the

experimentation in different identification diagnoses. One feature that is unique to bioeroding sponges is the erosion scars (pits) that are left on substrate. These pits have been used to identify sponge bioerosion in the fossil record (e.g. Perry & Bertling 2000) and more recently have been investigated as tool to aid speciation (Calcinai et al. 2003; 2004; 2007). However, while there were early indications that the macroscopic patterns of erosion pits differed between genera (Schönberg 2000a; Calcinai et al. 2004), the eroded substrate type appears to be an equally important determinant for these characteristics (Calcinai et al. 2007). Therefore the use of erosion pits requires caution and is not a solution to the potential inadequacies of traditional identification. Phylogenetic analysis offers the best resolution to these problems but has had particularly limited application in bioeroding sponges. Early work used a few nominal *Cliona* species to aid understanding of the relationship between families of the Hadromerida (Kelly-Borges et al. 1991; Borchiellini et al. 2000), but more recent Clionaidae-focused research is limited to the *C. viridis* spp. complex (Escobar et al. 2012; Leal et al. 2016) and a few other species (Barucca et al. 2007). For a fuller understanding of the systematics of this group, molecular analysis needs to be expanded to the less well studied species and genera of Clionaidae (such as *Sphaciospongia* and *Pione*), some of which have received little attention since their original description.

2.5.1. Conclusions

Regardless of our understanding of the systematic positioning of a species, the ability to differentiate between species in the field is critical to understanding how assemblages differ spatially and temporally. This chapter not only furthers our understanding of species composition on Indonesian reefs but provides the foundation for research into the environmental drivers that will potentially structure these assemblages on future degraded coral reefs.

Chapter 3: Bioeroding sponge assemblage distribution: the importance of substrate availability and sediment

3.1. Abstract

Despite coral reef health deteriorating globally, not all reef-associated organisms are in decline. Bioeroding sponges are a comparatively resilient group to the factors that stress and kill corals, and are increasing in abundance at many locations. However, there is a paucity of information on how environmental factors influence temporal and spatial variation in the abundance and diversity of these sponges, and how they might be affected by different stressors. I aimed to identify factors that explain differences in bioeroding sponge abundance and assemblage composition, and to determine whether bioeroding sponges benefit from dead substrate availability and from environmental conditions that contribute towards coral mortality. Abundance surveys were conducted in the Wakatobi region in Indonesia at reef sites characterised by different biotic and abiotic conditions. Bioeroding sponges occupied an average of 8.9% of suitable substrate with both abundance and assemblage composition differing significantly between sites, primarily attributed to differences in the availability of dead substrate. However, despite abundant dead substrate, sponge abundance was lowest at a highly sedimented and turbid site. My results suggest that if availability of dead substrate increases as a consequence of coral mortality, then bioeroding sponge abundance is also likely to increase. Conversely, these results also indicate that sedimentation mediated coral mortality, despite resulting in increased dead substrate, may not favour bioeroding sponges. Overall I demonstrate the importance of understanding the drivers of bioeroding sponge abundance and assemblage composition in order to predict possible impacts of different stressors on reefs communities.

3.2. Introduction

Coral reefs are among the most diverse ecosystems on Earth and harbour up to an estimated 9 million species (e.g. Small et al. 1998). They also provide critical ecosystem goods and services, with hundreds of millions of people reliant on them globally (Moberg & Folke 1999; Bouchet & Duarte 2006). Despite their importance, coral reefs worldwide are increasingly threatened by anthropogenic activities and have suffered from substantial declines in coral cover, habitat complexity and biodiversity over the past 50 years (e.g. Bruno & Selig 2007; Burke et al. 2011). In some locations, coral cover has already been reduced by 50% since the 1980's (Bruno & Selig 2007; De'ath et al. 2012). Such declines in spatially competitive scleractinian corals have the potential to provide less competitive benthic taxa with an opportunity to expand, and there are increasing reports of substantial reef community shifts (e.g. McManus & Polsenberg 2004; Norström et al. 2009). While the majority of the literature has focused on shifts from coral to macroalgal-dominated communities, many other groups of benthic taxa can potentially benefit from coral declines (Mumby 2009; Norström et al. 2009; Cheal et al. 2010; Bell et al. 2013). Bioeroding sponges are one such group, and are reportedly becoming more abundant on some degraded reefs in the Caribbean (e.g. Rützler 2002a; López-Victoria & Zea 2004), the eastern Pacific (Carballo et al. 2013), and on the Great Barrier Reef (GBR) (Schönberg & Ortiz 2009). Many bioeroding sponge species appear to be resilient to some of the stressors that are detrimental to corals (e.g. Schönberg & Suwa 2007; Enochs et al. 2015; Stubler et al. 2015), and some species are aggressive spatial competitors (e.g. López-Victoria & Zea 2005; Chaves-Fonnegra & Zea 2007; González-Rivero et al. 2011).

While a wide range of organisms contribute to bioerosion (e.g. Glynn 1997; Wisshak & Tapanila 2008), sponges regularly generate the majority of internal bioerosion on a reef and often represent 60-90% of macroborer activity (e.g. Risk et al. 1995; Mallela & Perry 2007). Rates of erosion can be very high, with some species capable of removing over 20 kg of calcareous substrate *per* m² sponge area *per* year (Schönberg 2002; Calcinaï et al. 2008). Furthermore, under certain environmental conditions that favour high abundances of bioeroding sponges, and in combination with reduced coral cover/calcification, the balance between calcification and reef erosion can be altered by sponge bioerosion, resulting in net carbonate erosion (e.g. Nava & Carballo 2008; Perry et al. 2008; Kennedy et al. 2013). Moreover, bioerosion has been identified

as a principal driver of the loss of structurally complexity (Alvarez-Filip et al. 2011). This is important, as the three-dimensional structure of coral reefs provides critical habitat and maintains densities and biomass of other common reef organisms, as well as being central to ecosystem services that support tourism and shoreline protection (e.g. Enochs & Manzello 2012; Graham & Nash 2012).

Given the potentially negative consequences of increases in bioeroding sponge abundance on reefs, it is important to understand the factors that influence their abundance and assemblage composition. As bioeroding sponges can only inhabit calcareous substrates, the availability of suitable substrate has been identified as a key factor influencing their abundance (Chaves-Fonnegra et al. 2007; Carballo et al. 2008a; Schönberg & Ortiz 2009; Schönberg 2015a). Other important environmental and abiotic factors that have been previously shown to regulate bioeroding sponge abundance include eutrophication (e.g. Holmes et al. 2000; Chavez-Fonnegra et al. 2007; Nava et al. 2014), light availability (e.g. López-Victoria & Zea 2005), and sedimentation and turbidity (Muricy 1991; Nava & Carballo 2013; see summary in Schönberg 2008). Many of these environmental parameters can be associated with reef degradation: polluted reefs are often eutrophic and have elevated chlorophyll *a* concentrations (chl *a*), and reefs that are subject to excessive terrestrial run-off are typically characterised by highly turbid water with high sedimentation rates, and may experience large fluctuations in salinity (Burke et al. 2011).

In this Chapter, I hypothesised that coral mortality, resulting in increased dead substrate availability, and the environmental conditions that contribute towards this mortality or reduce the severity of spatial competition, are beneficial for bioeroding sponges. To test this hypothesis I determined how different biotic and abiotic factors influenced the abundance and assemblage composition of bioeroding sponges on Indonesian reefs. Understanding these patterns will provide an increased understanding of how reef degradation may affect bioeroding sponge abundance and how future reefs might function if degradation continues.

3.3. Methods

3.3.1. Study area

The research for this chapter was conducted within the Wakatobi region of southeast Sulawesi, Indonesia. The Wakatobi supports a high diversity of marine species and was gazetted as a Biosphere Reserve by UNESCO in 2012 (UNESCO 2012). The region is also home to over 90,000 people who depend on the local reefs for food and other resources (Cullen et al. 2007).

Figure 3.1. Site map of wider survey region in the Wakatobi (top left) and the core survey sites around the islands of Hoga and Kaledupa.

Surveys were conducted at seven sites on the fringing reefs around the islands of Hoga and Kaledupa in March-April 2014 and then continued in June 2014 to include another four sites around the islands of Wanci and Tomia (Fig. 3.1). Survey sites were chosen to represent a variety of reef types, environmental conditions and levels of reef degradation. The initial core seven sites included three steep-wall reefs: Buoy 1 and 3, and Ridge 1; three sloping reefs: Kaledupa 1, Kaledupa Double Spur and Pak Kasim's; and Sampela 1, which is adjacent to a

stilted Bajo village and is considered to be highly degraded (McMellor & Smith 2010). The additional four sites were: Karang Gurita, a coral atoll located off the island of Wanci; Tomia 1 and 2, sloping reefs off the island coast of Tomia, which appear relatively healthy with high branching coral cover; and Wanci Harbour, a turbid and sedimented sloping reef within Wanci Harbour. Sites Buoy 1 & 3, Kaledupa 1 and Kaledupa Double Spur, Karang Gurita, Pak Kasim's, Ridge 1, Sampela 1, Tomia 1 & 2, and Wanci Harbour are abbreviated in figures as B1, B3, K1, KDS, KG, PK, R1, S1, T1, T2 and WA, respectively.

3.3.2. Bioeroding sponge abundance and benthic composition

Bioeroding sponge abundance and substrate characteristics were assessed *in situ* using line intercept transects at 5 and 10 m depth for the initial seven core survey sites in March-April 2014, and at just 10 m depth (due to logistical constraints) for the four additional sites surveyed in June 2014. At each site and depth, six 10 m transects were haphazardly deployed running parallel to the reef contours with a minimum separation of 10 m between replicate surveys. Sponge abundances and substrate composition were recorded by visually inspecting ten 1 m subsamples on each transect and recording the linear distance of each sponge species and substrate type that intercepted the measuring tape (after English et al. 1994; Schönberg 2015a). Schönberg (2015a) found linear distance to be proportional to areal extent, therefore linear distributions were treated as a proxy for percentage benthic cover. Substrate types were listed as 'live coral', 'live other' (excluding algal turf on dead substrate, which was counted as dead substrate), 'dead substrate' and 'sand'.

3.3.3. Environmental variables

Throughout March-August 2014 and May-June 2015, a XR-420 CTD data logger (RBR, Ottawa) was deployed at the seven core sites on haphazardly selected dates to measure turbidity and chl *a*. The CTD was set to record every minute with no averaging. Each deployment was for a minimum of 24 hours, with a minimum of three separate deployments at each site. This data collection methodology was identical (including same equipment and sites) to a previous study by Powell et al. (2014) in 2010. Given this, the data were combined to create average values for each environmental parameter for each site. Averages were based on each 24 h deployment with

minutes considered as subsamples within each 24 h period. Due to time constraints, no CTD data were collected from the four additional sites around Tomia and Wanci.

Sediment deposition and retention were indirectly evaluated by measuring depth of settled sediment on horizontal and 30-60° inclined surfaces without live cover. Measurements were taken at 3 m intervals along two haphazardly placed 30 m transects at each depth and site, and hence were limited to just 10 m depth at the four additional sites. The horizontal and inclined measurements were combined to create a mean measure of depth of settled sediment for each site.

Mean proportional current velocity for the seven core sites was quantified using plaster of Paris casts, commonly referred to as “clods” (e.g. Jokiel & Morrissey 1993). Clods were prepared in rubber moulds according to the manufacturer’s mixing instructions, to produce 5 cm diameter hemispherical casts with stainless steel nails embedded and passing through the centre. The plaster was allowed to air-dry for 24 h before being dried to constant weight in a 100 °C oven. The dry weight was recorded for each clod before deployment (mean weight = 59.3 g ± 0.54 SE). Three clods were gently nailed into bare substrate at each site at 10 and 5 m depth for three 24 hr periods, before recovering and repeating dry weight measurements. For each 24 h deployment, three control clods were placed on the reef within an anchored 40 l perforated bucket; this excluded water currents experienced by the freely deployed clods, but allowed limited water exchange and exposed the clods in the buckets to the same water temperature and salinity (which also affect clod dissolution; Jokiel & Morrissey 1993). Assessment of proportional differences in water movement between sites was achieved by converting dry weight lost by each clod into the percentage of initial clod weight lost, and subtracting mean control percentage losses (Doty 1971).

3.3.4. *Statistical analysis*

All univariate statistical analyses were performed in SPSS (version 21; IBM, Auckland, New Zealand) and multivariate analysis using the PRIMER-E v6 software package with the permutational multivariate analysis of variance (PERMANOVA) add on (Clarke & Gorley 2006).

Abundance of each bioeroding species for each transect was calculated using the mean linear extent across the ten subsamples on each transect and used as a proportional indicator for areal cover (see Schönberg 2015a). Previous studies have consistently found that bioeroding sponge abundance correlates with the abundance of calcareous substrate and therefore used substrate-standardised abundance data when analysing environmental drivers (Chaves-Fonnegra et al. 2007; Carballo et al. 2008a; Schönberg & Ortiz 2009; Schönberg 2015a). After finding similar correlations in the Wakatobi (see below), total bioeroding sponge abundance and individual species abundances were standardised to available dead substrate (including that which the sponges already occupy).

The absence of data from 5 m depth at the four additional survey locations meant that, where differences were found between depths, the analysis was separated into two sections: all eleven sites were evaluated for 10 m depth; and the seven core sites at both 5 and 10 m depth. In addition, the lack of CTD deployment at these four additional sites meant that the analysis of interactions between environmental variables and bioeroding sponges only incorporated data from the core sites. Due to the considerable differences in environmental conditions between Sampela 1 and the other sites, and the tendency for this site to drive collinearity amongst variables, the analysis of the core sites was conducted twice, once including Sampela 1 and once without.

Bioeroding sponge abundance and diversity

Differences in total bioeroding sponge abundance and species diversity (Shannon's index; H') between sites and depths were tested using a two factorial general linear model (GLM). Where differences occurred, Tukey's or Gabriel's (in the case of unequal sample sizes) *post hoc* procedures were used to identify where the differences occurred. Correlations between individual environmental/benthic factors and bioeroding sponge abundance and diversity were assessed with Pearson's product-moment correlation coefficients. Data were square-root or log transformed to meet the necessary assumptions of variance and generate normality for both tests. For any data that failed to meet these assumptions despite transformation, non-parametric tests were used; namely a Kruskal-Wallis or Spearman's Rank test.

Environmental characterisation

Environmental characterisation of each site was achieved using a multivariate analysis within PRIMER. All analyses were based on resemblance matrices calculated from normalised data using Euclidean-Distance similarity coefficients. Draftman's plots of all pairwise correlations were checked for collinearity and skewness in the abiotic and biotic data; these suggested that fourth-root transformation was appropriate for an increase in normality for all the variables. Biotic and abiotic differences between sites and depths were examined using one and two-factor PERMANOVAs (site and depth as factors with 7 levels or site as factor with 11 levels), and results were graphically displayed through principal coordinate analysis (PCO). The inter-site differences in abiotic and biotic variables were characterised with Pearson's correlations (>0.4) between PCO axes and the individual abiotic/biotic components.

Bioeroding sponge assemblage patterns

All biological assemblage data analyses were based on resemblance matrices calculated from square-root transformed data using Bray-Curtis similarity coefficients. The Bray-Curtis similarity index was chosen due to the large number of zeros in the data set, which this index ignores, and abundance data were transformed to preserve information on relative abundance, while reducing the effect of overly abundant or rare species (Clarke 1993). Due to the general sparseness or patchiness of bioeroding sponge abundances and the complete absence on one transect, a dummy species with the abundance value of 0.5 was added to each transect in order to diminish the erratic behaviour of the Bray-Curtis coefficient (Clarke et al. 2006). Differences in sponge assemblage compositions between sites were assessed using one- and two-factor PERMANOVAs of the same design as for the abiotic/biotic data. To identify those species that were contributing towards any assemblage dissimilarity between sites or depths, a SIMPER analysis was performed. Associations between bioeroding sponge assemblage structure and abiotic/biotic variables were investigated in a distance-based multiple linear regression model (DISTLM), which is a non-parametric permutation-based procedure that enables significance testing of explanatory variables against multivariate response variables (Anderson et al. 2007). In order to find the most parsimonious model, Akaike's Information Criterion (AIC), a step-wise procedure, adjusted for small sample sizes (AICc) was used (Burnham & Anderson 2004). As with univariate correlations, the DISTLMs were repeated twice; once with the outlier site

Sampela 1 and once without. DISTLM outputs were represented graphically with a distance-based redundancy ordination (dbRDA), including a 2D scatterplot to illustrate differences between sites and 2D bubble plots to illustrate differences in species abundance. The influence of the predictor variables selected by the DISTLM on the abundance of the individual species that were contributing the greatest difference between sites were tested using Spearman's Rank correlations.

3.4. Results

3.4.1. Biotic and abiotic site characteristics

Substrate composition of the core sites did not differ significantly with depth (PERMANOVA, Pseudo-F = 1.7118, $p = 0.143$; Table 3.1). Therefore, analyses referring to substrate composition across all 11 sites were performed including both depth categories. Substrate composition differed significantly between the sites (PERMANOVA, Pseudo-F = 9.1056, $p = 0.001$), with 59.2% of the variation being explained by the principal coordinate analysis (PCO; Fig. 3.2A). Tomia 1 and Buoy 3 were characterised by hard corals; Kaledupa Double Spur and Kaledupa 1 by dead substrate; Karang Gurita, Sampela 1 and Wanci Harbour by sand; and the other four sites were more heterogeneous in their substrate composition. The environmental conditions also varied significantly between the core sites where the CTD and clods were deployed (PERMANOVA, Pseudo-F = 26.572, $p = 0.001$), but not between depths. The two axes of the PCO together explained 63.4% of the variation (Fig. 3.2B), further characterising the sites: elevated chl *a* concentration, comparatively high settled sediment and turbidity at Sampela 1; low flow rates at Buoys 1 and 3; high flow rates at Kaledupa 1, Kaledupa Double Spur and Ridge 1; and comparatively heterogeneous environmental conditions at Pak Kasim's.

Figure 3.2. Principal coordinate analysis of site similarities with respect to their physical and water quality parameters. A) Comparison of all eleven study sites with regards to substrate composition and B) the seven core study sites regarding substrate composition and environmental factors. Overlaid vectors represent components that have a Pearson's correlation of greater than 0.4 with either of the PCO axes.

Table 3.1. Substrate characteristics and environmental factors of each site. Each value represents a site mean and error values are standard errors of these means.

Factor	Unit	Site										
		B1	B3	K1	KDS	KG	PK	R1	S1	T1	T2	WA
<i>Live coral</i>	% cover	19.29 (±2.57)	33.88 (±4.20)	11 (±1.79)	15.04 (±4.06)	19.25 (±8.91)	23.75 (±4.30)	27.98 (±4.55)	11.58 (±2.27)	64.58 (±7.05)	27.58 (±8.11)	18.0 (±2.55)
<i>Dead substrate</i>	% cover	37.96 (±3.80)	16.17 (±1.80)	39.98 (±4.07)	46.04 (±4.94)	24.33 (±4.53)	33.63 (±2.16)	41.17 (±4.05)	34.08 (±3.04)	20.33 (±4.96)	28.42 (±4.58)	41.92 (±2.41)
<i>Live other</i>	% cover	38.04 (±3.22)	45.12 (±3.35)	35.13 (±4.82)	35.38 (±4.50)	36.33 (±7.64)	33.91 (±3.76)	24.92 (±2.61)	23.25 (±4.84)	10.75 (±3.17)	14.42 (±1.93)	31.92 (±3.57)
<i>Sand</i>	% cover	4.52 (±1.46)	4.21 (±1.92)	7.67 (±2.18)	3.88 (±1.48)	20.08 (±9.34)	8.29 (±2.94)	8.39 (±3.39)	30.38 (±3.54)	4.42 (±3.05)	29.42 (±11.84)	7.67 (±2.66)
<i>Sediment thickness</i>	mm	0.78 (±0.18)	1.95 (±0.37)	0.25 (±0.12)	0.5 (±0.10)	2.23 (±0.54)	1.06 (±0.13)	0.85 (±0.16)	2.94 (±0.28)	0.5 (±0.17)	0.4 (±0.12)	2.45 (±0.86)
<i>Water movement</i>	% clod weight loss	8.36 (±0.84)	8.79 (±0.75)	18.73 (±0.67)	24.42 (±1.81)	n/a	12.78 (±2.60)	16.93 (±1.62)	13.88 (±0.81)	n/a	n/a	n/a
<i>Turbidity</i>	Standard turbidity units	2.66 (±1.22)	2.06 (±0.70)	1.69 (±0.50)	2.07 (±0.40)	n/a	1.75 (±0.20)	1.32 (±0.60)	4.10 (±1.04)	n/a	n/a	n/a
<i>Chl a</i>	µg/l	0.36 (±0.12)	0.36 (±0.02)	0.12 (±0.10)	0.31 (±0.08)	n/a	0.94 (±0.14)	0.33 (±0.03)	2.54 (±0.05)	n/a	n/a	n/a

3.4.2. *Sponge abundance, diversity and species composition*

Bioeroding sponges occupied an average of 3.1% (± 0.21 SE) of total reef area, and total abundance varied significantly between sites (GLM, $F_{(10,108)} = 5.721$, $p < 0.001$), but not between depths (GLM, $F_{(1,108)} = 0.242$, $p = 0.624$). Abundance was highest at Wanci Harbour (4.9% ± 0.63 SE) and lowest at Tomia 1 (1.3% ± 0.31 SE). Overall, bioeroding sponge abundance was positively correlated with availability of dead calcareous substrate (Pearson's, $r^2 = 0.345$, $p < 0.001$), thus justifying the standardisation of abundance data to the availability of dead substrate (%cover). Abundance was also negatively correlated with the abundance of sandy substrate (Pearson's, $r^2 = -0.199$, $p < 0.039$), but showed no significant correlation with either live coral or other live cover (Table 3.2). Following standardisation to dead substrate, bioeroding sponges were found to occupy an average of 8.9% cover (± 0.7 SE) of suitable habitat across all sites, up to 21.9% cover (± 2.7 SE) at Buoy 3 and as low as 3.5% cover (± 0.8 SE) at Sampela 1 (Fig. 3.3A). There was again a significant difference among sites and between depths (GLM, $F_{(10,108)} = 17.366$, $p < 0.001$ and $F_{(10,108)} = 10.445$, $p = 0.002$, respectively). Across the core sites, %cover decreased on higher water movement reefs and on those with high chl *a* concentrations (Table 3.2). Omitting Sampela 1, data still showed that within the remaining core sites, water movement limited %cover, but greater depth of settled sediment and turbidity were positively correlated with %cover and chl *a* concentration had no influence (Table 3.2). The abundance of different substrate types (with the exception of dead substrate) also had no effect on the %cover of these sponges (Table 3.2).

Species diversity of the bioeroding sponges differed significantly between the 11 sites, but not between depths (Kruskal-Wallis, $p = 0.003$ and $p = 0.986$, respectively). Species diversity was highest at Wanci Harbour and Buoys 1 & 3 ($H' = 1.173$, 1.098 and 1.102, respectively), and lowest at Karang Gurita and Tomia 1 ($H' = 0.380$ and 0.385, respectively; Fig. 3.3B). Sponge species diversity increased with increasing cover of "other live" benthos, regardless of whether or not Sampela 1 was included in the analysis. However, a significant negative correlation with chl *a* concentration only occurred when Sampela 1 was included in the analysis, and a significant negative correlation with turbidity only when Sampela 1 was omitted (Table 3.2).

Table 3.2. Results of bivariate correlations comparing total sponge abundance and species diversity with substrate characteristics and environmental factors. Abundance tests using Pearson's and diversity tests using Spearman's Rank. Significant correlation probabilities in bold. Analyses conducted with and without Sampela data.

Factor	Dependent variable	Sampela included		Sampela excluded	
		r	p	r	p
Live coral	Total abundance	-0.159	0.099	-0.287	0.005
	Standardised Total Abundance	0.186	0.054	0.031	0.765
	Species Diversity	0.048	0.622	-0.033	0.750
Live other	Total abundance	0.055	0.571	0.080	0.436
	Standardised Total Abundance	0.164	0.090	0.219	0.032
	Species Diversity	0.206	0.032	0.236	0.021
Dead substrate	Total abundance	0.345	>0.001	0.344	0.001
	Standardised Total Abundance	-	-	-	-
	Species Diversity	0.152	0.117	0.134	0.194
Sand	Total abundance	-0.199	0.039	-0.077	0.455
	Standardised Total Abundance	-0.126	0.1944	0.062	0.547
	Species Diversity	-0.073	0.451	0.019	0.855
Settled sediment	Total abundance	-0.110	0.256	0.176	0.087
	Standardised Total Abundance	-0.950	0.388	0.483	<0.001
	Species Diversity	-0.036	0.712	0.081	0.432
Turbidity	Total abundance	-0.364	0.001	0.306	0.009
	Standardised Total Abundance	-0.177	0.107	0.471	<0.001
	Species Diversity	0.070	-0.527	0.309	0.008
Chl <i>a</i>	Total abundance	-0.400	>0.001	-0.222	0.061
	Standardised Total Abundance	-0.440	<0.001	-0.159	0.183
	Species Diversity	-0.277	0.011	-0.161	0.177
Water movement	Total abundance	-0.191	0.082	-0.189	0.111
	Standardised Total Abundance	-0.328	0.002	-0.435	<0.001
	Species Diversity	-0.061	0.583	-0.097	0.415

Figure 3.3. Bioeroding sponge distribution patterns *per* sample site and across all depths. A) Total sponge abundance (standardised to substrate). B) Species diversity. Standard errors shown.

Although the field surveys recognised eight bioeroding sponge species as being dominant within the assemblage (Chapter 2), and rare species were not considered, 81.8% of the abundance of the sponges was represented by only three species – *Cliona* aff. *viridis* n. sp. B (39.1%), *Cliothosa* cf. *aurivillii* (23.2%) and *Spheciospongia* cf. *vagabunda* (19.5%). Species assemblage composition was significantly different among the 11 sites (PERMANOVA, Pseudo-F = 5.1843, $p = 0.001$; Fig. 3.4), and between 5 and 10 m depth (PERMANOVA, Pseudo-F = 6.3, $p = 0.001$). Given the influence of depth on assemblage composition, the multivariate analysis with regards to species composition was split into two analyses: the seven core sites including all depths (and CTD and clod data), and the full 11 sites with just 10 m depth surveys.

Figure 3.4. Average bioeroding sponge species abundance (standardised to substrate) at each core survey site. Standard errors shown.

Species composition at all eleven sites combined and for 10 m depth

At 10 m depth, species composition significantly differed among the 11 sites (PERMANOVA, Pseudo-F = 3.5829, $p = 0.001$), which had an average dissimilarity of 61.1%. The largest differences existed between Sampela 1 and either Buoy 3, Karang Gurita or Tomia 1 (86.0, 82.0 and 82.3%, respectively). The common *S. cf. vagabunda* at Buoy 3 had an average abundance of 19.3% cover, but at Sampela only an average cover of <0.1% cover, representing 45.6% of the site's assemblage difference. The abundance of another dominant species, *C. aff. viridis* n. sp. B, was the primary reason for the assemblage differences between Sampela 1 (0.9% cover) and both Karang Gurita (5.3% cover) and Tomia 1 (3.9 % cover), which contributed 45.0% and 39.8% towards the dissimilarities, respectively. The best sponge assemblage model in DISTLM found dead substrate to be the only benthic variable with a significant correlation with the biotic data before they were standardised to availability of dead substrate, explaining just 5.4% of the variation. Following standardisation to dead substrate, the best and only predictor of assemblage composition was live coral cover, accounting for just 3.7% of assemblage variation.

Species composition at the seven core sites

As above, 68.1% of the 52.6% difference in species composition between depths was attributed to the three most common species, *C. aff. viridis* n. sp. B, *Cl. cf. aurivillii* and *S. cf. vagabunda*. Variation in *Cl. cf. aurivillii* abundance contributed 25.7% of the difference; the species was more common in shallower water and had an average abundance of 2.6% cover on the 5 m surveys, but only 1.1% cover on the 10 m surveys. The reverse was true for *S. cf. vagabunda*, which at 5 m had an average abundance of 1.5% cover, but 4.3% cover at 10 m, accounting for 19.1% of variation between depths. Abundances of *C. aff. viridis* n. sp. B accounted for 23.4% of variation, and although average abundance was similar at 5 and 10 m depth (2.6% and 3.1% cover, respectively), there was high within-group variation.

The three largest inter-site differences in assemblage composition occurred with Buoy 3 *versus* Sampela 1, Kaledupa Double Spur and Kaledupa 1 (80.0%, 70.1% and 68.6%, respectively), and were largely driven by differences in the abundance of *S. cf. vagabunda*. This species was relatively abundant at Buoy 3 (average abundance of 13.3% cover and within-site assemblage similarity contribution of 58.0%), but had low abundance at Sampela 1 (< 0.1% cover), Kaledupa

Double Spur (0.7% cover) and Kaledupa 1 (0.5% cover), contributing 40.7%, 35.3% and 37.8% towards inter-site dissimilarity, respectively. The best sponge assemblage model in DISTLM explained 30.1% of variation in assemblage structure based on non-substrate-standardised abundance: dead substrate (14.0%), chl *a* concentration (6.4%), water movement (4.9%) and the proxy for sedimentation, sediment thickness (4.9%) (Fig. 3.5A).

Removal of the Sampela 1 data increased the total explanation value slightly to 33.0%. The explanatory power of dead substrate (16.1%) water movement (5.2%) and settled sediment (4.0%) changed little, there was no explanatory value for chl *a* concentration, and changes in turbidity (4.2%) and live coral cover (3.5%) were found to be slightly influential (Fig. 3.5B).

Figure 3.5. Distance based redundancy analysis (dbRDA) ordinations of fitted models for assemblage composition. A) Seven core sites and both depth categories. B) Core sites and both depth categories with the omission of Sampela.

When abundance was standardised to dead substrate availability, 23.9% of assemblage structure variation was explained by environmental variables including water movement (9.3%), settled sediment (8.2%) and chl *a* concentration (6.4%). The removal of Sampela 1 from this analysis explained a similar amount of variation (24.4%), but the explanatory value of settled sediment was greater (14.8%), water movement became less important (4.4%), chl *a* concentration no longer had an effect, and turbidity was found to be more important (5.2%).

Individual species

Greater abundance of dead substrate resulted in higher abundance by two of the three dominant boring sponge species: *C. aff. viridis* n. sp. B and *Cl. cf. aurivillii* (Spearman's Rank, $r_s = 0.245$, $p = 0.011$ and $r_s = 0.552$, $p < 0.001$, respectively). However, *S. cf. vagabunda* had an inverse relationship with dead substrate (Spearman's Rank, $r_s = -0.299$, $p = 0.002$) (Fig. 3.6). Substrate-standardising the abundance of these species and investigating their individual relationships with the explanatory variables identified by the DISTLM revealed that the abundance of *C. aff. viridis* n. sp. B correlated with none of these variables, increasing settled sediment limited the abundance of *Cl. cf. aurivillii* but positively influenced *S. cf. vagabunda*, and the abundance of *Spheciospongia cf. vagabunda* was limited by high water movement. (Appendix 1). Omitting Sampela 1 changed these relationships very little, but revealed a stronger relationship between *Spheciospongia cf. vagabunda* and settled sediment; it was also found that higher turbidity increased the abundance of this species (Appendix 1).

Figure 3.6. Distance based redundancy analysis (dbRDA) ordinations of fitted models for assemblage composition of the seven core sites (both depth categories), with the omission of Sampela 1. Overlapping 2D bubbles represent the abundance *Cliothosa cf. aurivillii* (top), *Cliona aff. viridis n. sp. B* (middle) and *Spheciospongia cf. vagabunda* (bottom).

3.5. Discussion

By identifying putative environmental drivers of bioeroding sponge abundances this chapter provides an opportunity to assess how different bioeroding sponges respond to environmental variability using a model reef system in the world's most biodiverse coral reef region. This is the first such study in the central Indo-Pacific. I hypothesised that factors leading to coral stress and mortality, resulting in decreased spatial competition and increased availability of dead substrate, are beneficial for bioeroding sponges. While I found that the availability of suitable dead substrate was consistently positively correlated with the overall abundance of bioeroding sponges and was the best predictor of differences in assemblage composition, I also found negative impacts of high levels of sedimentation on bioeroding sponges. This suggests that while coral health and abundance can decline as a result of intensifying sedimentation (e.g. Fabricius 2005; Erftemeier et al. 2012), promoting the availability of dead substrate, sedimentation will not necessarily also result in higher bioeroding sponge abundance. Furthermore, while dead substrate was the key predictor for differences in bioeroding sponge abundance and assemblage composition, at best it only explained 15.1% of biotic variation, indicating that while bioeroding sponges depend on dead substrate, they do not settle or survive on it uniformly (Driscoll 1967; Callahan 2005). Finally, inter-species variation in abundance with respect to environmental factors illustrated how largely ubiquitous patterns should not readily be generalised across the entire taxon, but that species-specific requirements apply (as they do for other bioeroders: Schönberg et al. 2017).

3.5.1. Abiotic and biotic influences on abundance, diversity and assemblage composition

A number of abiotic and biotic factors were evaluated as possible drivers of bioeroding sponge distribution patterns, but none of them explained more than 33% of the total variability. Among these factors, availability of dead substrate was consistently one of the most important factors causing differences in bioeroding sponge abundance and assemblage composition in Indonesia (present data; Holmes et al. 2000). This is consistent with earlier studies on the Australian GBR (Schönberg 2001; 2015a; Schönberg & Ortiz 2009), the Mexican Pacific (Nava & Carballo 2013), and in the Caribbean (Callahan 2005; Chaves-Fonnegra et al. 2007). This observation is a consequence of the sponges' endolithic habit that creates a dependency on calcium carbonate structures (see Schönberg 2008). Nevertheless, this relationship could not uniformly be shown

across all species studied, and differences were primarily driven by the abundances of the papillate *C. cf. aurivillii* and *C. aff. viridis* n. sp. B. Both species dominated at three sites with a high occurrence of dead substrate and little live coral. Conversely, *S. cf. vagabunda* became more common where dead substrate availability was low, but coral cover was relatively high. This suggests that biological requirements vary between these species and could be due to different levels of dependency on endolithic life style. Some *Spheciospongia* spp. are facultative endoliths, known to develop into fleshy or massive morphologies that are independent of the endolithic habit (Rützler 2002b). *Cl. cf. aurivillii* was originally described as occurring in a free-living, as well as in an endolithic form (Lindgren 1897), but the species is more typically associated with the endolithic form. Not enough is known about *C. aff. viridis* n. sp. B to assess how tightly it is associated with the substrate, but in Wakatobi it was only observed in endolithic form. Furthermore, dispersal capabilities of bioeroding sponges are thought to vary significantly, from the extremely limited (<10 m) to the extensive (>10 km) (Mariani et al. 2000; Chaves-Fonnegra et al. 2015; Bautista-Guerrero et al. 2010; 2016). Thus, depending on species-specific traits, distribution patterns can be further decoupled from substrate availability, as some recruits may settle close to the parent sponge rather than evenly spreading out across all available substrate (Callahan 2005).

Bioeroding sponges have repeatedly been shown to react strongly to gradients of eutrophication, with the abundance of a number of species, and resulting damage by bioerosion, increasing with increasing nutrient levels (e.g. Rose & Risk 1985; Holmes et al. 2000; Ward-Paige et al. 2005). However, my proxy for nutrient enrichment (chl *a* concentration) only correlated with boring sponge abundance and assemblage composition when data from Sampela 1 were included in the analysis. The otherwise lack of a clear nutrient stimulus may be explained by the generally low and similar chl *a* concentrations at most sites and interactions with other factors that can mask the effects of nutrient enrichment, leading to different net responses (e.g. Chaves-Fonnegra et al. 2007; Holmes et al. 2000; Reis & Leão 2000; Holmes et al. 2009; Nava et al. 2014). When including Sampela 1, chl *a* concentration was negatively correlated with sponge abundance, which appears inconsistent with the concept of nutrient enrichment being beneficial to these sponges. However, Sampela 1 was not only characterised by high chl *a* levels, but it was also the most turbid and sedimented of the surveyed sites. Low abundances of bioeroding sponges in eutrophic environments that experience excessive sedimentation or suspended particle

concentrations have also been found in other studies. For example, Edinger et al. (2000) noted that bioeroding sponges were rare on reefs in the highly eutrophic Jakarta Bay, which the authors attributed to high sedimentation levels. Nava and Carballo (2013) came to a similar conclusion when they observed no relationship between the distribution of boring sponges and chl *a* concentration on Pacific Mexican reefs.

Sedimentation can influence sponge distribution patterns by preventing settlement, by impeding vital physiological functions or by controlling survival and therefore selecting for adapted species over others (Bell et al. 2015; Schönberg 2016). Some bioeroding sponges can tolerate high levels of sedimentation, being covered by a thin layer of sand or are even adapted to live mostly buried in sediments (endopsammic; Holmes et al. 2000; Schönberg 2016). However even these tolerant species are thought to require a patch of free substrate for larval settlement and need to establish elevated, emerging structures before their main bulk becomes sediment covered. In the Wakatobi, up to 15% of the observed variance was explained by variation in the depth of settled sediment covering otherwise suitable substrate. The low total sponge abundance at Sampela 1 and the difference including or omitting this site's data has in regards to the importance of settled sediment implies that sedimentation resilience of the some bioeroding sponges has its limits. In this Chapter, sedimentation effects on individual species primarily emerged as a positive correlation of *S. cf. vagabunda* abundance with settled sediment depth, when excluding Sampela data. Several species within this genus are known to benefit from living embedded in sediments and are adapted to tolerate sediment deposition on their surfaces (e.g. Schönberg 2016). However, no endopsammic individuals were observed in this study, and it should be noted that the sites with high *S. cf. vagabunda* abundance and high levels of settled sediment were also wall sites (primarily Buoys 1 & 3). The presence of vertical surfaces represents sediment-free substrate and can decouple the impacts of sedimentation from horizontal substrates at the same site (Bell & Barnes 2000). This situation offers a refuge for less sediment-tolerant species (in the Wakatobi: Bell & Smith 2004). The almost entire absence of *S. cf. vagabunda* from Sampela 1, implies either a limitation in settled sediment tolerance or a vulnerability to the high concentrations of suspended material also associated with the site. The latter is potentially the case for *S. cf. vagabunda*, given that the species has been associated with sandy habitats in other studies (e.g. Bergquist 1965; Sutcliffe et al. 2010). However, as discussed

in Chapter 2, *S. cf. vagabunda* is potentially part of an unresolved species complex of which Wakatobi specimens represent a sediment intolerant species.

Holmes et al. (2000) found that the concentration of suspended material and turbidity were proportional to sponge bioerosion and explained this with collinearity to nutrient availability. Depending on the quality of the suspended materials, however, turbidity can counteract or be independent from the positive influence of nutrient enrichment (this Chapter; Holmes 2000). Whilst low levels of particle suspension in the water column were beneficial for the Wakatobi bioeroding sponges, evidence from Sampela 1 suggested that excessive turbidity may have limited bioeroding sponge abundance, a similar finding to that of Chaves-Fonnegra et al. (2007) in the Caribbean. Sponges have the capacity to be affected by suspended particles either by direct impairment of the pumping and filtration apparatus or indirectly through shading (Bell et al. 2015). If suspended particle concentration is limiting the abundance of *S. cf. vagabunda* at Sampela 1 it is likely due to direct impairment of vital functions rather than shading, as no photosymbionts were found in the species. However, turbidity induced shading may have contributed to the absence of two of the three locally abundant zooxanthellate species at Sampela 1. By altering the quality and quantity of photosynthetically active radiation, turbidity can regulate distribution patterns of phototrophic sponges (Caballero et al. 2009). For example, the zooxanthellate *Cliona orientalis* is most abundant near or below 5 m depth on clear-water reefs on the GBR, but at more turbid sample sites it dominates in the upper subtidal and intertidal regions (Bergman 1983, as *Cliona viridis*; Schönberg 2001). However, light requirements are likely species specific, as other zooxanthellate clionoids appear capable of persisting in conditions of greatly reduced light availability (Rosell & Uriz 1991).

3.5.2. Implications for reef management

Globally increasing abundances of bioeroding sponges on degraded coral reefs are primarily attributed to the sponges' ability to exploit newly available calcareous habitat released by coral mortality (e.g. López-Victoria & Zea 2005; Schönberg & Ortiz 2009). The spatial patterns of bioeroding sponge assemblages in this study could not be conclusively associated with coral mortality. Low overall values of sponge occurrence made spatial comparisons difficult, and the absence of baseline data prevented the recognition of a temporal sequence of events related to reef degradation. The Wakatobi bioeroding sponge occupation levels of 8.9% of the dead reef

substrate were somewhat lower than found on other reefs; e.g. 20 – 81% in the Mexican Pacific and 15% of dead substrate on the GBR (Schönberg & Ortiz 2009; Nava & Carballo 2013). However, the positive correlation between dead substrate availability and total bioeroding sponge abundance supports the hypothesis that further increases in the abundance of bioeroding sponges may occur if coral mortality increases in the region. Furthermore, the importance of dead substrate availability differed with species and had no overall association with sponge diversity, indicating that assemblages on degraded reefs are likely to be dominated by a few resilient species, a trend already observed by Schönberg and Ortiz (2009) on the GBR. Importantly, most of the local species had an apparent low resilience to sediment deposition and turbidity. This suggests that on reefs degraded by terrestrial run-off, which can cause declines in coral health and cover (Edinger et al. 1998; Fabricius 2005; Burke et al. 2011), bioeroding sponges may be prevented from exploiting increases in substrate availability.

3.5.3. Conclusions

In conclusion, not all factors that negatively affect corals are of benefit to bioeroding sponges. It is therefore vital to obtain a better understanding of the biological traits not just of calcifying, but also of bioeroding organisms, and of how they sustain or reduce the ecosystem health when reef function will be impacted by stress and degradation.

Chapter 4: Patterns of bioeroding sponge recruitment

4.1. Abstract

As coral bleaching events increase in severity and regularity on coral reefs across the globe, the ensuing mass mortality of hard corals is resulting in increased availability of dead calcareous substrates. Benthic taxa that exclusively inhabit calcareous substrates, such as bioeroding sponges, are consequently likely to increase their colonisation of these substrates through either lateral expansion or larval recruitment. However, very little is currently known about rates of recruitment in bioeroding sponges or the influence of factors such as local adult abundance or substrate cues. Rates and drivers of bioeroding sponge recruitment were investigated using the two year deployment of experimental calcareous substrates across seven reefs in the Wakatobi region of Indonesia. After two years, five of the eight locally abundant species had recruited, and recruits were present on 69% of the experimental substrates. Recruitment only occurred on coralline algae, encrusting bryozoans and dead calcareous substrate, with a preference for the latter. Differences in assemblage structure of recruits was primarily driven by local adult abundance and current flow, predominantly due to large recruitment events of *Cliona orientalis* at two sites where local abundance was high. However, phylopatric recruitment was not observed in all species, with cues from the adjacent substrate appearing more important for species such as *Cliothosa* cf. *aurivillii*. Overall, the results from my study suggest that coral mortality, and subsequent increases in dead substrate availability, is likely to result in rapid and widespread recruitment of bioeroding sponges in the region. Assemblage composition of recruits is likely to differ depending upon local adult abundance and local substrate cues.

4.2. Introduction

Coral reefs are in a global state of decline as sources of anthropogenic stress increase (Bellwood et al. 2004; Bruno & Selig 2007; De'ath et al. 2012; Jackson et al. 2014). In recent years, a large extent of these declines have been attributed to man-made climate change and mass coral bleaching with associated die-offs (e.g. Eakin et al. 2010; Hughes et al. 2003; 2017; DeCarlo et al. 2017). As the key-stone taxa on tropical reefs, historically corals have dominated substrate composition through competitive interactions with less-competitive taxa. However, increased coral die-offs, associated with bleaching events (e.g. Glynn 1984; Normile 2016) or other stressors (e.g. Aronson & Precht 2001; Kayal et al. 2012), is increasingly exposing new areas of bare calcareous substrate. Historically, on healthy reefs, space previously occupied by a coral could be colonised by any benthic taxa, but would predominantly follow a successional transition to eventual hard coral reoccupation (Endean 1976). However, on degraded and stressed reefs, where coral recruitment can be low (Kuffner et al. 2006; Hoey et al. 2011) and spatial-competitive ability reduced (e.g. Aerts 2000; Vermeiji et al. 2010), other taxa can colonise and competitively maintain this substrate. The classic example of this is in the Caribbean where coral disease, coral bleaching, and a die-off of a keystone herbivore *Diadema antillarum*, led to a dramatic region-wide coral cover decline and a regime shift to macroalgal dominance (Lessios et al. 1984; Aronson & Precht 2001; Gardner et al. 2003; Eakin et al. 2010; Mumby 2009; Jackson et al. 2014). The situation appears to be different in the Indo-Pacific, where despite large declines in coral cover (Bruno & Selig 2007), macroalgal dominated reefs are rare (Bruno et al. 2009). This has led to some authors (e.g. Norström et al. 2009; Bell et al. 2013) to question what other benthic taxa might occupy the space left by coral mortality and potentially dominate some degraded reefs. Recent bleaching events (and subsequent coral mortality) on the Australian Great Barrier Reef (GBR), in the east Pacific and in the Indian Ocean have been associated with large increases in bioeroding sponge abundance (Sheppard et al. 2002; Schönberg & Ortiz 2009; Carballo et al. 2013). These increases, and the resilience demonstrated by some bioeroding sponges to elevated water temperature and reduced pH, have led authors to propose that bioeroding sponges are likely to be among the “winners” on degraded coral reefs (Schönberg & Ortiz 2009).

The ability for bioeroding sponges to occupy newly available substrate following coral mortality is likely to happen through lateral encroachment, fragmentation, larval recruitment or a

combination of these processes (López-Victoria & Zea 2004; 2005; Zillberberg et al. 2006; Chaves-Fonnegra & Zea 2011). Broadly defined, recruitment is the addition of new individuals to populations (Caley et al. 1996). As with all animals, the supply of new individuals is vital for population maintenance in sponges (Pineda et al. 2009, 2010; McMurray et al. 2010; Knapp et al. 2016) but is also important for regulating distribution (Uriz et al. 1998) and likely the expansion of a population into novel habitats (as in formifera; Alve 1999). Recruitment rates in sponges are generally low (Zea 1993) and appear to be particularly low in bioeroding sponges from the few studies that indirectly assessed recruitment for this group (Kiene & Hutchings 1994; Pari et al. 1998; 2002). Recruitment of internal bioeroders has been studied in French Polynesia and the GBR and revealed a successional pattern from initial colonisation by polychaetes and sipunculans to an increasing abundance of boring molluscs and sponges over time (Kiene & Hutchings 1994; Pari et al. 1998; 2002; Tribollet et al. 2002).

Although sponges are capable of asexual reproduction and dispersal (e.g. López-Victoria & Zea 2004), the prevailing reproductive mode is sexual and dispersal relies on a free-living larval stage (Uriz et al. 2008). As such, recruitment is limited by larval production (e.g. Mariani et al. 2001; Piscitelli et al. 2011), survival (e.g. Uriz et al. 1996), dispersal (e.g. Maldonado 2006), habitat selection and settlement (e.g. Maldonado & Uriz 1998), and post settlement survival (e.g. Maldonado & Young 1996; de Caralt et al. 2007).

The pre-settlement lifespan of sponge larvae is short, normally only remaining in the water column for a matter of minutes to days and usually less than two weeks (Maldonado 2006). During this period, dispersal is thought to be largely passive and is a function of hydrodynamics that operate on a scale of tens of meters to kilometres (Pawlik 1992). Once larvae contact the sea bed dispersal transitions into active substratum exploration that occurs at a much finer scale of centimetres to meters, and can last longer than the planktonic phase (Maldonado 2006). Little is known about the mechanisms that govern the final selection of settlement location; it has long been hypothesised that chemical signals produced by conspecifics, competitors, or substrates etc play a role (as is the case for other invertebrate larva (e.g. Pawlik 1992)), but evidence for this is only beginning to emerge (e.g. Whalan et al. 2008; 2012; Wahab et al. 2011).

Our understanding of embryonic development and larval dispersal in bioeroding sponges is patchy and predominantly attributable to work by Mariani et al. (2000; 2001; 2005; 2006) on

Cliona viridis although *Cliona celata* and *Cliona tenuis* have also been studied (e.g. Piscitelli et al 2011; González-Rivero et al. 2013). From the few available studies it appears that oviparous embryonic development is the most widespread in bioeroding sponges (although potentially with internal fertilisation) (Rosell 1993; Mariani et al. 2000; Maldonado & Riesgo 2008; González-Rivero et al. 2013). Gamete development occurs on an annual cycle and release is a highly synchronised event that is related to water temperature (Mariani et al. 2000; Piscitelli et al 2011; González-Rivero et al. 2013). Clionidae larvae, unlike the majority of sponges which produce parenchymella larvae, are clavabastula ((Maldonado 2006; Maldonado & Riesgo 2008) and particularly weak swimmers, often demonstrating predominantly crawling rather than swimming behaviour (Mariani et al. 2000; 2001; 2006). Dispersal as a consequence is considered to be low and phylopatric (Mariani et al. 2006). As bioeroding sponges can only erode calcareous substrates it was assumed that larval settlement is limited to these substrates (Hartman 1958); however, settlement non-specificity has been also been observed in *C. celata* (Warburton 1966). Therefore it has been suggested that while bioeroding sponges are able to settle on a variety of substrates, post settlement development is reliant upon excavation on calcareous substrates (Rosell & Uriz 1992). The only available measure of post settlement survival (13% after 15 days in *C. viridis*) is unreliable as the experimental substrate was a plastic petri-dish (Mariani et al. 2000).

Despite some studies indirectly studying bioeroding sponge recruitment within the Indo-Pacific, (Kiene & Hutchings 1994; Tribollet et al. 2002), our knowledge of the drivers of recruit abundance and diversity and the timescales over which recruitment occurs is still very limited. Understanding these factors is important given the increase in potential habitat availability due to regional decreases in coral cover (Bruno & Selig 2007). This chapter therefore will focus on the recruitment on bioeroding sponges in the Wakatobi region of Indonesia. Through the use of a two year deployment of carbonate recruitment blocks, recruitment was analysed in relation to local environmental conditions, substrate composition and adult sponge abundance.

4.3. Methods

4.3.1. Study area

The research for this chapter was conducted within the Wakatobi UNESCO Biosphere Reserve (Wakatobi) in southeast Sulawesi, Indonesia. Bioeroding sponge recruitment was studied at seven reef sites fringing the islands of Hoga and Kaledupa, which were chosen to represent a variety of reef types, environmental conditions and levels of reef degradation (Fig. 4.1). The same sites constituted the “core” sites in Chapter 3; three steep-wall reefs; Buoy 1 and 3, and Ridge 1; three sloping reefs: Kaledupa 1, Kaledupa Double Spur and Pak Kasims; and Sampela 1, which is highly sedimented and considered to be highly degraded (McMellor & Smith 2010). Sites Buoy 1 & 3, Kaledupa 1 and Kaledupa Double Spur, Pak Kasim’s, Ridge 1 and Sampela 1 are abbreviated in the results and figures as B1, B3, K1, KDS, PK, R1 and S1 respectively.

Figure 4.1. Map of sponge recruitment study sites within the Wakatobi.

4.3.2. Bioeroding sponge recruitment

Bioeroding sponge recruitment was studied using a two year deployment of experimental calcareous substrates. The calcareous blocks (10 x 10 x 10 cm³) of cemented reef rock were obtained from a mine on the local coralline island of Wanci and deployed to reef sites in July and

August 2014. At each of the seven sites five blocks were attached 15 m apart to suitable patches of dead substrate at 10 and 5 m depth ($n = 70$) using marine epoxy (Fig 4.2A). Each block was then photographed in reference to notable reef features to aid future recovery.

Figure 4.2. Example field images of recruitment block deployed to the reef in 2014 (A) and on retrieval in 2016 (B).

Through the course of July and August 2016 the recruitment blocks were located (Fig. 4.2B) and retrieved from the relevant reef sites. Upon locating each block, the block was removed from substrate with a hammer and chisel and examined. Each exposed side of the block was examined for any bioeroding sponges, noting species present, sponge location on the block and the presence of any taxa that may be mistaken for sponges during image analysis. Blocks were then photographed *in situ* (every exposed side) and removed from the reef. In the lab each block was subsequently split open using a hammer and chisel to either confirm in-water observations or locate previously unobserved sponges.

4.3.3. Biotic and abiotic predictor variable data collection

The following data was collected to determine the degree to which bioeroding sponge recruitment is driven by the local adult population, substrate cues or environmental conditions.

The local adult sponge population and substrate composition was assessed using 1 m² photo-quadrats that were taken of the benthos surrounding each recruitment block during block deployment in 2014. Each quadrat was divided into sixteen subdivisions and in addition to taking

photos of each subdivision, field notes were taken of observations of any bioeroding sponges within each subdivision.

In order to augment environmental data already collected for Chapter 3 the XR-420 CTD (RBR, Ottawa) data logger was further deployed at the seven sites on randomly selected dates in June – August 2016 to measure turbidity and chl *a*. As per Chapter 3, each deployment took place for a minimum of 24 hours and the CTD set to record every minute with no averaging. The data was combined to create average values for each environmental parameter for each site, based on each 24 hour deployment with minutes considered as subsamples within each 24 hour period. In addition the clod data from Chapter 3 was used for estimations of site differences in current flow. A snapshot estimation of settled sediment for each block was obtained after deployment in 2014 and before retrieval in 2016 by measuring the depth of settled sediment on the top each block (mean of each corner and the centre) using callipers.

4.3.4. Image analysis

Figure 4.3. Example screen shots of Vidana software. Left image depicting one side of recruitment block pre-measurement and the right image showing the same block after the recruits have been located and tagged.

Recruitment was analysed using the *in situ* images and imaging software Vidana (freely available at marinespatialecologylab.org/resources/vidana). On each side of the block, recruits were located (with the aid of field notes) and marked (Fig. 4.3). Recruitment was then measured in terms of percentage cover of sponge recruits (per species) in relation to the total area of the

recruitment block side. Each side of the recruitment block was considered a subsample and data was averaged over all five sides of the block.

The 2014 abundance of bioeroding sponges adjacent to each block was also analysed using the Vidana software. The images of each subdivision of the photo-quadrat (and in combination with field notes) were examined for bioeroding sponge presence. As per the recruitment blocks, sponge cover was measured in terms of percentage cover of each subdivision. Sponge cover data for each photo-quadrat subdivisions were treated as subsamples and were averaged to create mean values for the entire square meter.

Benthic composition of both the substrate adjacent to each block and of each block surface was measured using Coral Point Count (CPC) software. CPC analysis of the photo-quadrat data involved the random allocation of 15 points per subdivision image ($n = 240$ per photo-quadrat). The substrate beneath each point was then allocated to one of the following categories; macro algae, coralline algae (CCA), hard coral, sponge, soft coral, dead coral + algae, rubble, dead platform, recently dead coral (bleached), sand, silt, sediment on rock or “other”. Data from all 16 subdivisions were then averaged across the photo-quadrat. The sponge recruitment images were used for CPC analysis of 2016 benthic composition of recruitment blocks. Percentage cover of ascidians, encrusting bryozoans, macroalgae, coralline algae, hard coral, soft coral, sponges, dead carbonate, settled sediment and “other” were measured. Twenty points were randomly allocated to each block side image ($n = 100$ per block) and the benthic taxa beneath each point identified as one of the categories above. Data from each side of the block was taken as a subsample and averaged to create mean block benthic composition.

The image analysis of the precise substrate beneath each recruit was judged by eye; the adjacent substrate around each recruit was inspected and allocated a substrate type (same categories as for the block the analysis). If more than one substrate type was present then the most contiguous was chosen.

4.3.5. Statistical analysis

The statistical analysis focused on site and depth based differences in bioeroding sponge recruit assemblages and abundance and the degree to which these were influenced by biological and environmental factors. In this context, biological factors constituted localised bioeroding sponge

abundance (adjacent photo-quadrat data) and reef-scale abundance (survey data from Chapter 3). Environmental data constituted recruitment block benthos, photo-quadrat benthos, CTD data, sediment and flow.

Multivariate analysis was performed using the PRIMER-E v6 software package with the permutational multivariate analysis of variance (PERMANOVA) add on (Clarke & Gorley 2006).

Differences in the benthic composition of the recruitment blocks and adjacent substrate was analysed using PERMANOVAs, constructed from normalised data and resemblance matrices constructed using Euclidean distance. Differences were further characterised graphically using principal coordinate analysis (PCO) with overlaying Pearson's correlation vectors.

Sponge recruitment was highly varied; recruit assemblage data (average percentage cover per species per recruitment block) ranged from the very small (e.g. a single papillae) to quite large (e.g. a large encrustation) and contained many zeros. Therefore the data was square-root transformed and resemblance matrices constructed using Bray-Curtis similarity coefficients. The transformation helping to preserve information on relative abundance, while reducing the effect of the overly abundant species and the Bray-Curtis similarity index ignores the large number of zeros in the data set (Clarke 1993). Due to the absence of bioeroding sponge recruits on many recruitment blocks, a dummy species with the abundance value of 0.5 was added to each recruitment block in order to construct the resemblance matrix and diminish the erratic behaviour of the Bray-Curtis coefficient (Clarke et al. 2006). Differences in recruit assemblages between site and depth (and any interactions) were assessed using a two-factor PERMANOVA and results were graphically displayed using PCO. The species of recruits that contributed most towards any site or depth differences were investigated using a SIMPER analysis. Differences in bioeroding sponge recruit assemblages were also analysed in relation to differences in explanatory biological and environmental data. These explanatory variables were either square-root transformed (biological data) or normalised (environmental data). Possible associations were investigated in a distance-based multiple linear regression model (DISTLM), which is a non-parametric permutation-based procedure that enables significance testing of explanatory variables against multivariate response variables (Anderson et al. 2007). In order to find the most parsimonious model, Akaike's Information Criterion (AIC), a step-wise procedure,

adjusted for small sample sizes (AICc) was used (Burnham & Anderson 2004). Biological and non-biological influences on recruitment were tested separately and DISTLM outputs were represented graphically with a distance-based redundancy ordination (dbRDA).

All univariate statistical analyses were performed in SPSS (version 23; IBM, Auckland, New Zealand). The large number of zeros in the data set meant that the data was inherently not normally distributed and variance high, therefore where data failed to meet the assumptions of the parametric tests data was square-root, fourth-root or log transformed. In the event that transformations failed to meet these assumptions non-parametric Kruskal-Wallis or Spearman's Rank tests were used.

Differences in total average recruit abundance (all species combined) between sites and depth (and interactions) were tested using a GLM on fourth-root transformed data. Correlations between recruit abundance (species combined and individual species) were tested against all biological and environmental data. As the data set contained a large amount of zeros, the correlation analysis for individual species was split into two analyses; 1) all data (Spearman's Rank, untransformed) and 2) positive abundance data (only using data from blocks that recruited bioeroding sponges; Pearson's correlation, fourth-root transformed). For correlations involving recruit data for individual species, only species that recruited to minimum of 10 recruitment blocks were included in the analysis.

Recruit substrate settlement choice was analysed using a means comparison (Kruskal-Wallis, untransformed) between the percentage of recruits (total) settling on a substrate type and the percentage of that substrate type on the block.

4.4. Results

4.4.1. Localised substrate and block characteristics

The local substrate composition in 2014 adjacent to each block differed significantly between sites (PERMANOVA, Pseudo-F = 5.6117, $p = 0.001$). The substrate composition was characterised by sand and rubble around blocks at KDS and S1; by soft coral, dead substrate, recently dead coral and macroalgae around blocks at K1 and PK; by sponges, coralline algae and settled sediment around blocks at B3; and a more heterogeneous composition around blocks at B1 and R1 (Fig. 4.4A). The local substrate composition adjacent to each block also differed significantly between depths (PERMANOVA, Pseudo-F = 3.8435, $p = 0.001$), which appears to be primarily driven by high cover of sponges, coralline algae and settled sediment around many 10 m recruitments blocks (Fig. 4.4B).

Figure 4.4. Two dimensional representation (principal coordinate analysis, PCO) of recruitment block similarities with respect to their adjacent substrate composition. A & B represent the same PCO but blocks are either designated by site (A) or depth (B). Overlaid vectors represent adjacent substrate components that have a Pearson's correlation of greater than 0.4 with either of the PCO axes.

Recruitment block benthos in 2016 was significantly different between sites (PERMANOVA, Pseudo-F = 1.772, $p = 0.002$) but not between depths. Recruitment blocks at KDS, R1 and S1 were predominantly characterised by coralline algae and “other”, while blocks at all other sites showed a more heterogeneous composition of coralline algae, macroalgae, sponges, dead substrate and “other”. Three blocks at B3 and one at R1 showed notably high ascidian cover (Fig. 4.5).

Figure 4.5. Two dimensional representation (PCO) of recruitment block similarities with respect to their benthic composition. Overlaid vectors represent recruit block benthic components that have a Pearson’s correlation of greater than 0.4 with either of the PCO axes.

4.4.2. Localised adult sponge abundance

All eight locally abundant species were identified in the photo-quadrats adjacent to the recruitment blocks with significant differences in assemblage composition occurring between sites (PERMANOVA, Pseudo-F = 3.3053, $p = 0.001$) and depths (PERMANOVA, Pseudo-F = 2.2846, $p = 0.047$). When assessing differences in these assemblages but not including those species that did not recruit (see below) local bioeroding sponge assemblage composition was still significantly different among the sites (PERMANOVA, Pseudo-F = 3.5373, $p = 0.001$) and depths (PERMANOVA, Pseudo-F = 2.9823, $p = 0.030$). The majority of sites were associated

with assemblages that were dominated by *Cliothosa cf. aurivillii*, however KDS was more characterised by the presence of *Cliona orientalis* and a number of blocks at K1, KDS and R1 were adjacent to assemblages characterised by the presence of *Cliona aff. viridis* n. sp. A. Although present in the local bioeroding sponge assemblage, neither *Cliothosa hancocki* nor *Cliona aff. viridis* n. sp. B were strongly associated with any particular site (Fig. 4.6)

Figure 4.6. Two dimensional representation (PCO) of recruitment block similarities with respect to their adjacent bioeroding sponge assemblage composition. Overlaid vectors represent Pearson's correlation of the same data with either of the PCO axes. Only *Cliothosa cf. aurivillii*, *Cliona orientalis* and *Cliona aff. viridis* n. sp. A have correlation coefficients higher than 0.4.

4.4.3. Recruitment

Of the 70 recruitment blocks deployed across the seven reef sites, 65 were recovered. Of the 65 recovered, 45 (69.1%) had at least one sponge recruit, however average cover was generally low ($0.42\% \pm 0.13$ SE) and of those blocks to which sponges recruited, species richness was also low (average of 1.2 species per block ± 0.06 SE). Average recruit cover was highest at KDS ($1.3\% \pm 0.8$ SE) and lowest at B1 ($0.1\% \pm 0.05$ SE), and higher at 5 m ($0.6\% \pm 0.3$ SE) than at 10 m depth ($0.2\% \pm 0.05$ SE). These differences were not significant (Fig. 4.7). Recruits only settled

on CCA ($60.4\% \pm 3.2$ SE), dead substrate ($38.8\% \pm 3.2$ SE) and encrusting bryozoans ($0.8\% \pm 0.5$ SE). The respective percentage of recruits settling on each of those substrates was significantly higher than the average cover of dead substrate on those blocks ($26.4\% \pm 2.0$ SE, $p = 0.017$), significantly lower than the average cover of encrusting bryozoans ($1.4\% \pm 0.4$ SE, $p = 0.049$) and similar (not significantly different) to the average cover of CCA ($57.5\% \pm 2.3$ SE).

Average total recruit cover correlated positively with local bioeroding sponge abundance ($r_s = 0.338$, $p = 0.006$), flow ($r_s = 0.333$, $p = 0.007$) and negatively with the abundance of algae-covered dead coral in the adjacent substrate ($r_s = -0.318$, $p = 0.010$).

Figure 4.7. Average percent coverage of bioeroding sponge recruits (all species combined) across sites. Standard error bars shown.

Of the eight bioeroding sponge species identified in Chapter 2, five were present on the recruitment blocks. These species were *Cl. cf. aurivillii* (11 blocks), *Cl. hancocki* (1 block), *C. orientalis* (11 blocks), *C. aff. viridis* n. sp. A (3 blocks) and *C. aff. viridis* n. sp. B (28 blocks). Absent were *Cliona cf. schmidtii*, *Sphaciospongia cf. vagabunda* and *Zyzzya criceta*. Despite recruiting the most regularly, *C. aff. viridis* n. sp. B was not as abundant overall as *C. orientalis* (see Table 4.1), predominantly due large recruitment events for the latter species at KDS at R1.

Table 4.1. Average percentage cover of bioeroding sponge recruits for individual species per site. Also shown is total average recruitment (all species combined) per site and average for recruitment for each species across all recruitment blocks. Not shown are species that did not recruit. Standard errors area shown.

Site	Species					Total
	<i>Cl. cf. aurivillii</i>	<i>Cl. hancocki</i>	<i>C. orientalis</i>	<i>C. aff. viridis</i> n. sp. A	<i>C. aff. viridis</i> n. sp. B	
B1	0	0	0	0	0.100 ± 0.060	0.100 ± 0.060
B3	0.004 ± 0.003	0.008 ± 0.008	0	0	0.092 ± 0.030	0.104 ± 0.025
K1	0	0	0	0.213 ± 0.140	0.058 ± 0.016	0.270 ± 0.194
KDS	0.036 ± 0.017	0	1.297 ± 0.500	0	0	1.333 ± 0.778
PK	0.218 ± 0.211	0	0	0.040 ± 0.040	0.026 ± 0.024	0.284 ± 0.220
R1	0.040 ± 0.040	0	0.364 ± 0.342	0.012 ± 0.012	0.290 ± 0.240	0.706 ± 0.402
S1	0.056 ± 0.030	0	0.007 ± 0.005	0	0.058 ± 0.013	0.120 ± 0.049
Average	0.052 ± 0.033	0.001 ± 0.001	0.237 ± 0.125	0.034 ± 0.027	0.092 ± 0.038	0.417 ± 0.134

Recruitment of the species, *Cl. cf. aurivillii*, *C. orientalis* and *C. aff. viridis* n. sp. B was high enough to warrant individual correlation analysis. Correlations are split into those using positive abundance data (only using blocks which the species recruited to) and all data. Correlation analysis (positive abundance) of *Cl. cf. aurivillii* recruits found their abundance to be only correlated with the cover of encrusting bryozoan on the recruitment blocks ($r^2 = 0.649$, $p = 0.031$). When including all data, the recruitment correlated with the cover of algae-covered dead coral and rubble in the adjacent substrate ($r_s = -0.381$, $p = 0.002$ and $r_s = -0.247$, $p = 0.048$,

respectively) and the cover of dead substrate on the recruitment blocks ($r_s = 0.318$, $p = 0.010$). Positive abundance correlations found *C. orientalis* to be positively correlated with the cover of dead substrate on the recruitment blocks ($r^2 = 0.603$, $p = 0.049$) and settled sediment on the adjacent dead substrate ($r^2 = 0.648$, $p = 0.031$), but negatively correlated with the cover of CCA on the recruitment blocks ($r^2 = -0.640$, $p = 0.034$). When including all data, *C. orientalis* recruit abundance correlated with flow ($r_s = 0.546$, $p < 0.001$), the local cover of CCA and sand ($r_s = -0.329$, $p = 0.007$ and $r_s = 0.397$, $p = 0.001$, respectively), the cover of macroalgae and CCA on the blocks ($r_s = -0.269$, $p = 0.030$ and $r_s = 0.276$, $p = 0.026$, respectively) and both the local and reef-scale abundance of adult *C. orientalis* ($r_s = 0.586$, $p < 0.001$ and $r_s = 0.506$, $p < 0.001$, respectively). Positive abundance of *C. aff. viridis* n. sp. B recruits only correlated with characteristics of the adjacent substrate; bleached coral ($r^2 = 0.474$, $p = 0.011$), settled sediment on dead substrate ($r^2 = -0.386$, $p = 0.042$) and “other” ($r^2 = 0.419$, $p = 0.026$). When including all data, *C. aff. viridis* n. sp. B recruit abundance negatively correlated with the species abundance at the reef-scale ($r_s = -0.311$, $p = 0.012$), as well as positively with turbidity ($r_s = 0.247$, $p = 0.047$), adjacent cover of CCA ($r_s = 0.279$, $p = 0.024$) and cover of encrusting bryozoans on the recruitment blocks ($r_s = 0.246$, $p = 0.048$).

Figure 4.8. Two dimensional representation (PCO) of site similarities with respect to recruited bioeroding sponge species assemblage.

The assemblage composition of the recruits differed significantly between the sites (PERMANOVA, Pseudo-F = 3.876, $p = 0.001$), but not between depths (Fig. 4.8). The highest differences occurred between KDS and K1 and B1 (both 100% dissimilarity), driven by the dominance of *C. orientalis* in the KDS assemblage, which was absent at K1 and B1. The smallest differences were between B3 and S1 (63.98% dissimilarity), K1 and S1 (72.4% dissimilarity), and B3 and K1 (70.52% dissimilarity). At these sites *C. aff. viridis* n. sp. B was abundant, but the relative importance of other species, such as *C. aff. viridis* n. sp. A and *Cl. cf. aurivillii* differed (Table 4.1).

26.6% of the variation in the recruit species assemblage composition was explained (DISTLM) by variations in the local adult population of *C. orientalis* (14.8%), *C. aff. viridis* n. sp. A (6.6%) and *Cl. cf. aurivillii* (5.2%) (Fig. 4.9). Using the abundance data from the whole reef surveys (Chapter 3 data) the best model from the DSTLM explained only 14.8% of the variation in the recruit assemblage, predominantly due to differences in the adult abundance of *C. orientalis* (11%) but also in *Cl. hancocki* (3.8%).

Figure 4.9. Distance based redundancy analysis (dbRDA) ordinations of fitted models for recruit assemblage composition. Overlaid vectors represent components that have a Pearson's correlation of greater than 0.4.

The best DISTLM models for substrate composition (both the local benthos and the block) and environmental predictors all only selected one variable; sand (9%) for the local benthos, dead substrate (3.7%) for the blocks and flow (16%) for the environmental variables.

4.5. Discussion

Over the course of the two year deployment, five species of bioeroding sponges recruited to the majority of deployed recruitment blocks and were present at every site and depth category. Generally low levels of recruitment and species richness made analysis problematic, however some clear trends did emerge. Bioeroding sponges only recruited to dead calcareous substrate, coralline algae or occasionally encrusting bryozoans and showed a preference for settling onto dead substrate. Recruitment, particularly in *C. orientalis*, showed signs of phylopatry and was potentially influenced by differences in hydrodynamic regime and substrate cues. Finally, although recruitment was low in terms of recruitment block coverage, relative to other studies (e.g. Kiene & Hutchings 1994; Pari et al. 1998; 2002), the proportion of blocks that exhibited bioeroding sponge recruitment was very high for this length of study.

4.5.1. Biotic and abiotic factors affecting recruitment

The local abundance of adult sponge species was one of the most important factors governing overall sponge recruitment and assemblage composition, largely driven by high recruitment of *C. orientalis* at KDS and R1 where the species was also locally abundant. This finding supports work on the Mediterranean zooxanthellate bioeroding sponge *C. viridis* by Mariani et al. (2000) who found that the abundance of adults and larvae were highly correlated. These authors attributed this correlation to the adherence of clusters of eggs to the substratum adjacent to mother sponges, the predominantly crawling (rather than swimming) behaviour of larvae and rapid larval settlement (< 24 hours) (Mariani et al. 2000; 2001; 2006). The significant correlation between *C. orientalis* recruitment and flow rate appears to counter to this hypothesis, suggesting that recruits accumulate at R1 and KDS due to hydrodynamics. However, this may not be the case if the larvae are predominantly crawling; at the boundary layer these larvae are subject to significantly less flow speed and turbulence than midwater larvae and should be able to manoeuvre and explore the substratum for settlement cues (Maldonado 2006). Limited dispersal and phylopatric aggregated recruitment is a strategy that facilitates fertilisation by proximity (e.g. Levitan 1991), settlement in favourable habitats (Pawlik 1992) and reduce the risk of mortality due to predators or being washed to unsuitable environments (Maldonado et al. 2006). Aggregated phylopatric recruitment might be particularly important for zooxanthellate bioeroding sponges, such as *C. orientalis* given their requirements for well-lit calcareous habitat

(López-Victoria & Zea 2005), which may be in a higher abundance close to adults than elsewhere. Not all bioeroding sponges in the Wakatobi assemblage showed a similar dispersal pattern. *C. aff. viridis* n. sp. B and *Cl. cf. aurivillii* were among the most consistent and abundant recruiters but recruitment was not correlated with local adult abundance. In the case of *C. aff. viridis* n. sp. B, recruitment actually showed a slight negative correlation with adult abundance at the reef scale. Not all bioeroding sponge larval dispersal is as limited as *C. orientalis* (current data) and *C. viridis* (Mariani et al. 2006), in fact larvae of *Thoosa* and *Alectona* are often found in offshore plankton (Karawaiew 1896; Trégouboff 1942). When Uriz et al. (1998) investigated the relationship between recruitment and adult spatial patterns in *Crambe crambe* and *Scopalina lophyropoda*, they found that the distribution of *C. crambe* was much less aggregated and philopatric than *S. lophyropoda*. The authors suggested that the comparatively active swimming and late crawling phase of the *C. crambe* larvae accounted for the differing patterns of recruitment (Uriz et al. 1998). While a wider dispersal and longer planktonic phase is likely to incur greater pre-settlement mortality, the advantages include higher chances of encountering optimal settlement cues and sites, the avoidance of localised extinctions and increased adaptation to a wider variety of environments (Uriz et al. 1998; Maldonado 2006).

Recruitment of bioeroding sponges was restricted to calcareous substrates. Despite some previous observations of larval settlement on non-calcareous substrates (Warburton 1966), these sponges are only able to erode and inhabit calcareous substrates (Rosell & Uriz 1992). Therefore while some larvae may have settled on non-calcareous substrates, it is unlikely that metamorphosis occurred. Adult substrate occupation patterns have demonstrated interspecies differences in substrate preferences, varying from mollusc shells, to dead massive or branched coral colonies to coral rubble (Hartman 1958; López-Victoria & Zea 2005; Calcinai et al. 2008; Chaves-Fonnegra & Zea 2011). My data suggests that overall, bioeroding sponges settled uniformly on CCA, tended to avoid bryozoans (but could settle on them) and preferred un-colonised dead substrate. A preference for clean, un-colonised substrate supports earlier studies by López-Victoria & Zea (2005) in the Columbian Caribbean who found that bioeroding sponges were more positively associated with recently dead coral skeletons than older incrustated substratum. Settlement on CCA, a ubiquitous calcareous substrate on coral reefs, is unsurprising given the evidence that it acts as a cue for settlement in hard corals (e.g. Ritson-Williams et al. 2010) as well as some sponges (Jackson et al. 2002; Whalan et al. 2012). In hard corals, settling

larvae exhibit a high degree of selectivity in regard to the CCA species on which they settle (Harrington et al. 2004). If bioeroding sponges also show some degree of preference between CCA species, then this is an important element to be incorporated into future recruitment studies. There is little available information about sponge recruitment to encrusting bryozoans. In scleractinians, bryozoans are generally thought to inhibit larval settlement (Birkeland 1977; Dunstan & Johnson 1998; Glassom et al. 2004) except on older substrates where CCA or dead substrate is rare (Arnold & Steneck 2011). It should be noted that these observations of settlement are based on the assumption that sponge recruitment occurred after the recruitment of CCA and bryozoans. This assumption is based on recruitment studies from other locations within the Indo-Pacific, where CCA and bryozoans are among the earliest colonisers of newly available substrate, often appearing on recruitment tiles within a few months of deployment (Fairfull & Harriott 1999; Field et al. 2007). Conversely, bioeroding sponges are often not present at all after a year or two of deployment (e.g. Pari et al. 1998; Tribollet et al. 2002). If the majority of sponge recruitment happened before the colonisation by CCA and bryozoans, then the interpretation of the observed bioeroding sponge occurrence is different. It would suggest that bioeroding sponges are slightly competitively inferior to CCA and more so to encrusting bryozoans. Unfortunately, it was logistically impossible to visit the blocks at more regular intervals, which could have provided a better timescale for recruitment and resolve the issue.

The relationship between recruitment and local substrate composition (both of the blocks and the adjacent 1 m² of substrate), varied greatly between species, making patterns in substrate cues for total bioeroding sponge recruitment difficult to infer. Many significant correlations also had low coefficients, casting doubt on their biological relevance. Nevertheless there were some stronger correlations that warrant discussion. For *Cl. cf. aurivillii* the strongest evidence for settlement cues was a moderately high correlation with the cover of encrusting bryozoans on the recruitment blocks. This is reflected in the settlement of this species, which was the only species to settle on bryozoans. As discussed previously there is little information on sponges recruiting to bryozoans but they could constitute an alternative substrate option for some sponge species when more preferable substrates are unavailable. If this is the case for *Cl. cf. aurivillii* then the species was potentially a late recruiter, consistent with evidence from other *Cliothisa* species (Pari et al. 1998; 2002). Settlement cues from the adjacent 1 m² indicate an aversion to rubble and algae-covered dead coral, which is also reflected in *Cl. cf. aurivillii*'s habitat choice on the

reef as the species is predominantly found in clean calcareous rock and dead massive corals. *C. orientalis* recruits exhibited a preference for blocks with high cover of dead substrate over blocks dominated by CCA. This is consistent with observations by López-Victoria & Zea (2005) on the substrate occupation preferences of the Caribbean zooxanthellate bioeroding sponges *Cliona aprica* and *Cliona caribbaea*. The positive correlation with cover of settled sediment on the adjacent substrate is perplexing as most sponges cannot colonise sediment, especially when it is moving (Schönberg 2016), which is likely at a high flow sites like KDS and R1. It's perhaps prudent to treat this correlation more cautiously; the snapshot nature of the data collection and the mobile dynamics of settled sediment mean that it is highly possible that the cover of settled sediment was very different during the time of larval settlement. This is especially the case where larval settlement is likely to occur over a very short period in a single annual recruitment (Mariani et al. 2000; 2001). The strongest and most notable correlation of *C. aff. viridis* n. sp. B recruitment was with the cover the recently dead (bleached) coral in the adjacent substrate. This positive relationship appears to strengthen the suggestion that recruitment on un-colonised and clean calcareous substrate is favoured among exploratory bioeroding sponge larvae (López-Victoria & Zea 2005).

Of the eight species identified in Chapter 2, three species, *C. cf. schmidtii*, *S. cf. vagabunda* and *Z. criceta* did not recruit at all and one species, *Cl. hancocki*, recruited to only one block. Interspecies differences in recruitment rates could be due to number of pre and post settlement factors and or due to interspecies differences in fecundity. Species that produce more offspring are likely to have a larger adult population (Uriz 1998), as has been postulated for the reason behind the population size differences in *C. viridis* and *C. celata* in the Western Mediterranean (Piscitelli et al 2011). Additionally, reproductive output can vary not only between species but within species over time. If I assume that the species in this study reproduce with the same frequency as many other bioeroding sponges, i.e. once annually (e.g. Mariani et al. 2000; Rosell & Uriz 2002; Piscitelli et al. 2011; González-Rivero et al. 2013), then a maximum of two recruitment events could have occurred during the duration of the block deployment. However, recruitment in sponges often varies with time, with “pulses” occurring some years and not others (e.g. McMurray et al. 2010). Therefore the timescale of this study could well be over- or underestimating the recruitment rates of some species depending upon the success of that species in those two recruitment events, and complete absence of a species being the ultimate example of

this. This could possibly be the case for *S. cf. vagabunda*; in Papua New Guinea the species is thought to recruit in pulses every three to nine years with lower reproductive output in the intervening years (Kelly 1986). The low numbers of small individuals of this species (J. Marlow pers. obs.) in the Wakatobi would support this. This could possibly also account for singular occurrence of *Cl. hancocki* on the recruitment blocks. In a five year study of bioerosion in French Polynesia by Pari et al (1998; 2002) *Cl. hancocki* was not found on experimental substrates after 24 months of exposure but was found after 60 months. Another possible explanation for the lack of recruitment of some species may be the unsuitability of experimental substrate. In this regard, *Z. criceta* is only found on coral rubble in the Wakatobi, a substrate that other sponge species have also shown a preference for (Jackson et al. 2002). Therefore the recruitment blocks may not have represented an ideal substrate for explorative *Z. criceta* larvae, especially if there was an abundance of preferable coral rubble in the vicinity. The sides of the blocks were also all equally exposed which could possibly deter settlement by sponges with a preference for cryptic habitats. Numerous studies have found large differences in sponge abundance between cryptic and exposed surfaces (e.g. Maldonado & Young 1996; Stubler et al. 2016), which is thought to be a function of negative phototaxis in settlement, reduced exposure to predators and or settled sediment (Maldonado & Young 1996). Species such as *C. cf. schmidtii* that are more common in cryptic habitats (J. Marlow pers. obs.) may require more cryptic substrate for recruitment then offered by the recruitment blocks.

4.5.2. Recruitment rates

The timescale of bioeroding sponge recruitment in the Wakatobi was very quick relative to other comparable studies. A deployment of experimental substrates by Tribollet et al. (2002) in the GBR found no bioeroding sponge presence after twelve months of deployment. A similar absence of bioeroding sponges was found after 15 months deployment on Palmyra Atoll in the central Pacific (Elmer 2016) and after 24 months in French Polynesia where only 5% of experimental substrates were colonised by bioeroding sponges (Pari et al. 1998). Kiene and Hutchings (1994) who found a similar trend around Lizard Island in the GBR, suggested that bioeroding sponges may take four or more years to appear after substrate becomes available. They also hypothesise that after new substrate becomes available, the macroboring community changes with increasing age of the substrate; following a successional path from small, short-lived polychaete species, to longer-lived, larger polychaetes, sipunculans, molluscs and sponges.

However, this hypothesis not only contradicts the results from the Wakatobi but also observations from other studies. As previously mentioned, López-Victoria & Zea (2005) found a positive tendency of *C. aprica* to occupy recently dead coral and a neutral (for *C. caribbaea*) to slightly negative tendency to occupy encrusted calcareous rock in the Colombian Caribbean. MacGeachy (1977) also found that bioeroding sponges were less abundant on heavily encrusted dead coral and hypothesised that “fouling” prevented larval settlement. These different recruitment timescales could be due to differences in substrate preferences of the individual species in the respective assemblages (this study; Hartman 1958; López-Victoria & Zea 2005; Calcinai et al. 2008; Chaves-Fonnegra and Zea 2011) or (as discussed earlier) differences in timing of reproductive output (Kelly 1986; McMurray et al. 2010).

4.5.3. Bioroding sponge recruitment and reef degradation

The results from this chapter further the suggestion that these sponges will benefit from reef perturbation. Recruitment was very quick relative to other studies (e.g. Kiene & Hutchings 1994; Pari et al. 1998; 2002), suggesting that newly available substrate could be rapidly colonised before other benthic taxa that may be unsuitable for recruitment. Indeed bioeroding sponges preferred to recruit to dead substrate over other live calcareous substrates, indicating that recruitment would be higher on recently dead substrate than more encrusted substrates. Nevertheless settlement does not appear to be inhibited by coralline algae, indicating recruitment would be successful even CCA were the earliest coloniser of newly available substrate. The degree of recruitment success following coral mortality therefore appears likely to be a product of timing. Successful species are likely to have reproductive modes that annually allocate considerable amounts of energy to egg production (e.g. *C. viridis*; Mariani et al. 2001; Piscitelli et al. 2011), have multiple spawning events (e.g. *Cliona delitrix*; Chaves-Fonnegra et al. 2016), display constant recruitment (e.g. *C. tenuis*; González-Rivero et al. 2013) or just fortuitous timing in the cases of those species that recruit at more irregular intervals (e.g. *S. vagabunda*; Kelly 1986). Finally, a mixture of dispersal strategies was observed; species that have a more restricted dispersion (e.g. *C. orientalis*) are potentially able to proliferate on more local scales (Uriz et al. 1998) while wider larval dispersal (e.g. *Cl. cf. aurivillii* and *C. aff. viridis* n. sp. B) is generally considered a more opportunistic strategy (Mariani et al. 2006). When taken into consideration the adult persistence of *Cl. cf. aurivillii* and *C. aff. viridis* n. sp. B at the degraded

Sampela (Chapter 3), the widespread and early recruitment of these two species, further indicates that they are likely to benefit from reef degradation in the region.

4.5.4. Conclusions

In conclusion, increased availability of calcareous substrate due to coral mortality is likely to result in increases in bioeroding sponge abundance through larval recruitment. However, interspecies differences in reproductive output, larval dispersal and larval settlement preferences will likely mean that some species will profit from reef degradation more than others. Species that recruit continuously or at least annually are expected to be particularly successful given the increased chances of larval settlement on clean substrates. While species with wider larval dispersal might benefit from more regional scales of coral mortality (given the right settlement cues), more limited dispersal strategies could result in localised proliferation and even dominance on some degraded reefs.

Chapter 5: Light limitation and *Cliona* aff. *viridis* n. sp. A, a photoacclimation response and recovery to shading

5.1. Abstract

Normally associated with coral hosts, photosynthetic *Symbiodinium* symbionts have an important function in many bioeroding sponges; enhancing growth, bioerosion and spatial competitiveness. In the Wakatobi, three such species have been identified as locally abundant, however two are absent from a turbid reef at Sampela. Increasingly a feature of coral reefs degraded by watershed-based pollution, high turbidity has the potential to negatively affect sponges through direct clogging of the filtering apparatus or shading of photosynthetic symbionts. In this chapter, I addressed the latter impact by examining the photoacclimatory capacity of *Cliona* aff. *viridis* n. sp. A in response to reduced light availability using *in situ* PAM fluorometry (rapid light curves; RLCs). Light availability was artificially reduced for individuals of *C. aff. viridis* n. sp. A at a clear-water reef using shades (70 & 95% reduction) for a period of 25 days, with a subsequent 14 day recovery period. Changes in ETR_{max} , E_k and qP in *C. aff. viridis* n. sp. A demonstrated an ability to photoacclimate to levels of extreme light reduction and recover within a relatively short period of time. A lack of corresponding tissue loss or evidence of necrosis during this period suggests that either photoacclimation resulted in sufficient nutritional provision for the host or that *C. aff. viridis* n. sp. A may not be an obligative phototroph. The abundance of *C. aff. viridis* n. sp. A is therefore unlikely to be limited by light availability on turbid reefs but its distribution may be restricted due to the other associated impacts of high sediment loading.

5.2. Introduction

Coral reefs are generally accepted as being one of the most stressed and threatened ecosystems in the marine environment (e.g. Hoegh-Guldberg & Bruno 2010; Frieler et al. 2013). In addition to climate change associated stressors (Hoegh-Guldberg et al. 2007; Normile 2016), reefs are at risk from local disturbances, which can further exacerbate the negative impacts of climate change (Ateweberhan et al. 2013; Ban et al. 2014; McClanahan et al. 2014). Of growing concern is watershed-based pollution that is increasing due to anthropogenic changes in land usage such as deforestation, agricultural intensification and coastal urbanisation (e.g. Munday 2004; Bartley et al. 2014; Stender et al. 2014). Watershed-based pollution can expose coral reefs to excessive levels of sedimentation, turbidity, eutrophication and pollutants (see Fabricius 2005 for review), and is responsible for reef degradation across the globe (e.g. Crabbe & Smith 2005; Wolanski et al. 2009; Golbuu et al. 2011). In some locations the negative impacts of terrestrial-runoff alone could outweigh those of climate change (Maina et al. 2013). In the case of increased turbidity, associated reductions in ambient light availability can have serious negative consequences for scleractinian corals, as they are reliant on endosymbiotic photosynthetic *Symbiodinium* algae for their nutritional needs. Corals in turbid environments can display reduced growth rates (Crabbe & Smith 2005), reduced diversity (e.g. De'ath & Fabricius 2010) and increased disease prevalence (Pollock et al. 2014).

While the impacts of turbidity are relatively well understood for scleractinian corals, few studies have considered how other photosynthetic reef taxa might be affected in these environments. The need for such information is increasing given the trend for regime shifts away from coral dominance towards dominance by other benthic taxa on degraded reefs (McManus & Polsenberg 2004; Norström et al. 2009). One such benthic group is bioeroding sponges, which in addition to increasing in abundance on many degraded reefs (see López-Victoria & Zea 2005; Schönberg & Ortiz 2009; Carballo et al. 2013), are also often hosts to photosynthetic endosymbiotic *Symbiodinium* (Rützler 1990). This symbiotic association is normally associated with cnidarian hosts, but unusually among sponges is common in Clionaidae (Rützler 1990). As in cnidarians, the relationship is generally assumed to be mutualistic; translocated carbon from symbiont to host enhances bioerosion and growth rates (Hill 1996; Schönberg 2006; Weisz et al. 2010). These zooxanthellate clionoids are also some of the most aggressive spatial competitors on coral reefs (Vicente 1978; Schönberg & Wilkinson 2001) and among bioeroding sponges are often the

primary species to opportunistically occupy recently dead substrate following coral mortality (Rützler 2002a; López-Victoria & Zea 2005; Ward-Paige et al. 2005). Abundance surveys of zooxanthellate clionoids regularly show a preferential occupation of well-lit substrate (e.g. López-Victoria & Zea 2005) and it is presently unclear what acclimatory mechanisms they have (if any) for prolonged exposure to turbid environments.

Coping with changes in ambient light availability for *Symbiodinium*-hosting holobionts has predominantly been studied in cnidarians. Some scleractinian corals have a capacity to modify their photophysiology and trophic mode that allows these animals to live and thrive in highly turbid environments and occupy a broad depth range (e.g. Anthony & Farbricius 2000; Hennige et al. 2008a; Morgan et al. 2016). Photoacclimation to low light is possible by adjusting pigmentation within *Symbiodinium* cells (Falkowski & Dubinski 1981), by increasing *Symbiodinium* density (Titlyanov et al. 2001), and by changing holobiont morphology (Einbinder et al. 2009). In the past, this information was derived from destructive sampling and *ex situ* respirometry analysis in the form of photosynthesis-irradiance curves (MacIntyre et al. 2002). However, the development of portable underwater pulse amplitude-modulated (PAM) fluorometry devices (DIVING-PAM) has allowed for non-destructive *in situ* assessments of photoacclimation by providing rapid collection of a suite of photophysiological data (Maxwell & Johnson 2000; Ralph & Gademann 2005). PAMs measure chlorophyll *a* fluorescence of photosystem (PS) II, providing information on the electron transport rate (ETR; equivalent to photosynthetic activity (Beer et al. 1998)), as well as photochemical and non-photochemical quenching (qP and NPQ, respectively) (Ralph & Gademann 2005). By plotting ETR (or relative ETR; rETR) against irradiance (PAR), rapid light curves (RLCs) can be constructed that allow for not only the determination of current photosynthetic capacity but also their responses over a broad range of ambient light conditions (Ralph & Gademann 2005), i.e. photoacclimatory capability. Of specific interest for investigating photoacclimatory potential is the minimum saturating irradiance (E_k) and maximum photosynthetic capacity (ETR_{max}) (Sakshaug et al. 1997; Schreiber 2004; Ralph & Gademann 2005). PAM fluorometry has had limited use in *in situ* sponge photophysiological studies but has been used to demonstrate photoacclimation in the zooxanthellate *Pione vastifica* and in cyanobacteria-hosting *Theonella swinhoei* and *Lamellodysidea herbacea* (Beer & Ilan 1998; Steindler et al. 2001; Biggerstaff et al. 2015).

This study was conducted in the UNESCO Wakatobi Biosphere Reserve (here: Wakatobi) in Southeast Sulawesi Indonesia. The surveys conducted in Chapter 3 found *Cliona* aff. *viridis* n. sp. A to be locally abundant and common around 10-14 m depth on patches of dead substrate. Notably this species is absent from a turbid and sedimented site, Sampela 1, despite abundant substrate availability. This absence suggests that the species is either unable to acclimate and survive in light-limited conditions or directly physiologically impacted by high levels of sedimentation, or a combination of both. The aim of this chapter was to address the first of these hypotheses: to determine whether *C. aff. viridis* n. sp. A is light limited at Sampela or capable of photoacclimating to similar and even more extreme levels of ambient light limitation. I artificially shaded individuals of *C. aff. viridis* n. sp. A for prolonged periods at a clear water reef and used *in situ* PAM fluorometry measurements to detect photoacclimatory changes in PSII. In addition, photographic analysis was used to analyse changes in holobiont health. Reductions in sponge size or signs of necrosis inferring that either photoacclimation failed to meet the host's nutritional requirements or in the absence of photoacclimation the same observation would indicate an inability to regulate heterotrophic feeding to compensate.

5.3. Methods

5.3.1. Study area

This study was conducted within the Wakatobi in July-August 2015. The photophysiological acclimatory capabilities of *C. aff. viridis* n. sp. A were assessed *in situ* at a reef site known locally as Pak Kasim's (Fig 5.1). Pak Kasim's is a section of the sloping fringing reef on the western side of Hoga Island and a location where *C. aff. viridis* n. sp. A is abundant. At this site (and within the wider Wakatobi), *C. aff. viridis* n. sp. A occupies dead calcareous substrate, predominantly in encrusting form, and is most abundant at 10-14 m depth.

Figure 5.1. Location of study area within the Wakatobi (inset black square) and position of reef sites Pak Kasim's and Sampela 1 in relation to the islands of Hoga and Kaledupa. Pak Kasim's and Sampela 1 abbreviated to PK and S1, respectively.

Ambient photosynthetically active radiation (PAR) was measured at Pak Kasim's and at the turbid site Sampela 1 (Fig 5.1). Sampela 1 is considered a degraded reef site; adjacent to the Bajau village of Sampela it is subject to destructive fishing, coral mining, and excessive sedimentation and turbidity thought to be due to mangrove removal, untreated sewage discharge and seasonal changes in currents (Crabbe & Smith 2005; Hennige et al. 2010; Salinas de Leon et

al. 2013). Bioeroding sponge abundance surveys in 2014 (see Chapter 3) found *C. aff. viridis* n. sp. A to be absent on the Sampela reef.

5.3.2. Chlorophyll fluorometry

All chlorophyll fluorometry was conducted using a Pulse Amplitude Modulated (PAM) fluorometer (RED DIVING-PAM, Walz, Iffeltrich Germany) and rapid light curves (RLCs). Prior to sponges being exposed to treatments, trial RLCs were performed on randomly selected sponges at 10 m depth at Pak Kasim's to identify a suitable dark adaption period, and RLC-PAR width and intensities. Full dark adaption took approximately 30 min, which was logistically unachievable when collecting data from multiple sponges on a single dive. Instead the initial fluorescence measurement (in the absence of actinic light) was collected after period of 10 s of quasi-darkness was applied (Ralph & Gademann 2005). This was followed by increasing actinic light steps of 270, 382, 510, 724, 954, 1399, 1957 and 2762 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$, each for a duration of 10 s. For all fluorometry measurements, the fibre optic cable was placed in the centre of the sponge, taking care to avoid patches of necrosis or algal growth. To maintain consistency in the distance to the sponge surface, a 1 cm spacer was attached to the end of fibre optic cable.

Maximum electron transport rates (ETR_{max}), light saturation coefficients and E_k , light-limited photosynthetic efficiency (α), effective quantum yield (Φ_{PSII}) and photochemical quenching (qP) were calculated in the software package WinControl (version 3.25). An absorption coefficient of 0.84 was assumed (Schreiber et al. 1994), but as absorption was not directly measured for these sponges, ETR and ETR_{max} are considered relative (rETR & rETR_{max}).

Shading experiment

Twenty individuals of *C. aff. viridis* n. sp. A were located and tagged at 10 m depth at Pak Kasim's. Sponges were selected based on organism size (5-10 cm^2), upwards orientation (to minimise self-shading) and minimal shading by other reef topographical features. Tagged sponges were randomly allocated treatments of control, procedural control, 70% light reduction and 95% light reduction ($n = 5$). Control sponges were left uncovered for the duration of the experiment, while procedural controls had the same transparent polymethyl methacrylate (Plexiglas GS Clear 0F00, Evonik Industries, Morrinsville NZ) suspended above the sponge as were used in the 70% and 90% shading experiments (Fig. 5.2). The Plexiglass was tested for

PAR attenuation using a spectrophotometer (USB4000, Ocean Optics Inc, Dunedin USA); approximately 10% attenuation at 380 nm and dropping to 0% at approximately 550 nm through to 750 nm (Biggerstaff et al. 2015). A light reduction of 70% was achieved by attaching shade-cloth (Redpath, Palmerston North NZ) to the underside of the Plexiglass and a 95 % reduction was achieved by painting both sides of the Plexiglass with marine paint. Shade and procedural control cover dimensions were 15 x 15 x 0.3 cm, and were suspended approximately 5 cm above sponges using cable ties and masonry nails embedded into adjacent dead substrate. Shades and procedural controls were cleaned every other day to clear algal growth and settled sediment. RLCs were applied on days 0 (just prior to treatment application) 5, 11, 18 and 25, after which the treatments were removed. Final RLCs were applied to each sponge 14 days post treatment removal (recovery). All RLCs were performed between 11 am and 12 pm to minimise inconsistency in the influence of circadian control.

Figure 5.2. Example images of shade treatments showing 95% (left) and 70% (right) light reduction treatments suspended above individual *Cliona* aff. *viridis* n. sp. A individuals.

Sponge size and colouration were monitored through the use of *in situ* images. Photos were taken of each sponge with adjacent scale bar and colour chart prior to treatment on day 0 and immediately after treatment on day 25. Images were subsequently analysed with the software

package ImageJ to assess any changes in sponge size before and after treatment, and tissue colour changes judged by eye in relation to the colour chart.

Transplant experiment

Ten individuals of *C. aff. viridis* n. sp. A were removed from 10 m depth at Pak Kasim's using a hammer and chisel. Sponges were removed in a manner that incorporated both sponge material and at least 3 cm of calcium carbonate beneath the sponge tissue. Sponges were stored in flow-through temperature controlled (28 °C) aquaria for three hours before relocation back to Pak Kasim's and Sampela reef, five sponges at each site. The transplanted sponges were attached to the reef at each site at 10 m intervals, using marine epoxy. The intention was to perform 25 days of chlorophyll fluorometry measurements parallel to the shading experiment. However, a high incidence of sponge mortality due to a combination of starfish predation and transplant dislodgement meant that these measurements had to be abandoned.

5.3.3. PAR assessment

In situ PAR measurements were taken for two distinct purposes: 1) to quantify the average daily PAR reaching reef benthos at Pak Kasim's and Sampela; and 2) to quantify the average daily PAR reaching the surfaces of the individual treatment sponges, when both shaded and unshaded. Individual sponge PAR levels were measured to assess not only the effect of treatment but also differences in PAR reaching sponges due to shading by reef topography and sponge orientation.

Average daily reef PAR was quantified using three separate 24 hr deployments of an ODYSSEY PAR logger (Dataflow Systems, Christchurch NZ) at 10 m depth, at both sites, set to record every minute and data averaged over daylight hours. Average PAR levels for individual sponges were measured using an external PAR sensor on the PAM. PAR measurements were taken once from the middle of the sponge surface and then immediately after in the water column at the same depth. This was repeated once for each sponge at 12 pm pre-treatment and for each sponge at 8 am, 12 pm and 4 pm during the treatment period (on non-cloudy days). PAR was calculated as a percentage of ambient light levels in the water column.

5.3.4. Statistical analysis

All statistical analyses were performed within the SPSS (version 23) statistical analysis package. Any data that did not meet the assumptions of variance, normality or sphericity for the relevant analysis were square root, fourth root or log-transformed.

Differences in ambient PAR between sites and between sponge treatment groups were tested using a One-Way Analysis of Variance (ANOVA) with Tukey's *post hoc* test where necessary. Differences in sponge size between days 0 and 25 were tested using a paired T-test.

Differences in $rETR_{max}$, E_k , α , Φ_{PSII} , F_0 and average qP among the different treatment groups over time were tested using a Repeated Measures ANOVA, with time and treatment as fixed factors, and with *post hoc* Bonferroni adjusted pairwise tests. Differences in RLCs and qP across time were tested using three general linear models (GLMs) for days 0, 25 and 39 (recovery), where $rETR$ and qP were the dependent variables, treatment a fixed factor and PAR as a covariate.

5.3.5. Molecular identification of symbiont cladal composition

Tissue samples of *C. aff. viridis* sp. A were obtained from six individuals at 10 m depth on Pak Kasim's reef, preserved in 96 % ethanol and transported to Wellington for analysis. DNA was extracted using a Qiagen extraction kit and PCR amplifications of the entire ITS region were carried using the primers S-DINO (forward) and L0 (reverse) as outlined by Pawlowski et al. (2001). PCR products were separated by horizontal gel electrophoresis and gel fragments containing the desired PCR products were cut out and purified using a freeze-squeeze methodology. Sequencing was completed in both directions by a third party service (Macrogen, South Korea) and symbiont clades identified using a BLAST search in GenBank.

5.4. Results

5.4.1. PAR and treatments

Average daily PAR at 10 m depth during the experimental period was $116 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$ (± 20 SE) at Sampela and $188 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$ (± 29 SE) at Pak Kasim's, an almost 60% difference and justifying the use of the 70% light reduction treatment. At Pak Kasim's, midday water column PAR at 10 m depth was $216 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$ (± 7 SE). Shading by reef topography and differences in sponge orientation meant that sponge surface PAR (pre-treatment) was less, at $170 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$ (± 18 SE), but there were no significant differences in PAR on the unshaded sponge surface between treatment groups. Following application of treatments, the average amount of PAR reaching each treatment group across a day (from 8 am, 12 pm and 4 pm readings) was $87 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$ (± 24 SE) for controls, $80 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$ (± 20 SE) for procedural controls, $25 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$ (± 6 SE) for 70% treatments and $3 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$ (± 1 SE) for 95% treatments, representing 52.1% (± 9.1 SE), 52.2% (± 6.7 SE), 15.1% (± 2.1 SE) and 2.1% (± 0.9 SE) of the available PAR in the water column, respectively. These differences were significant (one-way ANOVA, $F_{(3,56)} = 29.066$, $p < 0.001$), with *post hoc* tests revealing differences between the 95% treatments and all other treatments ($p < 0.001$), between the 70% treatments and all other the treatments ($p < 0.001$ for 95% treatments, $p = 0.02$ for controls, and $p = 0.08$ for procedural controls), and no differences between the controls and procedural controls.

Figure 5.3. Mean rETR_{max} of controls (filled circles), procedural controls (open circles), 70% light reduction (filled triangle), and 95% light reduction (open triangle) treatments over time (n = 5 for each). Standard errors are shown and the vertical dashed line represents the time when shades were removed.

5.4.2. *Sponge photophysiology*

There was a significant difference in rETR_{max} across time (Huyn-Feldt, $F_{(5,80)} = 44.366$, $p < 0.001$), and interaction with time and treatment (Huyn-Feldt, $F_{(15,80)} = 6.983$, $p < 0.001$) (Fig. 5.3). Pairwise comparisons show that, by day 11, average rETR_{max} across all treatments and controls was significantly lower than at days 0 and 5, or after recovery ($p < 0.001$, $p = 0.02$ & $p < 0.001$, respectively), a trend that continued on days 18 and 25 ($p < 0.001$ for all). However, after the recovery period, the average rETR_{max} was not significantly different from that found at days 0 and 5. Differences were primarily caused by a drop in the rETR_{max} for the 95% treatment group; by day 11 rETR_{max} was significantly lower than for the controls ($p = 0.010$), procedural controls ($p = 0.001$) and 70% treatment ($p = 0.011$), and this trend continued on days 18 and 25 ($p < 0.001$ for all). There were no other significant differences in rETR_{max} between any of the other treatment groups on any of the measured days, and after recovery no differences existed between any of the treatments. When examining differences across time within treatment groups, controls and procedural controls had a lower rETR_{max} on day 18 than after recovery ($p = 0.05$ & 0.016 , respectively). However, the main differences occurred for the 70 and 95% treatments; by

day 11, $rETR_{max}$ was significantly lower in these groups than it was on day 0 within the same groups ($p = 0.018$ & $p < 0.001$, respectively). On day 25, $rETR_{max}$ was at its lowest for the 70% and 95% treatments, and significantly lower than in the same treatments on days 0 ($p < 0.001$ for both), 5 ($p = 0.003$ & $p < 0.001$, respectively) and after recovery ($p = 0.011$ & $p < 0.001$, respectively). After the recovery period, $rETR_{max}$ was not significantly different from that of day 0 within each group.

Figure 5.4. Mean E_k of controls (filled circles), procedural controls (open circles), 70% light reduction (filled triangle) and 95% light reduction (open triangle) treatments over time ($n = 5$ for each). Standard errors are shown and the vertical dashed line represents the time when shades were removed.

There was a significant difference in E_k across time (Huyn-Feldt, $F_{(5,80)} = 5.917$, $p < 0.001$) but no significant interaction with time and treatment (Fig. 5.4). Mean E_k on day 11 (308.3 ± 18.6) was significant lower ($p = 0.009$) than on day 0 (377.6 ± 20.2). Mean E_k was also significantly lower on days 11 and 18 (332.4 ± 18.5) than after the recovery period (417.9 ± 25.7 ; $p = 0.003$ & 0.005 , respectively). On day 25, E_k appeared lower in the 70 and 95% treatment groups compared to both control groups (Fig. 5.4) and lower than within the same treatments on day 0 and after recovery. However, the lack of significant interaction between time and treatment fails

to significantly demonstrate this, probably due to the large amounts of within-treatment variation in E_k .

Figure 5.5. Mean α of controls (filled circles), procedural controls (open circles), 70% light reduction (filled triangle), and 95% light reduction (open triangle) treatments over time ($n = 5$ for each). Standard errors are shown and the vertical dashed line represents the time when shades were removed.

Light-limited photosynthetic efficiency (α) (Fig. 5.5) changed significantly with time (Huyn-Feldt, $F_{(5,80)} = 6.294$, $p < 0.001$); α at day 25 was significantly lower than at days 0 and 5 ($p = 0.41$ & 0.34 respectively), but was not significantly different from any other day, including after the recovery period ($p = 0.062$). Changes in α also occurred in an interaction between time and treatment (Huyn-Feldt, $F_{(15,80)} = 2.074$, $p = 0.020$) (Fig. 5.5). By day 11, α was significantly lower in the 95% treatment group than the controls and procedural controls ($p = 0.05$ & 0.017), however after day 11 no significant differences between treatments existed. Within treatment groups, the only change in α across time was in the 95% group, which by day 11 was significantly lower than at day 0 and after recovery ($p = 0.001$ for both), and remained so at days 18 ($p = 0.039$ & 0.018 , respectively) and 25 ($p = 0.016$ for both).

Effective quantum yield (Φ_{PSII}) across all treatment groups did not change significantly over time, however a significant interaction between time and treatment existed (Huyn-Feldt, $F_{(15,80)} = 2.004$, $p = 0.025$). Pairwise comparisons showed that this interaction was driven by changes in the Φ_{PSII} of the 70% treatments (Fig. 5.6); Φ_{PSII} was significantly greater at day 18 than at day 0 and or after recovery ($p = 0.017$ & 0.016 , respectively), and at day 25 was higher than after recovery ($p = 0.048$), but not significantly higher than at day 0 ($p = 0.055$).

Figure 5.6. Mean Φ_{PSII} of controls (filled circles), procedural controls (open circles), 70% light reduction (filled triangle), and 95% light reduction (open triangle) treatments over time ($n = 5$ for each). Standard errors are shown and the vertical dashed line represents the time when shades were removed.

F_0 declined significantly across time (Huyn-Feldt, $F_{(5,80)} = 36.511$, $p < 0.001$) but there was no significant interaction with time and treatment (Fig. 5.7).

Figure 5.7. Mean F0 across time in different treatment groups (n = 5 for each). Standard errors shown.

Mean qP changed significantly with time (Huyn-Feldt, $F_{(2,32)} = 113.071$, $p < 0.001$) and there was an interaction with treatment (Huyn-Feldt, $F_{(2,32)} = 2.686$, $p < 0.001$). Mean qP dropped significantly from day 0 to day 25 in the 70% and 95% treatment groups ($p < 0.001$ for both), and increased again after 14 days of recovery for the treatment groups (70%: $p = 0.001$; 95%: $p < 0.001$) and controls ($p = 0.024$) (Table 5.1).

Table 5.1. Mean qP and standard error for all controls and treatments at days 0 and 25, and after 14 days recovery.

<i>Treatment</i>	<i>Mean qP</i>		
	<i>Day 0</i>	<i>Day 25</i>	<i>14 days Recovery</i>
Control	0.48 ± 0.02	0.44 ± 0.04	0.51 ± 0.03
Procedural control	0.49 ± 0.01	0.44 ± 0.03	0.50 ± 0.02
70% light reduction treatment	0.51 ± 0.02	0.39 ± 0.03	0.49 ± 0.02
95% light reduction treatment	0.48 ± 0.03	0.22 ± 0.02	0.50 ± 0.02

Overall, RLCs and qP (Fig. 5.8) were not significantly different at day 0 or after recovery, but by day 25 there were significant differences (GLM, $F_{(3,175)} = 23.665$, $p < 0.001$ & GLM, $F_{(3,155)} = 43.592$, $p < 0.001$, respectively). At day 25, pairwise comparisons showed significantly shallower RLCs and qP for the 95% treatment in relation to the 70% treatments and both controls ($p < 0.001$ for all).

5.4.1. *Sponge size*

Sponge surface area for all controls and treatments was not significantly different between days 0 and 25 (Table 5.2), and no necrosis was observed in any sponge. 60% of sponges within the 95% reduction group were notably paler on day 25 than within the same group on day 0. No other group displayed obvious paling.

Table 5.2. Mean sponge size and standard error for all controls and treatments at days 0 and 25.

<i>Treatment</i>	<i>Sponge Size</i>	
	<i>Day 0</i>	<i>Day 25</i>
Control	18.4 ± 5	17.5 ± 2.9
Procedural control	20 ± 9.1	20 ± 10.4
70% light reduction treatment	15.4 ± 4.8	17 ± 5.3
95% light reduction treatment	17.8 ± 2.2	15.4 ± 4.5

5.4.2. *Symbiodinium cladal composition*

Symbiodinium of clades A, C and G were found in the six *C. aff. viridis* n. sp. A individuals. A combination of clade G and A occurred in three individuals, two sponges contained only clade C and one sponge contained only clade G.

Figure 5.8. Mean rETR (RLCs) and mean qP against PAR at day 0 (A&B) and day 25 (C&D), and after 14 days of recovery (E&F). Controls (filled circles), procedural controls (open circles), 70% light reduction (filled triangle) and 95% light reduction (open triangle) ($n = 5$ for each) Standard errors shown.

5.5. Discussion

In the context of reef degradation and stressor resilience, research on bioeroding sponges has primarily focused on resilience to global stressors such as increased water temperature and ocean acidification (e.g. Schönberg & Suwa 2007; Wisshak et al. 2012; 2013). Regional and local stressors (with the exception of eutrophication, e.g. Ward-Paige et al. 2005) have been largely overlooked. This is the first study to specifically focus on bioeroding sponge acclimation to light limitation on turbid reefs using PAM fluorometry. I demonstrate that *C. aff. viridis* n. sp. A is capable of rapidly photoacclimating to extreme changes in ambient light availability and furthermore, is capable of surviving for short periods in near darkness without any visible signs of necrosis. This resilience to a regionally common form of reef stress is important given that bioeroding sponges of the *C. viridis* spp. complex are frequently associated with abundance increases on degraded reefs (Rützler 2002a; López-Victoria & Zea 2005; Ward-Paige et al. 2005), indicating that zooxanthellate bioeroding sponges may be able to exploit coral declines on turbid reefs.

5.5.1. Photoacclimation of *C. aff. viridis* n. sp. A

Pertinent characteristics of *Symbiodinium* PSII in *C. aff. viridis* n. sp. A demonstrated altered states in relation to shading, that are consistent with photoacclimation. The most significant of which is the decline in $rETR_{max}$ and subsequent recovery. Numerous studies have shown a positive correlation between ETR_{max} and light availability in *Symbiodinium* (e.g. Steindler et al. 2001; Hennige et al. 2008a; Ziegler et al. 2015). In high light environments, high ETR_{max} allows *Symbiodinium* to capitalise on the elevated light availability by increasing photosynthetic rate (Ralph & Gademann 2005). However, reduced ETR_{max} in low light environments appears paradoxical to the increases in photosynthetic ‘units’ that are usually associated with low light acclimation (Falkowski 1980; Richardson et al. 1983; Ramus 1990). This is thought to be due to increased light attenuation due to the accumulation of pigments, resulting in less light reaching the reaction centres and saturating photosynthesis (Falkowski & Raven 2013). Reductions in ETR_{max} in the 95% treatment could also be a function of an extreme decrease in *Symbiodinium* density; in coral hosts ETR_{max} is up to 84% lower in bleached tissues in comparison to healthy parts of the same colony (Fine et al. 2004). Although the pale appearance of 60% of the sponges at the end of the 95% treatment would support this hypothesis, the observation of bleaching in *C.*

aff. *viridis* n. sp. A does not necessarily imply complete or even partial expulsion of symbionts, as is found in scleractinians (e.g. Fitt et al. 2000). *Cliona orientalis* relocates *Symbiodinium* deeper into sponge tissue at night or when experiencing light stress, giving a “bleached” appearance (Schönberg & Suwa 2007; Fang et al. 2016) and this same diurnal movement has also been observed in *C. aff. viridis* n. sp. A (J. Marlow pers. obs.). The absence of any significant difference in the initial F_0 value between the treatments and controls at day 25 would support this “bleaching” interpretation, as an initial F_0 is proportional to PSII reaction centre density (Ryan et al. 2009). Therefore, the reduction in ETR_{max} in shaded sponges is unlikely to be a consequence of a reduction in *Symbiodinium* density, but a function of photoacclimation.

Light reduction did not significantly alter one of the most reliable indicators of photoacclimation, minimum saturation irradiance (E_k). E_k is located on the RLC at the transition from the light limited to the light saturated region (Sakshaug et al. 1997) and is related to quenching; Q_p dominates below E_k and NPQ dominates above (Henley 1993; Ralph & Gademann 2005). *Symbiodinium* cells acclimatised to low ambient PAR are usually characterised by low E_k (Chalker et al. 1983) and reductions in E_k reflect changes in the effective absorption cross section of PSII (Kolber & Falkowski 1993; Rodolfo-Metalpa et al. 2008), as has been demonstrated in shaded seagrass (Collier et al. 2009) and sponges (Biggerstaff et al. 2015). E_k is constantly changing in relation to irradiance, only occasionally matching instantaneous irradiance and is hence highly variable (Sakshaug et al. 1997; Ralph & Gademann 2005). While this study found no significant difference between E_k in any of the treatments, E_k clearly declined in the shaded treatments, but variation was high and it is expected that more replication would have demonstrated this statistically. As E_k is an accurate measurement of photoacclimation, derived values are considered indicative of the ambient light levels to which an organism is photoacclimated. However, average control E_k values of $338 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ were substantially higher than ambient midday levels of $216 \mu\text{mol photons m}^{-2} \text{s}^{-1}$. This is potentially due to calibration error in the PAR sensor.

Another strong indication of photoacclimation that can be derived from the RLCs is photosynthetic efficiency in the light-limited region (α). High α values are usually associated with photosynthetic organisms that are low-light acclimated, as they are more effective at rapidly utilising low irradiances (e.g. Hennige et al. 2008a). I found that α showed a marked decline in

the 95% treatment over time but recovered rapidly to pre-shading levels after 14 days of recovery. In contrast, the 70% treatment showed no discernible difference over the course of the experiment. Neither reactions are typical for shade-adapted *Symbiodinium* and were unexpected. It is possible that the RLC sampling methodology had insufficient resolution to adequately estimate α in the shaded sponges, as estimates of α are strongly influenced by sampling frequency in the light-limited region of the RLC (Jassby & Platt 1976; Ralph & Gademann 2005). However, the very clear decline in α demonstrated by Figure 5.3 suggests that this is not the case and no alternative explanation is forthcoming.

The drop and subsequent recovery of photochemical quenching in the shade treatments is consistent with other studies that have demonstrated correlations between *in situ* light history and qP in aquatic phytoplankton (Harrison et al. 2015), seagrass (Ralph & Gademann 2005) and the sponge *L. herbacea* (Biggerstaff et al. 2015). The association between qP capacity and *in situ* light conditions is a reflection of the photochemical operating efficiency of PSII and hence photosynthetic organisms that display higher qP demonstrate a higher PSII efficiency in high light (Hennige et al. 2008a; Harrison et al. 2015). The decrease in qP over the first 25 days and subsequent significant increase over the next 14 days in the control sponges corresponds with the observed trend in $rETR_{max}$ and α . This is likely due to the increase and subsequent decrease in water column turbidity that was observed over this time and further demonstrates the photoacclimatory capabilities of this sponge. This confounding effect no doubt also contributed to the lack of significant difference in the overall shape of the qP plot between the 70% treatment and controls at day 25.

5.5.2. *Symbiodinium* clades

The discovery of clades A, C and G in individuals of *C. viridis* n. sp. A is consistent with findings from elsewhere in the Indo-Pacific (Schönberg & Loh 2005; Granados et al. 2008; Hill et al. 2011). Clade C has only previously been found in the Indo-Pacific *Cliona caesia*, clade G has been found in *C. orientalis* and the Caribbean sponges *Cliona caribbaea* and *Cliona varians* and clade A has only been found one Indo-Pacific sponge, *Cliona jullieni*, but also four Caribbean species (Schönberg & Loh 2005; Granados et al. 2008; Hill et al. 2011). To date 10 clionaid species have had their *Symbiodinium* symbionts identified and of the eight sponge species that are represented by more than one individual 63% are associated with only one clade

of *Symbiodinium* and the remaining 37% are associated with two (Schönberg & Loh 2005; Granados et al. 2008; Hill et al. 2011). The association of *C. aff. viridis* n. sp. A with three different clades is therefore a first for boring sponges but unsurprising given that this is common among cnidarian hosts (Baker & Romanski 2007). The existence of different clades within individuals of *C. aff. viridis* n. sp. A could have introduced some variation into the results as different clades of *Symbiodinium* are known to have different photoacclimation strategies (Hennige et al. 2008b). The capacity to host different and multiple clades, also suggests an ability for these sponges to photoacclimate through horizontal acquisition of other more suitable clades. This is unlikely to have occurred over the short period of my study but could represent a longer term (months) acclimatory mechanism as has been suggested for scleractinian corals (Cohen & Dubinsky 2015).

5.5.3. Reliance upon symbionts

A variety of sponges harbour *Symbiodinium* (Garson et al. 1998; Carlos et al. 1999), however the association is primarily associated with clonoid sponges (Sarà & Liaci 1964; Rützler 1990; Granados et al. 2008; Hill et al. 2011). In these sponges, heightened light availability and *Symbiodinium* density has been associated with increases in bioerosion rates, growth and competitive ability (Hill 1996; Schönberg 2006). Despite the apparent benefits of the symbiosis in some species, very few studies have addressed the mechanisms that underpin the relationship, or the level to which the sponge depends on *Symbiodinium* for survival. It was long assumed that, as in scleractinians (e.g. Rädcker et al. 2015), photosynthate is translocated from *Symbiodinium* to host in return for protection and inorganic nutrients. Weisz et al. (2010) found strong evidence for transfer of carbon from symbiont to host in *C. varians*, but were unable to detect any reciprocal transfer of nitrogen. Furthermore, heterotrophic uptake of particulate and dissolved organic carbon by *C. orientalis* is 39% lower than the sponge's metabolic carbon demand (Fang et al. 2016), further demonstrating the sponge's apparent reliance on symbiont-derived nutrition.

My study found that *C. aff. viridis* n. sp. A was able to photoacclimate to conditions of moderate to severe reductions in light availability. However, photoacclimation in *Symbiodinium* does not necessarily mean that the energetic needs of the sponge are met under the reduced light conditions. For instance, a comparable shading experiment by Biggerstaff et al. (2015) found that

the predominantly phototrophic sponge *Lamellodysidea herbacea* was able to photoacclimate and survive a similar period of near-darkness, but not without incurring significant partial mortality. There were no observations of necrosis in shaded *C. aff. viridis* n. sp. A, however 60% of the 95% treatment sponges were noticeably paler at day 25 of the experiment. As mentioned above, the observation of tissue paling in *C. aff. viridis* n. sp. A does not necessarily imply complete or even partial expulsion of symbionts. Nevertheless, it is indicative of a stressed sponge and likely to result in a significant decrease in photo-autotrophically supplied carbon. One possible explanation for differences in levels of necrosis between *C. aff. viridis* n. sp. A and *L. herbacea* is that the former is potentially a more capable heterotroph. If this hypothesis is valid, then *C. aff. viridis* n. sp. A is potentially able to survive, at least in the short term, in similar conditions without incurring necrosis due to a combination of photoacclimation and heterotrophically-acquired carbon. Increased feeding rates and CHAR (percentage contribution of heterotrophically-acquired carbon to daily animal respiration) has been observed in bleached corals (e.g. Grottoli et al. 2006) and is thought to support long-term bleaching resilience. However, this appears not to be the case in the closely related *C. orientalis*; heterotrophic carbon uptake has been shown to remain unchanged between day and night, in experimentally bleached individuals, and after 20 days of complete darkness (Fang et al. 2014; 2016; 2017a). In fact, Fang et al. (2017a) suggest that, in the absence of photo-autotrophic energy, *Symbiodinium* cells are sustained through heterotrophy at the expense of the *C. orientalis* host, i.e. a shift from mutualism to parasitism. If heterotrophic compensation is as insufficient in *C. aff. viridis* n. sp. A, my research suggests that this species is unlikely to survive and recover beyond short periods of extreme turbidity (akin to the 95% treatment).

5.5.4. Implications for survival on Sampela reef and other turbid Southeast Asian reefs

Reefs in Southeast Asia are increasingly threatened by anthropogenic terrestrial processes such as intensive deforestation and coastal urbanisation that are leading to substantial loads of sediment entering coastal waters (Spalding et al. 2001; Baum et al. 2015). Suspended sediment, particularly the finer particles, decreases light availability for photosynthetic taxa, resulting in compressed depth distribution zones, and reduced growth and survival (Fabricius 2005; Erftemeijer et al. 2012). For example, in Singapore, sediment input through land reclamation activities has resulted in such dramatic reductions in light availability that reefs below 6-8 m are considered coral dead zones (Dikou & van Woesik 2006; Todd et al. 2010). The capacity to

photoacclimate to changing light conditions is therefore vital to guarantee survival and possible proliferation of zooxanthellate sponges on degraded turbid reefs.

Photoacclimation in 70% and 95% shading treatments of *C. aff. viridis* n. sp. A demonstrated the sponge's ability to acclimate to a light regime associated with highly turbid reefs such as Sampela and beyond. Light conditions at 10 m depth on the Sampela reef are similar to the 70% treatment and this is considered a highly-degraded reef (Crabbe et al. 2004; Haapkylä et al. 2007), where the turbidity regime has resulted in significantly reduced coral growth rates and diversity (Crabbe & Smith 2002, 2005; Hennige et al. 2008a). This reef has a high abundance of the low-light and sediment tolerant *L. herbacea* (Powell et al. 2014; Biggerstaff et al. 2015; 2017), but *C. aff. viridis* n. sp. A is absent despite this studies' evidence suggesting that it can cope with the light regime. As previously mentioned, photoacclimation does not necessarily guarantee that *Symbiodinium* cells are able to transfer similar quantities of photosynthate to their host in light-limited environments. Therefore, to fully understand the functioning of the light-limited holobiont it is important to include concurrent analysis of symbiont-host nutrient translocation, host respiration and heterotrophic uptake (see Weisz et al. 2010; Fang et al. 2017a).

Another possible explanation for the sponge's absence at Sampela is that the timescale at which turbidity changes on the reef is out of sync with the timescale over which photoacclimation occurs (Anthony & Hoegh-Guldberg 2003). Photoacclimation in *C. aff. viridis* n. sp. A appeared to take approximately 11 days, however changing currents and tides can significantly alter the turbidity regime at Sampela over a matter of hours (J. Marlow pers. obs.). Under these timescales, photoacclimation would fail to enhance gross productivity, as downward- and upward-regulation of photosynthesis would compensate over longer timescales (current data; Fabricius 2005; Anthony & Hoegh-Guldberg 2003).

The absence of *C. aff. viridis* n. sp. A on Sampela reef could also be a product of the direct impacts (rather than indirect shading) of the high concentration of suspended sediment (Bell et al. 2015). As an organism that likely relies on filter-feeding to provide at least some of its nutritional intake, *C. aff. viridis* n. sp. A is potentially vulnerable to clogging by fine sediments, as is the case in other tropical sponges (Bannister et al. 2012). With only minor selective control over filtering intake (Reiswig 1971a), the clogging of a sponge's inhalent canals and aquiferous

system can cause reductions in feeding efficiency (Gerrodette & Flechsig 1979). Active responses to high suspended sediment loads include the reduction or cessation of pumping (Reiswig 1971b; Leys et al. 1999), and metabolically active mechanisms such as mucus production or flow reversal (Bannister et al. 2012; Bell et al. 2015; Biggerstaff et al. 2017). However, sediment tolerance in bioeroding sponges varies between species (Carballo et al. 1994) and the limitations of any tolerance is currently unknown in *C. aff. viridis* n. sp. A. Therefore, although this experiment has shown that *C. aff. viridis* n. sp. A can photoacclimate to compensate for reduced light availability associated with turbidity, it remains to be seen how the sponge copes with the actual direct impact of the same suspended sediment. Any conclusions about the persistence of *C. aff. viridis* n. sp. A and other zooxanthellate sponges on turbid reefs are consequently limited.

5.5.5. Conclusions

Symbiodinium of *C. aff. viridis* n. sp. A are capable of substantially and rapidly altering its photophysiology in response to conditions of significantly reduced light availability, and reversing these changes once light conditions are restored. Given that the sponge's *Symbiodinium* composition is predominantly made up of Clade G, it is possible to cautiously extrapolate these results to other zooxanthellate clionoids, as many either contain Clade G or are dominated by it (Hill et al. 2011). The absence of *C. aff. viridis* n. sp. A at Sampela appears unlikely to be largely due to light limitation but possibly related to the other potential impacts of high sediment loading. Finally, while results from the 95% treatment demonstrate that *C. aff. viridis* n. sp. A is capable of photoacclimation in response to extreme reductions of light availability, observations of bleaching suggest that this may not be sustainable over prolonged periods.

Chapter 6: Factors controlling the erosion rate of a *Spheciospongia cf. vagabunda*

6.1. Abstract

Coral reefs are increasingly threatened by anthropogenic disturbances and consequently coral cover and complexity are declining globally. However, bioeroding sponges, which are the principal agents of internal bioerosion on many coral reefs, are increasing in abundance on some degraded reefs, which is tipping them towards net carbonate erosion. The aim of this chapter was to identify the environmental factors that drive the erosion rates of the common Indonesian bioeroding sponge *Spheciospongia cf. vagabunda*. Sponge explants were attached to experimental calcareous substrates and deployed across seven sites characterised by different environmental conditions in the UNESCO Wakatobi Biosphere Reserve in Indonesia. Average bioerosion rates were $12.0 \text{ kg m}^{-2} \text{ sponge tissue yr}^{-1}$ ($\pm 0.87 \text{ SE}$), and were negatively correlated with depth of settled sediment ($r^2 = -0.717$, $p < 0.01$) and showed weak positive correlation with water movement ($r^2 = 0.485$, $p = 0.012$). My results suggest that although bioeroding sponges may generally benefit from coral reef degradation, bioerosion rates may be reduced on reefs that are impacted by high sedimentation, which is a common regional stressor in the Southeast Asian Indo-Pacific.

6.2. Introduction

Coral reefs are highly diverse ecosystems that globally provide critical ecosystem goods and services, such as food, tourism opportunities, fishing-derived income and shoreline protection for hundreds of millions of people (Veron et al. 2009; de Groot et al. 2012). However, these ecosystems are increasingly threatened by anthropogenic activities that have already led to a 50% decline in coral cover in the world's most biodiverse reef region, the Indo-Pacific (Bruno & Selig 2007). On coral reefs, which are traditionally characterised by intense spatial competition, declines in the cover of scleractinian corals can potentially benefit other benthic taxa (Norström et al. 2009). Bioeroding sponges are one potential 'winner', with a number of studies reporting increased abundance on degraded reefs (Lopez-Victoria & Zea 2004; Schönberg & Ortiz 2009; Carballo et al. 2013). Although bioeroding sponge infestation levels can differ relative to other boring taxa depending on environmental conditions (Tribollet et al. 2002; Tribollet & Golubic 2005), they are often the principle internal bioerosion agents on coral reefs (Risk et al. 1995). These sponges are capable of eroding substantial quantities of calcareous substrates; up to 20 kg m⁻² sponge tissue yr⁻¹ in the case of *Cliona orientalis* (Schönberg 2002) and up to 30 kg m⁻² sponge tissue yr⁻¹ for *Cliona albimarginata* (Calcinaï et al. 2007). While these rates are greater than the calcification rates of many scleractinian corals (e.g. De'ath et al. 2009), the relative difference in abundance between these two groups results in net reef growth on healthy reefs. However, changes in environmental conditions that result in coral cover declines without causing parallel declines in the abundance of bioeroding sponges may tip reefs towards a state of net erosion, as appears to be the case on some reefs in the Caribbean and eastern tropical Pacific (Glynn 1997; Perry et al. 2008; Nava & Carballo 2008). This shift from net accretion to net erosion results in a reduction in the topographic complexity of the reef, reducing the availability of habitat for other reef fauna and the provision of ecosystem services, such as shoreline protection (Sheppard et al. 2005; Pratchett et al. 2008).

Given the proliferation of bioeroding sponges on numerous degraded reefs and the implications this has for ecological functioning and ecosystem services, it is important to understand the rate at which sponges are eroding reefs and the factors that influence these rates. In this context, one of the most studied influences on erosion rates is nutrient availability. As many bioeroding sponges are heterotrophic (or at least partly), they are reliant on particulate and dissolved organic

carbon to meet energetic demands (Mueller et al. 2014). Nutrient availability, often measured using chlorophyll *a* concentration (chl *a*) as a proxy, has been shown to correlate with bioerosion rates that are typically higher on polluted eutrophic reefs than healthy reefs (e.g. Rose & Risk 1985; Holmes et al. 2000; Holmes et al. 2009). The erosion rates of some species that harbour endosymbiotic *Symbiodinium* are also dependent upon light availability, with reduced bioerosion in light limited conditions (Hill 1996; Schönberg 2006). Furthermore, the density and minerology of the substrate can also influence sponge erosion, with higher erosion rates occurring in denser substrates (e.g. Schönberg 2002; Calcinaï et al. 2007). Although no direct relationship has been found between sediment and sponge bioerosion rates, sediment can clog the filtering apparatus of sponges with subsequent effects on sponge ecology and physiology (see Bell et al. 2015 for review). Earlier studies have found that sedimentation can limit the abundance of specific bioeroding sponge species (Chaves-Fonnegra et al. 2007) and favour substrate infestation by microborers rather than sponge macroborers (Mallela & Perry 2007).

In this Chapter I focused on the erosion rates of a *Spheciospongia* cf. *vagabunda*, which is a common species across the Indonesian archipelago (J. Marlow pers. obs.). In the Wakatobi UNESCO Biosphere Reserve *S.* cf. *vagabunda* is common on steep reef walls, forming large (up to 1.5 m²) encrusting mats with conical oscula that rise up to 10 cm above the sponge surface (see Chapters 2 & 3). The objective of this Chapter was to compare the bioerosion rates of *S.* cf. *vagabunda* into experimental blocks across sites experiencing known variation in environmental conditions. Understanding how these different environmental factors influence erosion rates in this species provides an increased understanding of how reef degradation will influence sponge bioerosion and the reefs of the future.

6.3. Methods

6.3.1. Study area

This Chapter's research was conducted within the UNESCO Wakatobi Biosphere Reserve (Wakatobi) in southeast Sulawesi, Indonesia. Erosion rates of *S. cf. vagabunda* were measured at the seven sites around the Islands of Hoga and Kaledupa that were chosen to represent a range of environmental conditions and levels of reef degradation (Fig. 6.1). These sites constituted the “core” sites in Chapter 3; three steep-wall reefs; Buoy 1 and 3, and Ridge 1; three sloping reefs: Kaledupa 1, Kaledupa Double Spur and Pak Kasim's; and Sampela 1, which is highly sedimented and considered to be highly degraded (McMellor & Smith 2010). Sites Buoy 1, Buoy 3, Kaledupa 1, Kaledupa Double Spur, Pak Kasim's, Ridge 1 and Sampela 1 are abbreviated in results and figures to B1, B3, K1, KDS, PK, R1 & S1 respectively.

Figure 6.1. Map of Wakatobi region in southeast Sulawesi (top left) and the main study sites around the Islands of Hoga and Kaledupa.

6.3.2. Bioerosion rates

Sponge bioerosion rates were assessed using a modification of the methodology described by Holmes et al. (2009). This methodology uses the deployment of experimental blocks, half as treatment blocks with sponge explants attached and half as controls without sponges. Erosion

rates were determined by weight loss in the treatment blocks over the one year period of deployment whilst controlling for weight loss by factors such as chemical erosion or grazing.

Experimental calcareous (limestone) blocks ($10 \times 10 \times 10 \text{ cm}^3$) were obtained from a mine on the local corraline island of Wanci (as per Chapter 4; Fig. 6.2A). Each block was thoroughly cleaned before drying to constant weight at 150°C and then the volume was measured using water displacement. Blocks were then immersed in seawater for 48 hours before deployment. Deployment took place in July and August 2014 at each of the seven sites; ten blocks were attached to the bedrock at 10 m depth at 15 m intervals using marine epoxy, five controls and five with sponge explants of *S. cf. vagabunda*. The sponge cores were 3.5 cm in diameter and 2.5 cm deep and were attached using cable ties to the vertical side of each block. These sponge cores were haphazardly selected from 35 sponges at 10 m depth on Buoy 3, kept in laboratory aquaria for three hours and then transported to each of the seven sites (Fig. 6.2B). To assess the ecological relevance of using the calcareous blocks, five additional blocks of the recently dead *Porites lutea* were also deployed to Buoy 3 with attached sponge explants. *P. lutea* was chosen as it is a major reef building species in the Wakatobi, especially on reefs that have been degraded by previous bleaching events (J. Marlow pers. obs.). Unfortunately there was not enough recently dead *P. lutea* available to be used as the main treatment substrate, hence the use of calcareous blocks.

In July and August 2015 all blocks were retrieved (Fig. 6.2C), the remnants of any sponge graft removed and then immersed in household bleach. After 48 hours in bleach each block was removed, gently scrubbed with a wire brush to remove any epi- or endobionts, rinsed in fresh water and re-dried to constant weight. From visual inspection of blocks there was evidently a high amount of sponge bioerosion (Fig. 6.2E), however it was impossible to disentangle this from the weight loss due to extremely high external grazing pressure. Given this, an alternative methodology was developed to assess weight loss of treatment blocks independent to external weight loss due to grazing. The excavation region (including all erosion chambers) of each treatment block was hollowed-out using a fine chisel, retaining and weighing the non-eroded infrastructure (Fig. 6.2F). The volume of the excavated region was measured using a silicone mould and the mass of eroded calcium carbonate was then calculated by subtracting the weight of the non-eroded structure from the mass of the entire chamber (calculated from the mould volume and individual block density recorded pre-deployment). Rates were calculated in terms

of kg m^{-2} sponge tissue yr^{-1} based upon the final surface area of the sponge (measured using ImageJ software; Fig 6.2D).

Figure 6.2. Example images of treatment calcareous blocks in 2014; pre-deployment (A), and immediately after deployment in (B), and in 2015; on retrieving from the reef (C), measuring graft surface area (D), after 48 hrs in bleach (E), and after excavation of erosion zone (F).

6.3.3. *Environmental variables*

Environmental data was the same as data collected for Chapter 3:

Throughout March-August 2014 and May-June 2015 an XR-420 CTD (RBR, Ottawa) data logger was deployed at the seven sites on randomly selected dates to measure turbidity and chl *a*. The CTD was set to record every minute with no averaging. Each deployment took place for a minimum of 24 hours, with a minimum of three separate deployments per site. This data collection methodology was identical (including same equipment and sites) to a previous study by Powell (2014) in 2010. Given this, the data was combined to create average values for each environmental parameter for each site. Averages were based on each 24 hour deployment with minutes considered as subsamples within each 24 hour period.

Depth of accumulated settled sediment was used as a proxy for sedimentation; at each site two 30 m transects were haphazardly deployed at 10 m depth and depth of settled sediment was measured on abiotic horizontal and inclined surfaces at 3 m intervals using callipers ($n = 20$).

Between May and August 2015 average current velocity was quantified for each site, in the form proportional water movement, using plaster of paris “clods” (Doty 1971). Clods were deployed on randomly selected dates for three 24 hour periods at each site during this period. Clods were prepared in 5 cm diameter hemispherical casts with stainless steel nails through the centre and dry weighed pre deployment. Deployment consisted of gently nailing three clods at right angles to the substrate at each site at both 10 and 5 m depth. After 24 hrs all clods were recovered and the dry weight measurements repeated. For each of the three 24 hour deployments three control clods were placed on the reef within a weighted 40 ltr perforated bucket. This allowed limited water exchange, exposing the control clods to the same water temperature and salinity (which also affect clod dissolution) but excluded the water currents experienced by the freely deployed clods (Jokiel & Morrissey 1993). Percentage dry-weight loss of clods (subtracting mean control percentage weight loss) was used to determine relative differences in water movement between sites.

6.3.4. *Statistical analysis*

All statistical analyses were performed within the SPSS (version 23) statistical analytical package. Differences in environmental parameters and erosion rates between sites were tested

using a one-way analysis of variance (ANOVA) with relevant *post-hoc* tests. Tukey's *post-hoc* tests were used to identify individual site differences in environmental parameters and Gabriel's *post-hoc* test was chosen for erosion rates because it allows for unequal sample sizes. This was necessary due to differences in sponge explant survival between sites; only sites with three or more surviving explants were included in the analysis. If any data failed to meet the necessary assumptions of equal variance for the ANOVA (even after square-root or natural log transformation) then non-parametric Kruskal-Wallis tests were used with *post-hoc* Bonferroni adjusted pairwise comparisons between sites. Associations between environmental conditions and bioerosion rates were examined through Pearson's Correlation Analysis or Spearman's Rank when non-parametric testing was appropriate. Differences between the erosion rates of *S. cf. vagabunda* into the calcareous treatment blocks and into the *P. lutea* blocks at B3 were analysed using a one-way ANOVA.

6.4. Results

6.4.1. Site environmental characteristics

The mean values for each environmental variable at each site are presented in Table 6.1. Depth of settled sediment varied between sites (Kruskal Wallis, $H_{(6)} = 35.398$, $p < 0.001$). The highest average depth of settled sediment occurred at S1 ($2.94 \text{ mm} \pm 0.28 \text{ SE}$) and pairwise comparisons showed that this was significantly higher than at all other sites. The lowest average depth of settled sediment occurred at K1 ($0.25 \text{ mm} \pm 0.12 \text{ SE}$), which was significantly lower than at B3 and (Table 6.1). Water movement was significantly different between the sites (ANOVA, $F_{(6,75)} = 16.675$, $p < 0.001$) with significantly higher movement at KDS ($24.42\% \text{ clod weight loss} \pm 1.81 \text{ SE}$) compared to any other site and significantly lower movement at B1 ($8.36\% \text{ clod weight loss} \pm 0.84 \text{ SE}$) and B3 ($8.79\% \text{ clod weight loss} \pm 0.75 \text{ SE}$) compared to K1, KDS and R1 (Table 6.1). Significant differences in chl *a* (Kruskal Wallis, $H_{(6)} = 19.807$, $p = 0.003$) were detected between sites, however no significant individual inter-site differences were found in the pairwise comparisons. This is likely due to the conservativeness of so many *Bonferroni* corrections, however the greatest differences were between K1 and PK and S1 ($p = 0.06$ and 0.054 respectively). There were no significant differences in turbidity (Kruskal Wallis, $H_{(6)} = 3.350$, $p = 0.764$) between the sites.

Table 6.1. Environmental characteristics of each site. Standard errors shown.

Variable	Unit	Site						
		Buoy 1	Buoy 3	Kaledupa 1	Kaledupa Double Spur	Pak Kasim's	Ridge 1	Sampela 1
Settled Sediment	mm	0.78 (± 0.29)	1.95 (± 0.33)	0.25 (± 0.13)	0.5 (± 0.09)	1.06 (± 0.11)	0.85 (± 0.2)	2.94 (± 0.38)
Water Movement	% weight loss	8.36 (± 0.84)	8.79 (± 0.75)	18.73 (± 0.67)	24.42 (± 1.81)	12.78 (± 2.60)	16.93 (± 1.62)	13.88 (± 0.81)
Turbidity	NTU	2.66 (± 1.22)	2.06 (± 0.7)	1.69 (± 0.5)	2.07 (± 0.4)	1.75 (± 0.2)	1.32 (± 0.6)	4.10 (± 1.04)
Chlorophyll <i>a</i>	$\mu\text{g l}^{-1}$	0.36 (± 0.12)	0.36 (± 0.02)	0.12 (± 0.1)	0.31 (± 0.08)	0.94 (± 0.14)	0.33 (± 0.03)	2.54 (± 1.00)

6.4.2. Erosion rates

Sponge explant survival varied between sites (Fig. 6.3) and Sampela 1 was excluded from the analysis as only one sponge explant remained by 2015. All other sites had at least three surviving explants. The mean erosion rate of *S. cf. vagabunda* across all sites was $12.0 \text{ kg m}^{-2} \text{ sponge tissue yr}^{-1}$ ($\pm 0.9 \text{ SE}$) with significant differences between sites (ANOVA, $F_{(5,20)} = 6.725$, $p = 0.001$). The lowest average erosion rates occurred at B3 ($6.2 \text{ kg m}^{-2} \text{ sponge tissue yr}^{-1} \pm 0.9 \text{ SE}$), which was significantly lower than at K1, KDS and PK ($p = 0.002$, 0.003 and 0.014 , respectively) (Fig. 6.3). The highest erosion rates occurred at K1 ($16.5 \text{ kg m}^{-2} \text{ sponge tissue yr}^{-1} \pm 1.3 \text{ SE}$) but rates were not significantly different from at any other site other than B3.

Figure 6.3. Mean bioerosion rates of *Spheciospongia cf. vagabunda* and number of surviving individual grafts across the study sites. Standard error shown.

Inter-site differences can be partially attributed to variation in environmental characteristics that existed in between sites. The erosion rates of *S. cf. vagabunda* were negatively correlated with depth of settled sediment (Pearson's, $r^2 = -0.717$, $p < 0.001$) and positively correlated with water movement (Pearson's, $r^2 = 0.485$, $p = 0.012$) (Fig. 6.4). There were no significant correlations with chl *a* (Pearson's, $r^2 = 0.019$, $p = 0.925$) or turbidity (Pearson's, $r^2 = -0.234$, $p = 0.249$).

All sponges survived on the five blocks of *P. lutea*. The erosion rates into these blocks (average of $5.1 \text{ kg m}^{-2} \text{ sponge tissue yr}^{-1} \pm 1.4 \text{ SE}$) was not significantly different (ANOVA, $F_{(1,8)} = 0.374$, $p = 0.558$) from those into the limestone treatment substrate at the same site (B3, as above).

Figure 6.4. Pearson's correlations between erosion rates of *Spherospongia* cf. *vagabunda* and water movement ($r^2 = 0.485$, $p = 0.012$, left) and settled sediment ($r^2 = -0.717$, $p < 0.001$, right).

6.5. Discussion

This is the first study of the bioerosion rates of a *S. cf. vagabunda*, or any other *Sphaciospongia* sp. Bioerosion rates are similar to those found in other clionaid species; e.g. 3.4-17.6 kg m⁻² sponge tissue yr⁻¹ for *C. orientalis* and 2.9-29.5 kg m⁻² sponge tissue yr⁻¹ for *C. albimarginata*, depending on substrate density (Schönberg 2002; Calcinaï et al. 2007; Holmes et al. 2009). The variation in these rates in relation to the measured environmental factors provides insight into how anthropogenically mediated changes in environmental conditions could affect carbonate budgets on future degraded reefs.

6.5.1. Factors affecting erosion rates

The correlation between high water flow and high erosion rates in *S. cf. vagabunda* was weak. However, it is consistent with Rützler (1975) who suggested that strong water movement stimulated bioerosion in experimental grafts of *Pione lampa*. High water flow is likely to be especially important for heterotrophic boring sponges such as *S. cf. vagabunda* as it increases food availability (e.g. Duckworth et al. 2004), which increases sponge bioerosion rates (e.g. Rose & Risk 1985). This is particularly important in oligotrophic environments such as those in this study. Bioerosion rates did not correlate with chl *a* concentration, which initially appears contradictory to many studies that have found erosion rates to increase across gradients of eutrophication (e.g. Rose & Risk 1985; Edinger et al. 2000). However, with the exception of Sampela 1 (which was not included in the erosion analysis as all but one grafts died), chl *a* concentrations were low and uniform across treatment sites. Holmes et al. (2000) found similar results elsewhere in Indonesian, showing that while sponge erosion rates correlated with chl *a* concentration across polluted Javan reefs, this was not the case across less polluted Ambon reefs. On these less polluted reefs, factors such as water movement that increase food availability may be more important.

The inverse correlation between bioerosion rates of *S. cf. vagabunda* and depth of settled sediment and the survival of only one sponge explant at the highly sedimented Sampela reef indicates a negative influence of excessive sediment on this species. Some other studies have found a detrimental effect of sediment on bioeroding sponges. Abundance declines or the absence of bioeroding sponges have been attributed to excessive sedimentation in other studies (e.g. Edinger et al. 2000; Nava & Carballo 2013). However, bioeroding sponges are generally

quite sediment tolerant (Schönberg 2016). For example, both Hutchings et al. (2005) and Osorno et al. (2005) attributed high levels of sponge bioerosion at inshore sites on the GBR to high sediment deposition at these sites. *Spheciospongia* spp. in particular are thought to be sediment tolerant and often are capable of attaching to substrates buried in sediment up to 10 cm deep, surviving due to their fistular projections above the sediment surface (Schönberg 2016). This is also the case for previous descriptions of *S. cf. vagabunda*, which in other locations is often found buried in sediments (e.g. Bergquist 1965; Kelly-Borges & Bergquist 1988; Sutcliffe et al. 2010). In the Wakatobi, buried fistulated *S. cf. vagabunda* have not been observed and the observed negative impacts of sediment on erosion rates and survival of this species are clearly in conflict with these previous descriptions of sediment tolerance. However, as discussed in Chapter 2, previous descriptions of the species are highly varied and likely represent a species complex rather than a single species. *S. cf. vagabunda* in the Wakatobi closely resembles those described by Kelly (1986) and Kelly-Borges & Bergquist (1988) as “encrusting...form gently sloping mounds” and is potentially a less sediment tolerant reef-dwelling member of the complex. A sediment mediated reduction in bioerosion rate in *S. cf. vagabunda* could be due to the metabolic cost of active responses to sedimentation. Wakatobi *S. cf. vagabunda* in more sedimented environments often have mucus threads across their surface and have a more lamella-digitate surface, presumably allowing the body of the sponge to protrude above the sediment layer (as observed by Kelly-Borges & Bergquist 1988). Responses to sediment such as these can have a high metabolic cost (Bannister et al. 2012) and could mean the diversion of energy away from other activities such as bioerosion. However, considering the literature’s description of *S. vagabunda* as a sediment tolerant species and the snapshot collection of sediment data, this correlation should be viewed with some caution. In an effort to address this, I undertook an *ex situ* study into the impacts of settled sediment on the erosion rates of *S. cf. vagabunda* in 2016. Unfortunately data was highly variable and could not be used to prove or disprove the hypothesis that sedimentation constitutes a stressor for *S. cf. vagabunda* (more details in Appendix 2).

6.5.2. Carbonate budget

Caution is needed when interpreting the ecological relevance of this species’ bioerosion rates in relation to local carbonate budgets. Firstly, the methodology of using sponge explants can overestimate rates as boring sponges can display disproportionately high erosion activity during

the initial phases of colonisation (Rützler 1975). The use of limestone calcareous blocks was another potential source of error given the number of studies that have shown a strong link between substrate type and sponge bioerosion rates (e.g. Schönberg 2002; Calcinaï et al. 2007; Hernández-Ballesteros et al. 2013). However, similar rates of bioerosion into the calcareous blocks and into *P. lutea* suggest that the measured rates are representative of those that could be expected in a regionally common form of calcareous substrate. Assuming these rates are ecologically accurate, they approach that of the calcification rates reported from massive *Porites* in the GBR of $\sim 15 \text{ kg m}^{-2} \text{ coral yr}^{-1}$ (De'ath et al. 2009). This suggests that if the abundance of *S. cf. vagabunda* were to increase as scleractinian corals decline, then there would be significant negative consequences for a reefs carbonate budget. However, while *S. cf. vagabunda* is a common relative to other bioeroding sponge species in the Wakatobi, its actual abundance is low in comparison to calcifying benthic taxa. Data from Chapter 3 shows that it covers just 0.6% of total reef area and 2.9% of available dead substrate, equating to average erosion rates of 71.6 g m^{-2} of reef yr^{-1} . It has been suggested that high abundances of bioeroding sponges could tip a reefs carbonate budget towards net erosion (Glynn 1997; Nava & Carballo 2008). This appears to be currently unlikely in the Wakatobi where hard coral cover is still around 20% (Chapter 3; McMellor & Smith 2010). However for those reefs that are currently around 10% coral cover (Sampela 1 and Kaledupa 1), which in the Caribbean is considered to be indicative of reefs likely to have a neutral carbonate budget (Perry et al. 2013), increases in the abundance of this sponge (and others of similar erosive capabilities), could have serious consequences for reef framework.

6.5.3. Conclusions

In conclusion, bioeroding sponges generally benefit from reef degradation (e.g. Schönberg & Ortiz 2009; Carballo et al. 2013). In South-East Asia, a common cause of reef degradation is watershed-based pollution and its associated high levels of sedimentation and turbidity (Burke et al. 2011). The negative correlation between the depth of settled sediment and sponge bioerosion found in this study, suggest that these sponges are not resilient to all conditions that are adverse for corals. Excessive sedimentation in Southeast Asia may limit the potential additional damage of increased abundance of these sponges on the region's degraded reefs.

Chapter 7: General discussion

7.1. Summary of key findings

The overall aim of my thesis was to increase our understanding of the ecology of the bioeroding sponge assemblage on coral reefs within the Southeast Asian Indo-Pacific. Specifically, to gain an insight into how anthropogenically derived disturbances would affect the abundance and functioning of these sponges.

To address my aims, it was first important that I was able to identify the main species of the Wakatobi bioeroding sponge assemblage. Working at the species level is critical to understanding the impacts of reef degradation as many of the factors that contribute towards adult distribution of bioeroding sponges, e.g. larval recruitment, stress resilience, spatial competitiveness and food availability, differ between species (Chapters 3 & 4; Vicente 1978; Uriz et al. 1998; Holmes et al. 2000; Nava et al. 2014). This was only the second study within Indonesia to specifically address bioeroding sponge taxonomy and the first to employ phylogenetics. The assemblage of eight main species differed entirely in composition from the only other study in the region (Calcinai et al. 2005), despite a geographic separation of under 800 km. My findings have furthered the distribution of three known species to Indonesian waters and identified two new species, which I have confirmed phylogenetically. I was able to use these species identifications to show that although the availability of suitable dead substrate appeared to drive overall bioeroding sponge abundance, inter-species differences in environmental preferences and tolerances were important contributing factors to differences in assemblage composition (Chapter 3). This was highlighted by the generally low bioeroding sponge abundance and species richness at Sampela (despite a high availability of suitable substrate) but the persistence of two apparently sediment tolerant species, *Cliothisa* cf. *aurivilli* and *Cliona* aff. *viridis* n. sp. B. In my fourth Chapter I used a two year deployment of experimental substrates to show that bioeroding sponges are able to rapidly recruit to newly available calcareous substrates, countering the view that longer timescales are required (Kiene & Hutchings 1994; Pari et al. 1998; 2002; Tribollet et al. 2002). Recruitment rates, dispersal abilities and the relative importance of substrate cues for settlement also differed between species. In Chapter five I determined that the absence of a zooxanthellate species, *Cliona* aff. *viridis* n. sp. A, at the turbid and sedimented Sampela reef was unlikely to be due to light-limitation. Using a shading

experiment and PAM fluorometry I demonstrated that *C. aff. viridis* n. sp. A is capable of photoacclimating during prolonged periods of moderate to extreme reductions in light availability and rapidly recovering when returned to normal light levels. In my final research chapter I used a common Wakatobi species, *Spherospongia* cf. *vagabunda*, to investigate environmental drivers of erosion rates, finding a stimulatory effect of water flow and a suppressive effect of settled sediment.

7.2. Global and local reef threats and bioerosion

At the global scale, the biggest threat to the survival of coral reefs is man-made climate change and associated ocean warming and acidification (Hughes et al. 2003; Done & Jones 2006; Hoegh-Guldberg et al. 2007; De'ath et al. 2009; Hoegh-Guldberg & Bruno 2010; Eakin et al. 2016). This has predominantly (and most dramatically) manifested as large scale bleaching events (Eakin et al. 2016; Heron et al. 2016; Hughes et al. 2017) but ocean acidification is already reducing coral calcification rates (e.g. De'ath et al. 2009). The consensus is that climate change is likely to be largely beneficial for bioeroding sponges; ocean acidification has been found to increase bioerosion rates (Wisshak et al. 2012; Fang et al. 2013; Stubler et al. 2014), elevated temperatures has limited impact on bioerosion rates (Wisshak et al. 2013; Stubler et al. 2015), and bioeroding sponge abundance has increased after coral bleaching events (Sheppard et al. 2002; Schönberg & Ortiz 2009; Carballo et al. 2013). Although my thesis was primarily focused on localised reef degradation, abundance and recruitment data clearly indicate that bioeroding sponges are closely tied to the availability of dead calcareous substrate, which is likely to increase after bleaching events and subsequent coral mortality. Bioeroding sponge species that are particularly likely to be successful are those that either invest considerable resources in regular reproductive output, are highly spatially competitive or have high growth rates. Previous reports have found zooxanthellate bioeroding sponges to be among those that proliferate after bleaching events (e.g. *Cliona orientalis*; Schönberg & Ortiz 2009). However, a recent observation of a mass bleaching of *Cliona varians* in the Caribbean (Hill et al. 2016) indicated that bioeroding sponges may be more sensitive to thermal events than previously thought (Vicente 1990). A similar event in the Wakatobi in 2016 (Fig. 7.1) demonstrated that *C. aff. viridis* n. sp. A was rapidly able to recover from bleaching with minimal partial mortality. Whether these sponges could recover the lost tissue and invade bleached coral substrates before

other benthic taxa is unknown, although growth rates are high in many zooxanthellate encrusting bioeroding sponges (e.g. González-Rivero et al. 2013; López-Victoria et al. 2006). Also unknown is how bleaching would affect reproduction in these sponges. Gametogenesis is arrested in bleached corals (Szmant & Gassman 1990) and a similar physiological response in bioeroding sponges would likely constrain the sponge's ability to occupy bleached substrates through larval settlement.

Figure 7.1. Partially bleached *Cliona* aff. *viridis* n. sp. A in July 2016 (left image) and after recovery six weeks later (right image).

Ninety-five percent of coral reefs in Indonesia and the wider Southeast Asian region are at risk from local threats, predominantly fishing pressure (destructive fishing and overfishing) and watershed-based pollution (excessive levels of sedimentation, turbidity, eutrophication and pollutants) (Burke et al. 2011). These stressors are commonly implicated in regime shifts on coral reefs (Szmant 2002; Mora 2008; Fung et al. 2011) and have sometimes been associated with shifts to sponge dominance (Ward-Paige et al. 2005; Knapp et al. 2013; Powell et al. 2014). In Southeast Asia, watershed-based pollution threatens 45% of reefs (Burke et al. 2011) and using the Sampela reef as a model site, my thesis primarily focused on how this threat will affect sponge bioerosion. The low bioeroding sponge abundance, species richness and survival of sponge grafts at Sampela indicate that some aspects of either excessive sedimentation, turbidity, nutrient enrichment or some unmeasured variable do not provide favourable conditions for bioeroding sponges. The evidence from elsewhere in Indonesia (Holmes et al. 2000), the eastern Pacific (Nava et al. 2014) and from the Caribbean (Ward-Paige et al. 2005; Chaves-Fonnegra et

al. 2007) suggest that nutrient enrichment is actually likely to promote bioeroding sponge abundance and erosion rates through increased food supply. Therefore the impacts of either sedimentation or turbidity, which are often associated with nutrient enrichment (Edinger et al. 1998; 2000), appear to exceed any benefits derived from increased food supply at Sampela. The presence of *C. aff. viridis* n. sp. B at Sampela and the ability of *C. aff. viridis* n. sp. A to photoacclimate to light levels significantly below those found at Sampela, suggests that photosynthetic bioeroding sponges are not light-limited on turbid reefs, at least in the short term. In fact, nutrient enrichment on these reefs might compensate for any reductions in photosynthetically derived nutrients. It consequently seems likely that on reefs degraded by watershed-based pollution, occupation and erosion of available dead substrate is primarily restrained by sedimentation. This could be attributed to either adult mortality through the clogging of the aquiferous system (Gerrodette & Flechsig 1979), smothering (Illan & Abelson 1995) or abrasion (Nava & Carballo 2013) or by settled sediment hindering settlement of larvae (Maldonado et al. 2008). The low survival of *S. cf. vagabunda* grafts at Sampela and the negative correlation between depth of settled sediment and erosion rates in the species, further supports the negative impact that sedimentation can have on some bioeroding sponge species. Nevertheless the abundance and recruitment rates of both *Cl. cf. aurivillii* and *C. aff. viridis* n. sp. B demonstrate that some species are resilient to high levels of sedimentation and turbidity. Similar findings have been found in the GBR where *Siphonodictyon mucosum*, a sediment specialist, increased in abundance on reef flats after a coral bleaching event (Schönberg & Ortiz 2009). Nava et al. (2014) also found distinct differences in bioeroding sponge assemblage composition between reefs associated with differing levels of chl α , $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, turbidity and sedimentation. Therefore watershed-based reef degradation is likely to result in increased bioeroding sponge abundance but only limited to those sediment tolerant species. The impact this will have on the reef will largely depend on the erosion rates of those tolerant species.

While overfishing has been associated with regime shifts to macroalgal dominance on Caribbean reefs (Hughes 1994; Jackson et al. 2001), there is less evidence for involvement of overfishing in other regime shifts. In the Wakatobi widespread use of non-selective fish fences, more traditional line and speargun fishing, and destructive blast and cyanide fishing (Clifton et al. 2010) has led to significant declines in reef fish abundance (Curtis-Quick 2013). The consequence of reef fish abundance declines for bioeroding sponges is currently unclear but any impacts are likely to be

due to changes in the abundance of herbivorous grazers or spongivorous fish. Presently, there is very little information about bioeroding sponge mortality, either indirectly due to grazing pressure or directly by spongivorous fish, however both have been observed in the Wakatobi (J. Marlow pers. obs.). The only study to specifically study spongivory on bioeroding sponges (*C. varians*) found high rates of mortality inflicted by Angelfish (Hill & Hill 2002), which have also been identified as prominent spongivores in the Wakatobi (Powell et al. 2015). There is more evidence for the role of grazers in influencing sponge bioerosion but the conclusions are mixed. Risk & Sammarco (1982) measured bioerosion in *Acropora* inside and outside of damselfish territories and found erosion was highest inside territories. As damselfish aggressively exclude other reef fish from their territories, the authors attribute the difference in erosion to reduced bioeroder mortality by fish predators or grazers. Therefore a reduction in spongivorous fish or herbivorous grazers through over-fishing might result in a similar increase in bioerosion. However, a reduction in herbivorous grazers is also likely to result in increased macroalgae cover, which negatively correlates with the bioeroding sponge abundance and is a known spatial competitor (Wismer et al. 2009; Cebrian 2010; González-Rivero et al. 2012; Ramsby et al. 2017). Furthermore, there is evidence that grazing by parrotfish in the region between neighbouring corals and bioeroding sponges can facilitate the spread of the bioeroding sponge (Márquez & Zea 2012). Therefore it is currently unclear the degree to which overfishing will affect sponge bioerosion on coral reefs. A more foreseeable association between sponge erosion and fishing practices is in relation to destructive fishing methods such as blast fishing. Blast fishing is illegal but widespread in Indonesia (Erdmann 2000), reducing branching coral to fields of rubble and capable of splitting-open large massive corals (Alcala & Gomez 1987). It produces large areas of dead calcareous substrates suitable for colonisation by other taxa (Fox et al. 2003), such as bioeroding sponge. Blast fishing also potentially acts as a form of asexual dispersal for bioeroding sponges, as has been observed from other physical forms of reef disturbance (López-Victoria & Zea 2004)

7.3. Carbonate consequences of increased sponge bioerosion

The geomorphic status of coral reefs is a function of both calcium carbonate production (corals and coralline algae) and erosion (physical, chemical and biological) (Perry et al. 2008). A positive balance between these two is associated with healthy reefs but disturbance events that change the relative abundance of either coral accretors or eroders can tip this to a negative

erosional state (Eakin 2001). The best current examples of this are in the Caribbean and Eastern Tropical Pacific. Historically (Holocene), reef carbonate budgets in the Caribbean have been positive by approximately $10\text{--}17 \text{ kg CaCO}_3 \text{ m}^{-2} \text{ year}^{-1}$ (Vecsei 2001). However, recent surveys across four Caribbean nations by Perry et al. (2013) found current carbonate production ranged from -1.77 to $9.51 \text{ kg CaCO}_3 \text{ m}^{-2} \text{ year}^{-1}$; 21% of reefs had a negative budgets and a further 26% had positive budgets below $1 \text{ kg CaCO}_3 \text{ m}^{-2} \text{ year}^{-1}$. These authors attributed this to significant declines in coral cover across the region and suggest that 10 % coral cover is the tipping point below which net-erosion occurs. If a similar relationship occurs in the Indo-Pacific, reefs at Kaledupa and Sampela (Table 3.1) are likely to be approaching “accretionary stasis” (Perry et al. 2008), with further reductions in coral cover or increases in bioerosion tipping the balance towards net-erosion. This is particularly the case if there are large increases in the abundance of highly erosive species such as *S. cf. vagabunda*. A prolonged period of net-erosion is likely to have serious consequences for the stability and maintenance of reef framework. For example, a mass coral mortality in Galapagos Islands during the early 1980s and a subsequent population explosion of echinoid bioeroders resulted in a carbonate deficit of 10 to $30 \text{ Kg CaCO}_3 \text{ m}^{-2} \text{ year}^{-1}$ (Glynn 1988). The perseverance of the bioeroder population without any coral recovery over the past 35 years has resulted in virtually total reef frame loss in the central and southern islands (Glynn 1994; Reaka-Kudla et al. 1996; Glynn & Manzello 2015). The loss or reduction of reef framework is likely to have serious ecological and economic consequences. The three dimensional complexity afforded by intact coral growth forms and framework on healthy reefs facilitates the high diversity and abundance of other reef taxa by providing a range of habitats and refuges from predators and environmental stressors (Bruno & Bertness 2001; Willis et al. 2005). Reef rugosity and both height and variety of coral growth forms correlate strongly with reef fish diversity and abundance (Gratwicke & Speight 2004). Many of the fish that inhabit these refuges are commercially or ecologically important (Beukers & Jones 1997; Lee 2006; Graham et al. 2007). Additionally, a complex reef framework enhances coastal protection through the dissipation of wave energy (Lugo-Fernandez et al. 1998), which is of growing importance given predicted sea level rises. Therefore a state of net-erosion as a consequence of reduced coral accretion and increased sponge erosion is likely to have significant consequences for reef biodiversity, productivity and local socio-economics (Pratchett et al. 2008; Alvarez-Filip et al. 2009). One good example of this potential trajectory is the Seychelles. The reefs around these islands suffered a 90% coral mortality in the 1998 mass bleaching event (Sheppard 2003),

and by 2005 were a drastically altered ecosystem; benthic composition had shifted from a highly complex coral-dominated state to a low complexity rubble and algal-dominated state (Graham et al. 2006). The associated reef fish assemblage saw a local extinction of four species and a critical drop in abundance of six other species. Graham et al. (2006) found that the shift in species richness on these reefs was not a product of the reduction in coral cover but due to changes in complexity in habitat. In this regard, endolithic bioeroders often have a disproportion erosional effect on reef complexity as many preferentially occupy and erode the base of coral branches (Carballo et al. 2008b). Bioeroding sponges are therefore considered, among other bioeroders, to be key contributors to the flattening of reef framework and the reduction in habitat complexity (Glynn & Colgan 1992; Alvarez-Filip et al. 2011). In an increasingly acidic ocean, with decreased calcification rates (Orr et al. 2005), this is likely to be exacerbated by increased rates of sponge bioerosion (see Schönberg et al. 2017 for review).

7.4. Indonesian sponge bioerosion in a global context

Unfortunately, direct comparisons of bioeroding sponge space occupation and abundance patterns between Wakatobi and other regions are more problematic because of differences in survey methodologies. Other surveys have used % occurrence within rubble/coral (e.g. Carballo et al. 2013; Nava & Carballo 2013), numerical abundance or sponge size (e.g. Ward-Paige et al. 2005), but few have used percentage cover (e.g. Schönberg 2015a), which is surprising given the methods prevalence in coral studies (e.g. Edmunds & Elahi 2007; Green et al. 2008; Cleary et al. 2014). The most recent and analogous study to address the abundance of bioeroding sponges using percent cover has been in the GBR (Schönberg 2015a), which found that bioeroding sponges currently occupy 11.1% of suitable substrate, which is comparable to current occupation rates of bioeroding sponges in the Wakatobi (8.9% of suitable substrate). Bioeroding sponge cover on the GBR increased from 9.8% in 1997/1998 to 14.8% in 2003/2004 following bleaching events in 1998 and 2002 (Schönberg & Ortiz 2009) but abundance has since plateaued in some species (Schönberg 2015a; Ramsby et al. 2017). Conversely around the Caribbean island of Grand Cayman average cover (non-substrate standardized) of bioeroding sponges is 1.24% (Murphy et al. 2016), under half that of the Wakatobi (3.1%). While recent studies have demonstrated high bioeroding sponge cover in some parts of the Caribbean, the highest abundances appear to be concomitant with eutrophication (e.g. Rose & Risk 1985; Ward-Paige et al. 2005; Chaves-Fonnegra et al. 2007). Furthermore, recent declines in bioeroding sponge

abundance to very low levels in some parts of the Caribbean have been associated with reductions in nutrient input (Ruzicka et al. 2010; 2013). Outside of eutrophic environments, Indo-Pacific reefs (e.g. the GBR, Wakatobi) may support higher abundances of bioeroding sponges on degraded reefs as the majority of these reefs are yet to experience large shifts to macro-algal dominance (Bruno et al. 2009), which is known to be an important bioeroding sponge competitor on Caribbean reefs (Wismer et al. 2009; Cebrian 2010; González-Rivero et al. 2012).

7.5. Implications for monitoring and management

The 1998 El Niño and the subsequent global coral bleaching catalysed coral reef monitoring programmes around the world (Houk & Woesik 2013). However, the focus of these monitoring programmes remains largely coral-cover-centric, and it has been argued that a more question-orientated approach that encompasses more functional groups is required (Bellwood et al. 2004; Hughes et al. 2010). Given the proliferation of bioeroding sponges on certain degraded reefs (e.g. Schönberg & Ortiz 2009; Carballo et al. 2013) and the consequences this can have for carbonate budgets (Glynn 1997; Perry et al. 2008; Nava & Carballo 2008), it might be assumed that bioeroding sponges are regularly included in monitoring efforts. Unfortunately, with the exception of some instances in the Caribbean (Gilliam 2007; Lang et al. 2010), bioeroding sponges (and sponges more generally) have been largely excluded from long term monitoring efforts. This is presumably due to their cryptic habitat and the specialist knowledge that is required for species identification. However, the line intercept method described by Schönberg (2015a), and used in Chapter 3, could be readily incorporated into existing monitoring programmes. Direct incorporation may not be possible in all cases, as programmes that use point intercept (e.g. Reef Check) might lack the resolution to detect bioeroding sponges. However, many current monitoring programmes could incorporate bioeroding sponges with minimal changes to their current methodologies. Larger methodological changes would be required to incorporate assessments of carbonate budget into reef monitoring programmes (see Perry et al. 2012). Realistically however, without measuring carbonate accretion or bioerosion by other bioeroders, the monitoring of bioeroding sponge abundance or erosion rates alone is meaningless in the context of understanding reef carbonate changes.

Reef management is generally a localised process that aims to maintain biodiversity, sustain fisheries production and simultaneously allow resource extraction by the local populace (McClanahan et al. 2006; Christie & White 2007). An increase in reef sponge bioerosion has the potential to negatively affect both total reef biodiversity and fisheries production, as well as coastal protection and is therefore an important factor to be considered in reef management strategies. Fortunately, as the abundance of bioeroding sponges is tightly linked to the availability of suitable calcareous substrates (this thesis; Chaves-Fonnegra et al. 2007, Carballo et al. 2008a, Schönberg & Ortiz 2009, Schönberg 2015a), controlling their spread likely falls into the broad aims of most current reef management goals, i.e. maintaining or increasing coral cover. Some authors have argued that little can be done at the local scale to arrest coral declines from large-scale stressors such as climate change (Edwards & Gomez 2007). However, there is evidence that well managed long-term marine protected areas (MPAs) are capable of increasing resilience to global stressors through the maintenance of functional groups, accumulation of herbivorous fish, trophic cascades, and subsequently increasing coral recruitment (Hughes et al. 2007; Mumby et al. 2007; Mellin et al. 2016). Therefore on Southeast Asian coral reefs, the implementation of no take zones or “coral-friendly” and fishing regulations (Mumby & Steneck 2008) are likely to indirectly slow the proliferation of bioeroding sponges through the maintenance of coral cover.

Unfortunately, the funding for coastal zone management in Indonesia and other developing countries in the Region is sadly lacking, and many MPA or National Parks are better described as “paper parks”. The Wakatobi is prime example of this and where available, data suggest that the annual funds allocated to the park represent just 1% of the estimated US\$2.7 million required for effective management (Clifton et al. 2010). The lack of appropriate funding means that enforcement of the no-take-zones (NTZs) (3.4% of the park’s area) is constrained in all but the areas that are supported by local tourism operators (Clifton 2013). Even in these areas the NTZs are so small they are unlikely to offer any real protection to target species (Stacey et al. 2016). In the unenforced NTZs, compliance is minimal and reflects the insufficient consultation, education and participation of the Bajau fishers in the process of park zoning. Although now settled, the historical nomadism of Bajau means they are unlikely participants in local fisheries management as in the past fishers have simply moved on to new fishing grounds when catches decline (Satria & Masuda 2004). Further hindering the participation of the Bajau is that they do not perceive

time as linear, therefore have little perception of causality, i.e. that short-term restrictions in fishing activities could be outweighed by the long term benefits (Clifton & Majors 2012). The management and enforcement of sufficiently sized MPAs or fishing regulations in the Wakatobi and other similar regions is consequently unlikely to reverse or even slow declines in coral health or halt increases in other spatially competitive taxa such as bioeroding sponges. Local management of reefs in the Wakatobi, and others like it in the region, needs appropriate funding, scientific input and local stakeholder participation from the outset if conservation goals are to be met.

7.6. Limitations

From the outset, this thesis focused on the conspicuous bioeroding sponge species of the Wakatobi, i.e. those that could be observed by the naked eye. After spicule confirmation of observable macro-morphological differences in sponge species (Chapter 2), both abundance surveys and recruitment analysis relied upon visual identification of sponges. Schönberg (2015a), recommended the use of line intercepts and visual identification as they were the least spatially biased and provided the most statistical efficiency. However, the use of rubble surveys (e.g. Holmes et al. 2000), which are able to detect species with no observable surface presence, detected almost twice as many species as the line intercepts. Therefore focusing on only those species that are externally observable is likely to have underestimated the full extent of the bioeroding sponge assemblage composition and both levels of abundance and recruitment. Nevertheless, the inclusion of inconspicuous species into Chapters 3 and 4 would not have been possible in the field (as spicule identification is required). Perhaps more importantly, this thesis aims to address the impacts of habitat degradation on bioeroding sponges and a focus on the larger, more aggressive species (in terms of both erosion and spatial competition) is more appropriate. In this context, disregarding inconspicuous species is appropriate as they are generally less aggressive (Carballo et al. 2008a; Schönberg 2015a).

With exception of March-April 2014, all biological and environmental data was collected in short summer field seasons. The Wakatobi experiences seasonal changes in rainfall and prevailing wind direction; a dry season in April to October, when the prevailing wind is from the east, and a rainy season from November to March when the prevailing wind is from the west. Therefore the collection of data during only the dry season provided only a snapshot view and

could have failed to account for intra-annual variation in environmental and biological variables. Consequently, it's presently unknown how much seasonal variation occurs in the assemblage dynamics of bioeroding sponges in the Wakatobi. Evidence from elsewhere is mixed; sponge assemblage composition on reefs in the Mexican Pacific change with seasonal differences in wind, swell and sediments (Carballo 2006; Carballo et al. 2008b), conversely a study from the Caribbean found that the sponge assemblage remained relatively constant over the course of 16 years (Hughes 1996). Most likely a bigger source of error is the collection of environmental data during only these periods with seasonal changes in wind and rain likely affecting turbidity, chlorophyll α concentrations and water flow.

7.7. Future direction of research

Reef degradation in the Indo-Pacific is likely to continue due to stressors originating both locally and globally, and therefore research into the resilience and functioning of bioeroding sponges needs operate at these two levels.

This thesis highlighted the inter-species differences in sediment tolerance in bioeroding sponge species, but there is very little available information on the mechanisms that govern these differences (see Bell et al. 2015 for review) and is an important area of future research. Extensive research into sediment tolerance has been conducted in corals, with differences in passive and active response capacity determining abundances in highly sedimented habitats (Lasker 1980; Rogers 1990; Riegl 1995; Gleason 1998; Bongaerts et al. 2012). There is evidence of passive clearing of limited amounts of sediment in *C. orientalis* (Schönberg 2015b), but no studies have directly studied active clearing mechanisms in these sponges. Species composition data from Sampela suggest that α growth forms may be better equipped to inhabit highly sedimented environments, perhaps due to the sieve-like villi formations on the inhalant papillae. These morphological structures may aid sediment clearing or prevent sediment inhalation. In fact sponges were often found under a considerable depth of settled sediment suggesting that they are capable of pumping interstitial water (Illan & Abelson 1995). Although permanent burial is unlikely a long term option for zooxanthellate species such as *C. aff. viridis* n. sp. B (which is common at Sampela) and some form of active sediment clearing mechanisms is likely required. One aspect of passive sediment clearance that has received no attention is the role that non-sponge reef taxa can have. Time-lapse cameras deployed facing *S. cf. vagabunda* at B3 and B1

showed extensive surface feeding by Holothurians (*Synaptula* spp.) and reef fish (predominantly *Ctenochaetus* spp.), which reduced surface sediment (Electronic Supplementary Material). Whether these organisms are active spongivores or feeding on either surface biofilm or sponge mucus (potentially produced due to sedimentation; Biggerstaff et al. (2017)) and the importance of this feeding as a sediment clearance mechanism is an interesting area of future research. Finally, my data also suggest that moderate sedimentation inhibits erosion rates in *S. cf. vagabunda*, possibly through diversion of metabolic activity to morphological changes. For those bioeroding sponge species that are able to tolerate sedimented environments through active sediment rejection mechanisms, it is important that we understand how these responses effect erosion rates

My study and others have demonstrated that zooxanthellate bioeroding sponges are able to photoacclimate and survive during prolonged periods of extremely reduced or elevated light availability (Steindler et al. 2001; Pineda et al. 2016; Fang et al. 2017a). However, reduced erosion rates and unchanged heterotrophic feeding in shaded *C. orientalis* indicate that low light acclimated *Symbiodinium* are not necessarily providing the same nutritional content to their hosts as in higher light environments (Schönberg 2006; Fang et al. 2017a). Future research into photoacclimation could benefit from integrating not only PAM fluorometry, respiration assessments and measurements of organic carbon uptake, but also the use of stable isotopes to trace changes in translocated carbon.

At the global scale, the warming event in the Caribbean in 2015 was the first documented mass bleaching of bioeroding sponges (Hill et al. 2016) and a similar bleaching event and subsequent recovery in *C. viridis* n. sp. A was observed in the Wakatobi in 2016 (Fig 7.1). These observations are contrary to the previously held belief that the *Cliona-Symbiodinium* symbiosis was generally more thermally tolerant than in Cnidarian hosts (Vicente 1990; Schönberg & Loh 2005). It is critically important that we understand not just the thermal tolerance of these sponges but also the capacity to recover from bleaching and the physiological mechanisms that allow this. In particular, future research should focus on the ability for these sponges to regulate *Symbiodinium* cladal composition in relation to thermal stress. While some clionaid species appear to be only associated with one clade of *Symbiodinium*, e.g. Clade G in *C. orientalis* and *C. varians* (Schönberg & Loh 2005; Granados et al. 2008; Hill et al. 2011), my thesis has shown that *C. aff. viridis* n. sp. A is able to form symbioses with three separate clades and host multiple

clades within the same individual sponge. The ability to host different clades of *Symbiodinium* is important for term long term survival on thermally stressed reefs, as different clades are known to differ in their thermal tolerance (Rowan 2004; Tchernov et al. 2004). If zooxanthellate bioeroding sponges are able to shuffle the relative abundance of these clades or acquire more thermally tolerant *Symbiodinium* from the environment, then this would constitute a distinct adaptive advantage.

7.8. Concluding remarks

To conclude, bioeroding sponges within the Wakatabi are taxonomically and morphologically diverse and found to varying degrees in all reef environments. Bioeroding sponge adult abundance is primarily a function of the availability of dead calcareous substrate but species-specific differences in recruitment and stressor resilience further structure populations. Overall, reef degradation in the region is expected to stimulate abundance increases. However, the exact trajectory is expected to be dependent upon the nature of the disturbance and the biology of individual species. The consequences of increasing sponge bioerosion, coinciding with reductions in calcium carbonate accretion rates is likely to have substantial ecological and economic consequences for Southeast Asian reefs and coastal communities. To avoid the worst of these consequences, local monitoring needs to include assessments of carbonate budgets to best inform local management. Reef management at these scales needs to include increasing numbers of enforced MPAs and fishing regulations that prioritise the preservation of functional groups to enhance reef resilience. Unfortunately, the biggest drivers of bioerosion sponge abundance and erosion and continuing declines in coral reef carbonate budgets is likely to be climate change. Unless large reductions are made in atmospheric CO₂, even the most vigorous coral reef management and conservation is unlikely to avoid largescale coral mortalities and dismantling of calcareous framework.

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Appendices

9.1. Appendix 1

Results of bivariate correlations (Spearman's Rank, r_s) comparing the standardised abundance of individual species of bioeroding sponges with environmental factors. Only the three most dominant species are shown. Significant correlations are displayed in bold. Analyses were conducted with and without the inclusion of data for the outlier site Sampela 1.

Factor	Species	Sampela included		Sampela excluded	
		r _s	P	r _s	P
Depth of settled sediment					
	<i>Cliothesa</i> cf. <i>aurivillii</i>	-0.248	0.023	-0.343	0.003
	<i>Cliona</i> aff. <i>viridis</i> n. sp. B	-0.078	0.480	0.125	0.296
	<i>Spheciospongia</i> cf. <i>vagabunda</i>	0.260	0.017	0.601	<0.001
Water movement					
	<i>Cliothesa</i> cf. <i>aurivillii</i>	0.062	0.576	0.034	0.779
	<i>Cliona</i> aff. <i>viridis</i> n. sp. B	-0.148	0.179	-0.139	0.244
	<i>Spheciospongia</i> cf. <i>vagabunda</i>	-0.438	<0.001	-0.471	<0.001
Turbidity					
	<i>Cliothesa</i> cf. <i>aurivillii</i>	-	-	0.089	0.455
	<i>Cliona</i> aff. <i>viridis</i> n. sp. B	-	-	0.177	0.138
	<i>Spheciospongia</i> cf. <i>vagabunda</i>	-	-	0.472	<0.001
Chl <i>a</i>					
	<i>Cliothesa</i> cf. <i>aurivillii</i>	-0.125	0.258	-	-
	<i>Cliona</i> aff. <i>viridis</i> n. sp. B	-0.027	0.810	-	-
	<i>Spheciospongia</i> cf. <i>vagabunda</i>	-0.031	0.776	-	-

9.2. Appendix 2

Aim

My aim was to test the hypothesis that erosion rates in *Spheciospongia* cf. *vagabunda* are reduced by excessive sedimentation. My objective was to expose *ex situ* sponge grafts/blocks to a sediment regime comparable to Sampela for 45 days and infer erosion rates in comparison to non-sediment exposed sponge grafts/blocks.

Figure 1. Ten aquaria with paired blocks (left) and example image of sponge block and control block within sediment treatment aquaria (right).

Methods

In August 2015 32 calcareous blocks were attached to the B3 reef at 10 m depth using marine epoxy. Half had attached grafts *S. cf. vagabunda*, half were left as controls. In May 2016 10 blocks with surviving grafts and 10 controls were retrieved. Each block was buoyant-weighed using digital scales (Ohaus STX422, Greifensee) in an underhanging basket immersed in an aquaria. Blocks were then placed in ten flow-through aquaria, one sponge block and one control block in each. Over the course of 45 days sediment was added daily to half the aquaria and half were left as controls (Fig.1). Sediment was collected from Sampela, rinsed in freshwater and dried for 24 hrs at 180 °C before application in treatments. The amount of sediment added to each treatment was based on individual sponge surface area in relation to average daily sedimentation rates at Sampela (2015 sediment trap data): $3.5\text{mg cm}^{-2}\text{ day}^{-1}$; 20% > 250 μm ,

20% 125-250 μm , 40% 63-125 μm and 20% 38-63 μm . Control blocks within treatment aquaria were treated with the same amount of sediment as their reciprocal sponge block. After 45 days all blocks were reweighed using buoyant weight. Erosion rates were estimated in terms of kg m^{-2} sponge tissue yr^{-1} based on surface area at the end of the experimental period and in relation to their paired control block.

Results

Seventeen of the blocks gained weight over the experimental period (average $0.52\text{g} \pm 0.07 \text{ SE}$) and three lost weight (average $-0.47\text{g} \pm 0.03 \text{ SE}$). Sponge blocks in the sediment treatment gained an average of $0.36\text{g} (\pm 0.07 \text{ SE})$, while their reciprocal non-sponge control blocks gained an average of $0.72\text{g} (\pm 0.16 \text{ SE})$. In the control aquaria sponge blocks gained an average of $0.36\text{g} (\pm 0.25 \text{ SE})$ and non-sponge control blocks gained an average of $0.06\text{g} (\pm 0.23 \text{ SE})$. This equated to average erosion rates in the sediment treatment *S. cf. vagabunda* of $1.4 \text{ kg m}^{-2} (\pm 0.6 \text{ SE})$ sponge tissue yr^{-1} based, control sponge blocks actually gained 1.15 kg m^{-2} sponge tissue yr^{-1} ($\pm 0.79 \text{ SE}$).

Discussion

The difference in erosion rates between the treatments was in direct contrast to the results from the *in situ* erosion study. However, I do not believe that these are ecologically relevant results but instead a consequence of greater erosion by non-sponge endolithic bioeroders (e.g. polychaetes and molluscs) in the non-sponge blocks in the control aquaria. This hypothesis is supported by the buoyant weight data and visual observations of bioerosion (sediment production) in some of these blocks during the experimental period. Significantly greater replication and a longer experimental period would resolve this source of error.