Habitat scale variability in the rates of coral reef carbonate framework production and bioerosion on Grand Cayman

Submitted by ***Gary Noel Murphy*** to the University of Exeter as a thesis for the degree of Doctor of Philosophy in Geography, September 2016

I certify that all material in this thesis which is not my own work has been identified and that no material has previously been submitted and approved for the award of a degree by this or any other University.

Signature:

Abstract

Caribbean coral reefs have undergone changes in coral cover, structural complexity and assemblage composition since the 1970s. Although some of the ecological consequences associated with these changes have been well documented, the consequences for ecosystem functions dependent on reef structure are less well understood. In particular, there has been little research into the effects of change, on carbonate production and bioerosion; both are critical controls of structural complexity. Currently, there is only a very limited understanding of how both processes vary within and between different habitat types and what this means for ecosystem functioning.

Carbonate framework production and bioerosion were investigated within three habitat types (hardgrounds, *Acropora palmata* reef and *Orbicella* reef) under sheltered and exposed wave energy regimes on Grand Cayman. Census based assessments were used, allowing the identification of functionally important species. Additionally, habitat specific calcification rates were measured for calcareous encruster communities to improve estimations of carbonate production; mean rates of calcification ranged from 0.19 to 1.14 G (1G = 1 kg $CaCO_3$ m^{-2} yr^{-1}) within hardgrounds (4–7 m), *Acropora palmata* reef (1–8 m) and *Orbicella* reef habitats (8–15 m) and were significantly higher at wave exposed sites. The rates of bioerosion for two sponge species, *Siphonodictyon brevitubulatum* and *Cliona tenuis*, were also measured and new approaches to estimating excavating sponge community bioerosion were developed to improves bioerosion estimates.

Mean carbonate framework production was 0.38 G within hardgrounds, 2.65 G within *Acropora palmata* reef habitat and 3.54 G within *Orbicella* reef habitat but not significantly different between wave exposure regimes. Calcareous encruster communities, dominated by coralline algae, were identified as key carbonate producers within shallow reef habitats on the exposed south coast. They may be important to the maintenance of reef structure in these degraded reef habitats. *Orbicella* species were the most important carbonate producers within all reef habitats. Mean total bioerosion was 1.32, 2.27 and 2.28 G within hardgrounds, *Acropora palmata* reef and *Orbicella* reef habitats respectively.

Total bioerosion was not significantly different between wave exposure regimes for any habitat type, but almost completely dominated by parrotfish (29–86 %).

On Grand Cayman, both carbonate framework production and bioerosion were less than that measured in comparative habitats, across the Caribbean, despite the presence of a well-managed marine protected area on the sheltered west coast. The highest rates of net carbonate production occurred in the deepest habitat - *Orbicella* reef (exposed: +1.45 G, sheltered: +1.07 G). Sheltered and exposed *Acropora palmata* reef habitat had net production rates of +0.53 and +0.30 G respectively. Hardgrounds were net erosional (-0.94 G). Overall the results suggest a change in the focal point for reef accumulation on Grand Cayman that may alter geomorphology over time. Additionally, *Acropora palmata* reef habitats are likely to be in a state of accretionary stasis, which may have shutdown reef growth in reef crest environments as carbonate framework produced within these habitats is a major contributor to reef accumulation at the reef crest.

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GN Murphy, P Chin and C McCoy collected coral heads and short cores. GN Murphy performed all analyses. The manuscript was written by GN Murphy, with editorial contributions from CT Perry.

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A general introduction

The Caribbean eco-region is in the midst of a coral reef crisis. Coral cover has declined throughout the region (Caribbean sea, Gulf of Mexico and the western Atlantic from Bermuda south to Trinidad) since at least the 1970s (Jackson 1997, Gardner et al. 2003) and the biodiversity and abundance of reef associated species has synergistically changed (Done 1992, Jackson et al. 2014); sometimes due to local anthropogenic activities or more regional phenomena such as disease and bleaching, but often due to a combination of different factors. Compounding the ecological disruption of reef systems is new evidence that reef growth potential is greatly reduced in comparison to reef accretion rates over the past ~10,000 years (Perry et al. 2013). Furthermore, coral reefs face a bleak future as climate change models predict warming seas (Caribbean mean = + 0.5 to + 4.0 ºC) and decreasing aragonite saturation levels during this century (Meissner et al. 2012, IPCC 2014). It is unclear how coral reefs will respond to each of these threats. However, an increase in the severity and recurrence of bleaching events (Knowlton 2001, Sheppard 2003, Donner et al. 2005), a decrease in calcification rates (Johnson and Carpenter 2012, Kennedy et al. 2013) and an increase in the rates of bioerosion (Wisshak et al. 2012, Barkley et al. 2015) seem likely. Hence, the ability of coral reefs to continue accreting and to maintain their structural complexity as climate change alters the physical and chemical environment of reef communities already stressed by a myriad of existing pressures, is far from certain (Hoegh-Guldberg et al. 2007, Kennedy et al. 2013).

A reduction in the structural complexity of reefs has already occurred, accompanying declines in live coral cover across the Caribbean (Alvarez-Filip et al. 2009). This is likely to have had negative effects on biodiversity, biological carrying capacity and ecosystem functioning (Gratwicke and Speight 2005, Alvarez-Filip et al. 2013, Graham and Nash 2013). The ability of coral reefs to maintain their structures directly affects the habitat available to reef animals (Alvarez-Filip et al. 2011b, Graham and Nash 2013) and therefore the quantity of carbonate framework produced on a reef and which species produce it will

greatly influence the biodiversity and abundance of reef animals and plants (Alvarez-Filip et al. 2011a). Scenarios where current disturbance regimes (both regional, climate driven and localised, anthropogenic regimes) continue unabated or increase may lead to species extinctions, the failure of ecosystem functions and the loss of essential ecosystem services (Hoegh-Guldberg et al. 2007, Kennedy et al. 2013). Many of the ecosystem services provided by coral reefs and many ecosystem functions are dependent on the ability of coral reefs to maintain their physical structures. Hence, a quantitative understanding of carbonate framework production and erosion on coral reefs would be a useful management tool. However, at present there is little quantitative data available on the rates of calcium carbonate framework and sediment production within reef habitats or throughout wider reef systems to inform reef management paradigms.

1.1 The significance of calcium carbonate framework production to coral reef systems

Tropical coral reefs are not isolated habitats, although their dimensions are often limited spatially. Currents moving water between discrete reef habitats provide a link from one to the other (Roberts 1997) and many reef organisms have evolved to maximise their dispersion potential by using currents during mass spawning events, including the Nassau grouper (Colin 1992) and many coral species (Harrison et al. 1984, Wood et al. 2014). Ontogenetic migrations in many species reinforce the idea of connectivity between seemingly discrete habitats, as planktonic forms which settle in nursery habitats subsequently leave to find more suitable habitat for adult forms (Nagelkerken et al. 2000, Mumby et al. 2004). The ecological and physical relationships between coral reefs, hardgrounds, mangroves, seagrass beds and other reef associated environments are so numerous and complex that many authors have suggested studying or protecting coral reefs within the context of wider reef systems or seascapes (Ogden 1988, Harborne et al. 2006). Hence coral reef systems include all reef associated environments.

The idea of connectivity within a coral reef system can be extended to include the transport of calcium carbonate between reefs and other reef associated habitats, particularly those within sedimentary environments. Many of the ecological interrelationships between different coral reef system habitats are in some way dependent on the movement and production of calcium carbonate. Coastal protection from wave energy, by fringing and barrier reefs, allows the development of sedimentary environments in the lee of reefs because of a reduction in wave energy as waves break on the reef crest. Reef material (calcium carbonate) in the form of sediment and sometimes rubble, can be carried over the reef crest by wave energy and currents. Larger carbonate particles begin to settle first in back reef habitats and smaller particles settle further away as energy dissipates (Beanish and Jones 2002). The settlement of fine sediment promotes the growth of seagrasses which baffle currents further, allowing the growth and expansion of seagrass beds (Beanish and Jones 2002). Mangroves and muddy substrates may also benefit from a reduction in wave energy as both require calm, still water to establish and grow. Thus, sedimentary habitats could not exist in many locations without the protection from wave energy, afforded by coral reefs. The production of calcium carbonate framework by corals in fore-reef, reef crest and back reef environments increases structural complexity, while increasing wave energy dissipation and potentially increasing the biological carrying capacity. Degradation of the calcium carbonate framework on coral reefs through biological and physical erosion creates sediment and rubble which can promote habitats in the lee of coral reefs. These physical and biological processes benefit the overall functioning of coral reef systems.

The ecosystem function coral reefs provide by reducing wave energy and subsequently promoting habitats within reef associated sedimentary environments has been reduced by the decreases in reef structural complexity observed throughout the Caribbean (Sheppard et al. 2005, Alvarez-Filip et al. 2009). Naturally the relationship is perturbed by storms, which can redistribute large quantities of sediment and curtail habitat expansion or cause habitat contraction (Tongpenyai and Jones 1991, Burton 1994, Beanish and Jones 2002). The production of calcium carbonate on coral reefs benefits these sedimentary environments via the transport of sediment landward to allow their

establishment or expansion, but also by the accretion of reef framework which has continued to dissipate wave energy as sea-level has risen during the Holocene. In the Caribbean, sea-level is now increasing more rapidly than it has over the past 3,000 years (Toscano and Macintyre 2003, IPCC 2014) and therefore equivalent rates of reef accretion will be required to 'keep pace' with sea-level rise and allow coral reefs to continue providing that protectionary role.

The continued association of coral reefs with sedimentary habitats, over geological time-scales, has allowed the evolution of ecological connectivity within coral reef systems. Hence, coral reefs may be as dependent on other reef system habitats as those habitats are on reefs. Many reef fish and some invertebrates undergo ontogenetic and/or daily migrations between reefs and reef associated habitats (Ogden 1988, Appeldoorn et al. 2009). Seagrass beds and mangroves are important habitats for juvenile reef fish (Nagelkerken and Van der Velde 2004). Additionally, reef associated habitats may provide vital nutrients to coral reefs; Meyer and Schultz (1985) showed that *Porites furcata* colonies had significantly more tissue when associated with schooling grunts. The grunts feed on benthic invertebrates in seagrass or muddy habitats at night and return to the same coral colonies during the day, where they defecate. In some instances the provision of ecosystem services by coral reefs may benefit from the health of the wider coral reef system; Mumby et al. (2004) showed that the biomass of some reef fish species more than doubled when coral reefs were connected to mangroves.

Coastal communities throughout the Caribbean rely on coral reef systems in a number of ways, the most obvious of which are probably the provision of food and the economic benefits of fishing and tourism (Moberg and Folke 1999). Perhaps less obvious, but no less important, is the geomorphological role of coral reefs in coastal zone protection and the role coral reefs play in the maintenance of reef-associated sedimentary habitats and also sedimentary landforms such as beaches. Carbonate production by corals and other calcifying organisms and the transport of carbonate through entire reef systems, are not only central to the resilience and health of coral reefs and their associated sedimentary habitats, they also help regulate the social and economic benefits of coral reef systems to human communities.

Calcium carbonate can be lost from coral reef systems if it is transported over a shelf edge (Li et al. 1998, Kleypas et al. 2001). In some locations this may be a daily occurrence (Morgan and Kench 2014) but often large quantities of sediment are lost during storms (Neumann and Land 1975). Hence, the continued production of calcium carbonate within reef systems is essential to the provision of many ecosystem services and to the natural functioning of reef system habitats. Carbonate budgets (carbonate produced less carbonate lost) can be used to help understand the natural functioning of both coral reefs and the wider coral reef system.

1.2 Carbonate production on coral reefs

Coral reefs are focal points for the production of calcium carbonate framework within coral reef systems. Coral reefs form when the total accumulation of calcium carbonate, by growing coral colonies and other calcium carbonate secreting organisms and by the precipitation of diagenetic cements, exceeds the removal of calcium carbonate by biological, physical and chemical processes (erosion and dissolution) within a particular area for a prolonged period of time (100s – 1000s years). Coral growth accounts for the majority of calcium carbonate production on coral reefs in most reef environments (Stearn et al. 1977, Hubbard et al. 1990) and therefore it is a major driver of reef growth. However, under certain circumstances other organisms can be more important sources of calcium carbonate e.g. coralline algae in high energy reef crest and algal ridge environments (Steneck and Adey 1976). Additionally, *Halimeda* algae and benthic foraminifera can be major carbonate sediment producers both on reefs and also within reef associated sedimentary environments (Hallock et al. 1986, Bosence 1989, Hillis 1997, Harney et al. 1999).

1.2.1 *Seawater carbonate chemistry and the processes underpinning calcification on coral reefs*

The deposition of calcium carbonate ($CaCO_3$) by organisms, termed biomineralisation or calcification, is the biological process underpinning reef

formation. It is common to all marine ecosystems and expressed by many taxonomic groups (e.g. scleractinian corals, molluscs, foraminifera, cocolithophores etc.), although the biominerals/skeletons produced vary with species. $CaCO_3$ can also be precipitated inorganically through the reaction of calcium and carbonate ions:

$$Ca^{2+} + CO_3^{2-} \leftrightarrow CaCO_3$$

This equation is reversible and also describes inorganic dissolution. In seawater the relationship is governed by the saturation state (Ω) of calcium carbonate, which is described by the equation:

$$\Omega = [Ca^{2+}]\,[CO_3^{2-}] / K$$

Where, [ ] = the aqueous concentration of the ion

K = solubility product for $CaCO_3$

K changes depending on temperature, salinity and pressure and is different for different forms of calcium carbonate; aragonite (corals) and calcite (coralline algae) are the dominant forms produced on coral reefs. The inorganic precipitation of calcium carbonate is favoured in water which is super saturated ($\Omega > 1$) with respect to calcium carbonate and dissolution is favoured in water which is under saturated ($\Omega < 1$). Coral reefs undergo diel and seasonal fluctuations in aragonite and calcite saturation levels; Albright et al. (2013) report aragonite Ω fluctuations of 2.9–4.1 on a reef flat on the Great Barrier Reef. Carbonate saturation can vary due to changes in temperature, pressure and salinity but also due to fluctuations in the concentrations of calcium and carbonate ions. The chemistry of carbonate ions in seawater is complex and driven by dissolved inorganic carbon which exists as dissolved carbon dioxide (CO_2), bicarbonate ions (HCO^{3-}) and carbonate ions (CO_3^{2-}). The following equation describes the progression from one species to another and is reversible:

$$CO_2 + H_2O \leftrightarrow H_2CO_3 \leftrightarrow HCO^{3-} + H^+ \leftrightarrow CO_3^{2-} + 2H^+$$

The chemical speciation of dissolved inorganic carbon (CO_2:HCO^{3-}:CO_3^{2-}) seeks an equilibrium which is influenced by temperature, pressure and pH, but is often approximately 90:10:<1 in seawater of ≈ pH 8 (Gattuso et al. 1999). Any

biological or chemical process which alters the concentration of any of the three species alters the equilibrium. Hence, carbonate chemistry is very complex and in seawater there is a constant flux in dissolved inorganic carbon speciation and in carbonate saturation levels.

Inside corals, calcification occurs within an extra cellular calcifying medium controlled by adjacent specialised cells (calicoblastic cells). The source of Ca^{2+} ions is seawater (Allemand et al 2004). However, HCO_3^{1-} is used as the source of CO_3^{2-} ions and the biomineralisation process can be described simply by the equation:

$$Ca^{2+} + HCO_3^{2-} \rightarrow CaCO_3 + H^+$$

Hence, carbonate saturation states are vitally important for calcification in marine organisms and particularly aragonite saturation levels for corals. During calcification, the H^+ ions produced must be actively removed from the site of calcification and organic molecules are also included in the composition of the biomineral or skeleton produced (Constantz and Weiner 1988, Allemand et al. 2004). Hence there is a biological control of the calcification process and the extent to which seawater chemistry influences calcification within organisms is not clearly understood (reviewed in Gattuso et al. 1999, Allemand et al. 2004 and Tambutté et al. 2011). Calcification in zooxanthellate corals is light enhanced but not light dependent (Gattuso et al. 1999). Therefore, it is likely that photosynthesis plays an important role in the promotion of calcification. Several underlying mechanisms have been proposed including a suggestion that calcification may actually be repressed in the dark (reviewed in Gattuso et al. 1999, Allemand et al. 2004). However, the merits of each will not be discussed here.

The significance of these relationships to calcification, coral growth, habitat construction and ultimately reef growth is that environmental parameters such as light, temperature, aqueous CO_2 concentration and nutrient availability directly affect carbonate production on coral reefs and subsequently reef health and functioning. Localised anthropogenic disturbances of reef systems (e.g. nutrient enrichment, sedimentation, coral mining, dredging etc.) are increasingly altering environmental regimes often reducing light availability and increasing the availability of nutrients. Additionally, global changes in mean temperatures

and atmospheric CO_2 concentrations are driving increased severity and occurrences of bleaching events which directly reduce calcification on coral reefs. As atmospheric CO_2 concentrations increase (primarily from the burning of fossil fuels) the aqueous concentration of CO_2 in seawater also increases. This physical process (commonly called ocean acidification) alters the dissolved inorganic carbon species equilibrium, reducing CO_3^{2-} concentrations, seawater pH and the carbonate saturation state. There is a large quantity of experimental and model evidence which suggests that this process is and will continue to reduce calcification in shallow marine habitats while promoting the dissolution of sediment (Gattuso et al. 1999, Langdon and Atkinson 2005, Anthony et al. 2008, Veron et al. 2009, Eyre et al. 2014).

1.2.2 *Forms of calcium carbonate: sediment and framework*

The calcium carbonate produced on coral reefs can be separated into two components; framework and sediment. As already stated, corals are responsible for the majority of carbonate production on reefs and they produce coral reef framework. The other carbonate producers can also be important, not just for the quantity of calcium carbonate they produce but also for the ecosystem functions that they provide within reef systems. Coralline algae are often important contributors to sediment production, when they are encountered as epibionts on seagrasses (Bosence 1989), but on coral reefs they are mostly encountered as encrusting framework producers. These algae are common understory plants in macrophyte 'forests' within many different types of marine ecosystem including coral reefs (Steneck 1986, Steneck and Dethier 1994) and their success has implications for bioerosion, carbonate production and the maintenance of reef structure. Coralline algae help protect reef structures from biological and physical erosion, by competing for space with bioeroding organisms and by strengthening dead structural framework. Along with other calcareous encrusters they also play a role in reef stabilisation, binding dead coral rubble pieces together or overgrowing dead coral to create a solid and erosion resistant surface. Additionally, the inorganic precipitation of diagenetic cements, both within reef framework and at the surface also plays an important role in reef stabilisation and over time reef growth (reviewed in Rasser & Riegl 2002).

Sediment producers such as calcareous green algae, e.g. *Halimeda*, have calcium carbonate skeletons which do not remain connected to the reef framework when dead. *Halimeda* spp. generate carbonate sediment when they shed mature segments (Hillis 1997). These and other calcareous green algae grow in all coral reef system environments (coral reefs, lagoons, mangroves etc.) and play an important role in carbonate cycling within coral reef systems. The Foraminifera are shell forming protists, which may contribute to both framework production and sediment production on coral reefs. However, they are also found in many other reef system environments and may be most important as sediment producers. When growing on substrates such as seagrass, death leads to the break-up of their skeletons and the production of sediment (Hallock 1981). Large quantities of carbonate sediment can be produced by both calcareous green algae and the Foraminifera in lagoon environments (Neumann and Land 1975, Hallock et al. 1986). However, on coral reefs the quantities of carbonate sediment generated by these organisms is poorly understood and will not be investigated because it is of little direct relevance to carbonate framework dynamics.

1.2.3 *The framework producers*

Zooxanthellate corals and other calcareous encrusting organisms (e.g. coralline algae and foraminifera) build the structure and architectural complexity of the reef, creating reef habitat as they grow. More complex reefs have higher species diversity and larger fish biomass (Gratwicke and Speight 2005, Alvarez-Filip et al. 2011b). In the Caribbean, a small number of species have been responsible for the majority of reef growth during the Holocene and therefore carbonate production; *Acropora cervicornis*, *Acropora palmata* and the *Orbicella* spp. (Macintyre et al. 1981, 1985, Aronson and Precht 1997, Gischler and Hudson 2004, Hubbard 2009). The structural signatures of the reefs these corals build are obvious and often separated by depth and wave exposure regimes, as each species survives better in different physical environments (Goreau 1959). Consequently, reef habitat types or zones are often described in terms of these species. *A. palmata* reef habitats are shallow (usually <7 m) and visually dominated by the large robust branching colonies of this species (Figure 1.1). *A. cervicornis* habitats are deeper (usually 5–20 m) and often

found in lower wave energy environments, where the slender branching colonies can grow rapidly. *Orbicella* habitats usually begin around 8 m and can descend to 40 m or more with platy morphologies taking over from the more common massive forms as depth increases and light availability decreases. However, it should be noted that the range of each species overlaps the ranges suggested here for each habitat type and that environmental regimes may also alter the range over which these habitat types exist (Geister 1977). In the past, *A. cervicornis* and *Orbicella* spp. could often be found together across a large range and dominance would change from one to the other with depth (Goreau 1959). However, white band disease killed most *A. cervicornis* populations in the Caribbean during the 1980s and 1990s (Aronson and Precht 2001). Contemporary Caribbean reefs now have very little living *A. cervicornis*, although there are still some exceptions. The structures provided by this species have been destroyed by bioerosion and wave energy. Hence, habitat which once was appropriately described as a 'cervicornis zone' may now be more appropriately described as *Orbicella* habitat.

The zooxanthellate coral colonies of shallow tropical and sub-tropical reefs grow slowly, with most Caribbean species growing less than 10 mm each year (Vaughan 1916, Bak 1976, Hubbard and Scaturo 1985, Huston 1985, Dullo 2005). Growth is expressed in the extension of the calcium carbonate skeleton of the colony, upon which dwells the living coral tissue. Of the different growth forms of corals, the branching forms grow most quickly and in the Caribbean acroporids have the fastest growth rates. *A. cervicornis* growth rates can exceed 100 mm yr^{-1} (Shinn 1966, Tunnicliffe 1983). Zooxanthellate corals are reliant on light for growth and light availability is probably the primary environmental factor controlling colony growth and therefore carbonate production (Dullo 2005). Other important environmental influences are water temperature, salinity, suspended sediments and the availability of essential nutrients. These environmental factors impact individual coral polyps on a daily basis which in turn affects whole colony growth, health and reproduction over years. Colonies add calcium carbonate to a reef system through the creation of framework as they grow. Over time the calcium carbonate produced may remain in place and contribute to reef complexity and to the construction of new habitat. Over very long periods of time it may contribute to 'in-place' reef growth

(Fagerstrom 1987). However, physical and biological erosion may reduce much of the carbonate framework produced to rubble or sediment and this can be incorporated back into the reef as 'infilled' or 'displaced' reef growth (Hubbard et al. 1998) or transported to another area of the reef system where it may contribute to the development of other sedimentary habitats (e.g. seagrass beds).

Figure 1.1 An *Acropora palmata* colony at 5 m on Pallas reef, Grand Cayman

1.3 Bioerosion on coral reefs

The term bioerosion was introduced by Neumann (1966) to describe the 'removal of consolidated material or lithic substrate by the direct action of organisms'. On coral reefs this term refers to the biological erosion of framework and rubble. Often generating sand and silt, this process is a very important component of carbonate cycling in coral reef systems. Bioerosion has

been a natural part of the evolution of reef systems and is therefore beneficial, either as a creator of microhabitats or through the generation of sediment which contributes to other habitats. Indeed bioeroded sediment can be an important component of reef growth (Hubbard et al. 1990). Anthropogenic activities can increase bioerosion on reefs. The effects of eutrophication on bioerosion are well documented (e.g. Rose & Risk 1985; Holmes 2000) with increasing levels of bioerosion being correlated with increased nutrient enrichment. Overfishing can also result in increased bioerosion; McClanahan and Muthiga (1988) observed a loss of structural complexity in response to the removal of urchin predators and the subsequent increases in urchin populations, on Kenyan reefs.

Many species contribute to bioerosion on coral reefs and as a result it is a complex and difficult mechanism to measure. Glynn (1997) listed ten taxonomic groups which contain bioeroders; bacteria e.g. *Hyella* spp.; fungi e.g. *Aspergillus sydowi* (Kendrick et al. 1982); algae e.g. *Ostreobium* spp.; sponges e.g. *Cliona delitrix*; polychaete worms e.g. Eunicidae; Sipuncula (peanut worms); Crustacea e.g. *Lithotrya* spp.; Mollusca e.g. *Lithophaga* spp.; Echinoidea e.g. *Diadema antillarum*; and fishes e.g. *Sparisoma viride*. The smallest of these organisms, endolithic microboring taxa (bacteria, fungi and algae), dwell within the reef framework, but can also be found in cavities. These organisms use chemical dissolution to erode reef substrata (Disalvo 1969) and increase the porosity of reef framework, making it more susceptible to physical damage during storms or from grazing (Osorno et al. 2005, Grange et al. 2015). The diversity of microboring species is bathymetrically zoned with a change in the dominant species with depth (Vogel et al. 2000, Chazottes et al. 2009). Few studies exist which have investigated the rates of erosion by microborers (e.g. Chazottes et al. 1995; Chazottes et al. 2002; Tribollet & Golubic 2005; Carreiro-Silva et al. 2012) but these suggest that microbioerosion is an important element of total bioerosion on coral reefs.

Macroboring taxa (sponges, polychaetes, Sipuncula, Crustacea and Mollusca) are mostly endolithic, but some are epilithic. In addition to weakening coral reef framework (Schönberg 2002), these organisms also generate large quantities of sediment (Neumann 1966, Moore and Shedd 1977). Their diversity and abundance varies between different reef zones (Perry 1998), and in the

Caribbean the most important macroboring organisms are sponges (Scoffin et al. 1980), particularly in fore-reef environments (Perry 1998).

Sea urchins and parrotfish denude reef framework as they graze on turf and coralline algae. They are often the dominant bioeroders on coral reefs (Scoffin et al. 1980, Kiene 1988, Chazottes et al. 1995, Perry et al. 2014). Urchins are generally common in shallow reef environments (<5m) and when their fish predators are removed through overfishing their numbers can increase to levels where they become very damaging to reef structure by decreasing live coral cover and reducing topographic complexity (McClanahan and Muthiga 1988). The relationship between urchin erosion and test size is non-linear (Scoffin et al. 1980) with larger urchins eroding exponentially more than smaller ones. Urchin bioerosion also changes with species e.g. *Diadema antillarum* urchins erode more than *Echinometra viridis* urchins of the same test size (Perry et al. 2012).

The parrotfish can be divided into three groups, scrapers, excavators and browsers, based on their jaw structures and feeding behaviour (Bellwood and Choat 1990, Bellwood 1994). Browsing parrotfish feed on and remove macroalgae without disturbing the substrate, and therefore cause minimal or no bioerosion while feeding. Excavators are far more efficient eroders than scrapers; they target endolithic algae, bacteria and fungi in addition to the epilithic turf algae that the scrapers remove (Bruggemann et al. 1996). Size is an important control on the erosive capability of parrotfish and larger animals erode more per bite (Scoffin et al. 1980, Bruggemann et al. 1996). However, there are also changes in feeding rates as parrotfish grow and with changes in sexual phase (Mumby et al. 2006). Parrotfish are sequential hermaphrodites, changing sex from female to male at a size unique to the individual. The terminal phase males are most often larger, but have lower bite rates than the initial phase females as the males spend time defending territories (Bruggemann et al. 1994c, Mumby et al. 2006). Consequently, the relationship between parrotfish size and erosive capability is not linear, but a synthesis of species, life phase and size.

The measurement of bioerosion on coral reefs is challenging and often time intensive. One approach is to investigate total bioerosion using coral blocks

which can be placed in a reef environment for several years (Kiene 1988, Osorno et al. 2005). Changes in block mass and volume reflect bioerosion. This method can quantify bioerosion due to microborers, macroborers and grazers, but does have a number of disadvantages:

1. Experiments require at least 2 years to get meaningful results
2. For that bioerosion due to grazing, it is not possible to distinguish between species
3. Extrapolating results to an entire reef is tenuous (Chazottes et al. 1995)
4. There is an ethical issue with this method as usually live coral is sacrificed to cut the unbored coral blocks required.

An alternate approach is to quantify the bioerosion of the different taxa separately (Scoffin et al. 1980).

1.4 Carbonate budgets and framework production states

On coral reefs a carbonate budget is the sum of gross carbonate production from corals and calcareous encrusters, as well as sediment produced within or imported into the reef, less that lost through biological or physical erosion, dissolution or sediment export (Chave et al. 1972). The result of a carbonate budget is a value for net production which can be positive or negative and is often measured in terms of kg $CaCO_3$ m^{-2} yr^{-1}. Three methods have been used to calculate carbonate budgets for coral reefs:

I) Hydrochemistry

II) Accumulation of reef sediment

III) Census data

1.4.1 *Hydrochemical methods*

Changes in the pH and alkalinity of water flowing over a reef can be used to calculate net carbonate precipitation i.e. precipitation minus dissolution (Smith 1973, Kinsey 1985). This value would include all carbonate produced by framework builders, sediment producers and any inorganic precipitation. Consequently, this method does not allow the differentiation between organic or inorganic sources of calcium carbonate or the determination of the important agents of carbonate production. Additionally, they do not consider bioerosion or the physical processes associated with carbonate cycling. Hydrochemical methods can only be applied on shallow reef environments because of problems with water mixing at depth.

1.4.2 *Accumulation of reef sediment*

The accumulation of reef sediment over time, sampled using cores, can be examined to distinguish the contributions of different carbonate sources (Land 1979, Hubbard et al. 1990) and provide long-term net rates of carbonate production. These values only provide information on that carbonate (framework, sediment, precipitates or eroded material) which has remained in the reef system. Hence, they are good indicators of reef growth over time, but census based surveys and knowledge of the physical environment are still required to help understand the present reef state (Hubbard et al. 1990) in comparison to what has been deposited over time.

1.4.3 *Census based methods*

The use of census data to calculate carbonate production and erosion on reefs is survey intensive (Stearn et al. 1977, Scoffin et al. 1980) requiring data on organism abundance for the relevant carbonate producers and eroders. Annual calcification and erosion rates are combined with abundance data to determine carbonate production and bioerosion for a reef or reef area. Inevitably the results are dependent on the accuracy of the calcification and erosion rates used and data for some organisms are very limited; data for sponge bioerosion and microbioerosion rates, calcification by some coral species and calcareous encruster communities and in general on the effects of depth are particularly

limited. However, in the Caribbean there is good calcification rate data for many coral species, bioerosion rate data for parrotfish and urchins and adequate data available for other taxa to give confidence in results (Perry et al. 2012).

Census data cannot consider the effects of water chemistry. Hence, the inorganic precipitation of calcium carbonate from the water column and the dissolution of reef framework and sediment are not considered by census approaches. However, quantitative data on these processes is very limited and neither of these two chemical processes are important drivers of carbonate framework production on coral reefs (Eyre et al. 2014). The dissolution of sediment is a very important process on coral reefs and would need to be considered for carbonate budgets investigating the production of sediment (Eyre et al. 2014). Census based approaches have distinct advantages. Specific reef habitats can be investigated and there is also the potential to extrapolate results to larger spatial areas. Differentiating between different reef habitats is important as different environmental characteristics may yield different rates of net production. Another important advantage of census based methodologies is that they allow the evaluation of the contributions of different taxa to both carbonate production and bioerosion. These can be viewed as quantitative measures of an ecological function and therefore the importance of different species to habitat construction (carbonate production) and destruction (bioerosion) can be assessed. As already described some carbonate producers and eroders are more important than others. Hence, changes to the population size of specific species can have far reaching effects on ecological functions and the provision of ecosystem services reliant on the physical structure of a reef.

1.4.4 *Carbonate framework production states*

An understanding of the physical and biological processes which act on the structure of a reef gives rise to four theoretical reef types or framework production states: (i) production-dominated, (ii) bioerosion-dominated, (iii) export-dominated and (iv) import-dominated (Kleypas et al. 2001). Most modern reefs are (or were) examples of production-dominated states; biogenic carbonate production by corals and encruster communities greatly exceeds

carbonate loss through bioerosion and physical processes and therefore there is a net positive budget. Typically, production-dominated reefs would be considered 'healthy' and would have complex framework structures. On bioerosion-dominated reefs, carbonate production is exceeded by erosion and the sediment produced is generally exported.

Import and export-dominated states consider the physical forces that transport carbonate sediment and rubble. On import-dominated reefs physical processes such as currents on a daily basis or storms sporadically over time accumulate calcium carbonate in areas where the carbonate was not originally produced. Storms, in particular, can create and move large quantities of carbonate rubble which can be an important source of reef growth; e.g. evidence from cores of the reef crest and shallow fore-reef (1–4 m) on Grand Cayman's south coast, suggests that storm generated rubble is the main contributor to the reef matrix and therefore to reef growth in this area (Blanchon et al. 1997). Hardgrounds are good examples of an export-dominated state, because calcium carbonate framework does not accumulate over time. However, such habitats may not necessarily be bioerosion-dominated.

Coral reef systems have areas which are export-dominated and some which are-import dominated e.g. a fore-reef habitat may provide carbonate rubble for the growth of a reef crest environment (Blanchon et al. 1997) or sediment to a lagoon (Morgan and Kench 2014). The lagoon itself may be import-dominated during fair-weather conditions but become export dominated during a storm (Li et al. 1997). Coral reef systems will usually be production-dominated, but they may also have areas or habitats which are bioerosion-dominated. Hence, these classifications are spatially variable and production states will depend on the extent of the area investigated. Additionally carbonate production states can change over time. In 1982/3, an unusually strong El Nino led to extensive bleaching in the eastern Pacific. As with other areas, the reefs around Uva Island, Panama, suffered very high coral mortality which led to decreased carbonate production. Overall, the reefs changed from a net depositional state (probably the 'Production-dominated' classification) to a net erosional state (probably the 'Bioerosion-dominated' classification) due to the complex ecological changes that occurred to community structure in the years following this bleaching event (Eakin 1996, 2001). However, Eakin (1996) also reported

large variations between reef zones or habitats, with some areas remaining net depositional.

1.5 *ReefBudget*: A census based approach to carbonate framework budgets

ReefBudget is a census based carbonate framework budget protocol developed for Caribbean coral reefs (Perry et al. 2012). It does not consider sediment production, physical erosion or the export/import of calcium carbonate and is solely focused on the dynamics of carbonate framework production and bioerosion. Hence, it yields a snapshot of net calcium carbonate framework production within a defined area at a specific moment in time. As the protocol is census based, it also identifies species which are important drivers of carbonate budget dynamics and therefore provides a quantitative measure of particular functional roles associated with carbonate production and bioerosion. In comparison to previous census based carbonate budget studies (e.g. Stearn et al. 1977, Scoffin et al. 1980) this protocol allows relatively rapid assessments and therefore affords interested parties the ability to investigate carbonate budget dynamics on scales that would have been logistically unrealistic before. In terms of the management of coral reef systems, *ReefBudget* provides an opportunity to begin to understand the links between ecology, geomorphology and the wider health of reef ecosystems, an essential step toward a truly ecosystems based approach to management.

The *ReefBudget* protocol was developed during a Leverhulme Trust funded project that ran from January 2010 to January 2012. I was an integral member of the team that developed and subsequently used the protocol to gain an overview of carbonate budgets dynamics on Caribbean reefs; a detailed methodology is published in Perry et al. (2012). Three additional *ReefBudget* journal articles have been published during my PhD thesis (Perry et al. 2013, 2014, 2015c), the major findings of which I will describe here because they form the background for my study and because I have contributed to them during my PhD. The three papers present a general overview of carbonate budget dynamics on contemporary Caribbean coral reefs. Grand Cayman data (5 sites)

published in those articles were collected in April 2012, after the Leverhulme project had ended, and form a part of my PhD thesis work.

1.5.1 *Changing patterns in Caribbean reef carbonate production*

Caribbean wide declines in coral cover (Gardner et al. 2003) and structural complexity (Alvarez-Filip et al. 2009) suggest that carbonate production rates have also declined on Caribbean coral reefs (Knowlton 2001, Perry et al. 2008). This was confirmed using the *ReefBudget* protocol for 19 reefs sites across the Caribbean (Perry et al. 2013). The overview of reef carbonate production, presented in that paper, suggested a decrease of 50% in comparison with mid- to late-Holocene estimates. It is likely that accretion rates have also been affected by the decline in carbonate production and Perry et al. (2013) suggest that shallow reefs (<10 m) may now be accreting at rates an order of magnitude lower than Holocene estimates.

Trends of declining coral cover in the Caribbean, mainly due to sources of anthropogenic disturbance, have affected some coral species more than others (Aronson and Precht 2001, Bruckner 2012). Hence, coral species assemblages on contemporary reefs have changed from those evident on 'pre-decline' reefs (Aronson and Precht 1997, Knowlton 2001, Green et al. 2008, Burman et al. 2012). An assessment of carbonate production by coral assemblages at 75 Caribbean sites (only 22 using the *ReefBudget* protocol) estimated that 68% of gross carbonate production was due to non-reef-building species (Perry et al. 2015c). Typically, carbonate production on 'pre-decline' reefs was dominated by long lived, competitive species which formed complex reef habitats in different zones constrained by natural environmental factors such as light, depth and wave energy. Carbonate production on contemporary reefs is now often dominated by short lived 'weedy' and 'stress tolerant' species (*sensu* Darling et al. 2012) which cope well with frequent disturbance events but do not compete well for space against more long-lived and often more rapidly growing, reef-building species (Knowlton 2001, Darling et al. 2012). Darling et al. (2012) use the term 'weedy' to describe some of these species, but I prefer the term 'opportunistic' and will use it here. Common species include *Porites astreoides* (opportunistic/weedy), *Agaricia agaricites* (opportunistic/weedy) and *Siderastrea*

siderea (stress tolerant) which have lower calcification rates and therefore produce less calcium carbonate per unit area than reef building taxa (*Orbicella* or *Acropora* spp.). Additionally, these species form less complex and usually much smaller structures, which will alter the types of habitat constructed on Caribbean reefs over time.

1.5.2 *Changing patterns in Caribbean reef bioerosion*

Gross bioerosion has also decreased on many reefs across the Caribbean. Perry et al. (2014) estimate that bioerosion rates are 75% lower than rates reported for 'pre decline' coral reefs. A key function of bioerosion is in carbonate cycling within coral reef systems and the effects of this widespread decrease in sediment generation by bioeroding taxa remain unclear. The most important bioeroding taxa were the parrotfish at all reef sites and therefore fishing has undoubtedly contributed to the decrease in bioerosion on many coral reefs; fishing reduces parrotfish biomass and as previously explained larger parrotfish erode more (Bruggemann et al. 1996, Mumby et al. 2006).

Sea urchins contributed so little to bioerosion at the 19 reef sites investigated by Perry et al. (2014) that they were essentially functionally irrelevant. However, they may have been the most important bioeroders at many 'pre decline' reefs (e.g. Ogden 1977, Scoffin et al. 1980). In 1983/84 populations of *Diadema antillarum* (the largest and often most common urchin found on Caribbean reefs) were decimated by an unknown pathogen (Lessios et al. 1984). This mass mortality event may have altered ecosystem functioning on many coral reefs as *D. antillarum* are important herbivores and contribute to both grazing and bioerosion (Ogden et al. 1973, Hunter 1977, Scoffin et al. 1980). Populations have not recovered to date (Lessios 2016).

Much less is known about the changing patterns of both sponge and micro-bioerosion on Caribbean reefs. However, it is likely that bioerosion by both has increased; decreasing seawater pH (due to ocean acidification) may create environments which make the dissolution of reef carbonates more energetically efficient for organisms using chemical methods (Zundelevich et al. 2007, Wisshak et al. 2012, Reyes-Nivia et al. 2013). Additionally, bleaching induced coral mass mortality reduces competition for space on reefs which has led to

larger bioeroding sponge populations on some reefs (Lopez-Victoria and Zea 2005). Despite this the relative importance of sponges to total reef bioerosion remains lower than that for parrotfish or microborers (Perry et al. 2014).

1.6 Research rationale, aims and objectives

The three *ReefBudget* papers (Perry et al. 2013, 2014, 2015c) provide an overview of carbonate production and bioerosion on contemporary Caribbean coral reefs and comment on the changes that have occurred since the 1970/80s. However, only a relatively small number of sites have been investigated and these they do not provide a comprehensive assessment of carbonate budget dynamics at the scale of individual reefs or within specific habitat types. Additionally, the three papers do not attempt to describe how carbonate production and bioerosion are affected by environmental regimes; *e.g.* neighbouring reefs may be exposed to very different wave energy regimes which could impact on carbonate production and bioerosion, as they influence coral assemblages (Geister 1977). Despite this, two conclusions can be drawn from the three *ReefBudget* papers:

1. Carbonate production and bioerosion have both decreased across the Caribbean since the 1970/80s.

2. The reef communities responsible for carbonate framework production and bioerosion are different on many contemporary reefs, from those that existed on 'pre-decline' reefs, and therefore the nature of habitat construction and destruction has also changed.

The consequences of these changes for ecosystem functioning and the provision of ecosystem services to people remain unclear. Aside from the *ReefBudget* studies, very little quantitative data exist on carbonate production and bioerosion in the Caribbean. Hence, there is an urgent need for more basic data on the quantities of calcium carbonate produced and eroded on coral reefs throughout the Caribbean. Additionally, studies which address different spatial

scales, both within and between distinct habitat types are required to begin to understand how ecological changes may have altered ecosystem functioning and how contemporary reefs function now. There is also a need to understand the functional roles of individual species and how they contribute to natural carbonate cycling within coral reef systems and over time to geomorphology.

1.6.1 *Aims and objectives*

The aim of this study is to provide a quantitative assessment of biological calcium carbonate framework production and bioerosion, within specific habitat types that are common across the Caribbean, but at a spatial scale relevant to a reef system. Three marine habitats are investigated on a wave exposed and wave sheltered coast, on Grand Cayman, to a depth of approximately 15 m. The three habitats are coral reefs structurally dominated by (i) *Acropora palmata* framework, (ii) *Orbicella* spp. framework and (iii) areas with no reef accumulation known as hardgrounds. Many previous similar studies have defined a specific area in which to calculate a carbonate budget. However, this study is focused on the mean rates of carbonate framework production and bioerosion within specific habitat types and makes no attempt to quantify the area over which these habitats exist, although the survey work is restricted to specific coastal areas.

A census based approach to carbonate budgets is used to investigate species contributions to both carbonate framework production and bioerosion. As previously described (Section 1.4.3) census based carbonate budgets are reliant on species specific calcification and bioerosion rates to generate accurate data. Hence, this study also estimates calcification rates for calcareous encruster communities on Grand Cayman within the habitats investigated on both sheltered and exposed coastlines, to improve the carbonate budgets. Bioerosion rates for two common sponge species (*Cliona tenuis* and *Siphonodictyon brevitubulatum*) are investigated on Grand Cayman reefs and a new approach to estimating bioerosion by sponges populations developed; this approach combines life history strategies and appropriate bioerosion rates to improve on the previous *ReefBudget* method for estimating sponge bioerosion. Additionally, ecological changes caused by human

disturbance regimes have altered marine habitats throughout the Caribbean and the implications of measured carbonate budget data are considered in relation to potential changes to ecosystem functions associated with the production and bioerosion of calcium carbonate framework.

Specific objectives include:

1. Measure calcification rates for calcareous encruster communities in *Acropora palmata* reef, *Orbicella* reef and hardground habitats.
2. Measure the rates of bioerosion by two sponge species, *Cliona tenuis* and *Siphonodictyon brevitubulatum*.
3. Develop an improved method for estimating bioerosion by excavating sponge communities.
4. Quantify the relative contributions of specific organisms to carbonate framework production and bioerosion within different habitat types.
5. Quantify mean rates of carbonate framework production and bioerosion within *Acropora palmata* reef, *Orbicella* reef and hardground habitats.
6. Determine a carbonate framework budget for *Acropora palmata* reef, *Orbicella* reef and hardground habitats along both wave exposed and wave sheltered shorelines.

1.6.2 *Thesis structure*

Chapter 2 introduces the study area, defines the habitat types investigated and describes site selection.

Chapter 3 describes an experiment to quantify encruster community calcification rates for the three habitat types investigated, under different regimes of wave exposure. This chapter addresses objective 1 and the calcification rates measured improve the accuracy of carbonate production estimates at all sites, because the data used for calcareous encruster communities is specific to Grand Cayman.

Chapter 4 presents data on carbonate framework production within *Acropora palmata* reef, *Orbicella* reef and hardground habitats, for wave exposed and sheltered coasts. This chapter addresses objectives 4 and 5.

Chapter 5 describes experiments to quantify bioerosion rates for two sponge species, *Cliona tenuis* and *Siphonodictyon brevitubulatum* and addresses objective 2. This chapter also describes a new approach to estimating bioerosion by sponge communities using census surveys, available bioerosion rate data and the growth and erosion strategies of each species (objective 3). Overall this chapter improves the accuracy of estimates for sponge bioerosion at all sites and therefore the carbonate budgets for habitat types.

Chapter 6 presents data on total bioerosion within *Acropora palmata* reef, *Orbicella* reef and hardground habitats, for wave energy exposed and sheltered coasts. This chapter addresses objective 4 and 5.

Chapter 7 presents a carbonate framework budget for each habitat type, under different wave exposure regimes and addresses objective 6. It also presents overall conclusions and suggests future research directions.

Study location, habitat types and site selection

2.1 Grand Cayman

Grand Cayman is located in the north western Caribbean about 300 km south of Cuba and north-west of Jamaica (Figure 2.1). It is part of the Cayman Islands which are a United Kingdom Overseas Territory and have been under British control since they were first inhabited by people in 1661. The three Cayman Islands, Grand Cayman, Cayman Brac and Little Cayman, are low-lying carbonate platforms which do not support rivers. Grand Cayman is far removed from the influence of other large land masses and both politically and economically stable with almost no subsistence fishing. It is surrounded by clear, open sea waters which are relatively unpolluted in comparison to other Caribbean islands.

In 2014, Grand Cayman had 58,238 residents, up from approximately 10,000 in 1970 (source: Cayman Islands Economics and Statistics Office). The rapid increase in population has mirrored the island's success in the banking and tourism industries during this time. 2014 saw 1.99 million visitors to Grand Cayman, up from just 403 air visitors in 1970 and 971 cruise ship passengers in 1973 (Smith 1988). Hence, although Grand Cayman is largely free of heavy industries and only has a very limited agricultural industry, it is not without potentially detrimental factors to reef health (Turner et al. 2013). Specifically, the large tourist industry has a number of potential impacts on reefs; sewage (Rose and Risk 1985, Paytan et al. 2006), construction (Rogers 1990), scuba diving (Tratalos and Austin 2001), noise pollution (Simpson et al. 2016) and boat and anchor damage (Davis 1977, Smith 1988).

To help protect coral reefs on Grand Cayman from anthropogenic impacts, the government set up a marine protected area in April 1986, which covers most of the west coast (Figure 2.1). All fishing is banned within the marine protected area, although there are two 200 m wide 'Replenishment zones' which divide

this area into three sections (Figure 2.1). Line fishing and anchoring is allowed within ‘Replenishment zones’. Fishing from shore is also permitted. In addition to protected areas, there is a public mooring scheme in operation that currently provides over 180 moorings for use by dive operators, snorkelers and yachts. Since the 1980s Grand Cayman has also strengthened environmental laws in an attempt to avoid much of the anthropogenically induced coral decline that has affected other Caribbean reefs. Despite this, mean coral cover on coral reefs in the Cayman Islands was only 25% in 1997 and had declined further to 15% in 2008 (DaCosta-Cottam et al. 2009). Earlier investigators comment on abundant corals but do not specify a mean percent coral cover (Rigby et al. 1976, Roberts 1994). However, it is clear that the benthic communities described in detail by Rigby and Roberts (1976) do not exist anymore, from the back reef communities dominated by *Orbicella annularis* to shallow fore-reef communities dominated by *Acropora palmata* and *Acropora cervicornis*. In these descriptions most of the coral species abundant today, within shallow reef communities, were understory members of a highly complex physical structure dominated by branching corals. Fish biomass on Grand Cayman reefs is dominated by herbivores (parrotfish and surgeonfish) and it seems likely that most of these species are not overfished. However, parrotfish are targeted using fish traps and by spear fishing, which is legal on Grand Cayman with the appropriate license. Spear fishing can quickly reduce both the population density and mean size of target fish (Frisch et al. 2012). Hence, it is possible that the populations of some species of parrotfish have been reduced by fishing. The two largest Caribbean parrotfish species (Midnight, *Scarus coelestinus* and Rainbow, *Scarus guacamaia*) are rarely encountered (Figure 2.2) on Grand Cayman reefs. Visibility in the water column is generally good (20 – 30 m, *pers. obs.*) on Grand Cayman and there does not appear to be obvious problems with eutrophication or pollution. However, water quality on Caymanian reefs may have much to do with their physical location, at the edge of a narrow shelf (Figure 2.1).

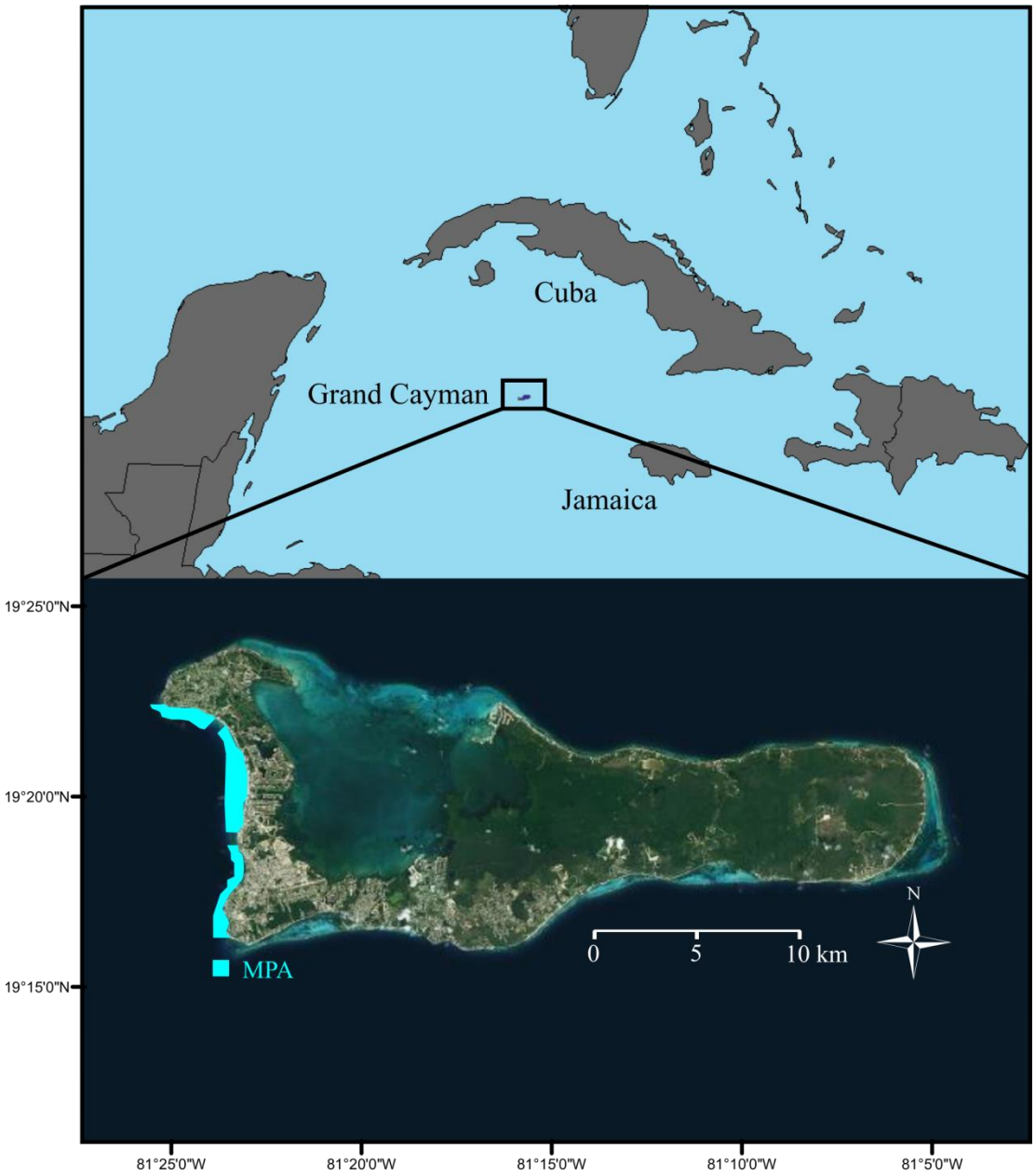

Figure 2.1 A map of Grand Cayman showing its location in the Caribbean. A marine protected area (MPA) is indicated in blue.

Figure 2.2 A large terminal phase rainbow parrotfish (*Scarus guacamaia*) feeds at 5 m on Pallas reef, Grand Cayman.

2.2 Setting

At its widest points, Grand Cayman is 35 km long (east-west) and 15 km wide (north-south). It has an area of almost 200 km^2 and is almost completely surrounded by fringing reefs which sit upon a narrow shelf up to 3 km in width. Seaward of the shelf edge, at 110 – 170 m depth, a steep slope descends to abyssal depths; 4,000 m to the north and 7,000 m to the south. Despite being close to a tectonically active transform fault and spreading centre known as the Mid-Cayman Rise, Grand Cayman has undergone little or no vertical movement over the past 500,000 years (Emery 1981, Vezina et al. 1999). Two discrete terraces characterise the submarine topography of the shelf surrounding Grand Cayman and are separated by a mid-shelf scarp (Blanchon and Jones 1995). Both terraces were eroded during the Holocene and may be the result of periods of slow sea level rise separated by a period of relatively rapid sea level rise (Blanchon and Jones 1995). The contemporary coral reefs of Grand Cayman have accreted on these terraces during the Holocene.

The deep terrace surrounding Grand Cayman supports spur and groove coral reefs which track the coast line from approximately 12 to 30 m depth. These give way to impressive sheer walls which can drop to depths of 170 m. The shelf edge reefs on this terrace form massive buttresses at the wall interface and lead to spur and groove formations and/or joined up reef; variations are largely determined by wave energy, with lower wave energy coastline more likely to have more joined up reef (Roberts 1994). Spurs can continue to the mid-shelf scarp, but generally give way to a sand plain as one proceeds landward. Again, higher wave energy coastline is more likely to have better developed coral spurs. The sand plain circumnavigates the island and is only occasionally interrupted by coral spurs. Beyond the sand plain spur and groove reefs form, and these can join with coral buttresses, denoting the location of the mid-shelf scarp. However, this break is often obscured by sediment and reef.

On the shallow terrace an almost continuous fringing reef tracks the south, east and north coasts, breaking the surface at low tide. Spur and groove formations often begin at 4–5 m and the spurs can form impressive buttresses at the mid-shelf scarp. As with reef formations on the deeper terrace, wave energy plays a role in structuring reef growth. Coral reef formations on the shallow terrace of the west coast are less regular and these fringing reefs do not break the surface. The shallow terrace on the west coast also supports a small number of patch reefs which are surrounded by sand or hardgrounds.

There are only limited reports available on coral reef health during the 1970s and 1980s, however, declines in coral cover since the 1980's have taken place and it is reasonable to assume that calcium carbonate production has also reduced on the coral reefs across both terraces. Rigby and Roberts (1976) provide detailed descriptions of the marine communities of Grand Cayman with numerous photographs illustrating high coral cover in both shallow and deep terrace habitats. Additionally, Smith (1988) reported coral cover ranging from 36 – 56% on deep terrace reefs unaffected by cruise ship anchor damage along the south coast. More recently the Cayman Islands Department of Environment have estimated mean coral cover at just 11% (31 sites, unpublished data from 2011). It is likely that coral cover declines during the 1980s along with major bleaching events in 1998, 2005 and 2009 and also hurricanes in 1988, 2004

and 2008 are responsible for current low coral cover and potentially the lack of any visible recovery.

2.2.1 *Wind and wave energy regime*

Grand Cayman has an average tidal amplitude of just 26 cm with a maximum range of 1 m (Burton 1994). Winds are predominantly from the east and north-east but also regularly approach from the south-east making the west coast the only leeward side to the island (Figure 2.3), although occasionally strong winds will blow in from the north-west. Figure 2.3 displays a wind rose for Grand Cayman along with a model of wave exposure regimes. Data on wind speed and direction was provided by the Cayman Islands National Weather Service and was recorded hourly over ten years (2004 – 2014) at Owen Roberts International Airport in the south west corner of the island. The freeware WRPLOT View was used to plot a wind rose (Lakes Environmental 2016). The wind data was also used to model wave energy around Grand Cayman using the method of Perry et al. (2015b). This wind fetch based model includes a minor modification of the original U.S. Geological Survey scripts (Rohweder et al. 2012), that uses a spatial offset to cater for the increased computational requirements that would result from the large areas over which fetch must be calculated for Grand Cayman. The original scripts considered lake environments with relatively small fetch lengths. Hence the spatial offset used in Perry et al. (2015b) decreases the computational requirements. The original U.S Geological Survey scripts are available as a free download from:

http://umesc.usgs.gov/management/dss/wind_fetch_wave_models_2012update.html

Average wave energies (Joules m^{-3}) were higher on the south and north coasts than on the west coast (Figure 2.3) and are displayed for each survey site in Table 2.1.

These average wave energy values are a good indication of the wave exposure regimes that occur at each site however, they apply to sea level conditions and do not consider the effect of depth. Hence, shallower habitats are more likely to be affected by this measure of average wave energy than deeper ones. The

effect of periodic storms may have more direct control on reef structural formations (Blanchon and Jones 1997) and also on the populations of long lived coral species (e.g. broadcast spawning species like *Orbicella annularis*) than measures of average wave energy. However, populations of short lived coral species which mature quickly (e.g. many brooding species like *Porites astreoides*) may be more controlled by these chronic wave energies than periodic storms.

Hurricanes and other major storms commonly affect Grand Cayman and have been implicated as the major structuring force of the deep terrace reef architecture (Blanchon and Jones 1997). Shallow terrace reefs are also structured uniformly along the south, east and north coasts, showing systematic variations in geomorphology which correspond to their orientation in relation to the approach of hurricanes and also shelf width (Blanchon and Jones 1995). Hurricanes and other storms generally approach Grand Cayman from the east, south east or north east and the wave energy transmitted to the reefs is controlled by the length of water over which the winds have blown (fetch). The habitat types of the fringing reef complex on the south coast of Grand Cayman vary systematically with exposure to wave energy (Blanchon and Jones 1995); coastal areas with an easterly orientation are considered open and have the most reef development, whereas coastal areas with a westerly orientation are considered somewhat protected. These windward 'protected' areas have limited reef development extending from the mid-shelf scarp, but still distinct spur and groove formations which develop into hardgrounds as one proceeds landward. As the orientation becomes less 'protected', reef habitats expand; in the most open areas (south facing) large spur and groove formations have developed over time and *A. palmata* colonies came to dominate the coral assemblages on top of the spurs. Indeed most of the spurs have been constructed by *Acropora* species (Blanchon et al. 1997) and here, I classify these shallow spur and groove formations as *Acropora palmata* reef habitat. As one proceeds landward from the mid-shelf scarp, spur and groove formations decrease until they develop into a continuous reef dominated by *A. palmata* structures (or hardgrounds in 'protected' areas). Here, I classify this continuous reef as stump and boulder habitat. Reef formation below the scarp (on the deeper terrace) also increases in these 'open' areas with spur and groove formations that may

extend to the shelf edge reefs. Here, I classify these reef formations as *Orbicella* reef habitat. The south coast is predominantly south to east facing and has very little coastline orientated west.

The west coast of Grand Cayman is sheltered from high average wave energies (Figure 2.3) and offers a different physical environment to the south coast, in which equivalent habitats to *Acropora palmata* reef, *Orbicella* reef and hardgrounds can be found. However, reef formations on the west coast are not as regular and predictable as they are on the south and north coasts, except in the very southern and northern portions of the coastline and along the shelf edge where the deeper terrace reefs have developed large spur and groove formations that often extend seaward from continuous reefs. On the shallow terrace *Acropora palmata* reef habitat is limited and patchy. *Orbicella* reef habitat is common along the southern portion of the west coast, becoming patchy as sand becomes more common in these more sheltered areas and reappearing as regular formations along the northern portion of the west coast (pers. obs.). The formation of patch reefs may be due to a decrease in wave energy (Figure 2.3) which would encourage the settlement of sediment. Hardgrounds can be found along the length of the west coast from 1-7 m, although sandy areas are also common over this depth range.

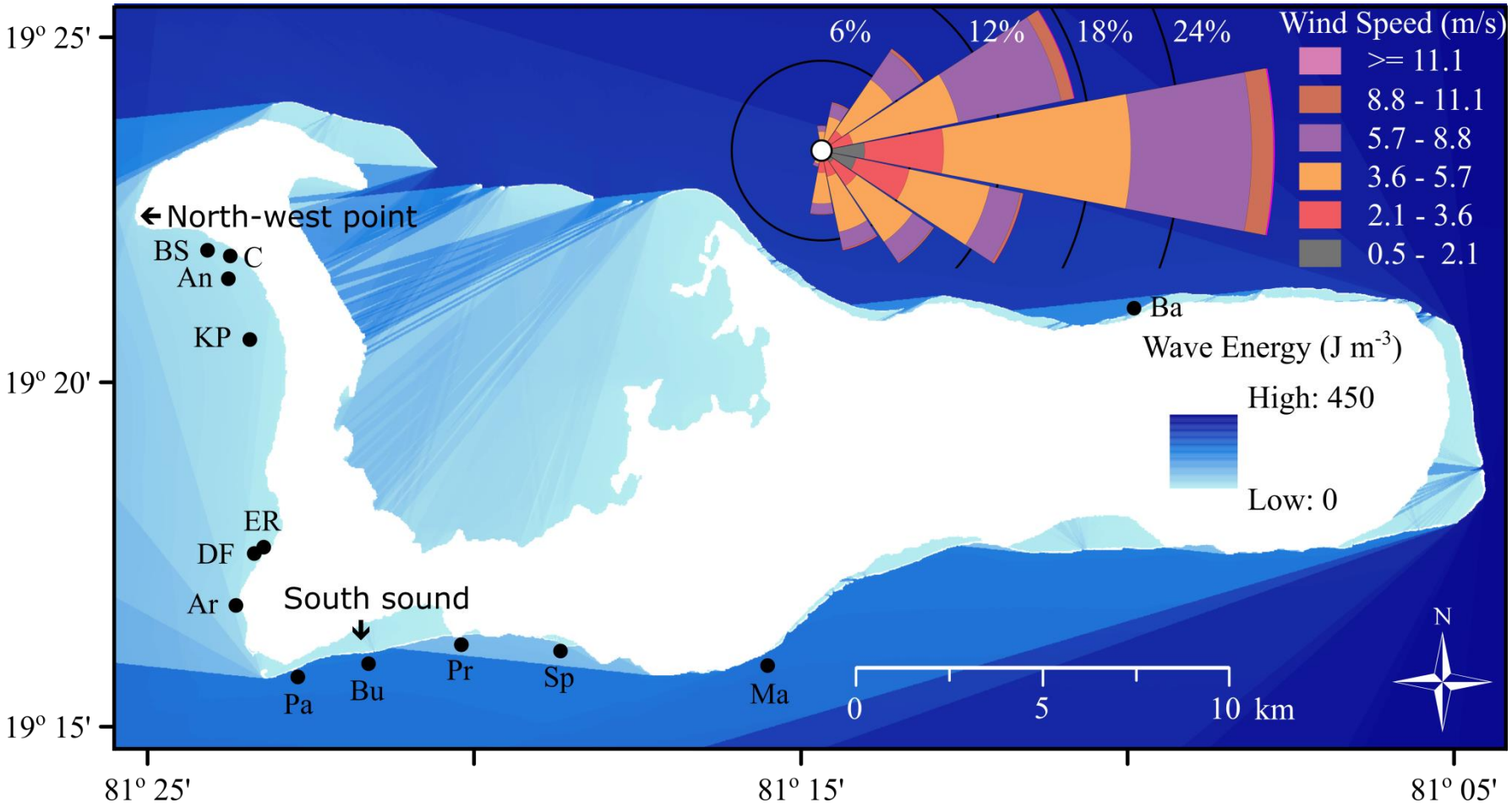

Figure 2.3 Wind and wave exposure regimes around Grand Cayman. Hourly wind data (2004 – 2014) sourced from the Cayman Islands National Weather Service and used to model wave energy (Rohweder et al. 2003, Perry et al. 2015b). The locations of survey sites are indicated by dots. West coast (top to bottom): BS – Boggy Sands, C – Cemetery, An – Anchor, KP – Killer Puffer, ER – Eden Rock, DF – Don Fosters, Ar – Armchair. South coast (left to right): Pa – Pallas, Bu – Bullwinkle, Pr – Prospect, Sp – Spotts, Ma – Manse. North coast: Ba – Babylon.

2.3 Habitat types

On any coral reef the physical environment corals are exposed to changes rapidly with depth, such that a series of discrete habitats or zones can be distinguished as one proceeds seaward from the reef crest of a typical fringing reef (Goreau 1959, Geister 1977, Blanchon and Jones 1995). Throughout the Caribbean, specific habitats were dominated by particular coral species which constructed distinctive reef structures. Hence, their names provide useful descriptions of the habitats. Three structurally distinctive, reef-building species/groups are recognised in the Caribbean.

1. *Acropora palmata*

This species (Figure 1.1) naturally dominates shallow reef habitats between 1 and 8 m, but especially in wave exposed environments. Individual colonies up to 5 or 6 m high were reported by Rigby and Roberts (1976) on Grand Cayman. However, live colonies are now rare and usually only the structures of dead *A. palmata* colonies remain. Figure 2.4 shows one of the few large living colonies of *A. palmata* on Grand Cayman, surrounded by the more typical dead structures of this distinctive species and reflects the now degraded shallow reef habitats that exist. Here, this type of reef is classed as an *Acropora palmata* habitat and has spur and groove formations. It is equivalent to the buttress zone of Goreau (1959) and the spur and groove zone described in Blanchon et al. (1997).

Stump and boulder habitat (*sensu* Blanchon et al. 1997) occurs in more shallow (0 – 5 m) areas, along wave exposed coastline, and does not have spur and groove formations. This geomorphological difference reflects an increase in wave energy forces due to decreasing depth which may alter the mode of reef accretion; ‘inplace’ reef growth on the spurs gives way to detrital growth (Blanchon et al. 1997) as the reef shallows. This area is equivalent to the lower palmata zone of Goreau (1959). *A. palmata* colonies tend to dominate this type of habitat and their structures are still obvious in many areas, although overgrown by coralline algae and bioeroding sponges (Figure 2.5). As with

Acropora palmata habitat, these areas are now very degraded in comparison to what they once were (Rigby and Roberts 1976), with few living corals.

2. *Acropora cervicornis*

This species (Figure 2.6) can dominate substrate cover in relatively calm settings across a depth range of about 5 – 25 m. However, even in exposed settings this species can become plentiful with depth, as wave energy becomes less effective at structuring benthic communities (Geister 1977).

3. *Orbicella* spp.

Three species (*Orbicella annularis*, *Orbicella faveolata* and *Orbicella franksii*) form this genus (formerly *Montastraea*, see Budd et al. (2012)) and dominate coral reefs in deeper water than *A. palmata* and in more energetic settings than *A. cervicornis*. *Orbicella* species may be abundant from back reef environments to the deeper fore reef but only tend to dominate where the two *Acropora* species are less successful (Goreau 1959, Rigby et al. 1976). Figure 2.7 shows an image of the typical columnar formations of *Orbicella annularis* colonies at 10 m on Grand Cayman. Although they form less structurally complex reefs than *Acropora* species, they are long lived and over time large columns can grow close together creating relatively complex habitat in comparison to many other species. All three species can form massive domes or sheets depending on environmental conditions.

Together, both *Acropora* and *Orbicella* species have been responsible for most reef growth in the Caribbean, during the Holocene (Bosscher 1992, Blanchon et al. 1997, Hubbard 2009). However, a combination of bleaching and white band disease killed most colonies of both *Acropora* species across the Caribbean (Aronson and Precht 2001) and populations of *Orbicella* species are in decline (Bruckner 2012). The fragile branching structures of dead *A. cervicornis* colonies are easily destroyed and have mostly disappeared on Grand Cayman,

while the thick, robust basal structures of dead *A. palmata* colonies have resisted bioerosion and physical damage. Hence, a lot of their structures are sufficiently intact to identify the species and therefore relict *Acropora palmata* reef habitats are still evident in many shallow areas. The structures associated with *Orbicella* species are largely intact on Grand Cayman and dominate reefs from about 7 m to the shelf edge reefs at 30 m. Many of these locations may have had thriving *A. cervicornis* populations in the past but colonies are presently rare and the structures that may have distinguished an *Acropora cervicornis* zone or habitat are no longer present on Grand Cayman. As the contemporary structure providers are dominated by *Orbicella* species, these reefs are considered to be *Orbicella* reef habitats. Hardgrounds (Figure 2.9) are a common marine habitat surrounding Grand Cayman. These are mostly flat areas with some coral growth but no reef accumulation.

Coral reef habitats (predominantly dominated by relict *A. palmata* structures and *Orbicella* species) comprise 46% of the shelf area (excluding lagoons) to a depth of approximately 30 m (DaCosta-Cottam et al. 2009). Hardground habitat is the next largest contributor to shelf area, covering 41% (DaCosta-Cottam et al. 2009). Shelf edge reefs cover much of the available shelf area surrounding Grand Cayman to 30 m, however they are deep (usually >20 m) and therefore safe dive times would limit the amount of survey work that could be achieved each day. Hence, only shallow reefs (<17 m) were investigated – i.e. shallow terrace reefs and those extending seaward from the mid shelf scarp on the deep terrace, to the sand plain.

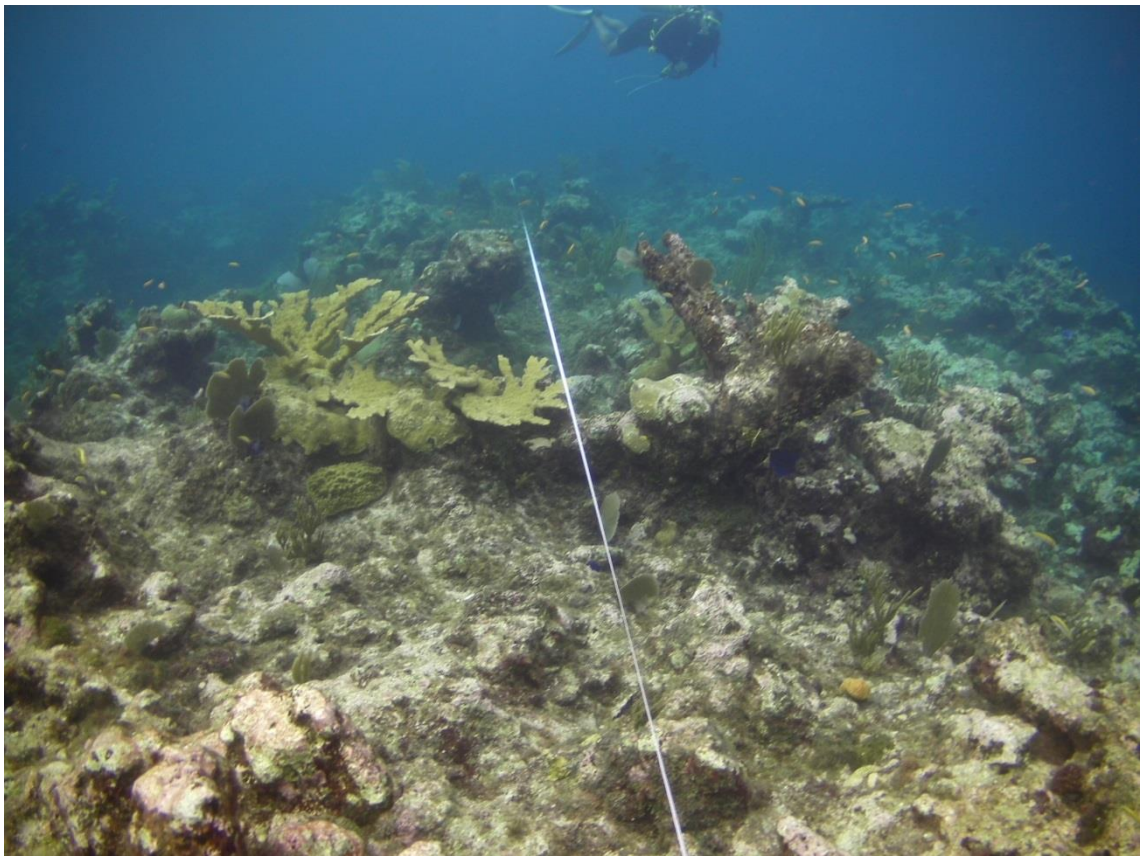

Figure 2.4 A degraded *Acropora palmata* reef habitat on the south coast of Grand Cayman, at Manse.

Figure 2.5 A degraded stump and boulder habitat at Pallas reef on Grand Cayman. *Acropora palmata* colonies grow over the coralline encrusted structures of dead ones.

Figure 2.6 The slender branches of an *Acropora cervicornis* colony at Anchor reef on Grand Cayman.

Figure 2.7 *Orbicella annularis* colonies at 10 m on Pallas reef, Grand Cayman.

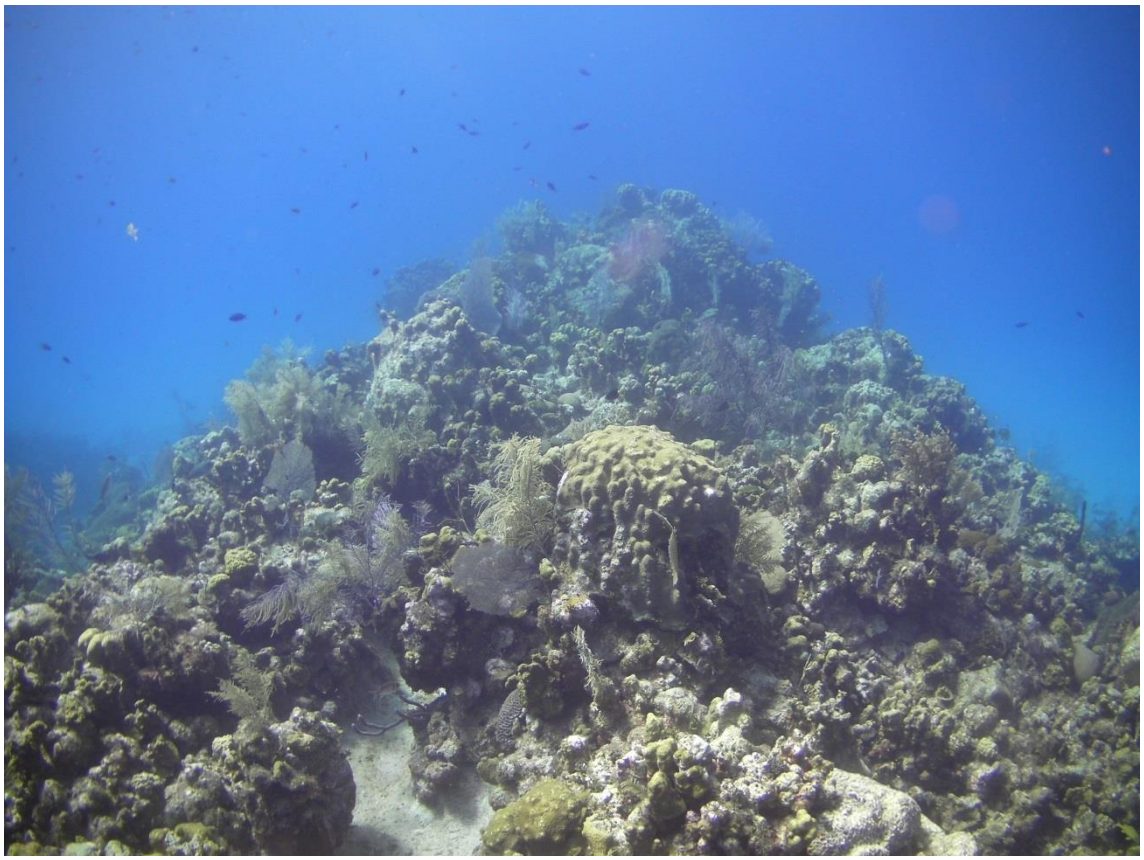

Figure 2.8 An *Orbicella* reef habitat on the west coast of Grand Cayman, at Killer Puffer.

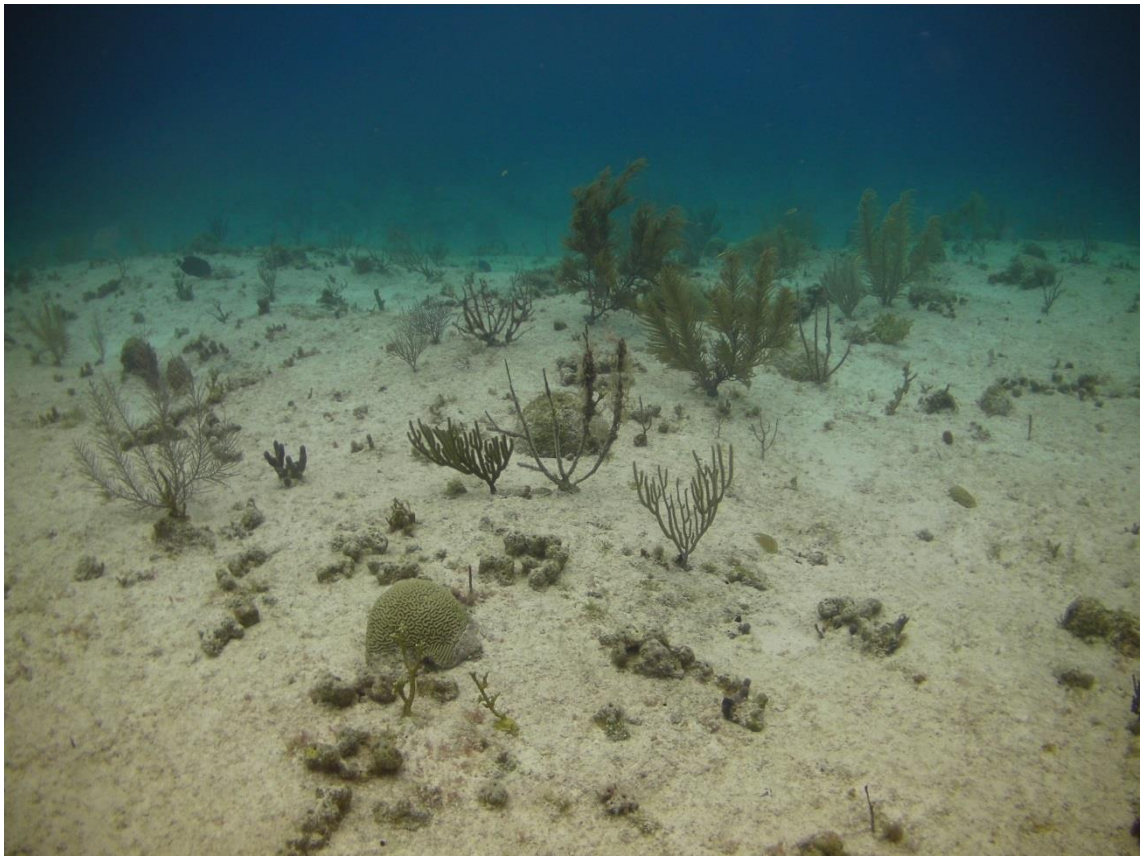

Figure 2.9 A hardground habitat on the west coast of Grand Cayman at Armchair reef.

2.4 Site Selection

An area of approximately 12.25 km^2 (*pers comm* J. Olynik, Cayman Islands Department of Environment) was selected to investigate carbonate production and bioerosion within the major habitat types that occur on Grand Cayman. This area comprised two sections of coast: (i) on the wave exposed south coast and (ii) on the wave sheltered west coast. On the south coast, a 14 km stretch of coastline was selected for investigation because this area provided a range of wave energy regimes representative of most of the south coast and because of the logistical considerations (time and cost) associated with surveying reefs further from the Cayman Islands Department of Environment base on the western peninsula. Sites were chosen on the south coast, based on the orientation of the fringing reef which was determined by examining satellite images of the reef crest; south facing sections of reef are less exposed to wind generated wave energy than east facing sections as the prevalent wind direction is from the east (Blanchon et al. 1997). Variation along the coast was also considered and sites were selected to be roughly similar distances apart. This provided sites with a range of exposure regimes to wind generated waves which also spanned the total section of coast being investigated. Hence, from Pallas to Spotts there is a decrease in the exposure to the average wind generated waves (Figure 2.3) and the most exposed sites are located at Manse (252.9 J m^{-3}). Where possible more than one habitat type was investigated at these locations, but see Table 2.1 for a description of which habitats were investigated at each location. A single *Orbicella* reef site, Babylon, was investigated on the north coast.

On the sheltered west coast, sites were investigated along a 12 km stretch of coast from North-west point to the southern-most reefs. Sediment laden currents exiting South Sound, in the south-west (Figure 2.3), limit the growth and development of shallow reefs and so this area was avoided. Coral reefs further north of North-west point become more exposed to wave energy, particularly from winter storms, and were not deemed sufficiently sheltered to be included. Sheltered shallow reef habitats along the west coast are not as predictable as the fringing reef formations on the south coast. The leeward setting allows the settlement of large quantities of sediment which may curtail

prolific reef growth; winter storms remobilise sediment and this is likely to cause intense events of sediment scour in many areas of the shallow terrace. Although *Orbicella* framework dominated habitats were present along almost the entire west coast, *A. palmata* framework dominated habitats were much less common and only occurred as patch reefs. Hence, only two sites were surveyed. These habitats were not present in the southern portion of the west coast. Hardgrounds exist along the entire west coast. Hence, sites were chosen to reflect the range of habitats that existed while considering the wave exposure regimes (Figure 2.3) along the west coast. Although there are reefs within the area surrounding Georgetown harbour, this area was avoided because of safety concerns in relation to constant boat traffic.

Table 2.1 A list of all sites investigated along with the habitats that were surveyed, average wave energies modelled, approximate depths of transects and co-ordinates. SB = stump and boulder, PR = *Acropora palmata* reef, OR = *Orbicella* reef, HG = Hardgrounds.

Site	Coordinates (dec degrees)	Wave energy (Joules m^{-3})	Habitats	Depth (m)
Boggy Sands	19.365265 -81.401652	23.8	PR	1.5
			HG	5.0
Cemetery	19.36392 -81.39593	20.7	PR	2.4
Anchor	19.35849 -81.396265	23.9	OR	9.5
			HG	7.0
Killer Puffer	19.34367 -81.39073	24.4	OR	9.5
			HG	7.0
Eden Rock	19.29363 -81.38712	6.1	OR	9.5
			HG	4.2
Don Fosters	19.291963 -81.389538	9.8	OR	10.5
			HG	5.0
Armchair	19.27952 -81.39425	20.4	OR	14.7
			HG	6.0
Pallas	19.26215 -81.37842	243.3	SB	3.3
			PR	5.0
Bullwinkle	19.26548 -81.36032	242.3	OR	11
			PR	7.7
Prospect	19.27012 -81.33667	101.7	PR	7.0
			OR	15
			HG	7.3
Spotts	19.26862 -81.31138	97.8	OR	10.0
Manse	19.265120 -81.25848	252.9	PR	5.5
			OR	11.5
Babylon	19.35332 -81.16432	208.45	OR	10.5

Calcification rates of calcareous encruster communities

3.1 Abstract

Benthic calcareous encrusting organisms are ubiquitous on coral reefs and their communities are often dominated by coralline algae. These organisms have important functional roles which include the promotion of coral settlement and helping to cement reef structure, making it more resistant to physical damage. Their growth or calcification rates are little studied and therefore estimations of their contribution to carbonate production on reefs are based on few data. As coral populations have decreased across the Caribbean, the calcium carbonate produced by calcareous encrusting communities has become relatively more important to reef carbonate budgets. Additionally, the protective function they provide to dead coral structures may be more significant now, to halt or slow the collapse of reef structural complexity. Here, I estimate calcification rates by calcareous encruster communities, after 1 year on artificial substrate, over a depth range of 3–30 m on coral reefs and hardgrounds exposed to different wave energy regimes. Additionally the benthic cover of these organisms was measured at 24 coral reef and hardground sites. Calcification ranged from 0.097 to 1.274 kg $CaCO_3$ m^{-2} yr^{-1} at the sites investigated. Mean calcification rates were significantly lower at sheltered sites than at exposed sites and significantly decreased with depth. Mean benthic cover by calcareous encruster communities was 58.7 % at the 17 coral reef sites investigated and crustose coralline algae dominated these communities at all sites. The data presented here provide calcification rates for calcareous encruster communities within different habitat types and under different wave energy regimes, informing reef carbonate budget estimates on Grand Cayman and may be applied to other Caribbean reef systems. The data also reveal the importance of considering wave energy regimes when considering carbonate production by these encruster communities.

3.2 Introduction

Benthic calcareous encrusters are ubiquitous on coral reefs and include non-geniculate coralline algae, serpulid worms, bryozoans, foraminifera and bivalves (Hepburn et al. 2014). These epilithic communities perform a variety of important ecological and geomorphological functions on coral reefs. Some species of coralline algae induce the settlement of specific coral species (Morse and Morse 1996, O'Leary et al. 2012) and therefore they are clearly important to the recruitment success of those corals. Calcareous encrusters also bind rubble together and help "cement" the structure of the reef, making it resistant to physical damage from wave energy and bioerosion (Bak 1976, Spencer 1985, Rasser and Riegl 2002). This may be particularly important after mass coral mortality events (*e.g.* bleaching) where large areas of coral substrate become available for settlement by other species, including bioeroders (López-Victoria and Zea 2005). Calcareous encruster communities also contribute to calcium carbonate production on coral reefs and can dominate this important function in certain habitats *e.g.* on reef flats (Smith 1973) and on algal ridges (Bosence 1984). However, calcification by benthic encrusting communities has not been widely investigated in the Caribbean. To the author's knowledge, there have to-date only been 4 published accounts of Caribbean calcification rates for these carbonate producers (Bak 1976 – coralline algae only, Mallela 2007; Mallela 2013; Hepburn et al. 2014), although Stearn et al. (1977) reported rates for specific coralline algae species and other authors have reported expansion and accretion rates (Adey and Vassar 1975, Steneck and Adey 1976).

In reef environments, newly available benthic substrate is colonized by various flora and fauna through a succession of different species. Filamentous turf algae colonise first, usually within a few days, followed by fast growing and rapidly maturing coralline algae species. A successional climax community takes a little over a year to develop (Adey and Vassar 1975). Hence, the taxonomic make-up of benthic encruster communities will vary through time, but it also varies in space as different species compete more successfully in specific habitat types (Martindale 1992). Coralline algae often dominate encruster communities on light exposed substrates, particularly where wave

energy is strong. Although they can also be abundant in shaded areas, experiments suggest that calcification rates are often lower (e.g. Mallela 2013).

Many calcareous encruster species are abundant within reef cavities, in caves or beneath canopies formed by corals, macroalgae and sponges (Logan 1981, Jackson and Winston 1982, Steneck 1986). As a result these light shaded communities are often missed by contemporary reef surveys (Goatley and Bellwood 2011); however, their functional importance remains. Different calcareous encruster communities develop in relation to light, wave exposure and sedimentation (Martindale 1992, Mallela 2013, Hepburn et al. 2014). Therefore the quantity of calcium carbonate produced by encruster communities is also likely to vary in relation to these environmental factors (Mallela 2007, Hepburn et al. 2014, Roik et al. 2016). Calcareous encruster communities cover extensive areas on coral reefs and although their calcification rates are somewhat lower than corals, their contribution to total carbonate production can approach and could potentially exceed that for corals. On an isolated fringing reef in Barbados, Stearn et al. (1977) estimated carbonate production by coralline algae to be 4.3 G (where 1 G = 1 kg $CaCO_3$ m^{-2} yr^{-1}) and this was 40% of that produced by corals. Environmental disturbance can alter carbonate production regimes on coral reefs, such that encruster communities become the dominant contributor (Eakin 1996, Perry et al. 2008).

Here calcification by encruster communities is investigated in different reef habitats at sites around both wave exposed and sheltered shorelines of Grand Cayman, over a depth range of 3–30 m. Benthic cover by these calcareous encruster communities is also described for 24 coral reef and hardground sites. Calcification rates are estimated for *Acropora palmata* stump and boulder reef, *Acropora palmata* reef and *Orbicella* reef habitats along with hardgrounds. In addition calcification is also estimated for deeper shelf edge reef habitats to examine changes that occur across the range of reef types that exist on Grand Cayman. Hence, the results of this experiment will add considerably to the limited data available for encruster community calcification rates in the Caribbean, while providing appropriate rates for use in carbonate budgets within the habitat types investigated in this thesis. It is hypothesised that calcification by calcareous encruster communities will decrease with depth, in response to diminishing light penetration.

Null hypothesis: The rates of calcification by calcareous encruster communities do not change with depth or exposure to different wave energy regimes.

Specific objectives:

1: To measure the rates of calcification by calcareous encruster communities at 5 depths (3 m, 5 m, 10 m, 20 m and 30 m) using ceramic tiles, within the major marine habitats that exist on Grand Cayman, over a year.

2: To measure the rates of calcification by calcareous encruster communities at similar depths exposed to different wave energy regimes, over a year.

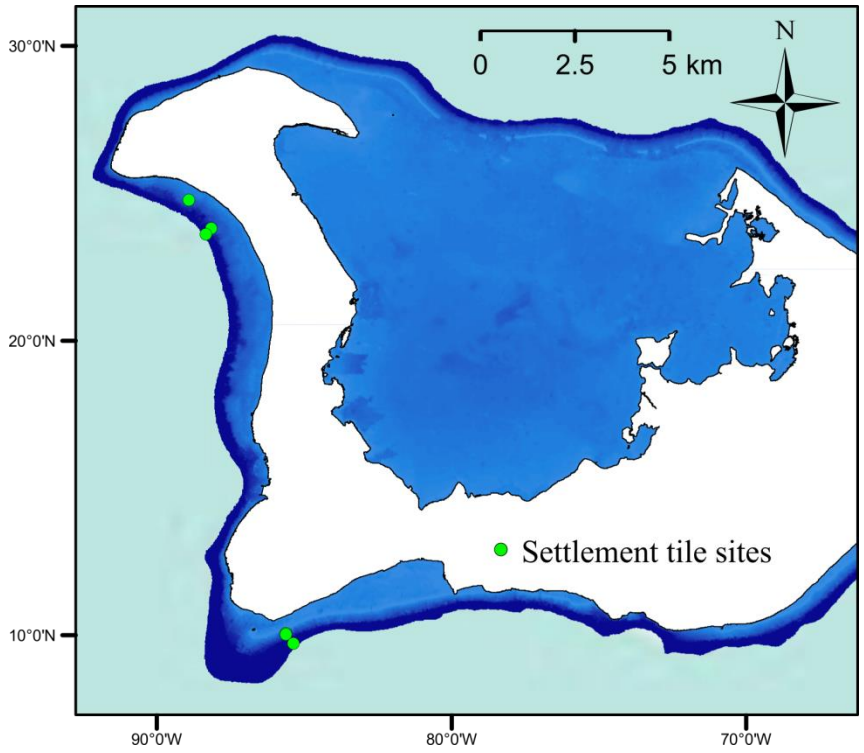

Figure 3.1 Location of the settlement tiles deployed at 10 sites on Grand Cayman. Green dots represent locations, which contain at least one site depending on depth and habitat availability.

3.3 Methodology

3.3.1 *Experimental design*

The calcification rates of calcareous encruster communities were measured across a depth range of 3 – 30 m at sites on the south (exposed) and west (sheltered) coasts of Grand Cayman (Figure 3.1). Five depths were investigated for each wave exposure regime and each of the ten sites corresponded to one of 6 discrete habitat types identified around the island; hardgrounds (~5 m, sheltered only), *Acropora palmata* stump and boulder (~ 3 m, exposed only), *Acropora palmata* reef (~ 3 m – sheltered, ~ 5 m exposed), *Orbicella* spur and groove (~10m), and deeper shelf edge habitats (at 20m and 30m). At each site light exposed and light shaded communities were investigated using 12 replicate ceramic tiles, totalling 240 settlement tiles.

The unglazed backs of ceramic tiles are ideal for settlement experiments because minute surface irregularities facilitate recruitment and growth of calcifying communities (Adey and Vassar 1975). Tiles were stuck together in pairs, using a marine silicone adhesive on the glazed sides. Two pairs were fixed to either end of a PVC pipe using a stainless steel screw and subsequently the pipe was hammered into the desired location with rebar. Figure 3.2 illustrates the setup employed. Light exposed and light shaded tile pairs provide an approximation for the range of light regimes that exist naturally on a coral reef and the results from both were combined to calculate a calcification rate for encruster communities. All tiles were 15 cm * 15 cm and separated from other replicates by 30 cm. None of the tiles touched the substrate or living organisms when they were installed.

Settlement tiles were deployed during October 2012 and monitored for the first signs of calcareous encrusters. After 21 days coralline algae (probably *Leptoporolithon* – Figure 3.3) had recruited to the settlement tiles. Successional experiments by Adey and Vassar (1975) found that the first corallines appeared on PVC pipes after 20 days. Hence, the settlement tiles were left underwater for as close to 1 year and 3 weeks as logistically possible, allowing a brief period for calcareous encrusting species to recruit. The mass of calcium carbonate on the tiles after this period provides a good indication of calcification rates by encruster communities over 1 year. Time at sea ranged from 54 to 58 weeks

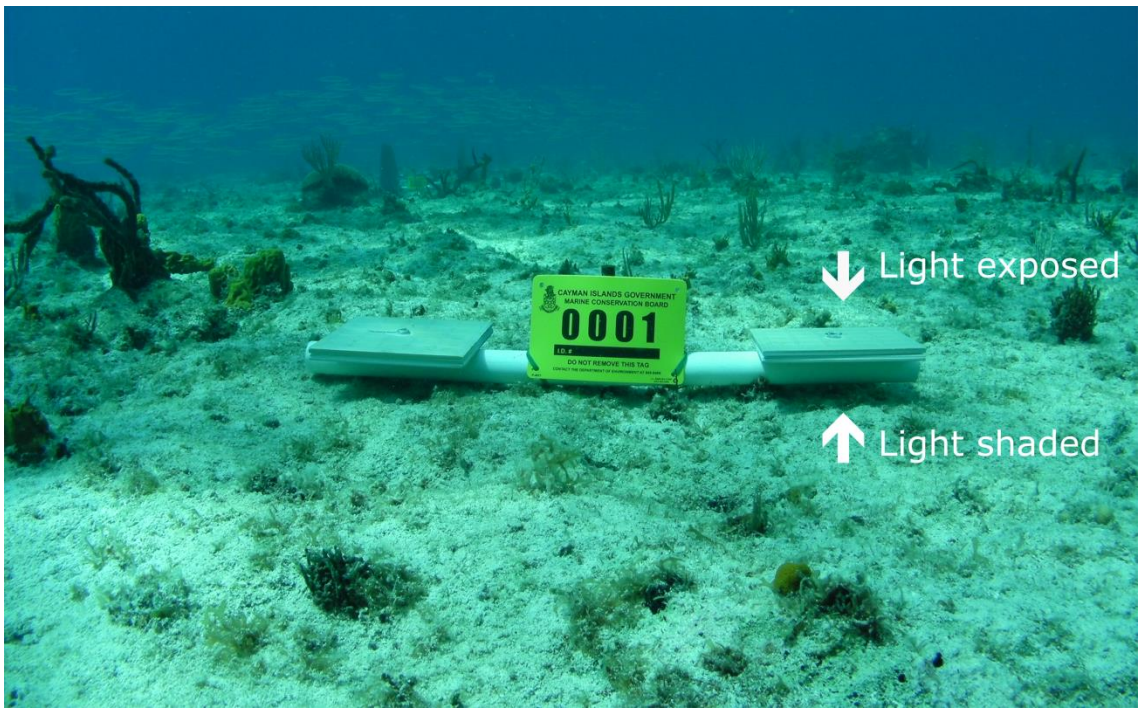

Figure 3.2 Four settlement tiles attached to the substrate in a hardground habitat at 5m.

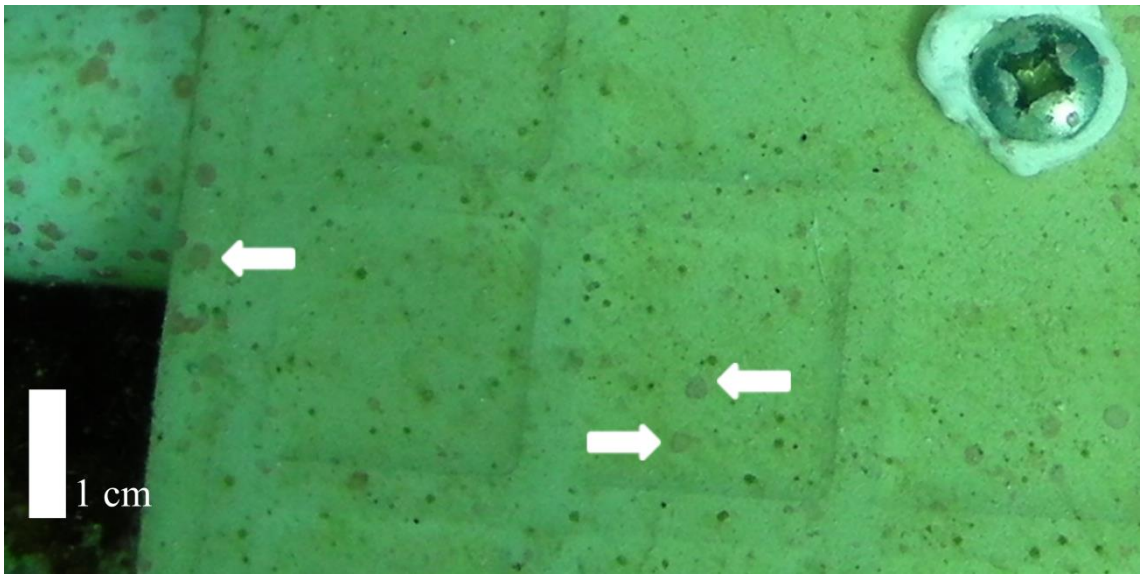

Figure 3.3 Close up of a settlement tile after 21 days at 10 m in *Orbicella* spur and groove habitat. White arrows indicate pink spherical patches of coralline algae.

across all sites and this was taken into account when calculating a calcification rate. In total, 216 settlement tiles were recovered with 20 of those lost coming from the shallow (<5 m) exposed sites. Recovered tiles were left in freshwater overnight and then air dried in the sun. Each tile pair (light shaded and light exposed) was removed from its frame, scanned at 600 dpi using a Ricoh Aficio MP C4500 multifunctional printer/scanner and placed in a marked plastic bag. Subsequently, each tile was individually wrapped in bubble wrap, carefully packaged and shipped to the UK for further analysis.

3.3.2 *Calcium carbonate production by light exposed and light sheltered communities.*

To investigate carbonate production by calcareous encruster communities on recovered settlement tiles, a portion (approx. 40%) was cut from each tile pair using a diamond blade rotary wet saw. Tile portion edges were also removed to avoid complications arising from any edge effects. The light exposed and light shaded parts were separated using the saw. Individual tile portions were then bleached overnight using a thin bleach solution (1% sodium hypochlorite) to aid the removal of fleshy algae. Tile portions were washed and soaked in deionised water and subsequently dried to constant weight at 60°C. Each tile was placed in a bath of 10% HCl until all the carbonate had dissolved (usually <2 hrs), rinsed and soaked in deionised water and then dried to constant weight as before. Any remaining non-calcareous material was either captured and placed back on the tile pieces before drying or filtered from the acid bath solution and subsequently dried and weighed. The area of each tile portion was measured and used to calculate calcium carbonate production (kg $CaCO_3$ cm^{-2} yr^{-1}). Both unused ceramic tiles and the set of four tiles found in a sand groove were used as controls. As the set of four had calcareous encrusters attached, these were removed using sand paper prior to the bleaching stage.

3.3.3 *Encruster community cover*

Percent cover by encruster communities was investigated at 24 sites around Grand Cayman, using *ReefBudget* style benthic surveys. Site selection is described in Chapter 2 and the benthic surveys employed, in Chapter 4. However, briefly, three to six transects were surveyed at each site, recording the benthic taxa covering every cm of substrate beneath 10 m of a taut transect line; see Perry et al. (2012) for a full description of the *ReefBudget* methodology.

Calcareous encruster community taxa were recorded differently within hardground habitat than they were within coral reef habitats. On hardgrounds, limestone pavement accounted for most of the area and this was recorded instead of the individual taxa that lived upon it. This was because calcareous encruster communities living on limestone pavement covered lengths of each transect from a millimetre to tens of centimetres. They were mixed in with turf algae, macroalgae and sediment in a transient way that made recording data an arduous and time consuming task. Hence, the first 1m of each transect was used to estimate the contribution of encruster communities, turf algae, macroalgae and sediment to the limestone pavement of that transect and thereafter only limestone pavement was recorded. Live corals, sponges and anything (including encruster community taxa) living on substratum raised above the limestone pavement were recorded as normal (Perry et al. 2012).

3.3.4 *Statistical analyses*

The mean calcification rates for settlement tiles were not normally distributed or equally variable, so the non-parametric Kruskal-Wallis test was used to investigate the effect of depth and habitat. Differences between sites were assessed by the appropriate use of a Student's t test (t) or the Wilcoxon rank sum test (W). The influence of tile orientation (light shaded vs exposed) on mean calcification was investigated using paired t tests, where joined tiles were treated as pairs (see Figure 3.2). All data was checked to ensure that the differences between pairs were normally distributed, as this is an underlying assumption of the paired t test (Crawley 2007).

3.4 Results

3.4.1 *Spatial variation in calcification by encruster communities*

Control tiles (n = 27) lost 0.5 +/- 0.05 % of their mass when exposed to acid for 3 hours. Hence this value was used to correct for mass loss not due to the dissolution of encruster calcium carbonate. Mean calcification (including cryptic and exposed tiles) by encruster communities ranged from 0.097 +/- 0.008 (SE) to 1.274 +/- 0.067 kg $CaCO_3$ m^{-2} yr^{-1} at the sites investigated. Calcification was significantly higher on the south coast than on the west coast (Kruskal-Wallis chi squared = 44.788, df = 1, $p < 0.001$) and also influenced by habitat (Kruskal-Wallis chi squared = 52.567, df = 5, $p < 0.001$); habitat types have approximately the same depths on both coasts, so this test is equivalent to testing for the effect of depth.

Figure 3.4 plots encruster community calcification rates within each site. On the exposed south coast (Figure 3.4a), mean calcification rates for encruster communities at 20 m and 30 m were very similar; 0.328 +/- 0.01 and 0.335 +/- 0.01 kg $CaCO_3$ m^{-2} yr^{-1} respectively. Calcification was higher within *Orbicella* spur and groove habitat (0.513 +/- 0.048 kg $CaCO_3$ m^{-2} yr^{-1}) at approximately 10 m on Pallas reef (Figure 2.3). The two shallow sites on the south coast, Pallas reef (5m) and (3m), had the highest calcification rates of any site; 1.135 +/- 0.049 kg $CaCO_3$ m^{-2} yr^{-1} at 5 m and 1.274 +/- 0.067 kg $CaCO_3$ m^{-2} yr^{-1} at 3 m. Although calcification was consistently higher in the *Acropora palmata* stump and boulder habitat (3 m), it was not significantly different from the slightly deeper *Acropora palmata* habitat (5 m) where spur and groove formations dominated ($t = -1.662$, $p = 0.123$).

Mean calcification by encruster communities on the sheltered west coast paralleled the depth related trends recorded on the south coast (Figure 3.4b), with depth playing a major role in the rates of calcification recorded. However, the two shallowest sites at 3 and 5 m were significantly different on the west coast ($W = 120$, $p < 0.001$) in contrast to the finding for the south coast. Mean calcification was 0.283 +/- 0.019 kg $CaCO_3$ m^{-2} yr^{-1} at 5 m, but 0.565 +/- 0.059 kg $CaCO_3$ m^{-2} yr^{-1} at 3 m with only a little overlap in their respective ranges (Figure 3.4b); 0.18 to 0.422 kg $CaCO_3$ m^{-2} yr^{-1} at 5 m and 0.283 – 0.906 kg

$CaCO_3$ m^{-2} yr^{-1} at 3 m. Both sites were located at Boggy Sands, but within different habitat types. It may be that environmental factors within the 5 m hardground habitat were suppressing calcification below that, which one might expect, within a west coast reef habitat at the same depth. At the 10 m site (*Orbicella* spur and groove) on the west coast calcification was lower, with a mean of 0.191 +/- 0.005 kg $CaCO_3$ m^{-2} yr^{-1}. This was almost 2.7 times lower than the corresponding habitat on the south coast. On the deeper shelf edge reef sites mean calcification by encruster communities was 0.113 +/- 0.005 kg $CaCO_3$ m^{-2} yr^{-1} at 20 m and 0.097 +/- 0.008 kg $CaCO_3$ m^{-2} yr^{-1} at 30 m, but these values were not significantly different ($t = 1.75$, $p = 0.096$; Figure 3.4b).

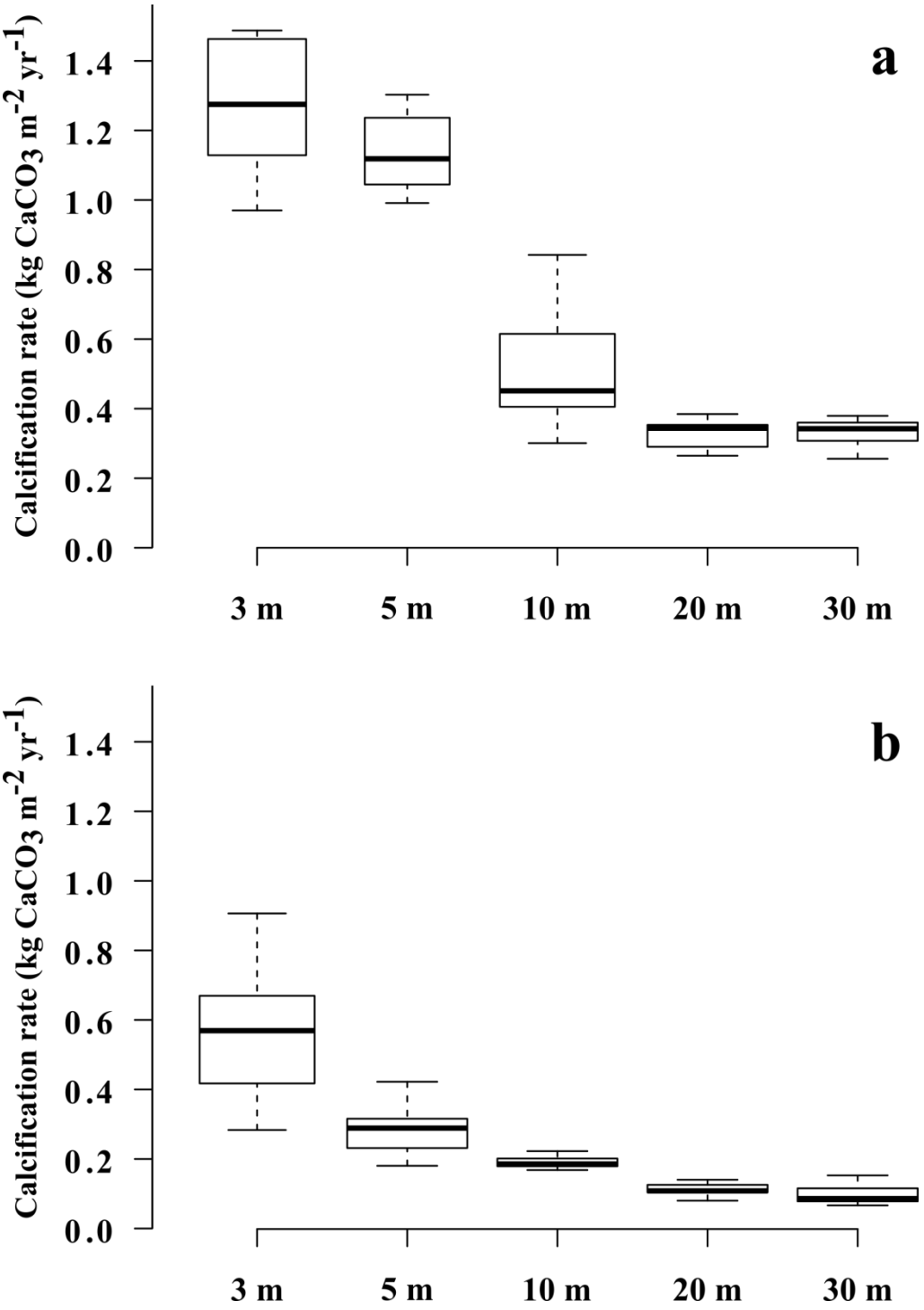

Figure 3.4 Box (median and 50% quantile) and whisker (95% quantile) plot showing calcification within each site. A) South coast. B) West coast.

3.4.2 *Calcification by light exposed and light shaded encruster communities*

Within site differences in calcification between light shaded and light exposed encruster communities were investigated using paired t tests (Table 3.1). Light exposed tiles had significantly higher mean calcification rates than light shaded ones at all sites, except for two sites on the west coast – at 5 m and 10 m. Settlement tile orientation did not influence the calcification rates within the hardground habitat (West 5 m). However, at the deeper (West 10 m) *Orbicella* spur and groove habitat, light shaded tiles had calcification rates that were on average 18% higher than light exposed tiles and this difference between means was significant (Table 3.1).

Both light exposed (Figure 3.5a) and light shaded (Figure 3.5b) encruster communities responded to depth in a similar fashion to the overall mean calcification rates for each site (Figure 3.4). Data from hardground and stump and boulder habitats were excluded from Figure 3.5, as these habitats were not investigated on both coasts. Regardless, both habitats had higher calcification rates than deeper sites and thus fit the overall trend of decreasing calcification by encruster communities with depth (Table 3.1). However, there were some exceptions to this trend. On the south coast, light exposed tile calcification rates decreased with depth until 20 m. At 30 m calcification rates were higher (Figure 3.5a), although the differences were not significant. Nevertheless even a levelling off of calcification on exposed tiles is an unexpected result as light availability should decrease from 20 to 30 m. Light shaded tiles at 20 and 30 m on the south coast also reversed the trend of decreasing calcification with depth having higher calcification rates than tiles at 10 m (Figure 3.5b, Table 3.1). This did not occur on the west coast where the calcification rates measured on both light exposed and light shaded tiles decreased with depth (Figure 3.5b), although calcification rates for encruster communities at 20 and 30 m were very similar (Table 3.1).

A detailed examination of the taxa responsible for the measured calcification rates was beyond the scope of this thesis. However, it was clear that the communities found on light shaded and light exposed tiles were very different. Coralline algae dominated the communities on light exposed tiles, particularly at shallower depths (e.g. Figure 3.6a). However, light shaded tiles (e.g. Figure 3.6b) had much more diverse communities, in part reflecting the change in light

availability from the outer edges to the centre where tiles were joined to a PVC pipe (Figure 3.2). Common taxa were coralline algae, foraminifera, serpulid worms and bryozoans on the light-shaded tiles.

Table 3.1 Mean (+/- SE) calcification rates (kg $CaCO_3$ m^{-2} yr^{-1}) for light shaded and light exposed tiles at 10 sites around Grand Cayman. The results of paired t tests between the means for shaded and exposed tiles are also displayed.

Site	Light Shaded	Light Exposed	df	T	p
West 3 m	0.461 +/- 0.08	0.669 +/- 0.07	10	-2.242	0.049
West 5 m	0.281 +/- 0.03	0.286 +/- 0.02	11	-0.180	0.860
West 10 m	0.207 +/- 0.01	0.175 +/- 0.01	11	2.257	0.045
West 20 m	0.062 +/- 0.01	0.163 +/- 0.01	11	-8.505	< 0.001
West 30 m	0.068 +/- 0.02	0.125 +/- 0.01	11	-2.831	0.016
South 3 m	0.804 +/- 0.06	1.744 +/- 0.10	7	-10.072	< 0.001
South 5 m	0.617 +/- 0.08	1.655 +/- 0.07	5	-9.904	< 0.001
South 10 m	0.194 +/- 0.03	0.832 +/- 0.10	10	-6.088	< 0.001
South 20 m	0.290 +/- 0.02	0.366 +/- 0.01	11	-2.948	0.013
South 30 m	0.274 +/- 0.01	0.396 +/- 0.02	11	-4.697	< 0.001

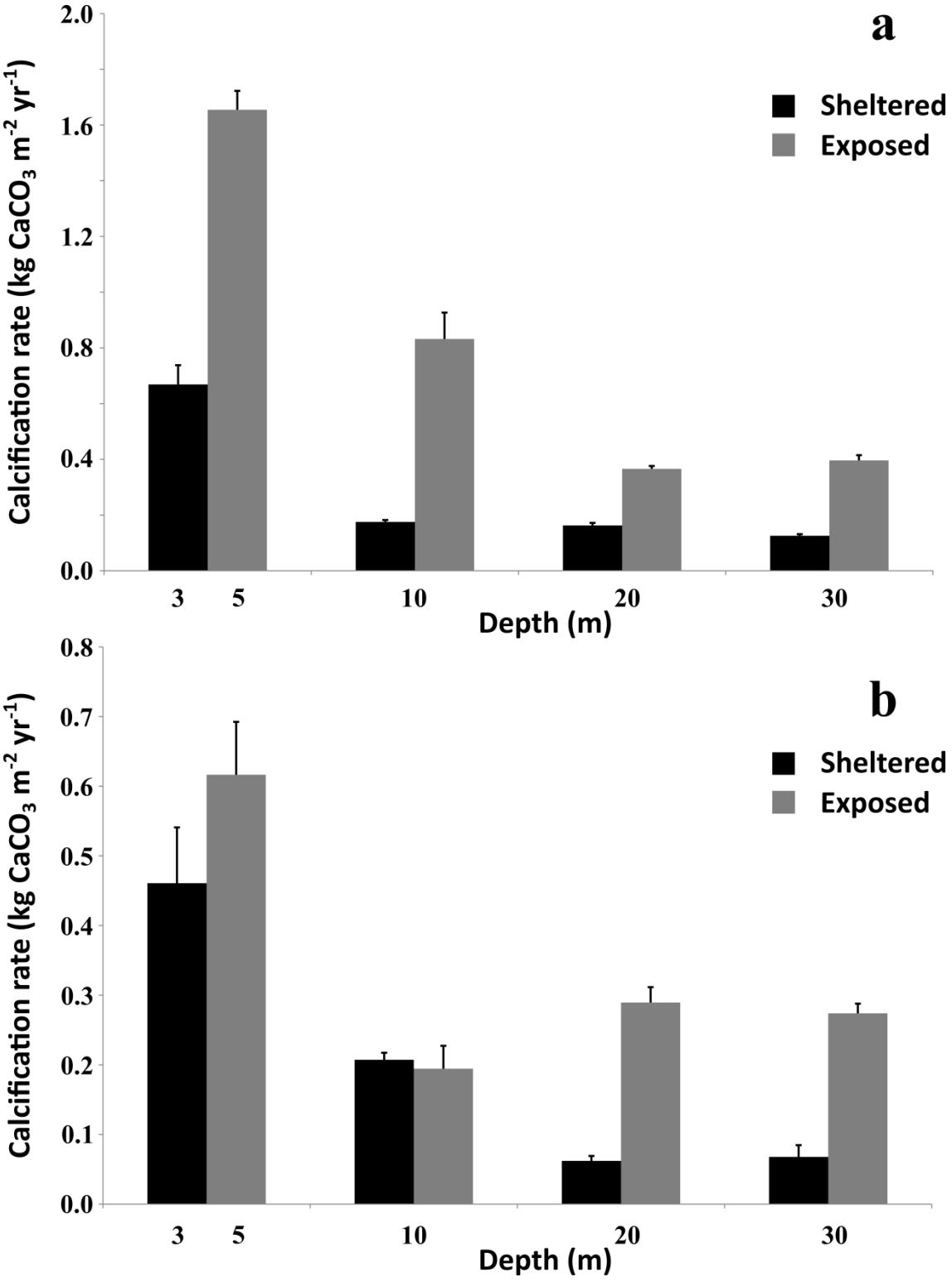

Figure 3.5 Light exposed (a) and shaded (b) encruster community calcification rates from 8 sites on the South and West coasts of Grand Cayman. Note the differences in scale on the y axis.

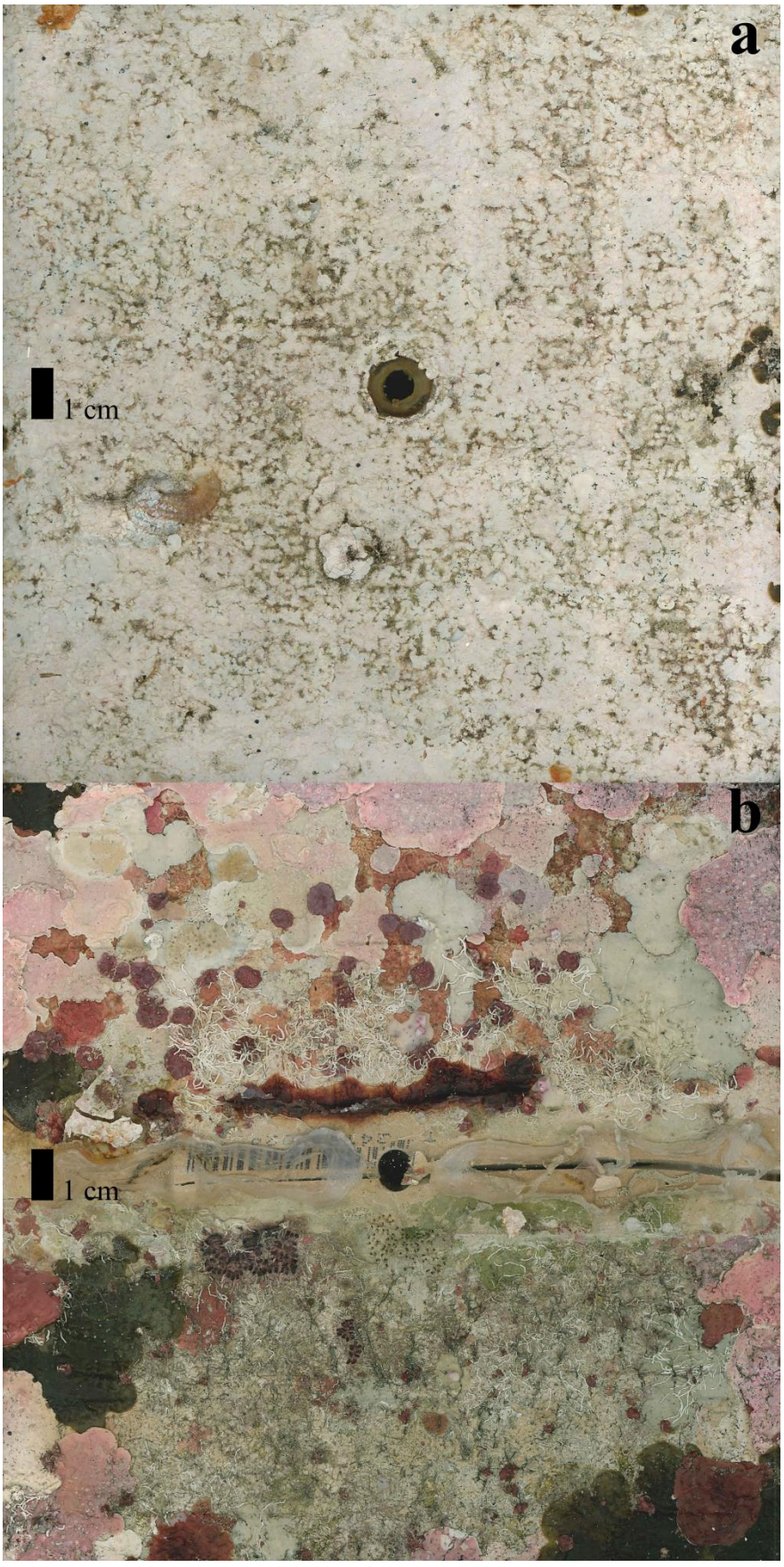

Figure 3.6 Settlement tiles (15 * 15 cm), showing typical (a) light exposed and (b) light shaded encruster communities after one year at 5 m within an *Acropora palmata* reef habitat.

3.4.3 *Encruster community cover on Grand Cayman reefs*

Calcareous encruster communities were recorded on all benthic transects investigated (n = 83) and observed to be dominated by crustose coralline algae. Often, they were hidden by canopies of macroalgae. Within coral reef habitats, 90% of the macroalgae recorded had living calcareous encrusters beneath them. Figure 3.8 illustrates the percentage of substrate covered by calcareous encruster communities at coral reef sites, both beneath macroalgal canopies and where no canopy was present. Percent cover by these organisms ranged from 27.4 +/- 2.0 % at Boggy Sands (2 m) to 82.8 +/- 2.0% at Pallas (5 m). Mean overall cover was high at 58.7 +/- 3.3% across the 17 coral reef sites investigated. In general sites on the shallow terrace had a greater proportion of canopy free calcareous encrusters.

The mean percent cover by calcareous encrusters was relatively similar within each habitat type. Mean cover for *Orbicella* spur and groove habitats was 56.8 +/- 3.4%. For the two fore reef slope habitats mean cover was 69.4 +/- 5.6%. However for *Acropora palmata* reef habitats, there was a distinct difference in encruster community cover between the exposed and sheltered coasts (exposed: 68.8 +/- 5.1%, sheltered: 34.5 +/- 7.1%, overall: 57.1 +/- 8.1%). Both sheltered sites (Boggy Sands (~2 m) and Cemetery (~2 m) were shallower than their exposed coast counterparts where mean depths ranged from 5 – 8 m. The stump and boulder site at Pallas ranged from 2 – 4 m and had mean encruster community cover of 60.2 +/- 5.6%. In deeper water within *Orbicella* spur and groove habitat there was little difference between exposed (59.9 +/- 3.9 %) and sheltered coasts (53.8 +/- 5.7 %).

Calcareous encruster communities within hardground habitats were dominated by coralline algae, but macroalgal canopies were rare. The substratum was predominantly exposed limestone pavement, on which encruster communities were recorded. Each site was subtly different but the pavement generally supported a combination of coralline algae, turf algae (often thick), some macroalgae and various quantities of fine sediment. Frequently, brightly coloured and presumably living coralline algae and/or other calcareous encrusters were concealed beneath a layer of fine sediment or amongst algal turfs with fine sediment (Figure 3.7). It may be that encruster communities are quite ephemeral on limestone pavements, with limited succession. The large

quantity of sediment may indicate that scouring is an important control on encruster community development.

Percent cover data for hardground sites are presented in Figure 3.9, which is divided between pavement and other raised substrates. Most sites were covered by limestone pavement (38–87%). Macroalgal canopies with calcareous encrusters were rare; a maximum of 13% cover was recorded at Don Fosters hardground, while Boggy Sands and Eden Rock had none. The single wave exposed hardground site (at Prospect) had calcareous encruster communities that resembled the other sites and there did not appear to be an obvious influence from wave energy. However species diversity and abundance was not investigated.

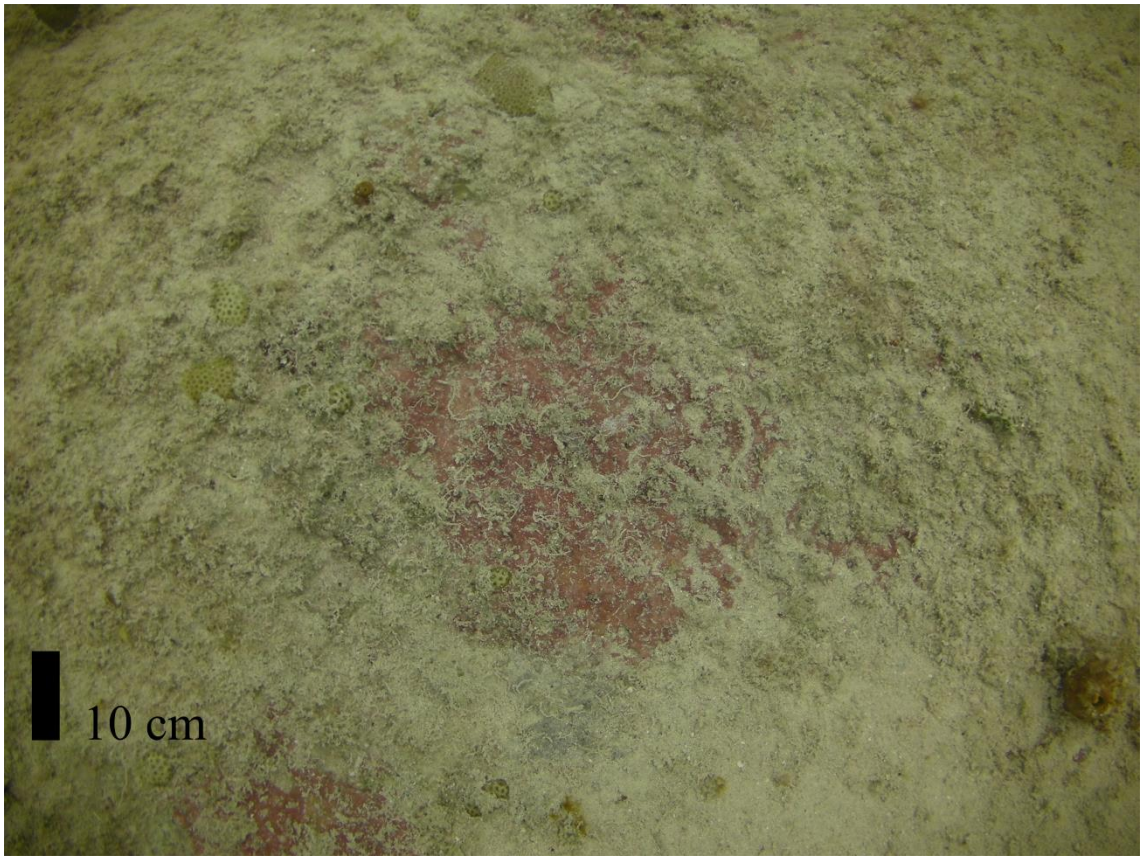

Figure 3.7 Live coralline algae revealed from beneath fine sediment within a hardground habitat at Armchair reef, Grand Cayman.

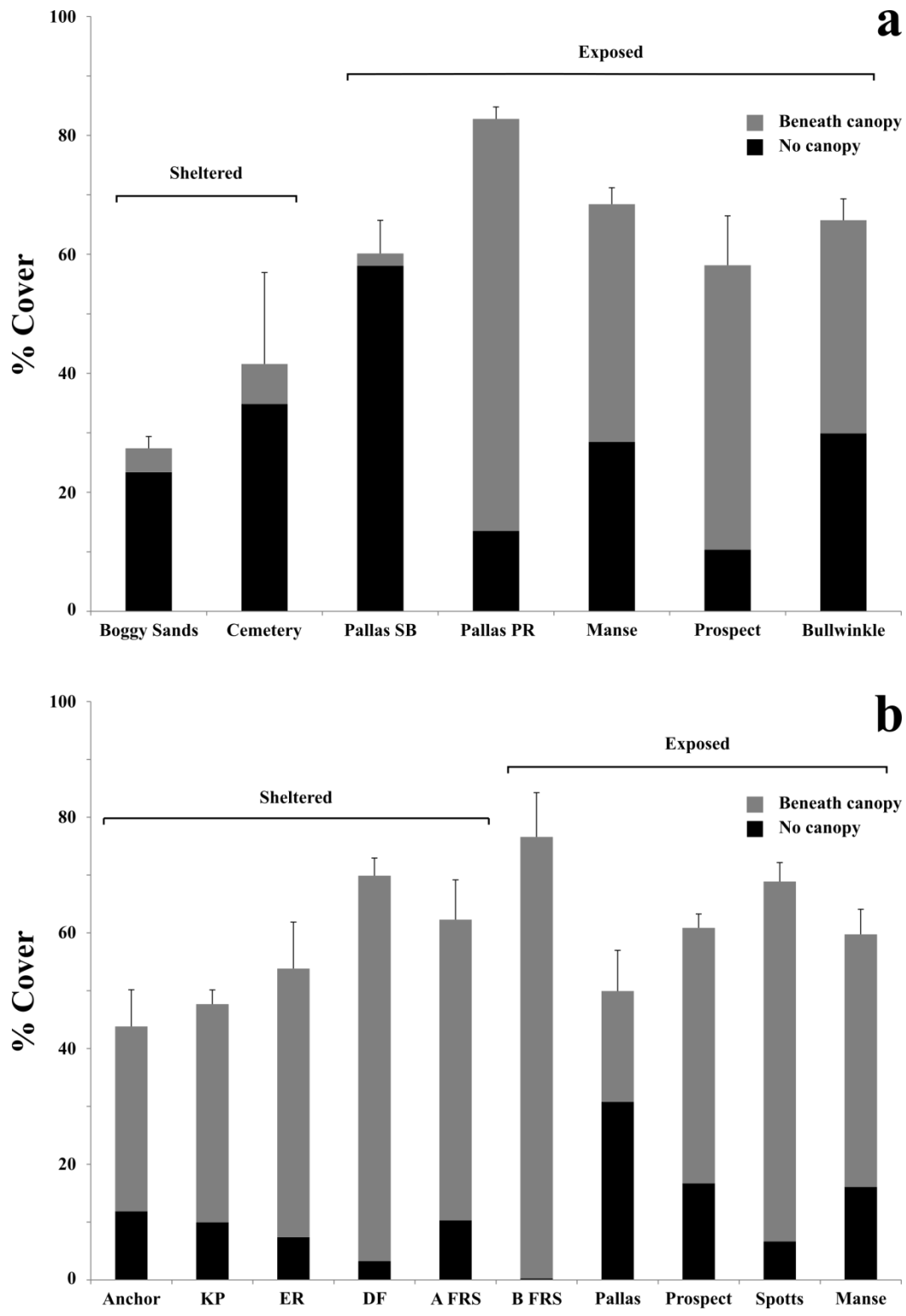

Figure 3.8 Mean percentage of substrate covered (+ SE) by calcareous encrusters. a) all sites were *Acropora palmata* reef (PR) habitat except Pallas SB which was a stump and boulder habitat. b) all sites were *Orbicella* spur and groove habitat, except FRS which was fore reef slopes. KP – Killer Puffer, ER – Eden Rock, DF – Don Fosters, A FRS – Armchair fore-reef slope, B FRS – Babylon fore-reef slope.

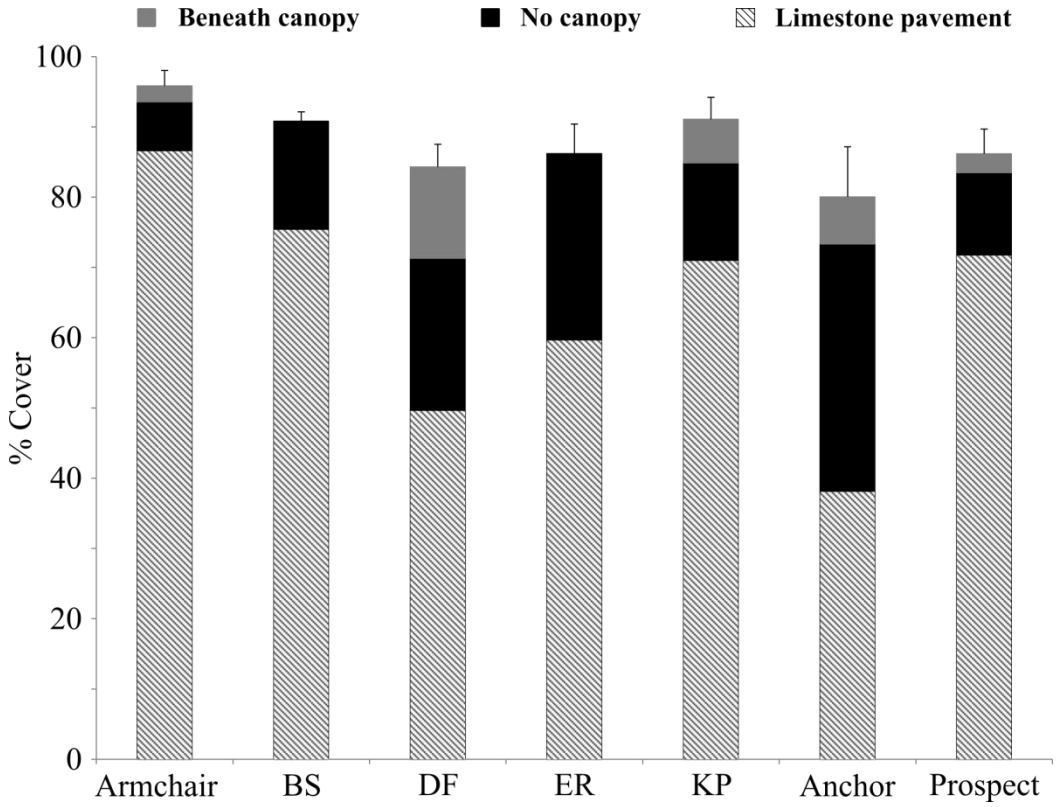

Figure 3.9 Mean percent cover (+ SE) by calcareous encrusters on elevated substrate and limestone pavement, at different hardground sites. Limestone pavement supported encruster communities but was not completely covered by them. BS – Boggy Sands, DF – Don Fosters, ER – Eden Rock, KP – Killer Puffer. All sites are sheltered, except for Prospect which was exposed.

3.5 Discussion

3.5.1 *Encruster community calcification on coral reefs and hardgrounds*

The settlement tile experiment, described here, sought to improve the data available for encruster community calcification rates in various coral reef and hardground habitats around Grand Cayman. Appropriate means could then be used at each site to generate estimates of carbonate production by these communities from benthic cover data (see Chapter 4). The rates of calcification measured for encruster communities decreased with depth, but were also very different between coasts (Figure 3.4). Hence, appropriate rates for encruster communities on Grand Cayman were selected based on depth, coast and habitat type. The selected calcification rates are presented in Table 3.2.

Table 3.2 Appropriate calcification rates (kg $CaCO_3$ m^{-2} yr^{-1}) for encruster communities on Grand Cayman.

Habitat type	Sheltered Coast (kg $CaCO_3$ m^{-2} yr^{-1})	Exposed Coast (kg $CaCO_3$ m^{-2} yr^{-1})
Hardgrounds	0.283	0.283
Stump and boulder	-	1.274
Acropora palmata reef	0.565	1.135
Orbicella reef	0.191	0.513

These rates describe the likely calcification on newly exposed substrate over the course of a year, allowing a short period for initial settlement. They are applied to encruster community cover to estimate carbonate production in Chapter 4. These communities exist across a range of successional stages which would achieve a climax community after 1 year if allowed to develop However, for hardground habitat the calcification rate is also applied to the percent cover by limestone pavement. This is because settlement tiles from the hardground habitat at Boggy Sands had communities that were representative of those living on the surrounding pavement and not on the elevated substrate (dead coral heads). Encruster communities on elevated substrate within hardground habitats did not have the same quantities of sediment and did not reflect the seemingly ephemeral nature observed for those on the pavement. Calcification rates measured on settlement tiles at Boggy Sands were significantly lower within the hardground habitat (5 m) than within the *Acropora palmata* reef habitat (3 m). However, the same was not true of Pallas reef where settlement tiles at 3 and 5 m, within reef habitats, did not have significantly different calcification rates (see section 3.4.1; Figure 3.4). Hence, light availability is unlikely to be responsible for the differences observed and there must be a physical process at the Boggy Sands hardground habitat suppressing calcification that is not present at 5 m on Pallas reef. The shallow terrace on the west coast stores large quantities of sediment which would begin to mobilise under high energy conditions. Hardground habitat makes up most of the area of the shallow terrace on this coast and there is very little physical structure available to stop or channel the movement of sediment within this habitat type. Therefore, sediment scouring may be common and I suggest that

the continued resuspension of sediment and subsequent scouring allows short lived encruster communities to develop briefly before dying. As a result, calcification during a year by these ephemeral encruster communities on limestone pavement is better described by the area of substrate available, than by an estimate of the percent cover by these communities at any one point in time. This may mean that estimates for carbonate production by encruster communities on elevated substrate within hardground habitats were conservative.

3.5.2 *Trends in calcification due to depth and wave exposure*

Light and exposure to wave energy are two of the main controls on encruster community growth (Adey and Vassar 1975, Martindale 1992, Hepburn et al. 2014, Roik et al. 2016), but other important factors include herbivory (Steneck 1986) and sedimentation (Mallela 2007, 2013). Other studies have measured similar but often lower calcification rates for encruster communities, to those measured here for coral reefs. Mean calcification was 0.34, 0.25 and 0.27 kg $CaCO_3$ m^{-2} yr^{-1} at 1 m, 5 m and 8 m, respectively, at Puerto Morelos in the Mexican Caribbean (Hepburn et al. 2014) within fore reef environments. The mean calcification rate measured here for an exposed fore-reef habitat at 5m is 1.135 kg $CaCO_3$ m^{-2} yr^{-1}. It is not clear why the environment on Grand Cayman was so much more supportive of calcification than that at Puerto Morelos.

Depth (and therefore light availability) was a clear influence on calcification by encruster communities at the sites investigated here. However, there were also large differences in the rates of calcification measured for sites at the same depths, but subject to different exposure levels (Figure 3.4). Roik et al. (2016) report similar trends for the Red Sea; calcification rates by encruster communities increased with exposure level. At Rio Bueno in North Jamaica, Mallela and Perry (2007) recorded calcification rates that ranged from 0.003 – 0.030 kg $CaCO_3$ m^{-2} yr^{-1} within sheltered and turbid reef habitat, but which increased in exposed clear water reef settings (0.07 – 0.16 kg m^{-2} yr^{-1}). Although this was not investigated, Grand Cayman is unlikely to have different light or sedimentation regimes on the exposed and sheltered coasts; there are no rivers or heavy industries and the limited agriculture that exists is far

removed from the sites investigated. Hence, wave exposure may be driving the differences measured for sheltered and exposed sites on Grand Cayman.

Wave action in shallow reef habitats reduces competition from organisms which cannot cope with the physical energy of these systems. However, it should be noted that herbivory is also an important process in controlling fleshy algae which would otherwise overgrow coralline algae (Steneck 1986, Williams et al. 2001, Steneck et al. 2014) even in high wave energy environments. Despite this, in deeper water where physical forces are reduced, the level of competition between encruster communities and other organisms should be similar between exposed and sheltered coasts. The calcification rates measured in this study were not similar between exposed and sheltered sites at any depth. Potentially, the constant movement of water generated by inshore wind driven waves (undertow) boosts calcification by calcareous encrusters even as deep as 30m at the exposed site investigated.

Another possibility is that herbivorous parrotfish play a role in suppressing calcification at sites on the sheltered west coast as they are situated within a marine protected area, where fishing is illegal. Bak (1976) reported an increase in calcification for coralline algae with depth (0.16 kg m^{-2} yr^{-1} at 3m and 0.41 kg m^{-2} yr^{-1} at 25 m) attributing the increase to a release from herbivore pressure. The exposed south coast is outside of the marine protected area (Figure 2.1) and presumably experiences higher fishing pressure. Coralline algae species with thick thalli are selected for in areas undergoing intense herbivore driven disturbance (Steneck 1988) and therefore species comparisons between exposed and sheltered sites at the same depths may indicate herbivory as a potential cause. However such a study is beyond the scope of this thesis. Parrotfish grazing scars were present on settlement tiles down to 30 m, but obvious scars were rare and herbivory, whether influential or not, may not completely explain the differences between coasts.

Light shaded encruster communities were protected from parrotfish and other large herbivores. Urchins are rare on Grand Cayman reefs (see Chapter 6) and therefore herbivory could not be an important factor influencing calcification rates for these communities. However, calcification was much lower on light shaded tiles from the west coast than on the south coast (Figure 3.5b), with the

exception of the sites at 10 m. Hence, herbivory is probably not the underlying cause of differences in calcification rates between the coasts at all sites. At the 10 m site on the west coast (Anchor), light shaded tiles had calcification rates that were on average 18% higher than light exposed tiles. This difference between the means was significant (Table 3.1) and also the only occurrence of light shaded communities contributing more calcium carbonate to mean calcification rates than light exposed ones, across all sites. At the 10 m site on the south coast (Pallas) light shaded communities had similar calcification rates to those on the sheltered west coast at 10 m. This suggests that the difference between mean calcification rates at both sites was due to the exposed tiles only, which were far higher at Pallas. Bioerosion by parrotfish at Anchor was nearly twice that for Pallas (see Chapter 6) and this suggests that herbivory may be influencing the measured encruster community calcification rates at these sites. Bak (1976) attributed low calcification rates by coralline algae at 13 m to herbivory, which became intense after 6 months. Additionally, mean calcification by encruster communities at 10m on fore-reef sites in Tobago was 0.76 kg $CaCO_3$ m^{-2} yr^{-1} (Mallela 2013) and much higher than that measured here for Grand Cayman. Tobago reefs are over fished (Burke et al. 2008) and it may be that parrotfish are an important control on encruster community calcification rates throughout the Caribbean. This possibility means that measured rates of calcification by encruster communities are net figures. Hence, for the purpose of estimating a carbonate budget, the application of rates of bioerosion to encruster community cover might double count the effect of herbivores. Studies which limit grazing by specific parrotfish species (e.g. Steneck et al. 2014) may be useful in understanding the impact of bioeroding parrotfish on calcification by coralline algae.

Nevertheless, herbivory cannot be driving the differences in calcification between coasts at 20 m and 30 m because light shaded communities on the south coast had calcification rates which were approximately 4 times those on the west coast. Hence, another mechanism must be in place which promotes calcification by encruster communities on the south coast above that on the west coast or alternatively, suppresses calcification on the west coast. Perhaps the most obvious potential mechanism is undertow due to wave energy at the surface, which may deliver more nutrients and oxygen to shelf edge habitats on

the south coast. But other potential mechanisms exist; nutrient enrichment via submarine groundwater discharge (Paytan et al. 2006) may suppress coralline algae on the west coast. However, there are no available data and this suggestion is purely speculative.

3.6 Conclusions

Appropriate habitat means for calcification by calcareous encruster communities on Grand Cayman are displayed in Table 3.2. It is clear that there are differences between habitat types, which are influenced by depth and exposure to wave energy. The underlying mechanisms that drive the differences are less certain. However, light availability undoubtedly plays a role in the decrease in calcification rate with depth. Differences in calcification measured between levels of exposure to wave energy are most likely influenced by undertow which may provide encruster communities on the south coast with greater access to nutrients and/or oxygen. Additionally, parrotfish may also play a role in suppressing the measured rates of calcification on the west coast where their biomass is greater.

Carbonate framework production by benthic communities along exposed and sheltered shores of Grand Cayman

4.1 Abstract

Caribbean coral reef systems have undergone extensive, and largely anthropogenically driven, changes in species abundance and diversity over the past forty to fifty years. Research into the sources and consequences of this change has usually focused on ecology. Hence, links between the ecological functioning of reef systems and their geomorphology are not well understood and this precludes an understanding of how ecological changes have affected ecosystem functions that are dependent on the physical structure of coral reefs. A fundamental barrier to the development of knowledge in this area is a lack of basic data on the quantities of calcium carbonate produced in reef habitats and on which species are responsible. In this chapter, carbonate framework production data is presented from 24 sites within coral reef and hardground habitats along sheltered and exposed coastlines of Grand Cayman. The contributions of individual coral species are examined for each habitat and wave energy regime along with carbonate production by calcareous encruster communities. In Chapter 3, habitat specific encruster community calcification rates were calculated and the percent cover by these communities described; the synthesis of both, carbonate production, is examined here. Mean carbonate framework production was highest within *Orbicella* reef habitat (3.54 G, kg $CaCO_3$ m^{-2} yr^{-1}). Shallow *Acropora palmata* reef habitat had carbonate framework production rates of 2.65 G and hardgrounds had the lowest rates (0.38 G). The increase in carbonate framework production from shallow (< 8 m) to deeper reefs (8–15 m) is a reversal of a natural biophysical relationship and is concerning for the management of coral reef systems on Grand Cayman. Wave energy regimes (sheltered vs exposed) did not affect the rates of

carbonate production within habitats. Calcareous encrusters contributed most (57%) to carbonate production within hardground habitats, but corals were the dominant carbonate producers within coral reef habitats. However, calcareous encrusters were relatively more important on shallow exposed sites; 46% within exposed and 13% within sheltered *Acropora palmata* habitat. Hence, coralline algae are actively maintaining the structural complexity of shallow reef communities on the exposed south coast and therefore providing an important ecosystem service. *Orbicella annularis* was the most important carbonate producing coral species within both *Acropora palmata* reef and *Orbicella* reef habitats.

4.2 Introduction

Calcium carbonate framework production is critical to the natural functioning of coral reef systems. Most framework is produced by corals (Bak 1976, Dullo 2005, Hubbard 2009) within fore-reef environments. Much of the carbonate produced is subsequently remobilised through a combination of biological (Neumann 1966) and physical erosion (Hubbard et al. 1990) and transported as sediment or rubble to other environments within a coral reef system (Johns and Moore 1988, Blanchon and Jones 1997, Kleypas et al. 2001). This supplementary sediment and rubble may add to existing stores or allow habitats to expand (e.g. seagrass beds – Beanish & Jones 2002). In many instances environments in the lee of fringing or barrier reefs would not exist without the protection afforded them, from wave energy, by reef structure and require replenishment of sediment after storm events (Neumann and Land 1975). Hence, the influence of calcium carbonate framework production may travel well beyond the location in which it was produced. The physical structure of coral reefs provide important ecosystem services to people and the rates at which this structure is produced is an important function within coral reef systems. Over time (10^1 – 10^3 years) habitat construction on coral reefs (carbonate framework production and inorganic cementation) interacts with habitat destruction (via bioerosion, wave energy and calcium carbonate dissolution) to produce complex physical structures (Blanchon et al. 1997, Hubbard et al.

2013), that support diverse communities, which provide yet more ecosystem services to millions of people worldwide (Moberg and Rönnbäck 2003, Harborne et al. 2006). Beneath this surficial reef complexity, coral reef geomorphology has been fashioned, over very long time periods (10^2 – 10^5 yrs.) against a background of the fluctuating balance between carbonate production and erosion, by temporally varying physical forces (currents, wave energy, hurricanes, earthquakes etc.) and sea level rise/fall (Neumann and Macintyre 1985, Blanchon and Jones 1997, Hubbard 2009).

However, the growth and continued existence of coral reef systems begins with the benthic communities that produce calcium carbonate. On coral reefs this function is usually dominated by corals (Stearn et al. 1977, Hubbard et al. 1990, Mallela and Perry 2007, Perry et al. 2013), although coralline algae can be very important in shallow, high wave energy environments (Smith 1973, Bosence 1984). Coral reef communities have evolved against a backdrop of natural disturbance (both chronic and acute) and specific reef habitats tend to have coral assemblages which reflect the physical environment in which they exist; Goreau (1959) described reef zones based on the diversity and abundance of species within similarly structured reef habitats, while Geister (1977) used changes in depth and wave energy to describe the same zonation. Light availability, temperature, depth and wave energy are the four main controls of species diversity and abundance (Huston 1985, Dullo 2005). However, extrinsic environmental factors are increasingly forcing changes to reef community assemblages either through chronic or intermittent disturbance events.

On Caribbean coral reefs, coral cover has declined dramatically over the past 40 years (Aronson and Precht 2001, Gardner et al. 2003, Green et al. 2008). Consequently, both carbonate production and reef structural complexity have decreased (Alvarez-Filip et al. 2009, 2013, Perry et al. 2013) and benthic communities have changed (Green et al. 2008, Burman et al. 2012). Within different reef zones or habitats the dominant and structurally important species (*Acropora palmata, Acropora cervicornis, Orbicella annularis* and *Orbicella faveolata*) have suffered severe population losses (Aronson and Precht 2001, Bruckner and Bruckner 2006, Green et al. 2008, Bruckner 2012, Burman et al. 2012). Core records suggest that these species were the most important carbonate framework producers on Caribbean reefs during the Holocene

(Blanchon et al. 1997, Gischler and Hudson 2004, Hubbard 2009) and that similar community transitions are unprecedented during this epoch (Aronson and Precht 1997, Aronson et al. 1998, Greenstein et al. 1998). Given the relative speed and magnitude of change and its apparent uniqueness in the geological record, it is not clear how ecosystem functioning has been affected. Contemporary Caribbean reef habitats now have very different benthic communities (Green et al. 2008, Bruckner and Hill 2009, Burman et al. 2012, Perry et al. 2015c) to those that were originally described by early reef researchers – Goreau (1959), Geister (1977). Hence, a decoupling of the natural biophysical relationships (*sensu* Williams G et al. 2015) which normally determine coral reef assemblages may have occurred across much of the Caribbean (Williams S et al. 2015). It has been hypothesised that the myriad of modern anthropogenic disturbances affecting coral reefs are drowning out or superseding natural disturbance regimes leading to novel assemblages (Nystrom et al. 2000, Knowlton 2001, Riegl et al. 2012) which could not persist indefinitely in a completely natural setting. The consequences of these novel assemblages for reef carbonate production remain unclear but may include decreased rates of habitat construction, reduced structural complexity and slower reef growth (Alvarez-Filip et al. 2013, Perry et al. 2013, 2015c). Ecosystem services dependent on specific habitat types, reef structural complexity or reef geomorphology may be threatened.

Research into reef carbonate production is generally rather limited and in the Caribbean there have only been six field based publications assessing the contributions of different taxa to benthic community carbonate production (Stearn et al. 1977, Hubbard et al. 1990, Mallela and Perry 2007, Perry et al. 2012, 2013, 2015c). Hence, very little data exist for contemporary reefs and basic data on the quantities of calcium carbonate produced by reef communities is required to develop our understanding of how habitat construction affects ecosystem function under different environmental regimes and over time how this may affect essential ecosystem services. In this chapter, carbonate framework production by benthic communities is estimated within discrete *a priori* selected habitats (hardground, *Acropora palmata* reef and *Orbicella* reef) along exposed and sheltered coasts of Grand Cayman. The questions posed are the same as those originally posed by Stearn et al. (1977) for a small reef in

Barbados, but expanded to include several different reef habitats across a range of wave energy regimes. Census surveys are used to investigate the contributions of individual coral species and calcareous encruster communities. It is anticipated that carbonate framework production will vary between habitat types and be driven by different species in each habitat. Different wave energy regimes (sheltered vs exposed) are also likely to affect carbonate framework production.

Null hypothesis 1: Carbonate framework production does not vary between different habitat types or exposure regimes.

Null hypothesis 2: Individual species contribute uniformly to total carbonate framework production within coral reef and hardground habitats.

Specific objectives:

1. To measure benthic cover by individual coral species and calcareous encrusters using benthic transects within *Acropora palmata* reef, *Orbicella* reef and hardground habitats.

2. To estimate the contributions of individual species to carbonate framework production within *Acropora palmata* reef, *Orbicella* reef and hardground habitats.

3. To estimate the total carbonate framework production within *Acropora palmata* reef, *Orbicella* reef and hardground habitats.

4. To compare total carbonate framework production within similar habitat types exposed to different wave energy regimes.

4.3 Methodology

A description of Grand Cayman, its reefs and the environment in which they grow is presented in Chapter 2. Carbonate framework production was investigated using the census approach of Perry et al. (2012). Four *a priori* selected habitats were investigated (hardground, stump and boulder, *Acropora palmata* reef and *Orbicella* spur and groove reef) as these made up the majority of submarine area to a depth of 15 m. Shelf edge reefs and hard bottom communities in deeper water were not investigated. Site selection is described in Chapter 2. On two occasions sites originally selected as *Orbicella* spur and groove habitats were found not to possess characteristic spur and groove formations and were classed as fore-reef slopes. Hence, this habitat type was not chosen in advance and data analysis needed to incorporate this fact.

4.3.1 *Benthic community surveys*

Benthic surveys were conducted at 24 sites around Grand Cayman within 5 habitat types – hardgrounds (HG, 4 – 8 m, n = 7), stump and boulder (SB, 2 – 4 m, n = 1), *Acropora palmata* reef (PR, 1 – 8 m, n = 6), *Orbicella* spur and groove (OSG, 8 – 17 m, n = 8) and fore-reef slope (FRS, 10 – 15 m, n = 2). The habitat types, sites and their locations are described in Chapter 2. Although habitat types were sometimes contiguous, all five never occurred at the same site. Different habitats were surveyed, where possible, at each site such that their locations provided a description of benthic communities over a range of different wave exposure regimes within each habitat type (see Chapter 2 for details). The stump and boulder habitat type does not exist on the west coast and only one site was surveyed.

At each site three to six 10 m transects were surveyed. Transects were laid along spurs for reef sites and randomly for hardgrounds, where spurs did not exist. All reef sites contained spur and groove formations with the exception of the stump and boulder habitat at Pallas and the two fore-reef slope sites. However, these sites did have visible sand channels which were avoided and transects were laid perpendicular to shore as with spur and groove sites. This meant that some fore-reef slope transects spanned up to 3 m in depth. Transect

placement was controlled by the selection of a random starting point, usually a convenient hole, roughly in the centre of each spur into which a 50 cm rigid plastic stake was hammered. The transect line was attached to the stake using a 50 cm rope. A second stake was hammered into the reef >11 m from the first stake seaward along the spur and because a suitable location needed to be found for the second stake, the transect lines were never completely straight down the centre of the spur. This meant that the beginnings, ends and trajectories of transects were never chosen. Transect lines were pulled taught between the stakes and secured so that a planar length of 10m could be measured above the reef (Fgure 4.1). Using this method, a representative area of the spur could be surveyed without having to decide that the area was representative, avoiding potential surveyor bias. A benthic category was assigned to each cm of substrate beneath the planar 10 m transect by using a 1 m flexible plastic tape to conform to substrate contours (Figure 4.1). All hard corals were identified to species level (Humann and DeLoach 1996, Budd et al. 2012, Coralpedia 2016). Algal species were recorded using a functional group approach (Steneck 1988, Steneck and Dethier 1994). Four groups were used: algal turfs (<10 mm), macroalgae (>10 mm), articulated calcareous algae (e.g. *Halimeda* and *Amphiroa*) and crustose coralline algae. Benthic marine communities often support canopies of macroalgae, beneath which live coralline algae and other calcareous encrusters (Steneck 1986). A unique category was used to record this, but the same calcification rate was applied to encruster communities living with or without macroalgal canopies. Soft corals and sponges were recorded, but not identified to lower taxonomic levels.

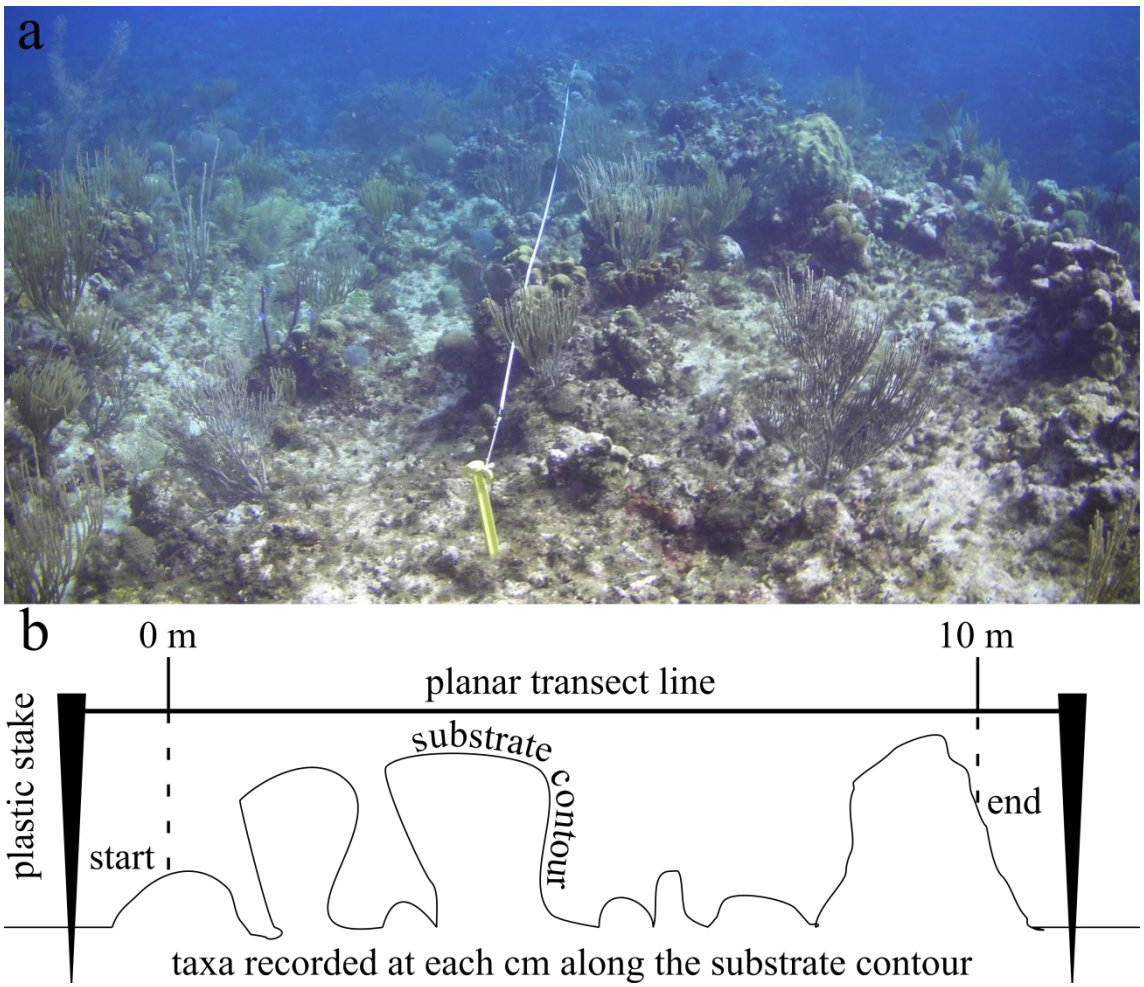

Figure 4.1 a) Benthic transect at Pallas *Orbicella* reef habitat. b) A diagrammatic representation of the side view of transects.

4.3.2 *Calcification rates*

Percent cover data were combined with rugosity and species specific calcification rates (Appendix A) to calculate calcium carbonate production for each relevant taxonomic group and summed for each transect. Calcification by calcareous encruster communities was based on the measured rates calculated in Chapter 3 for each habitat. For corals, calcification rates were tailored to each species dependent on available Caribbean data for coral growth and density. Data from outside the Caribbean Sea (Gulf of Mexico, Florida, Bahamas and Bermuda) was not considered because coral growth rates tend to decrease with decreasing mean temperatures (reviewed in Dullo 2005). Data were pooled for depths 1–8 m and used to calculate calcification rates for hardgrounds, stump and boulder and *Acropora palmata* reef in both exposure regimes. Data were pooled for depths 8–15 m and used to calculate calcification rates for *Orbicella* spur and groove and fore-reef slope habitats in both exposure regimes.

Wherever possible, species data were used preferentially, followed by data at the genus level, then family/morphology. The mean growth and density selected for each species is reproduced for shallow (1–8 m) and deep (8–15 m) calcification regimes in Appendix A. Where studies provided a mean growth/density rate, this was used. Where studies provided a range of growth rates, the mid-point was used and where studies provided data for more than one site, a mean value from all relevant sites was used. As an example, the growth rate data selected for *Porites astreoides* are reproduced in Table 4.1.

Table 4.1 Data selected for *Porites astreoides* to calculate a mean growth rate in habitats from 7 – 15 m.

Reference	**Location**	**Depth (m)**	**Growth rates (cm/yr)**	**Mean growth (cm/yr)**
Gladfelter et al. 1978	Buck Island, St. Croix	10		0.300
Chornesky & Peters 1987	Discovery Bay, Jamaica	10		0.310
Hubbard & Scaturo 1985	Cane Bay, St. Croix	12.2		0.310
Huston 1985	Discovery Bay, Jamaica	10	0.22 – 0.45	0.335
Torres & Morelock 2002	La Parguera, Puerto Rico	7	0.25	0.325
Torres and Morelock 2002	Guanica, Puerto Rico	7	0.4	
Crabbe 2009	Rio Bueno, Jamaica	5 – 8.5	0.433	0.413
Crabbe 2009	M1, Discovery Bay, Jamaica	5 – 8.5	0.367	
Crabbe 2009	DL, Discovery Bay, Jamaica	5 – 8.5	0.357	
Crabbe 2009	Dairy Bull, Jamaica	5 – 8.5	0.537	
Crabbe 2009	Pear Tree Bottom, Jamaica	5 – 8.5	0.373	
Mean used in this study				**0.332**

4.3.3 *Data analysis*

The benthic communities recorded on each transect were investigated using a multivariate approach which, at first, focused solely on the biological information present. Multivariate analyses were performed in Primer 5. Data were first normalised using percentages as the actual length of each transect was different and dependent on structural complexity. Although the structural complexity of a reef site is often a result of the biological communities that exist there, antecedent topography may also influence it. Additionally, and perhaps more importantly, declines in coral cover and any synergistic ecological changes may mean that the current benthic communities are not similar to those that were responsible for building the habitat. Storms can also move large quantities of coral framework and sediment from one location to another altering the structural complexity of sites. Hence, it is likely that the underlying rugosity at each transect would influence the abundances recorded (cm cover) and so similarity matrices constructed from this data would be affected by a non-biological factor. Normalising the data to percent cover removed this possibility. It is important to note that, here, percent cover refers to the entire three dimensional structure of the area surveyed and cannot be directly compared to percent cover figures based on assessments of planar surface area, such as those taken from line point count or photographic surveys.

Rare species were defined as anything that did not occur on at least two of the 83 transects and removed from the analysis as they could not be representative of their communities. The data were square root transformed to diminish the influence of very common taxa which could have masked the influence of less abundant taxa. A Bray-Curtis similarity matrix was constructed and interpreted using cluster analysis and non-metric multi-dimensional scaling (MDS). Finally, analysis of similarity (ANOSIM) was used to test for differences between benthic communities within habitats. All of the multivariate analyses were used to interpret the influence of depth and wave energy on the benthic communities investigated.

4.4 Results

Benthic communities present on 83 surveyed transects are described using a multivariate approach (section 4.4.1) to establish typical community assemblages for each habitat type. In the next section (4.4.2) the structural differences of each habitat are described using rugosity. The benthic cover by taxonomic groups including corals is then discussed in section 4.4.3 for each site and habitat. Finally (section 4.4.4), carbonate production is described at each site and within habitat types. The percent cover by calcareous encrusters was described in Chapter 3 and therefore is not reproduced here. However, carbonate production by these communities is described at each site and within habitat types.

4.4.1 *Benthic community structure*

Benthic transects, surveyed on both reefs and hardgrounds, revealed biological communities which tended to be more similar within habitat types. Figure 4.2 shows a dendrogram of Bray Curtis similarities constructed from square root transformed percent cover data and group-average linkage. At 66% similarity each transect was assigned to one of four groups, although a single transect from Boggy Sands (an *Acropora palmata* reef habitat) was grouped on its own. Group 1 contained all of the *Orbicella* spur and groove and fore-reef slope transects along with all south coast *Acropora palmata* reef transects. Hardground transects were spread across three groups. Group 2 contained hardground transects from one site – Don Fosters. Groups 3 and 4 contained transects from the remaining hardground sites, both west coast *Acropora palmata* reef sites (Boggy Sands and Cemetery) along with the stump and boulder transects. Transects from shallow terrace coral reef habitats (*Acropora palmata* reef and stump and boulder) were found in all the groups. This suggests that contemporary biological communities inhabiting these shallow reefs have similarities with communities inhabiting both the *Orbicella* reef and hardground habitats. However, there was also a distinct division between *Acropora palmata* reef transects from the south (Group1) and west (Groups 3,

4) coasts which was not apparent for communities within *Orbicella* reef sites or hardgrounds.

Further investigation of the benthic community data was achieved using a two dimensional MDS plot of the Bray-Curtis similarity matrix (Figure 4.3). The stress value was 0.16, which suggests that the two dimensional plot is broadly representative of the similarities between biological communities within each transect. Hence, it is clear that hardgrounds have very different biological communities to fore-reef slope and *Orbicella* spur and groove habitats. Four groups were tentatively drawn in Figure 4.3 and these match the groups assigned in Figure 4.2 well. Group 1 included transects from *Orbicella* spur and groove, fore-reef slope and south coast *Acropora palmata* reef habitats. Group two included hardground transects from Don Fosters, the remaining south coast *Acropora palmata* reef transects and a single *Orbicella* spur and groove transect. Group 3 contained all the west coast *Acropora palmata* reef transects along with a single hardground transect. Finally group 4 contained the remaining hardground transects and the stump and boulder transects. Similar patterns were observed using the cluster analysis technique (Figure 4.2) and both techniques provide mutually consistent representations of the similarity between the surveyed biological communities. However, the stress value of 0.16 in the MDS plot was not sufficiently low to draw definitive conclusions about the communities within groups or about whether some transects belonged in adjacent groups. Hence it is not clear whether *Orbicella* spur and groove, fore-reef slope and south coast *Acropora palmata* reef transects have similar enough biological communities to be considered the same or whether further subdivision is appropriate for any of the other groups. Certainly, a case could be made for further divisions within Groups 2 and 3.

Despite this, it is clear that there is a general change in biological communities from relatively deep *Orbicella* reef habitat to shallow *Acropora palmata* reefs and to hardgrounds. Hence depth is having a structuring effect on the benthic communities investigated. Figure 4.3b examines the effect of exposure and the plot reveals that *Acropora palmata* reef communities on the south and west coasts are very different, as they are split between Groups 1 and 3. The effect of exposure (if any) is less clear within *Orbicella* spur and groove and fore-reef slope habitats. There were only 3 transects from exposed hardgrounds.

However, each fits well into Group 4 with most of the other hardground transects. Additionally, each transect had benthic communities which were more similar to communities from some west coast hardground transects than to one another.

Analysis of Similarity (ANOSIM) was used to test for differences between habitat types (Table 4.2). Three of the *a priori* selected habitats (hardground, *Acropora palmata* reef and *Orbicella* spur and groove) had benthic communities that were significantly different from one another. However, stump and boulder transects (n = 3) did not have significantly different benthic communities to either hardground or *Acropora palmata* reef habitat types. The MDS plot (Figure 4.3) positions all three stump and boulder transects in Group 4 and each was plotted relatively far from *Acropora palmata* reef transects. This suggests a divergence in the conclusions made by both techniques. However, the cluster analysis technique (Figure 4.2) suggests that stump and boulder and west coast *Acropora palmata* reef transects were 66% similar (excluding one transect at Boggy Sands, which was 59% similar). South coast or exposed *Acropora palmata* reef transects had benthic communities which were only 57% similar to their sheltered counterparts. The differences between exposed and sheltered *Acropora palmata* reef benthic communities can be visualised in Figure 4.3 and it seems likely that exposure is playing a role in defining the benthic communities within these shallow coral reef habitats. Fore-reef slope benthic communities were not significantly different (Table 4.2) from those within *Acropora palmata* reef or *Orbicella* spur and groove habitat types and again the obvious differences between *Acropora palmata* reef benthic community structure on both exposed and sheltered coasts suggested that wave exposure needed to be considered. Hence, the structuring effects of a categorical wave exposure level (sheltered/exposed) were included in a 2 way crossed ANOSIM (Table 4.3).

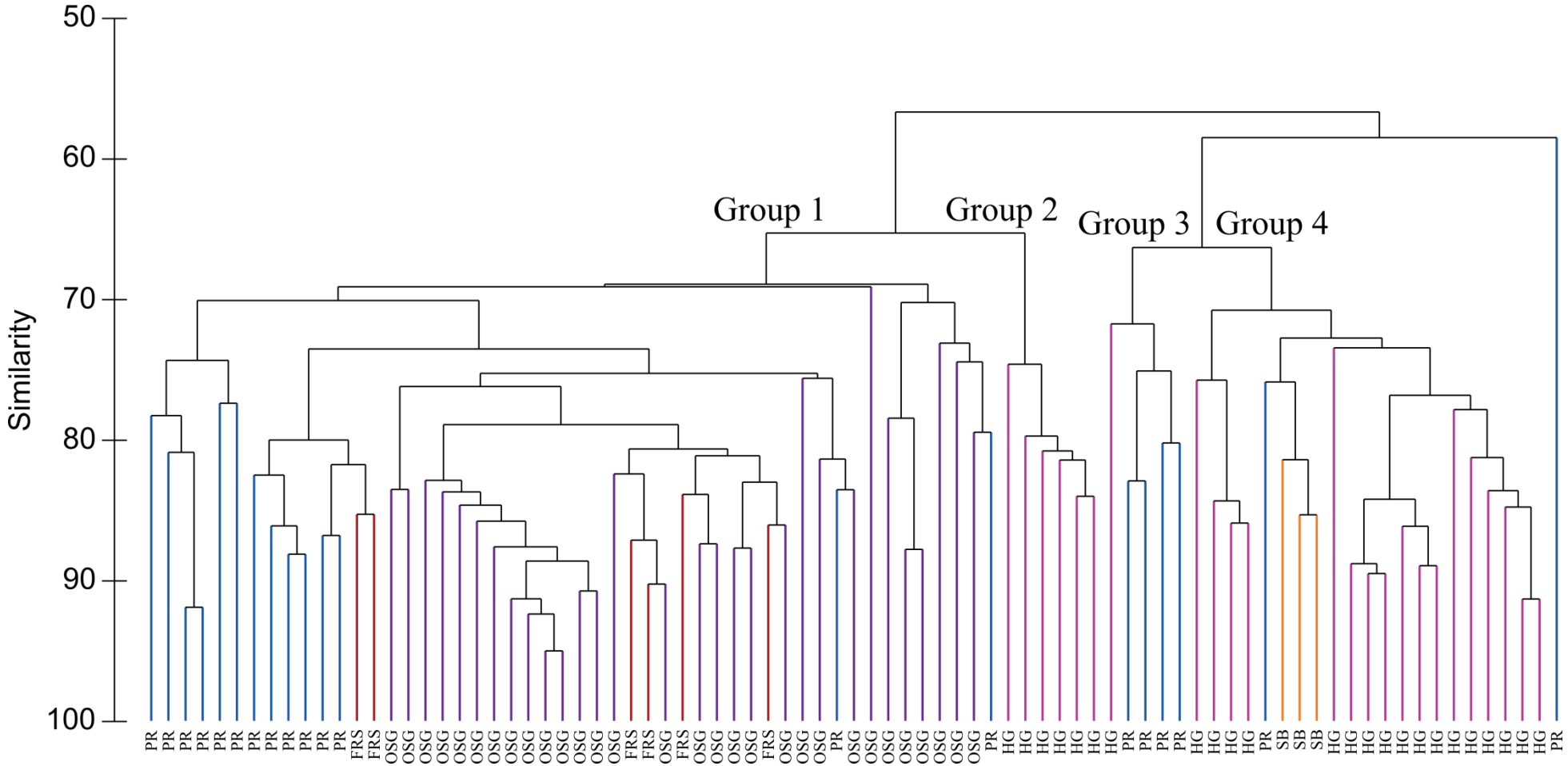

Figure 4.2 Dendrogram for hierarchical clustering of 83 benthic community transects, using group-average linkage of Bray-Curtis similarities calculated from square root transformed data. Transect habitats are listed along the base; PR – *Acropora palmata* reef, FRS – fore-reef slope, OSG – *Orbicella* spur and groove, SB – stump and boulder, HG – hardgrounds. Data in Appendix B.

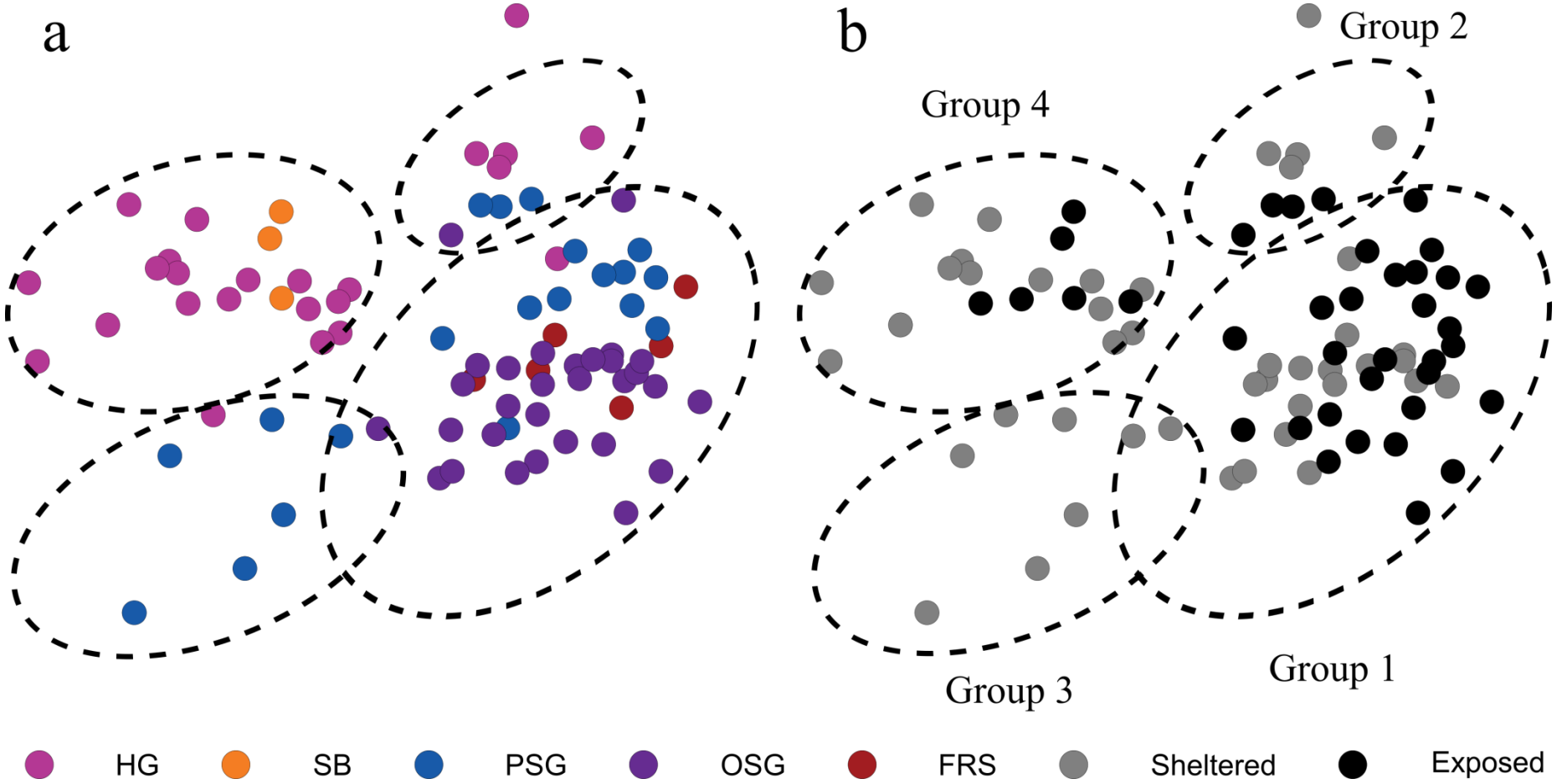

Figure 4.3 Two dimensional MDS plot of benthic community data taken from 83 transects of coral reef habitats in Grand Cayman. Percent cover data was square root transformed and the bi-plot was composed from a Bray-Curtis similarity matrix. Stress = 0.16. a) Transects are colour coded for a) habitat type and b) wave exposure; HG – hardgrounds, SB – stump and boulder, PR – *Acropora palmata* reef, OSG – Orbicella spur and groove, FRS – fore reef slope. Data in Appendix C.

Table 4.2 ANOSIM of transect data with habitat as a grouping. HG – hardgrounds, SB – stump and boulder, PR – *Acropora palmata* reef, OSG – *Orbicella* spur and groove, FRS – fore reef slope.

Global R	**Significance**	**Permutations**	**Permutations ≥ R**	
0.455	p < 0.001	9999	0	
Pairwise Tests	**R Statistic**	**p**	**Permutations**	
			Actual	≥ R
HG vs FRS	0.522	< 0.001	9999	0
HG vs PR	0.411	< 0.001	9999	0
HG vs OSG	0.714	< 0.001	9999	0
HG vs SB	- 0.077	0.653	2925	1910
FRS vs PR	- 0.068	0.668	9999	6683
FRS vs OSG	- 0.039	0.576	9999	5762
FRS vs SB	0.988	0.012	84	1
PR vs OSG	0.372	< 0.001	9999	0
PR vs SB	0.169	0.125	1771	221
OSG vs SB	0.919	< 0.001	5456	1

Both exposure and habitat significantly influenced the benthic communities on the surveyed transects (Table 4.3). Pairwise tests between habitat types (taking exposure into account) revealed that hardground transects had benthic communities that were significantly different from fore-reef slope, *Acropora palmata* reef and *Orbicella* spur and groove transects. Stump and boulder benthic communities were not significantly different from hardground communities, however, there were only 10 possible permutations as the stump and boulder habitat type does not occur on the sheltered coast. ANOSIM tests involving small numbers of permutations are unreliable. Both the cluster analysis (Figure 4.2) and MDS (Figure 4.3) techniques suggested that hardground benthic communities did not differ between exposure levels. Hence, it is appropriate to use the 1 way ANOSIM pairwise test for hardground vs stump and boulder (Table 4.2; R = -0.077, p = 0.653). All three analysis techniques used agreed that the benthic communities within hardground and

stump and boulder habitats were not sufficiently different to be considered as separate groups.

Table 4.3 Two way crossed ANOSIM of benthic community data with habitat and wave exposure as groupings. Percent cover data were root transformed and the matrix constructed using Bray Curtis similarities.* SB transects only occurred on the exposed coastline and therefore the results are a 1 way ANOSIM between habitats using data form the exposed coast only. Tests with a low number of permutations (e.g. 10) are unreliable. HG – hardgrounds, SB – stump and boulder, PR – *Acropora palmata* reef, OSG – *Orbicella* spur and groove, FRS – fore reef slope.

Global R	**Significance**	**Permutations**	**Permutations ≥ R**	
Exposure				
0.192	p = 0.011	9999	113	
Habitat				
0.503	p < 0.001	9999	0	
Pairwise Tests	**R Statistic**	**p**	**Permutations**	
			No. run	No. ≥ R
HG vs FRS	0.035	0.008	9999	83
HG vs PR	0.534	< 0.001	9999	0
HG vs OSG	0.647	< 0.001	9999	0
*HG vs SB	0.667	0.1	10	1
FRS vs PR	0.273	0.036	9999	356
FRS vs OSG	- 0.027	0.566	9999	5656
*FRS vs SB	1	0.1	10	1
PR vs OSG	0.551	< 0.001	9999	0
*PR vs SB	0.927	0.001	680	1
*OSG vs SB	0.952	0.001	816	1

Table 4.4 A summary of benthic community dissimilarities for each habitat type investigated. HG – hardgrounds, SB – stump and boulder, PR – *Acropora palmata* reef, OSG – *Orbicella* spur and groove, FRS – fore reef slope.

	Are benthic communities different?			
Habitat Type	Hardground	SB	PR	OSG
Hardground	-			
SB	no	-		
PR	yes	yes	-	
OSG	yes	yes	yes	-
FRS	yes	yes	yes	no

However, stump and boulder transects did have significantly different benthic communities to both *Acropora palmata* reef and *Orbicella* spur and groove habitat types (Table 4.3). It was not possible to reliably test between stump and boulder and fore-reef slope habitats when considering exposure level because of the small number of permutations. Despite this, an examination of the MDS plot (Figure 4.3) and dendrogram (Figure 4.2) revealed large differences between both benthic communities. Fore-reef slope transects were significantly different to *Acropora palmata* reef transects, when exposure was considered (Table 4.3). As before, an examination of Figure 4.2 and Figure 4.3 agreed. The 2 way ANOSIM results also show that *Acropora palmata* reef habitats had significantly different benthic communities to *Orbicella* spur and groove habitats. However, benthic communities within fore-reef slope and *Orbicella* spur and groove habitats did not differ significantly ($R = -0.027$, $p = 0.566$), when exposure level was considered. Both Figure 4.2 and Figure 4.3 plot fore-reef slope transects within Group 1 and often they had more similar benthic communities to *Orbicella* spur and groove transects than to one another.

Table 4.4 summarises benthic community differences between the habitat types. Don Fosters hardground site had very different benthic communities to other hardground sites and therefore it will be considered separately. Fore-reef slope sites were initially selected as sites within *Orbicella* spur and groove habitat but lacked the distinguishing spur and groove formations. However, there is no evidence to suggest that both habitats have different benthic communities. The structural complexity (rugosity) of each is discussed in the

next section and was also similar. Hence, they will be treated together as *Orbicella* reef habitat in subsequent analyses. Benthic communities within *Acropora palmata* reef habitat were very different between exposure regimes. Hence, they will be considered separately and identified as sheltered and exposed *Acropora palmata* reef. Of the hardground sites, Don Fosters had an atypical benthic community. All transects at this site had benthic community assemblages that were more similar to exposed *Acropora palmata* reef habitat than to the other hardgrounds (Figure 4.3). In addition, one of these transects had coral cover as high as 10% which may be a critical point for the creation of net positive carbonate budgets (Perry et al 2013). Hence, it is likely that the area surveyed was too close to the reef proper to be considered representative of hardground habitat in general, but may be representative of the area which marks the transition between coral reef and hardground habitats.

4.4.2 *Rugosity*

Although hardground and stump and boulder sites had indistinguishable benthic communities, the geomorphology of these habitats remained very different (Chapter 2). The single stump and boulder site ranged from 2 – 4 m and had a mean rugosity of 1.40 +/- 0.04. In contrast hardground sites ranged from 5 – 7 m and had a mean rugosity of 1.11 +/- 0.03. The other coral reef habitats had greater structural complexity (Figure 4.4). Mean rugosity was 1.61 +/- 0.06 for *Acropora palmata* reef, 1.82 +/- 0.11 for *Orbicella* spur and groove reef and 1.67 +/- 0.1 for fore-reef slope habitat. Transect structural complexity varied significantly between habitat types ($F = 48.56$, $p < 0.001$, based on reciprocal transformed data). Hochberg multiple pairwise comparisons revealed three significantly different groups (Figure 4.4). Hardground transects were structurally different to all other habitat types. Stump and boulder, *Acropora palmata* reef and fore-reef slope transects did not have significantly different rugosity. However, it should be noted that there were only 3 transects for the stump and boulder habitat type. Finally, the third group was comprised of transects from *Orbicella* spur and groove and fore-reef slope habitat types, as these did not have significantly different rugosity (Figure 4.4). Differences in structural complexity between habitat types aligns well with the differences observed for benthic communities (Table 4.4) and corroborate the

amalgamation of *Orbicella* spur and groove with fore-reef slope habitats to the *Orbicella* reef habitat type.

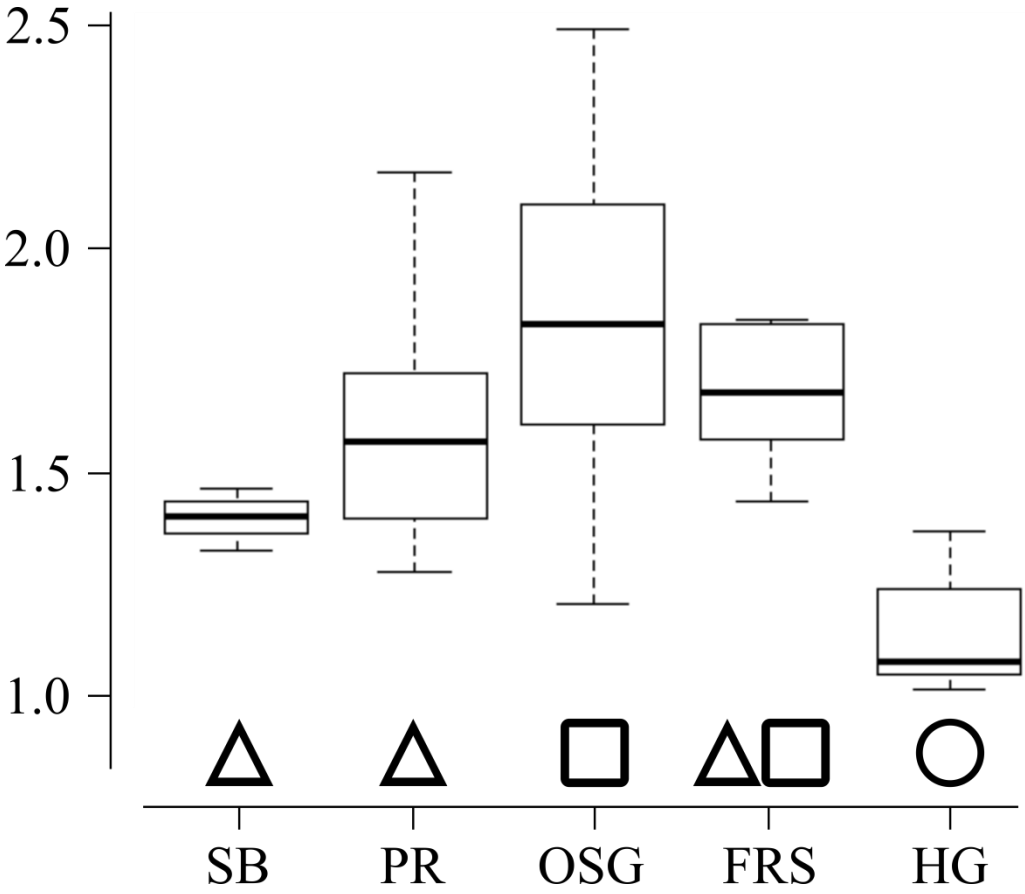

Figure 4.4 Boxplot of median rugosity values recorded within surveyed habitat types. SB = stump and boulder, PR – *Acropora palmata* reef, OSG – *Orbicella* spur and groove, FRS – fore-reef slope, HG – Hardground. Significant differences between habitat types are marked using geometric shapes – circle, triangle and square.

4.4.3 *Benthic community cover*

The percent coral cover (+/- SE) at all coral reef sites varied from 2.81 +/- 2.3 % at Pallas stump and boulder (2 – 4 m) to 22.37 +/- 8.0 % at Boggy Sands (1 – 2 m), a sheltered *Acropora palmata* reef habitat. Mean cover by corals was 13.34 +/- 1.1% for all coral reef sites. At hardground sites coral cover ranged from 1.04 +/- 0.5 % at Armchair to 4.22 +/- 1.9 % at Anchor, with a mean of 2.16 +/- 0.6 %. The site at Don Fosters hardground is not included in the mean for hardgrounds but had live coral cover of 5.66 +/- 1.4%. The coral cover recorded at each site is displayed in Figure 4.5. All of the hardground sites had less coral cover than sites within reef habitats, with the exception of Pallas SB (the stump

and boulder site at Pallas reef). This area is analogous to the lower *palmata* zone of Goreau (1959) and the stump and boulder zone described by Blanchon et al. (1997). Within *Acropora palmata* reef habitat mean coral cover was 12.47 +/- 2.2 % overall, but 10.32 +/- 2.1% at the exposed sites and 16.76 +/- 3.4 % at the two sheltered sites. *Orbicella* reef sites ranged from 11.35 +/- 0.8% at Armchair to 18.45 +/- 1.9% at Spotts. Mean coral cover was 14.92 +/- 0.8 % within *Orbicella* reef habitat.

The percent cover by reef building corals (*Acropora* spp. and *Orbicella* spp.) is presented in Figure 4.6 for each site. The species *A. palmata* was only recorded within stump and boulder and *Acropora palmata* reef habitat, while *A. cervicornis* was only recorded within *Orbicella* reef habitat (Figure 4.6a). Both species were rare. However, *A. palmata* covered 5.2 % of the substrate within the *Acropora palmata* reef habitat at Manse on the south coast and was the most abundant coral species recorded at that site. Total coral cover at this site was 12.1 +/- 0.8 % (Figure 4.5). *A. palmata* was recorded at 3 other sites: Pallas stump and boulder (0.3 %), Boggy Sands (2.4 %) and Bullwinkle (0.5 %). *A. cervicornis* was recorded at 5 sites but did not cover more than 0.35 % of the substrate at any site. Four of the five sites where this species was recorded were on the sheltered west coast.

In contrast, *Orbicella* species (predominantly *O. annularis*) were relatively abundant corals at almost all reef sites (Figure 4.6b). Mean cover for *Orbicella* species was 1.12 +/- 0.3 % and 2.7 +/- 0.9 % within sheltered and exposed *Acropora palmata* reef habitats respectively. Deeper *Orbicella* reef sites supported greater substrate cover by *Orbicella* species, ranging from 1.39% at Armchair to 6.47% at Manse. Mean cover by these corals was 4.45 +/- 0.4 % within *Orbicella* reef habitat. With the exception of the hardground site at Don Fosters (2.1 % cover, Figure 4.6b), *Orbicella* species were not recorded on hardgrounds.

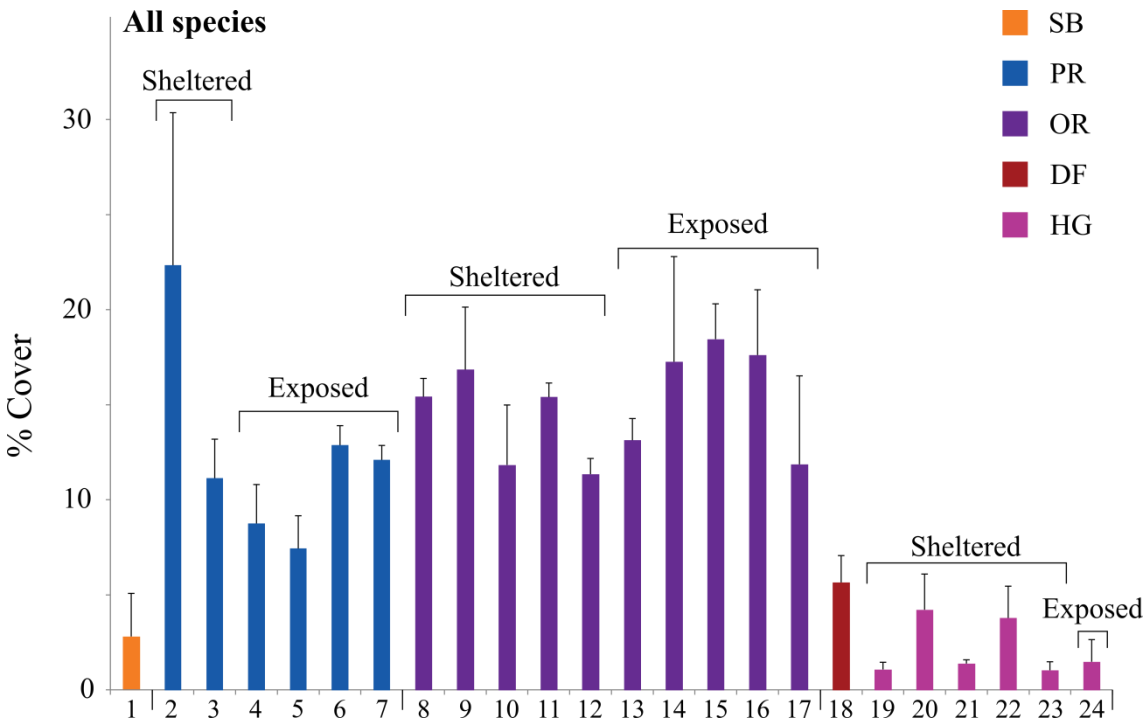

Figure 4.5 Percent coral cover (+ SE) at each site. Colours represent habitat types and exposure regime is indicated for each site. Stump and boulder (SB) site: 1 – Pallas; *Acropora palmata* reef (PR) sites: 2 – Boggy Sands, 3 – Cemetery, 4 – Pallas, 5 – Bullwinkle, 6 – Prospect, 7 – Manse; *Orbicella* reef (OR) sites: 8 – Anchor, 9 – Killer Puffer, 10 – Eden Rock, 11 – Don Fosters, 12 – Armchair, 13 – Pallas, 14 – Prospect, 15 – Spotts, 16 – Manse, 17 – Babylon; Reef/HG transition (DF) site: 18 – Don Fosters; Hardground (HG) sites: 19 – Boggy Sands, 20 – Anchor, 21 – Killer Puffer, 22 – Eden Rock, 23 – Armchair, 24 – Prospect.

Mean substrate cover by *Agaricia* species (Figure 4.7a) was similar to that for *Orbicella* species, in terms of abundance and distribution within habitat types. *Agaricia* corals were recorded at all 17 coral reef sites, two of the six hardground sites and also at the atypical hardground site, Don Fosters. Mean substrate cover by *Agaricia* species was 1.56 +/- 0.2% on sheltered *Acropora palmata* reef, 1.15 +/- 0.3 % on exposed *Acropora palmata* reef and 4.91 +/- 0.5 % on *Orbicella* reef habitat. At the two hardground sites where they were recorded, the substrate cover by *Agaricia* species was minor at Boggy Sands (0.19 %) but higher (1.88 %) at Anchor, accounting for 45 % of all coral cover.

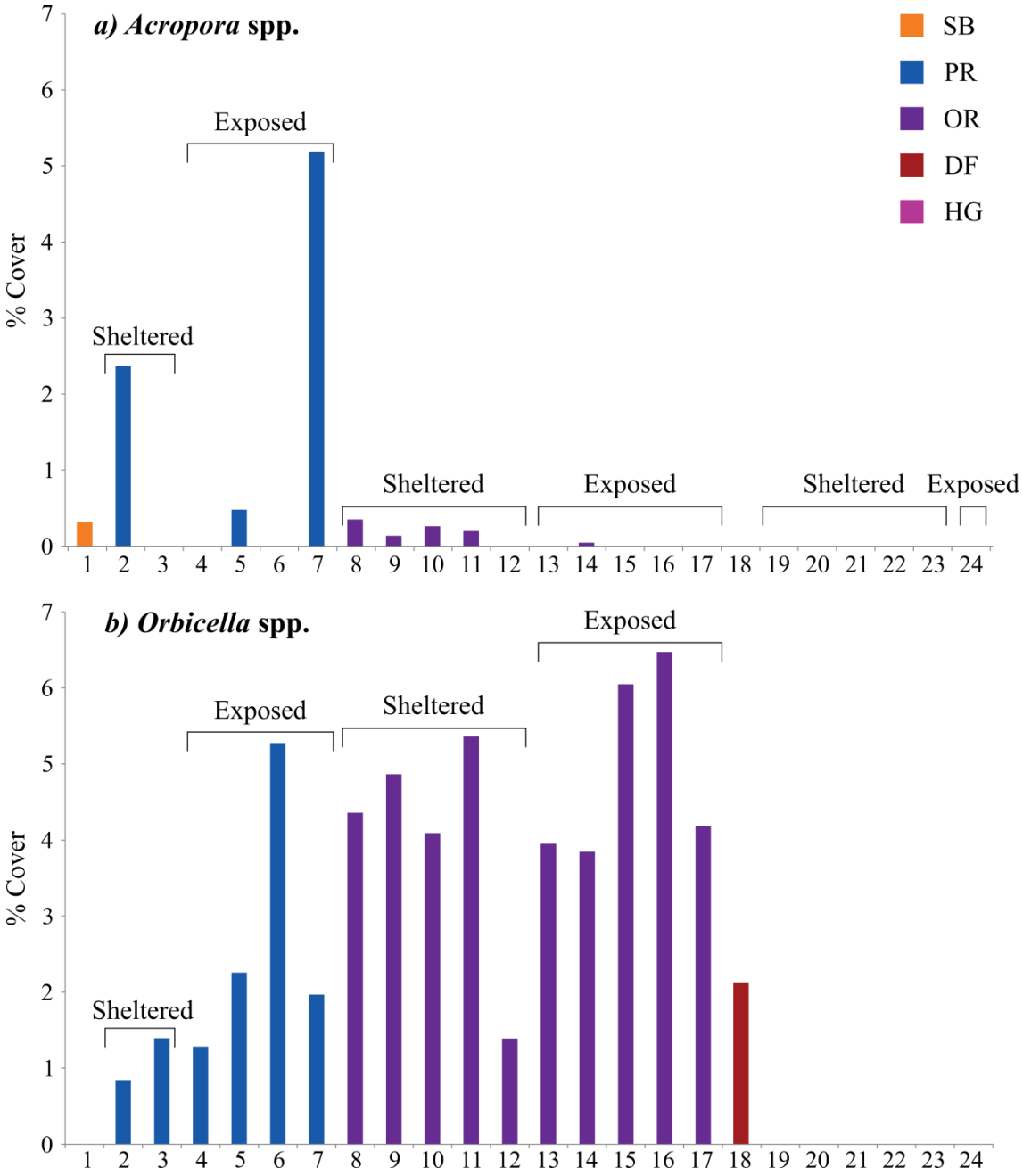

Figure 4.6 Percent cover by reef building coral species on Grand Cayman a) *Acropora* species and b) *Orbicella* species. Colours represent habitat types and exposure regime is indicated for each site. Stump and boulder (SB) site: 1 – Pallas; *Acropora palmata* reef (PR) sites: 2 – Boggy Sands, 3 – Cemetery, 4 – Pallas, 5 – Bullwinkle, 6 – Prospect, 7 – Manse; *Orbicella* reef (OR) sites: 8 – Anchor, 9 – Killer Puffer, 10 – Eden Rock, 11 – Don Fosters, 12 – Armchair, 13 – Pallas, 14 – Prospect, 15 – Spotts, 16 – Manse, 17 – Babylon; Reef/HG transition (DF) site: 18 – Don Fosters; Hardground (HG) sites: 19 – Boggy Sands, 20 – Anchor, 21 – Killer Puffer, 22 – Eden Rock, 23 – Armchair, 24 – Prospect.

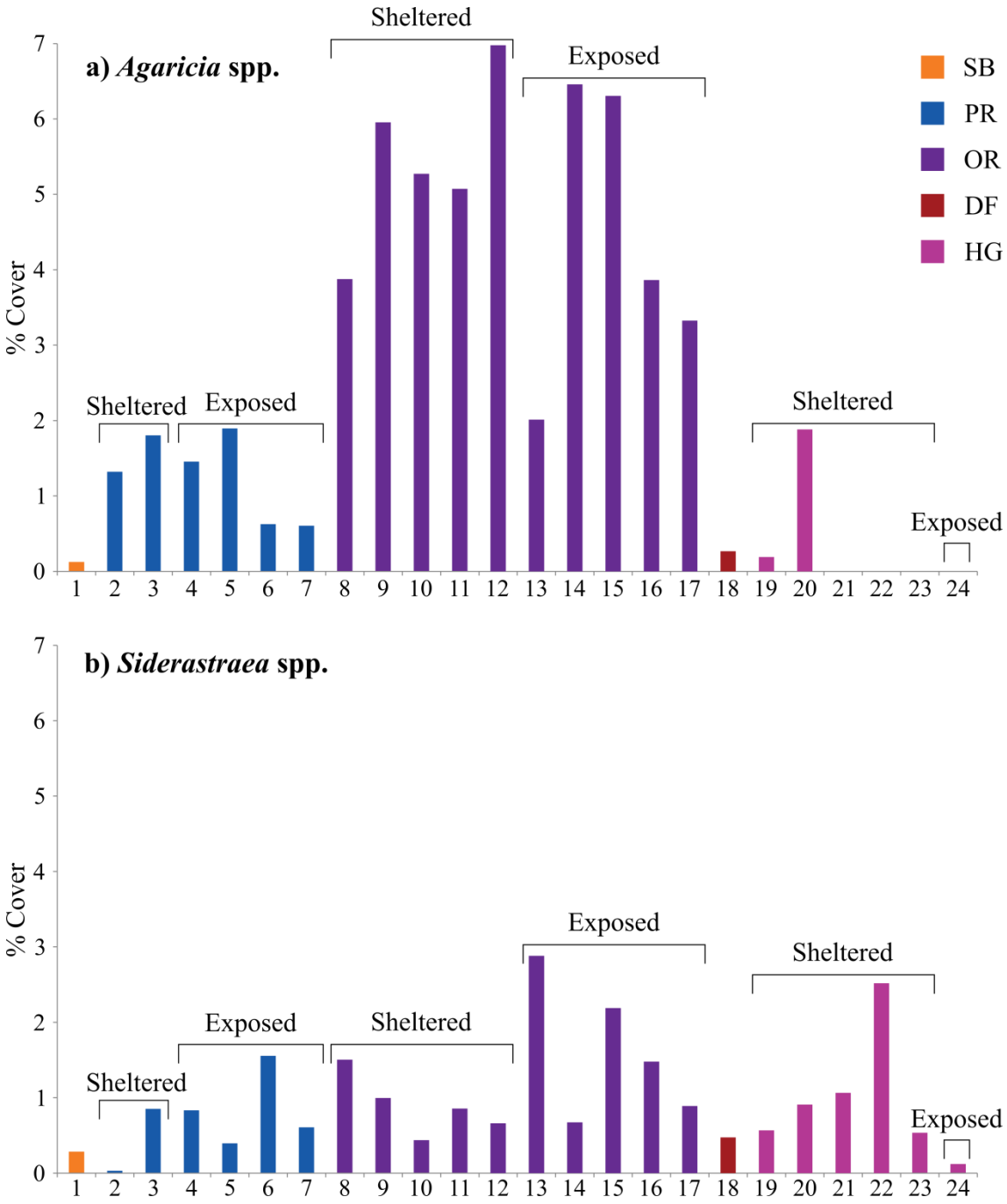

Figure 4.7 Percent cover by two non-reef building coral species at 24 sites on Grand Cayman. Colours represent habitat types and exposure regime is indicated for each site. Stump and boulder (SB) site: 1 – Pallas; *Acropora palmata* reef (PR) sites: 2 – Boggy Sands, 3 – Cemetery, 4 – Pallas, 5 – Bullwinkle, 6 – Prospect, 7 – Manse; *Orbicella* reef (OR) sites: 8 – Anchor, 9 – Killer Puffer, 10 – Eden Rock, 11 – Don Fosters, 12 – Armchair, 13 – Pallas, 14 – Prospect, 15 – Spotts, 16 – Manse, 17 – Babylon; Reef/HG transition (DF) site: 18 – Don Fosters; Hardground (HG) sites: 19 – Boggy Sands, 20 – Anchor, 21 – Killer Puffer, 22 – Eden Rock, 23 – Armchair, 24 – Prospect.

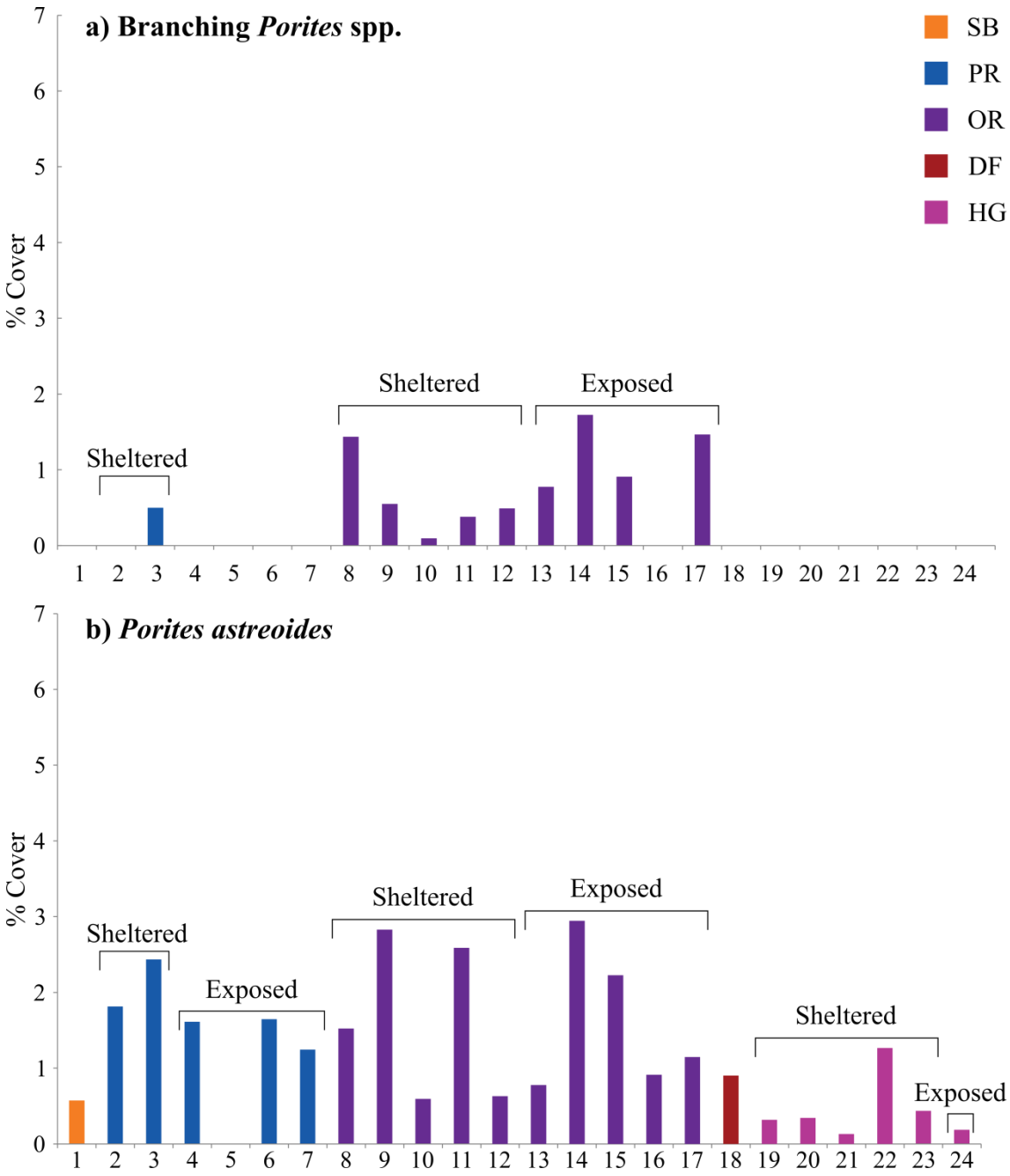

Figure 4.8 Percent cover by *Porites* species at 24 sites on Grand Cayman. Colours represent habitat types and exposure regime is indicated for each site. Stump and boulder (SB) site: 1 – Pallas; *Acropora palmata* reef (PR) sites: 2 – Boggy Sands, 3 – Cemetery, 4 – Pallas, 5 – Bullwinkle, 6 – Prospect, 7 – Manse; *Orbicella* reef (OR) sites: 8 – Anchor, 9 – Killer Puffer, 10 – Eden Rock, 11 – Don Fosters, 12 – Armchair, 13 – Pallas, 14 – Prospect, 15 – Spotts, 16 – Manse, 17 – Babylon; Reef/HG transition (DF) site: 18 – Don Fosters; Hardground (HG) sites: 19 – Boggy Sands, 20 – Anchor, 21 – Killer Puffer, 22 – Eden Rock, 23 – Armchair, 24 – Prospect.

Other relatively abundant corals included *Siderastrea* species and *Porites astreoides* (Figure 4.7 and Figure 4.8). These species were less abundant than *Orbicella* or *Agaricia* species at most sites, but were recorded at more sites. *Porites astreoides* was recorded on more transects than any other coral species (76%) and was absent from only one site (Bullwinkle, an exposed *Acropora palmata* reef). Mean cover by *Porites astreoides* ranged from 0.13 % at Killer Puffer hardground to 2.94 % at Prospect *Orbicella* reef. The mean substrate cover within hardgrounds was 0.45 +/- 0.2 % and 1.62 +/- 0.3 % within *Orbicella* reef habitat. On sheltered and exposed *Acropora palmata* reef, mean cover was 2.12 +/- 0.3% and 1.13 +/- 0.4% respectively (Figure 4.8b). *Siderastrea* species were recorded at every site, but predominantly *Siderastrea siderea* at reef sites. Mean substrate cover ranged from 0.03 +/- 0.03 % at the Boggy Sands *Acropora palmata* reef site to 2.9 +/- 0.9 % at the Pallas *Orbicella* reef site. Hence, they were similarly distributed to both *Porites astreoides* and *Agaricia* species, although *Agaricia* species were generally more abundant (Figure 4.7a).

Other coral species were uncommon and often limited to specific habitats. Branching *Porites* species were relatively abundant in *Orbicella* reef habitat (mean cover = 0.78 +/- 0.2 %), but absent from hardgrounds and the stump and boulder site (Figure 4.8a). Within *Acropora palmata* reef habitat, they were only recorded at Cemetery (0.5% cover, sheltered). *Millepora* species (particularly *Millepora complanata*) were abundant within sheltered *Acropora palmata* reef habitat (mean cover = 9.91 +/- 5.9 %, 2 sites). However, mean substrate cover by *Millepora* species was 0.80, 0.94, 0.12, and 0.19 % within stump and boulder, exposed *Acropora palmata* reef, *Orbicella* reef and hardground habitats respectively.

4.4.4 *Carbonate Production*

The mean carbonate production (G, where 1G = 1 Kg $CaCO_3$ m^{-2} yr^{-1}) calculated for each site is displayed in Figure 4.9 along with the contributions of both corals and calcareous encrusters. Crustose coralline algae were by far the most abundant and often the only recorded calcareous encrusters on the surveyed transects (see Chapter 3). *Orbicella* reef sites often had greater gross carbonate production than shallower reef sites within *Acropora palmata* reef and

stump and boulder habitats. Mean carbonate production within *Orbicella* reef habitat ranged from 1.791 +/- 0.19 G at Armchair to 5.515 +/- 2.48 G at Anchor (Figure 4.9). At shallower coral reef sites carbonate production ranged from a low of 1.609 +/- 0.44 G at the only stump and boulder site to a high of 3.115 +/- 0.45 G at Manse. It is interesting to note that Manse and Anchor are the only sites without dive moorings and therefore they have considerably less scuba diving. Carbonate production was much lower at hardground sites than at any coral reef site, ranging from 0.097 +/- 0.04 G at Boggy Sands to 0.545 +/- 0.19 G at Anchor, with a mean of 0.378 +/- 0.07 G. The transitional zone between hardground and reef at Don Fosters had a mean carbonate production rate of 1.002 +/- 0.20 G. Mean carbonate production within habitat types was highest for *Orbicella* reef (3.544 +/- 0.15 G). Differences in carbonate production between *Orbicella* reef sites on the sheltered (mean = 3.873 G) and exposed (mean = 3.213 G) coasts were not significant ($t = 0.96481$, $p = 0.374$). The mean carbonate production at sites within *Acropora palmata* reef habitat was 2.649 +/- 0.15 G. Despite having very different benthic communities, sheltered and exposed *Acropora palmata* reef habitats had mean carbonate production of almost exactly the same values (2.646 +/- 0.22 and 2.651 +/- 0.17 G respectively). The mean rates of carbonate production for each habitat type are displayed in Table 4.5 .

Contributions of calcareous encruster communities

The percent contributions by calcareous encrusters to total carbonate production varied across sites (3 – 81 %) but tended to be larger at sites on the exposed coast (Figure 4.9). This was mainly due to the higher calcification rates used to calculate gross production on exposed sites, which were measured using settlement tiles and are described in Chapter 3. Table 4.5 describes the % contribution of calcareous encrusters to total carbonate production within habitat types and by exposure regime. It is clear that even at depth (e.g. within *Orbicella* reef habitats) calcareous encruster communities at exposed sites provide two to three times more calcium carbonate to total carbonate production, than their sheltered counterparts.

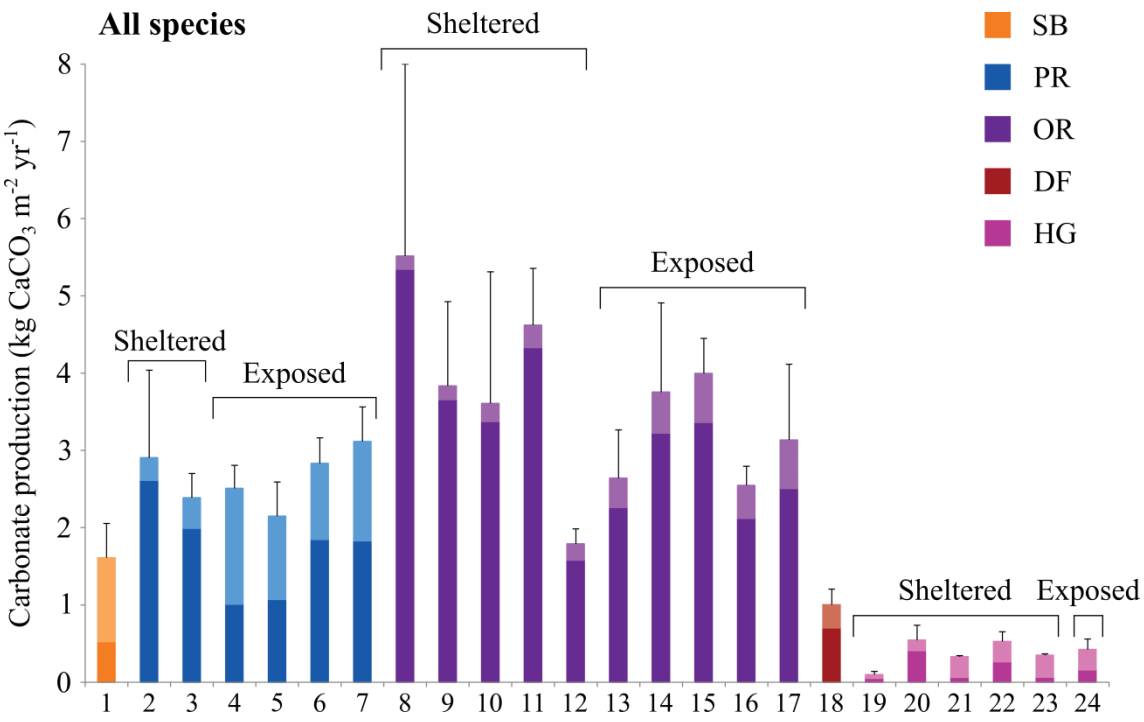

Figure 4.9 Mean (+ SE) gross carbonate production (kg $CaCO_3$ m^{-2} yr^{-1}) by corals (dark shade) and calcareous encrusters (light shade) at 24 sites on Grand Cayman. Colours represent habitat types and exposure regime is indicated for each site. Stump and boulder (SB) site: 1 – Pallas; *Acropora palmata* reef (PR) sites: 2 – Boggy Sands, 3 – Cemetery, 4 – Pallas, 5 – Bullwinkle, 6 – Prospect, 7 – Manse; *Orbicella* reef (OR) sites: 8 – Anchor, 9 – Killer Puffer, 10 – Eden Rock, 11 – Don Fosters, 12 – Armchair, 13 – Pallas, 14 – Prospect, 15 – Spotts, 16 – Manse, 17 – Babylon; Reef/HG transition (DF) site: 18 – Don Fosters; Hardground (HG) sites: 19 – Boggy Sands, 20 – Anchor, 21 – Killer Puffer, 22 – Eden Rock, 23 – Armchair, 24 – Prospect.

On reef sites, corals were usually more important contributors to total carbonate production than calcareous encrusters. However, this was not the case within the stump and boulder habitat surveyed at Pallas, where calcareous encrusters contributed 67.2 % to total carbonate production. Carbonate production by encruster communities, also at Pallas but within *Acropora palmata* reef habitat was also high at 60 % (Figure 4.9). At other *Acropora palmata* reef sites this percentage ranged from 10% at Boggy Sands (a sheltered site) to 50% at Bullwinkle (an exposed site). The contributions to total carbonate production by calcareous encruster communities at *Orbicella* reef sites ranged from 3% at Anchor to 20% at Babylon. Sites within hardground and stump and boulder habitats had similar benthic communities and carbonate production at these sites was often dominated by calcareous encrusters (Figure 4.9). Mean carbonate production by encruster communities was 1.082 G at the Pallas

stump and boulder site, but only 0.527 G by corals at that site. Hence, habitat construction at this coral reef site has become dominated by taxa which shield the existing reef structure from biological and physical erosion, rather than by the structure producing corals, which build more complex habitats. At hardground sites, low coral cover and low calcification rates for encruster communities provided the lowest rates of carbonate production. These sites had low rugosity (Figure 4.4) and were generally flat (Figure 2.9). The highest contribution to carbonate production by calcareous encruster communities was 1.49 G and occurred at the Pallas *Acropora palmata* reef site.

Table 4.5 Mean gross carbonate production (G, kg $CaCO_3$ m^{-2} yr^{-1}) within discrete habitats on Grand Cayman along with the percent contributions from coral and calcareous encruster taxa. Habitat types: HG – hardgrounds, SB – stump and boulder zone, PR Shel – Sheltered *Acropora palmata* reef, PR Exp – Exposed *Acropora palmata* reef, OR – *Orbicella* reef.

Habitat	**Mean G +/- SE**	**no. of transects**	**% Contribution** Coral	CE
SB	1.61 +/- 0.4	3	32.8	67.2
PR Shel	2.65 +/- 0.22	6	86.7	13.3
PR Exp	2.65 +/- 0.17	14	53.6	46.4
OR	3.54 +/- 0.15	36	88.7	11.3
HG	0.38 +/- 0.05	18	42.7	57.3

	Sheltered Sites % Contributions		Exposed Sites % Contributions	
	Corals	CE	Corals	CE
SB	-	-	32.8	67.2
PR	86.7	13.3	53.6	46.4
OSG	93.6	6.4	83.8	16.2
Hardground	43.6	56.4	38.1	61.9

Reef building corals versus non-reef builders

In total, 31 coral species contributed to carbonate framework production within the investigated habitats. *Orbicella annularis* was by far the most important species, contributing 25% to the total quantity of calcium carbonate produced across all transects. The next most important coral species were *Porites porites* (9%), *A. cervicornis* (8%), *Agaricia agaricites* (8%) and *P. astreoides* (5%). Calcareous encrusters were ubiquitous and as a result very important to carbonate production contributing 21% to total carbonate production across all the surveyed transects. This overview of contributions by different taxa is influenced by the number of transects within each habitat type and therefore biased toward taxa from benthic communities within the most surveyed habitat type (*Orbicella* reef, n = 36). Despite this, it is clear that carbonate production on Grand Cayman was almost completely dominated by a small number of coral species and calcareous encruster communities; 85% of carbonate production was due to just seven coral species and the calcareous encrusting community.

Figure 4.10 displays carbonate framework production at each site by reef building taxa (*Acropora* spp. and *Orbicella* spp.). The species *A. palmata* was only recorded within stump and boulder and *Acropora palmata* reef habitats, while *A. cervicornis* was only recorded within *Orbicella* reef habitat. Although live cover by *A. palmata* was low (Figure 4.6a), carbonate production by this species was relatively high at two of the four sites where it did occur – 0.530 G at Boggy Sands and 0.892 G at Manse. Mean carbonate production by *A. palmata* was 0.047 +/- 0.05 G at the Pallas stump and boulder site, 0.265 +/- 0.26 G within sheltered *A. palmata* reef habitat and 0.241 +/- 0.22 within exposed *A. palmata* reef habitat. The high standard errors reflect the rarity of this species. *A. cervicornis* was recorded at half of the *Orbicella* reef sites investigated and carbonate production was high where it did occur (Figure 4.10a). Mean carbonate production by this species was 0.469 +/- 0.20 G within *Orbicella* reef habitat.

Orbicella species were much more wide ranging and occurred at 16 of the 17 coral reef sites, being absent from hardgrounds and the Pallas stump and boulder site. Mean carbonate production by these species was 0.291 +/- 0.04 G

within sheltered *Acropora palmata* reef habitat, 0.576 +/- 0.18 G within exposed *Acropora palmata* reef habitat and 1.138 +/- 0.12 G within *Orbicella* reef habitat. Relative to other taxa, *Orbicella* species provided 31.0% of total carbonate framework production within *Orbicella* reef habitat and together with *A. cervicornis* (12.8%) the reef building taxa provided only 43.8% of carbonate framework production. Within sheltered and exposed *Acropora palmata* reef habitats, reef building taxa provided 21.0% and 31.1% respectively, to total carbonate framework production. At the Pallas stump and boulder site, this figure was just 2.9%.

Carbonate framework production by the important non reef building taxa is presented in Figure 4.11 and Figure 4.12. *Agaricia* species were important carbonate framework producers at all reef sites. Mean carbonate production by these corals was 0.121 +/- 0.01 G and 0.079 +/- 0.02 G at sheltered and exposed *Acropora palmata* reef sites respectively (Figure 4.11a). Within *Orbicella* reef habitat mean carbonate production by *Agaricia* species was much higher at 0.385 +/- 0.04 G and within hardground habitat only 0.02 +/- 0.02 G. Both *Siderastrea* species (Figure 4.11b) and *Porites astreoides* (Figure 4.12b) contributed broadly similar quantities to carbonate framework production. In sheltered and exposed *Acropora palmata* reef habitats mean carbonate production was 0.051 +/- 0.05 G and 0.096 +/- 0.03 G for *Siderastrea* species, but higher for *Porites astreoides*; 0.260 +/- 0.02 G and 0.123 +/- 0.04 G for sheltered and exposed habitats respectively. Mean carbonate production within *Orbicella* reef habitat was 0.174 +/- 0.03 G for *Siderastrea* species and 0.135 G +/- 0.03 G for *Porites astreoides* and therefore much lower than the contributions of *Agaricia* species. On hardgrounds mean carbonate production by both *Porites astreoides* (0.15 G +/- 0.01 G) and *Siderastrea* species (0.019 +/- 0.01 G) was marginally lower than that for *Agaricia* species.

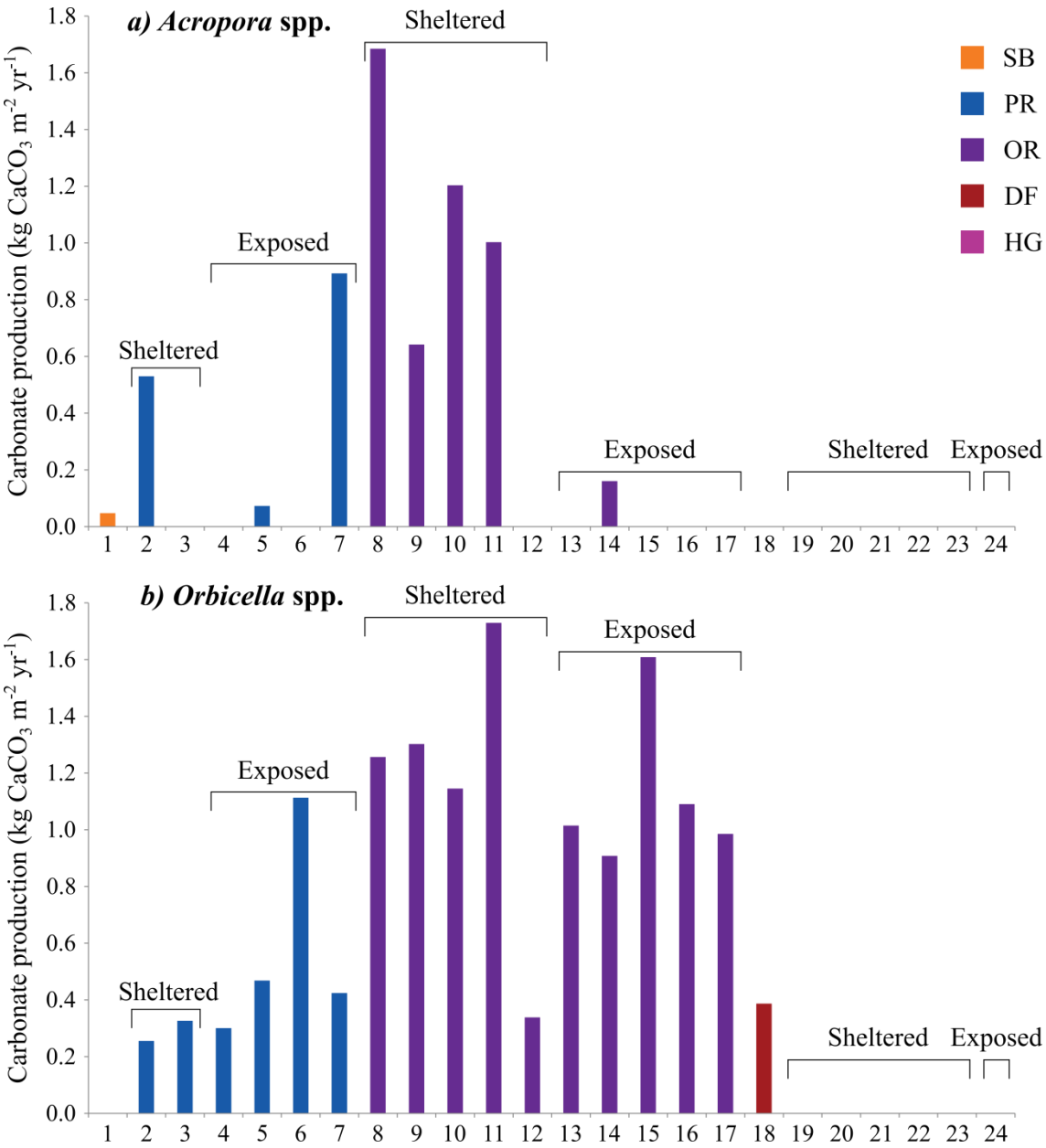

Figure 4.10 Mean calcium carbonate production (kg $CaCO_3$ m^{-2} yr^{-1}) by reef building taxa at 24 sites on Grand Cayman. Colours represent habitat types and exposure regime is indicated for each site. Stump and boulder (SB) site: 1 – Pallas; *Acropora palmata* reef (PR) sites: 2 – Boggy Sands, 3 – Cemetery, 4 – Pallas, 5 – Bullwinkle, 6 – Prospect, 7 – Manse; *Orbicella* reef (OR) sites: 8 – Anchor, 9 – Killer Puffer, 10 – Eden Rock, 11 – Don Fosters, 12 – Armchair, 13 – Pallas, 14 – Prospect, 15 – Spotts, 16 – Manse, 17 – Babylon; Reef/HG transition (DF) site: 18 – Don Fosters; Hardground (HG) sites: 19 – Boggy Sands, 20 – Anchor, 21 – Killer Puffer, 22 – Eden Rock, 23 – Armchair, 24 – Prospect.

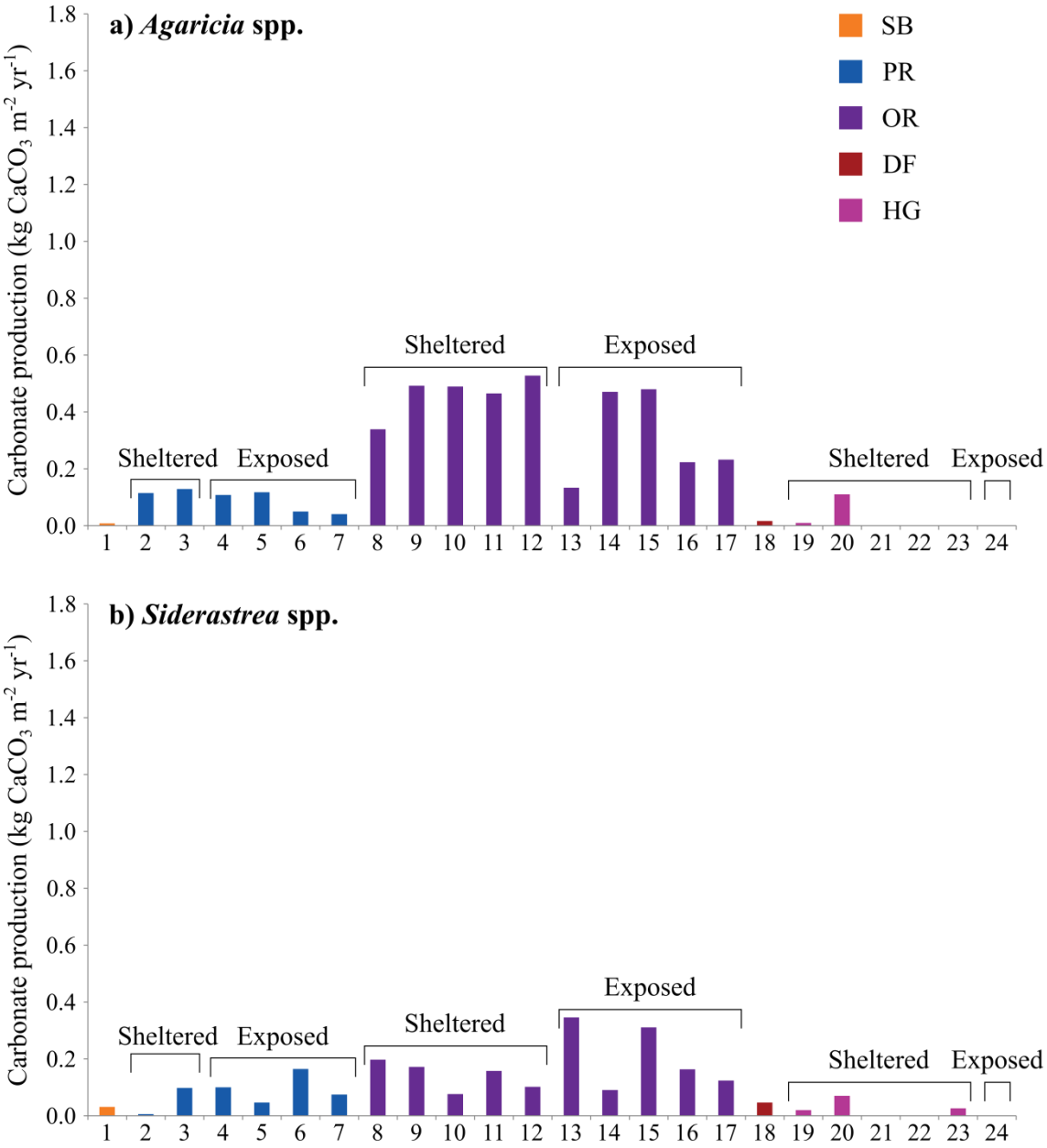

Figure 4.11 Mean calcium carbonate production (kg $CaCO_3$ m^{-2} yr^{-1}) by selected non-reef building corals at 24 sites on Grand Cayman. Colours represent habitat types and exposure regime is indicated for each site. Stump and boulder (SB) site: 1 – Pallas; Acropora palmata reef (PR) sites: 2 – Boggy Sands, 3 – Cemetery, 4 – Pallas, 5 – Bullwinkle, 6 – Prospect, 7 – Manse; Orbicella reef (OR) sites: 8 – Anchor, 9 – Killer Puffer, 10 – Eden Rock, 11 – Don Fosters, 12 – Armchair, 13 – Pallas, 14 – Prospect, 15 – Spotts, 16 – Manse, 17 – Babylon; Reef/HG transition (DF) site: 18 – Don Fosters; Hardground (HG) sites: 19 – Boggy Sands, 20 – Anchor, 21 – Killer Puffer, 22 – Eden Rock, 23 – Armchair, 24 – Prospect.

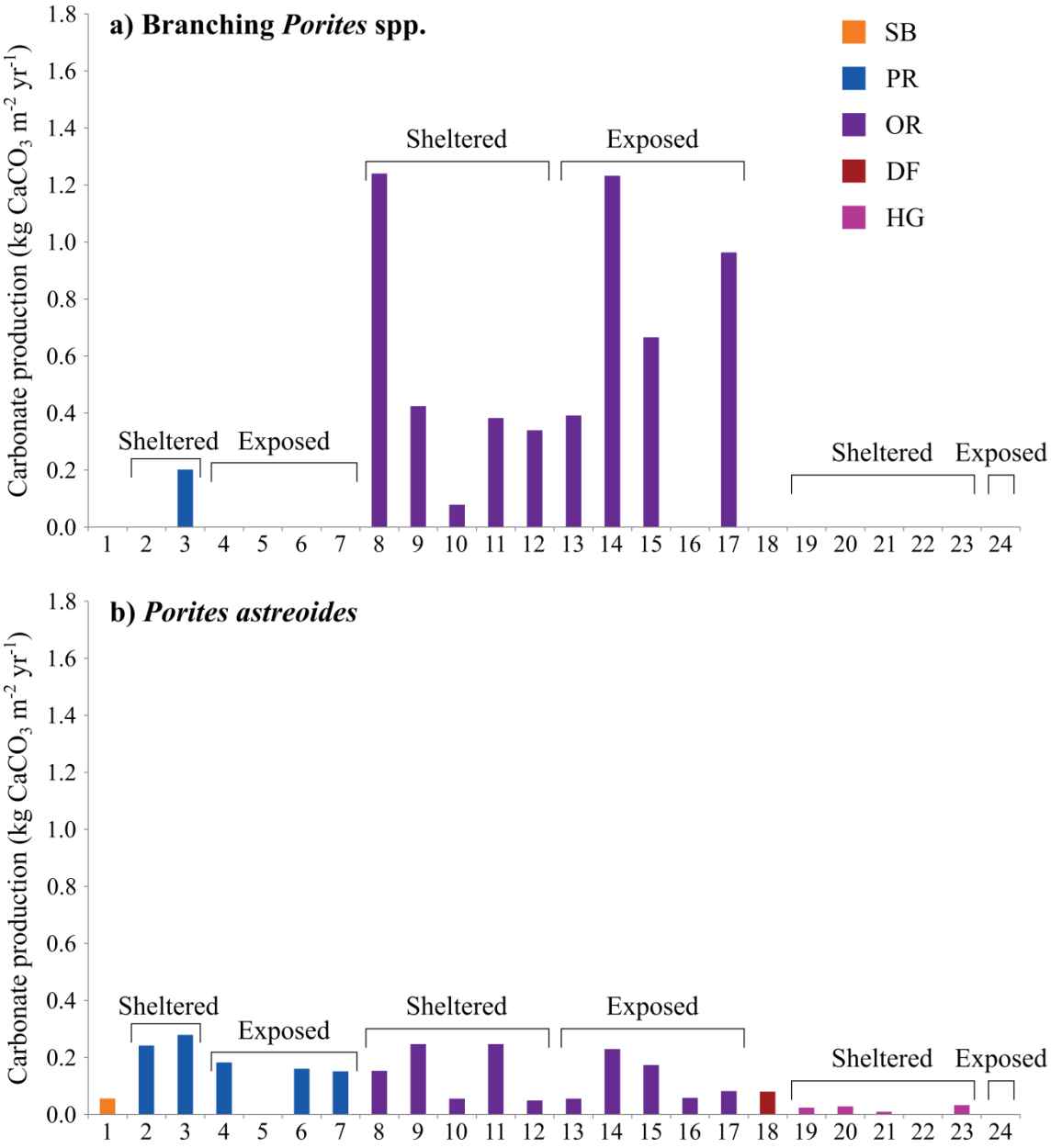

Figure 4.12 Mean calcium carbonate production (kg $CaCO_3$ m^{-2} yr^{-1}) by selected non-reef building corals at 24 sites on Grand Cayman. Colours represent habitat types and exposure regime is indicated for each site. Stump and boulder (SB) site: 1 – Pallas; *Acropora palmata* reef (PR) sites: 2 – Boggy Sands, 3 – Cemetery, 4 – Pallas, 5 – Bullwinkle, 6 – Prospect, 7 – Manse; Orbicella reef (OR) sites: 8 – Anchor, 9 – Killer Puffer, 10 – Eden Rock, 11 – Don Fosters, 12 – Armchair, 13 – Pallas, 14 – Prospect, 15 – Spotts, 16 – Manse, 17 – Babylon; Reef/HG transition (DF) site: 18 – Don Fosters; Hardground (HG) sites: 19 – Boggy Sands, 20 – Anchor, 21 – Killer Puffer, 22 – Eden Rock, 23 – Armchair, 24 – Prospect.

Other important carbonate producing corals included species from structurally complex branching genera – *Porites* and *Millepora*. Mean carbonate production by branching *Porites* spp. ranged from 0.078 G at Eden Rock to 1.240 G at Anchor with a mean of 0.571 +/- 0.14 G within *Orbicella* reef habitat (Figure 4.12a). Outside of *Orbicella* habitat, branching *Porites* spp. were only recorded at one site – Cemetery and here carbonate production was calculated to be 0.202 G. *Millepora* species were present at most sites but carbonate framework production was dominated by *Millepora complanata* (94% of total *Millepora* spp. carbonate production) within *Acropora palmata* reef and stump and boulder habitats and by the encrusting species *Millepora alcicornis* (77%) elsewhere. Mean carbonate production was 1.193 +/- 0.26 G and 0.127 +/- 0.05 G within sheltered and exposed *Acropora palmata* reef habitat respectively. At the Pallas stump and boulder reef site, carbonate production by *Millepora* species was 0.326 G. Within *Orbicella* reef habitat, mean carbonate production by *Millepora* species was only 0.033 +/- 0.01 G.

4.5 Discussion

Calcium carbonate framework production on Grand Cayman reefs (excluding hardground) is relatively low in comparison to other recent investigations in the Caribbean. Mean carbonate production at 17 reef sites on Grand Cayman was 3.1 G but 4.1 G at 75 sites from across the Caribbean (Perry et al. 2015c). However, both these figures are in startling contrast to the gross production calculated for a ‘typical’ sheltered reef in Barbados in the 1970s: 15 G – Stearn et al. (1977). Using regionally averaged coral cover data in the Indo-Pacific, Vecsei (2001) estimated that carbonate framework production within shallow (<10 m) fore-reef habitats, dominated by branching corals, should range between 10 and 17 G. Similarly shallow reefs (<10 m) on Grand Cayman that were formerly dominated by the branching coral *A. palmata* currently have mean framework production rates of just 1.61 G (2 – 4 m) within stump and boulder habitat and 2.65 G within *Acropora palmata* reef habitat (1 – 8 m). Clearly the loss of live coral cover and in particular contributions from branching corals has reduced the ecosystem functions that are provided by framework

production on Grand Cayman reefs. Vecsei (2001) also estimated that carbonate production rates for fore-reef habitats at 10 – 20 m should range between 4.5 and 8.1 G. *Orbicella* reef habitat (8 – 17 m) on Grand Cayman had mean carbonate framework production rates of 3.54 G, a reduction of 21 to 56%. Two very obvious conclusions result from these observations. Firstly, the natural function of carbonate framework production within shallow reef habitats (<8 m on Grand Cayman) has been far more affected by anthropogenic impacts (the ultimate cause of coral cover loss) than deeper reefs (8–15 m on Grand Cayman) and secondly, carbonate framework production is now higher on these deeper reefs, reversing a natural biophysical relationship for these coral reefs. The shelf edge reefs surrounding Grand Cayman were not surveyed and therefore it is not known how much carbonate framework is produced in these environments. However, the depths at which this habitat exists (20–30 m) would reduce the calcification rates for all corals and certainly the calcareous encrusters (Chapter 3), limiting carbonate framework production; the calcification rate of *Orbicella annularis* decreases from 1.48 g cm^{-2} yr^{-1} at 8 - 15 m to 0.38 g cm^{-2} yr^{-1} at 20 - 30 m (published data compiled in Appendix A, *ReefBudget* database).

4.5.1 *Benthic communities, depth, exposure and carbonate framework production*

Natural biophysical relationships structure benthic communities on coral reefs and on Grand Cayman the primary controls are depth and wave energy; both temperature and light attenuation are similar on the coral reefs around this small island. Recent research has suggested that anthropogenic disturbances are superseding these natural structuring forces on many coral reefs (Williams G et al. 2015, Williams S et al. 2015) and this process has been identified as an increasing trend in many marine ecosystems (Polunin 2008). The results described here also provide evidence for this process occurring on Grand Cayman reefs.

The *a priori* selection of habitat types for this study was based on depth, wave energy and geomorphology. Benthic community analysis justified the determination of habitat types in this way, with the exception of stump and

boulder habitat. The benthic community present in this habitat was similar to that present on hardgrounds (Figure 4.3). At 2 – 4 m, these communities are shallower than hardground (3 – 8 m) communities, but the influence of depth was not apparent. Additionally, these communities are subjected to a very different wave energy regime, particularly in comparison to sheltered hardground habitat, but again this was not apparent in the benthic community data. It should be noted that the diversity of non-carbonate producing taxa (e.g. macroalgae and sponges) was not investigated and it may be that habitat distinctive taxa exist which were not considered. However, these species are not important when considering carbonate production and it is the production of calcium carbonate framework (and usually accumulation) that characterises a coral reef.

Hardground habitats have relatively low levels of carbonate framework production but they do not exhibit framework accumulation over time and this is due to natural processes which limit the growth of adult corals (e.g. sediment scour) along with biological and physical erosion which removes any growth. Stump and boulder habitat was significantly more rugose than hardground habitat (Figure 4.4) clearly demonstrating past carbonate framework accumulation. Hence, the similarities between the contemporary carbonate producing benthic communities of hardground and stump and boulder habitats suggest that the environment which allowed the development of a reef producing benthic community has changed. Past disturbances (hurricanes/disease/bleaching) have degraded the stump and boulder habitat, but little or no recovery is underway (Turner et al. 2013). Hence, it may be that chronic anthropogenic disturbance is preventing a recovery and therefore superseding natural community structuring forces.

Acropora palmata reef habitat supported benthic communities that were different between wave exposure regimes. Sites surveyed on the sheltered west coast were also shallower than their exposed south coast counterparts. Hence it is likely that both wave energy and light regimes combine to support distinctive benthic communities in these reef habitats. Exposure to wave energy did not affect benthic communities within *Orbicella* reef habitat. However, the depth of these reefs would limit the influence of wave energy. This habitat had different benthic communities to the reefs within *Acropora palmata* reef and stump and

boulder habitats suggesting that depth is still a natural structuring force on these reefs. Hence, intact biophysical relationships were still apparent at most reef sites.

Despite this, there is evidence to support the hypothesis that anthropogenic disturbance is becoming increasingly important in structuring benthic reef communities on Grand Cayman. *A. palmata* can be identified as a habitat distinctive coral for both stump and boulder and *Acropora palmata* reef habitats (Figure 4.6a, Goreau 1959; Rigby & Roberts 1976), while abundant *Orbicella* species (Figure 4.6b) and *A. cervicornis* (Figure 4.6a) are indicative of *Orbicella* reef habitat (Goreau 1959). Disease, hurricanes and bleaching have probably all combined to reduce the adult populations of *A. palmata* and *A. cervicornis* on Grand Cayman. Ultimately both bleaching and disease outbreaks can be linked to anthropogenic activities (Fabricius 2005, Baker et al. 2008, Sutherland et al. 2010) and are therefore anthropogenically induced sources of disturbance. The last hurricane to directly hit Grand Cayman was Ivan in 2004, although two hurricanes passed close (Gustav – 110 km and Paloma – 80 km) to Grand Cayman in 2008. Hence, the last completely natural major disturbance event was in 2004 and no recovery in coral cover has been evident from Cayman Islands Department of Environment data since about 1997 when the average was 25% (DaCosta-Cottam et al. 2009). Indeed coral cover has been broadly stable since 2006, when it was just 14% (DaCosta-Cottam et al. 2009). Bleaching events have been reported on Grand Cayman reefs in 1983, 1991, 1994, 1998, 2003 and 2005 (Turner et al. 2013) suggesting that coral assemblages on Grand Cayman have experienced a period of relative thermal tolerance since 2005.

Remote reefs which are largely free of localised anthropogenic influences can often recover from major disturbance events relatively quickly. At Ashmore reef in the north of Western Australia live hard coral cover increased from 10% to 29% in four years, after a severe bleaching event in 2005 (Ceccarelli et al. 2011). Remote reefs in the Chagos archipelago experienced severe bleaching in 1998 (>90% mortality), but after eight years live hard coral cover had recovered (Sheppard et al. 2008), although mature populations were not present suggesting that a complete restoration of ecosystem function takes a longer time period. Subsequent surveys in 2015 on these remote reefs

estimated high rates of carbonate production (mean 6.6 G, Perry et al. 2015b) for reefs at approximately 10 m. This would suggest that the function of carbonate production had been restored to these reefs, despite several more minor bleaching events and isolated outbreaks of crown of thorns starfish in the period since 1998 (Sheppard et al. 2008, Perry et al. 2015b). My survey work took place 8 – 10 years after Hurricane Ivan and 7 – 9 years after the last reported bleaching event in 2005. This is likely to have been sufficient time to allow a recovery to take hold or at least become evident, unless an underlying chronic disturbance regime was in place. Without any additional data it is difficult to comment on what this disturbance regime might be. However, it may be different within different habitats and include combinations of natural ecosystem functioning and anthropogenic disturbance. For instance, an allele effect (*sensu* Knowlton 2001) could increase the time over which a recovery by *A. palmata* and *A. cervicornis* would become evident and this process could occur against a background of discrete ephemeral pollution events through subterranean groundwater discharge.

The lack of recovery is not the only evidence implicating the influence of anthropogenic disturbance on the benthic communities of Grand Cayman reefs. Generalist taxa such as *Porites astreoides*, *Siderastrea siderea* and *Agaricia* species are relatively and similarly abundant within all habitat types (Figure 4.7 and Figure 4.8) and often dominate the coral assemblages. This biotic homogenization of disparate habitat types has occurred as populations of habitat distinctive species (*A. palmata*, *A. cervicornis* and *Orbicella* spp.) decline and those of stress tolerant or generalist taxa increase or remain stable. Evidence for this process occurring on the Florida reef tract has been reported by Burman et al. (2012).

4.5.2 *Maintenance and construction of reef framework - functional roles for corals and coralline algae.*

On Grand Cayman differences between the coral assemblages of distinct habitat types still exist, but this does not ensure that the functional roles of past benthic communities remain intact (Alvarez-Filip et al. 2013). Carbonate production on Grand Cayman reefs has been greatly reduced since the 1970s

and therefore the quantity of reef framework construction has also decreased. Additionally, coral assemblages have changed and therefore the character of reef framework constructed and the structural complexity maintained in each habitat type has also changed.

Within *Orbicella* reef habitat, structurally important *Orbicella* species are still relatively common and most carbonate production is due to these species (1.138 G). The complex three dimensional structures constructed by *A. cervicornis* have all but vanished and therefore many of the ecosystem functions associated with it are reduced. However, where this species does occur, carbonate production is high and within *Orbicella* reef habitat *A. cervicornis* contributes (0.469 G). Branching *Porites* corals (mostly *P. porites*) form smaller three dimensional structures and are still commonly observed on these reefs, albeit in low abundances (Figure 4.8). Their contribution to carbonate production was relatively high (0.572 G) and hence they may also provide many of the functions associated with complex reef structures. However, relatively abundant generalist and stress tolerant species (e.g. *Agaricia agaricites*, *Porites astreoides* and *Siderastrea siderea*) produce less calcium carbonate (Figure 4.11, Figure 4.12) and form less complex structures than reef building taxa (Alvarez-Filip et al. 2011a). Hence, it is clear that contemporary *Orbicella* reef habitat on Grand Cayman has subdued rates of habitat construction, which consists of less complex framework than existed in the 1970s. More complex habitats support higher fish biomass (Gratwicke and Speight 2005, Alvarez-Filip et al. 2011b) and therefore it is likely that contemporary *Orbicella* reef habitat can support less fish than it once did. This is independent of fishing regimes, but may have had knock on effects to ecosystem functions dependent on fish diversity and biomass which are likely to have changed synergistically with the available habitat (Alvarez-Filip et al. 2015).

Carbonate production within *Acropora palmata* reef habitat did not significantly vary between exposed and sheltered sites but the coral assemblages did. Hence, the character of framework construction changes with exposure regime. At these sites mean carbonate production was just 2.65 G, which is 16 - 26% of the estimated range in carbonate production made by Vecsei (2001) for shallow reefs (1 – 10 m) dominated by branching corals. Carbonate production was

dominated by corals at sheltered west coast sites but particularly by structurally complex corals – *M. complanata* and to a lesser degree *A. palmata*. On exposed *Acropora palmata* reef habitat carbonate production was dominated by calcareous encruster communities (Figure 4.9) with minor contributions from the complex reef structure building coral *A. palmata*. Hence the construction of new reef framework favoured more complex forms at the sheltered sites. However, rugosity was similar at both sheltered and exposed sites but bioerosion was not significantly different between exposure regimes; this is discussed in Chapter 6. If structurally complex corals dominate carbonate production in a low wave energy habitat, it may be expected that the structural complexity of the habitat would be greater than that for a high wave energy environment which had similar rates of bioerosion and carbonate production, but framework construction dominated by encrusting organisms. This is not the case and it seems likely that a key functional role for coralline algae, which were the dominant carbonate producers in exposed *Acropora palmata* habitat (Figure 4.9), is in the protection of existing reef framework from physical destruction. Calcification rates by encruster communities were much higher on the exposed coast (Chapter 3) and this may help protect the structural complexity of shallow reefs exposed to high wave energies on Grand Cayman.

It has been well reported that certain coral species preferentially recruit to coralline algae (e.g. Morse & Morse 1996; O'Leary et al. 2012) and therefore higher calcification rates by corallines on the south coast may result in larger numbers of coral recruits. Additionally, the sheltered west coast of Grand Cayman is exposed to occasional winter storms coming from the north-west, which may last for several days. This could mean that coral recruits settling on the west coast in autumn are more at risk from damage by storm generated rubble than recruits on the south coast where the reef structure is better protected by coralline algae. Hence, although speculative, it is possible that the recovery potential of shallow exposed reefs may be better than that for shallow sheltered reefs, after a major disturbance event.

4.6 Conclusions

Coral reefs are focal points for the production and accumulation of calcium carbonate within reef systems and highest rates of production are generally in shallower water. On Grand Cayman, a reversal of this natural biophysical relationship has probably occurred for *Acropora palmata* reef and *Orbicella* reef habitats. Currently the focal point for carbonate framework production on Grand Cayman reefs occurs within *Orbicella* reef habitat at approximately 8–15 m. Historically, this focal point would have occurred within shallower reefs (1–8 m) dominated by living *A. palmata* colonies. The consequences of this shift in carbonate framework production to a deeper setting are not clear, but over time (10^2 - 10^3 yrs.) may alter the geomorphology of the entire reef system, particularly on the south coast where shallow reef development is extensive.

Carbonate framework production has been reduced on Grand Cayman reefs and again the consequences of this loss are unclear, but may include reduced reef growth and a reduction in the quantities of calcium carbonate sediment transported to back reef areas and into lagoons. Sediment transport studies are required to help determine the probable outcomes.

Coralline algae are important in maintaining the structural complexity of *Acropora palmata* reef and stump and boulder habitats on the exposed south coast.

Bioerosion by sponge communities on Grand Cayman

5.1 Abstract

Bioerosion is a critical process on coral reefs, influencing reef structural integrity and complexity. Excavating sponges are important bioeroders, especially in the Caribbean where sponges dominate macroborer communities. However, the contribution of bioeroding sponge communities to total bioerosion on coral reefs is not well understood; census surveys are rarely employed by monitoring agencies, and there is little data on the erosion rates of different species. Here, I investigate bioerosion by two Caribbean sponge species with different growth forms (*Siphonodictyon brevitubulatum* — α-form and *Cliona tenuis* — β-form) and describe new approaches to estimating bioerosion by sponge communities. By categorising the growth form of different species, suitable growth form related bioerosion rates are applied to census surveys, along with a previously published rate for *Cliona delitrix* (γ-form), to estimate bioerosion by sponge communities on Grand Cayman reefs. Results indicate distinct habitat preferences for the two most abundant sponge species, *C. tenuis* and *C. caribbaea*. Mean sponge bioerosion across eight sites was 0.1 kg CaCO3 m^{-2} yr^{-1}. Visible cover by α-growth-form excavating sponges caused a disproportionately high level of bioerosion in comparison with cover by β-growth-form species. Therefore, it is important to consider growth forms and excavation strategies when assessing bioerosion by sponge communities. Our present level of understanding of bioerosion by sponge species is limited, and more research is clearly required. However, the approaches described here can generate instant, meaningful results on sponge abundance and bioerosion and would complement many current benthic monitoring regimes. Furthermore, they create a framework for the provision of data, which is relevant to both coral reef management and to developing our understanding of how bioeroding sponge populations influence reef structure and carbonate budgets.

This chapter is based on a previously published journal article (Appendix D).

5.2 Introduction

The biological erosion of hard substrates (bioerosion; sensu Neumann 1966) occurs through the feeding and excavating activities of a range of external grazers, including various parrotfish (Bruggemann et al. 1996) and urchins (Bak 1994), but also both macro- and micro-endolithic taxa (reviewed in Hutchings 2011). On coral reefs, bioerosion is a critical process which can influence reef structural integrity and complexity (Goreau and Hartman 1963, Scott and Risk 1988) while generating significant amounts of sediment (Fütterer 1974). The sediment produced is often important as a contributor to reef framework accretion (Hubbard et al. 1998) and also as a source of reef island sediment (Perry et al. 2015a). Bioerosion is also a key determinant of carbonate budgetary states on coral reefs (*i.e.* the balance between calcium carbonate production and erosion) (Perry et al. 2008, 2014). Rates of bioerosion greatly in excess of carbonate production have been measured at some reef sites, resulting in net negative carbonate budgets (*e.g.* -6.9 kg $CaCO_3$ m^{-2} yr^{-1}; Edinger et al. 2000). Although their contribution to total bioerosion may often be less than external grazers, the endolithic macroboring taxa can be responsible for a significant proportion of bioerosion occurring on coral reefs (*e.g.* up to 1.2 kg $CaCO_3$ m^{-2} yr^{-1}; Tribollet & Golubic 2005). In the Caribbean, most macroboring communities are volumetrically dominated by bioeroding sponges and this is particularly true for fore-reef habitats where sponges commonly contribute to over 90% of substrate removal (MacGeachy and Stearn 1976, Scoffin et al. 1980, Perry 1998).

Despite the importance of sponges to reef bioerosion, species specific erosion rate data are limited (*e.g.* Schönberg 2002) and only a few studies have attempted to investigate the relative contributions of sponge species to total bioerosion on coral reefs (*e.g.* Perry et al. 2014). However, there is a growing consensus that understanding sponge bioerosion is vitally important to the management of coral reef systems – particularly from the perspective of understanding carbonate budget dynamics (Perry et al. 2008). It has been widely reported that reefs affected by nutrient enrichment support larger sponge populations (Rose and Risk 1985, Holmes 2000, Ward-Paige et al. 2005), which inevitably leads to increased sponge bioerosion on reefs affected by agricultural

run-off, sewage or other sources of nutrients. Additionally, ocean acidification is likely to increase the rates at which endolithic sponge species erode (Fang et al. 2013, Wisshak et al. 2014, DeCarlo et al. 2015). Hence, a major concern for the management of coral reefs must be that atmospheric changes which influence ocean pH and temperature, in association with localised anthropogenic influences, will increase bioerosion while simultaneously decreasing the ability of coral reef communities to calcify. Such a scenario would push reefs toward negative carbonate budget states (Perry et al. 2015c), threatening reef growth (Perry et al. 2013) and potentially leading to catastrophic habitat loss (Eakin 2001). Hence, there is an urgent need to better understand how sponge populations contribute to overall bioerosion and how the rates and patterns of bioerosion are changing on coral reefs, while integrating this knowledge into monitoring and management efforts.

Recent attempts to investigate bioerosion by sponge populations have involved methods that relate the percent cover of bioeroding sponge tissue to erosion rates (*e.g.* Perry et al. 2012 for the Caribbean and Calcinai et al. 2011 in the Adriatic). In the Caribbean, this approach correlated the visible presence of bioeroding sponge tissue with a predicted bioerosion rate. Published data on the relationship between the rate of bioerosion by macroborers and the volume of substrate removed (Scoffin et al. 1980, Chazottes et al. 1995, Tribollet and Golubic 2005) were used with data relating the volume of substrate excavated by *Cliona delitrix* (a common Caribbean sponge) to the visible tissue area on the surface of individual coral heads (Rose and Risk 1985). Whilst this approach provided an initial step towards understanding and monitoring population level bioerosion, it is not clear how suitable this relationship is for species other than *Cliona delitrix*. Typically, bioeroding sponges have three growth forms (α, β or γ; Vosmaer 1931) and different species can grow in only one form or change forms as they mature. A species will typically erode either large single cavities (Figure 5.1c) or a series of small interconnected chambers (galleries; Figure 5.1f). In the α-form, only the inhalant and exhalant fistules are visible and most of the tissue is hidden. In the β-form, the sponge encrusts the substratum above excavated galleries or cavities. γ-form sponges become massive, overgrowing the surrounding substratum. It is thus reasonable to hypothesise that the relationship between the area occupied by visible tissue

and the volume of internally eroded substrate is likely to be inherently different for species with different growth forms (α, β or γ) and endolithic chambers (galleries or cavities). However, these relationships are at present poorly understood.

To address this, the relationship between excavated substrate and visible tissue area was investigated for two common Caribbean sponge species, *Cliona tenuis* (Zea and Weil 2003) and *Siphonodictyon brevitubulatum* (Pang 1973). Both species exhibit different growth forms to *C. delitrix*. *S. brevitubulatum* only grows in the α-form and individual sponges excavate a single cavity (Pang 1973), which contains the vast majority of tissue. Water exchange occurs through bright yellow inhalant and exhalant fistules which are the only visible evidence for the sponge's presence within the substratum (Figure 5.1 a-c). *C. tenuis* is a brown, encrusting, β-growth-form sponge (Figure 5.1d-f) which hosts endosymbiotic dinoflagellates (*Symbiodinium* spp.) and prefers shallow windward habitats (Zea and Weil 2003, López-Victoria and Zea 2005). This species excavates tissue galleries within the substratum and the visible area of epilithic tissue corresponds closely to the area of substrate excavated (López-Victoria et al. 2003). The aim here is therefore to expand the potential of using census-based sponge cover data to estimate rates of bioerosion at the growth form/species level, and thus to improve our understanding of the impact of bioeroding sponge populations on coral reef carbonate budgets. These newly developed approaches are then applied to a subset of sheltered and exposed sites around Grand Cayman, to investigate population level bioerosion by sponge species. As the methods were developed during the course of my thesis they could not be applied to all sites.

Null hypothesis 1: Bioerosion by excavating sponge species is not proportional to the visible tissue area covered by those species.

Null hypothesis 2: Individual species contribute uniformly to sponge bioerosion on Grand Cayman coral reefs.

Specific objectives:

1. To measure the volume of substrate eroded by *Siphonodictyon brevitubulatum* in dead coral heads, which are visibly infested with this species.

2. To determine a relationship between the percent cover of visible *S. brevitubulatum* tissue on dead coral heads and the volume eroded.

3. To measure the mean quantity of substrate eroded from beneath colonies of *Cliona tenuis*.

4. To develop a method which predicts bioerosion by *C. tenuis* colonies over a year based on the current colony size.

5. To use the developed methodology to estimate bioerosion by populations of excavating sponge species on selected coral reef sites in Grand Cayman.

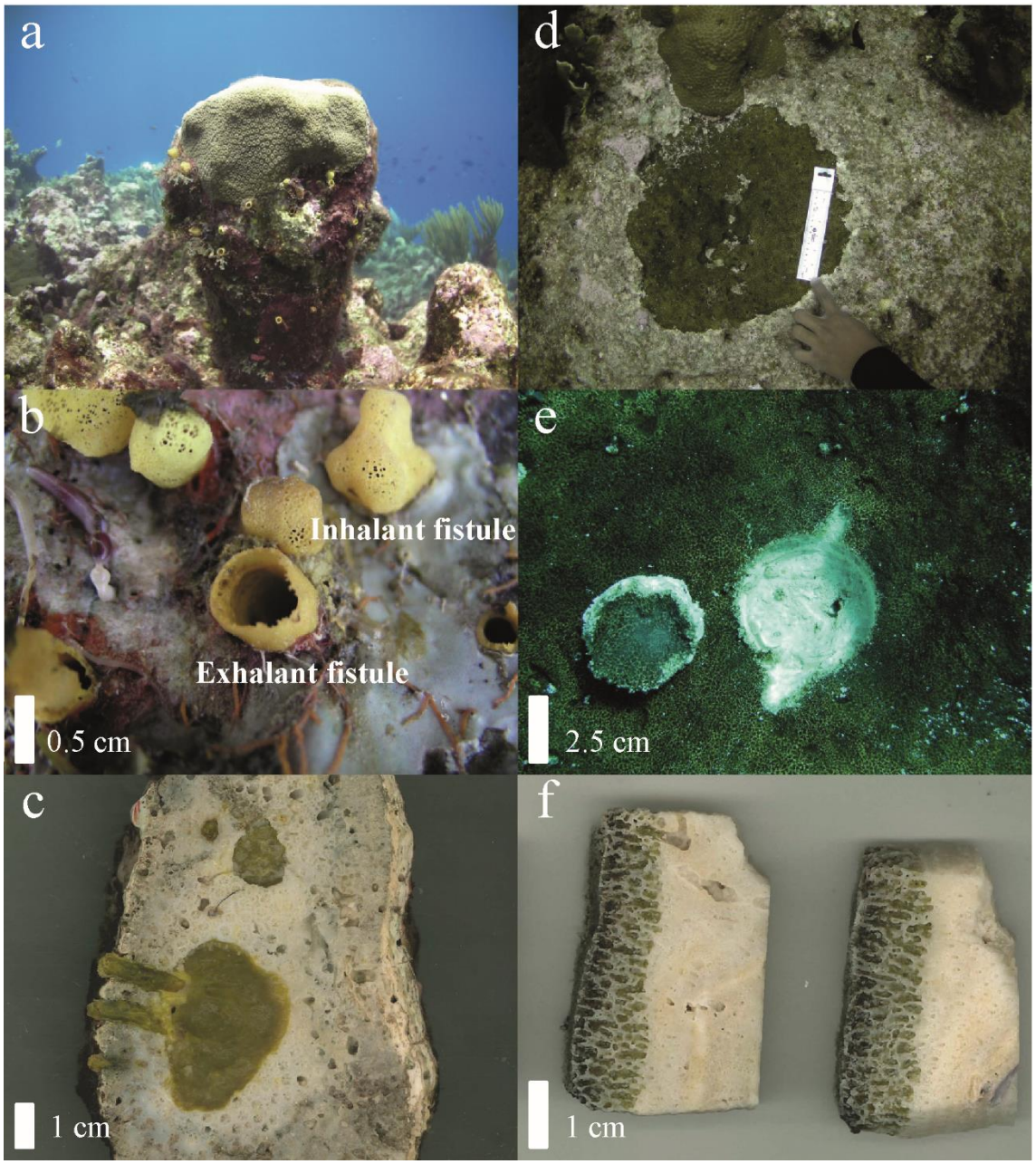

Figure 5.1 Bioeroding sponge images showing visible tissue and endolithic structures. **a** Bright yellow fistules indicating the presence of *Siphonodictyon brevitubulatum* (α-growth-form) below the living portion of an *Orbicella annularis* colony. **b** Close-up of the inhalant and exhalant fistules of *S. brevitubulatum*. **c** Slab cut from an infested coral head illustrating the large cavities generated by *S. brevitubulatum* and fistules which link the colony to the surface. **d** Roughly circular colony of *Cliona tenuis* (β-growth-form). **e** 5 cm core taken from *C. tenuis*. **f** Slabbed core from a *C. tenuis* individual illustrating the green tissue galleries that exist beneath the surface.

5.3 Methodology

Two different methodologies were used to calculate a relationship between visible sponge tissue at the substrate surface and the volume of substrate eroded. The method of Rose and Risk (1985) was adapted for use with *S. brevitubulatum*, whilst the method used for *C. tenuis* was based on an assessment of erosion in slabs cut from short cores of the coral substrate beneath the sponge. Both relationships were then used along with existing published data to estimate total sponge bioerosion at 8 reef sites in Grand Cayman.

5.3.1 *Calculation of a rate of bioerosion for Siphonodictyon brevitubulatum*

Dead *Orbicella annularis* coral heads (n = 25, volume range: 250 – 2800 cm^3) visibly infested with *S. brevitubulatum* were removed from fore-reef spur and groove habitats at depths between 6 and 14 m, on the west and south coasts of Grand Cayman. After removal, the coral heads were kept in seawater prior to an analysis of the number and dimensions of *S. brevitubulatum* fistules. Exhalant fistules had approximately circular oscula and so the maximum dimension was used as a proxy for diameter. Inhalant fistules were irregularly shaped and therefore the maximum lengths and widths were recorded. Height was not recorded for either fistule type. Coral head volumes were estimated using water displacement (Rose and Risk 1985) and the surface area of each (excluding the base) was also measured, by using tissue paper to conform to the coral head shape. After sponge fistule measurements were obtained, coral heads were cut into slabs (mean thickness = 1.53 cm, standard deviation (SD) = 0.35) using a wet saw and returned to freshwater to avoid desiccation. Slabs were then gently washed with water and blotted dry. Each slab was colour scanned at 600 dpi using a Ricoh Aficio MP C4500 multifunctional printer. A portion of *S. brevitubulatum* tissue was taken from each coral head to confirm species identity using spicule morphology (Schönberg and Beuck 2007).

The percent cover of sponge tissue on the scanned images of both sides of each slab was measured by tracing around visible sponge tissue using Image J software (Rasband 2007) along with the Livewire plugin. Sponge tissue volume

within each slab was then calculated by multiplying mean cover by slab volume (mean slab area * slab thickness). Sponge tissue volumes were summed for each coral head and the % volume of sponge tissue within the coral head calculated, using the sum of all slab volumes. In this way the % volume of sponge tissue within each coral head (*i.e.* that substrate removed through sponge erosion) was calculated so that it could be related to the area covered by fistules at the surface. Correlation was checked for significance using simple linear regression in the R statistical environment (R Development Core Team 2011) and the assumptions of linear regression verified using plots of the residuals and a Breusch – Pagan test.

Data generated from previous macroborer studies (Caribbean – Scoffin et al. 1980, Indo-Pacific – Chazottes et al. 1995; Tribollet & Golubic 2005) suggest that there is a strong linear relationship between the rate of bioerosion and the volume of substrate removed by macroborers. Equation 1 (Perry et al. 2012) describes this relationship:

Eq 1: Bioerosion (kg m^{-2} yr^{-1}) = 0.0636 * % substrate volume removed

Here I calculate a relationship between the percent cover of *S. brevitubulatum* fistules on the surface of coral heads and the volume of substrate removed from those coral heads. To calculate the rate of bioerosion (kg $CaCO_3$ m^{-2} yr^{-1}) by *S. brevitubulatum* on coral reefs, this newly developed relationship is substituted into Equation 1 (see 4.4 Results).

5.3.2 *Calculation of a rate of bioerosion for C. tenuis*

The growth and erosional strategies of *C. tenuis* (and other β-form species) are so different to that for α-form species like *S. brevitubulatum*, that a different method for extrapolating a relationship between visible tissue and bioerosion is required. Short 5 cm diameter cores (recovered using a carpenter's brace and hole saw) were used to assess chamber development and depth of substrate erosion by *C. tenuis* (n = 20 cores taken from the centre of individual sponges).

All cores were recovered *in situ*, using SCUBA, at a depth of approximately 5 m on the south coast of Grand Cayman. It was usually not possible to visually determine the underlying coral species and this was not considered during sponge selection. Additional cores were recovered from across the tissue/substrate boundary to investigate the consistency of boring across the sponge and these revealed a rapid transition from the average boring depth to unbored substrate (*pers obs*). Tissue samples taken *in situ* from each individual sponge were frozen upon returning to the lab. Subsequently, six tissue samples were randomly selected to confirm sponge species by spicule analysis (Rützler 1974, Zea and Weil 2003). Each core was left in freshwater overnight and subsequently cut into vertical slabs approximately 1 cm thick (see Figure 5.1f). Slab sides were scanned and investigated as described for *S. brevitubulatum*. The maximum depth of penetration of sponge tissue was recorded for each image and the highest value (1.4 cm) used in assessments of tissue cover. A polygon, 1.4 cm deep, was drawn around the area of each slab image. Lateral slab edges and any damaged or crumbling areas were avoided as tissue retention may have been affected by the coring or sawing processes. Sponge tissue was traced within this polygon and an average % cover was calculated from the cut slabs taken from each core. An overall mean was then calculated. This was assumed to be equivalent to the mean % of substrate eroded beneath *C. tenuis*, down to a standardised depth of 1.4 cm.

To calculate a rate of bioerosion for *C. tenuis*, the growth and boring strategies of gallery-forming sponges need to be considered. These sponges excavate downwards forming tissue filled chambers which connect to an encrusting surface layer (see Figure 5.1d-f). López-Victoria et al. (2003) report that *C. tenuis* and other gallery-forming species do not continue downward excavation once maximum penetration has been achieved and therefore, only lateral expansion was considered in the calculation of a bioerosion rate. The expansion of an individual sponge is typically uniform in all directions (Acker and Risk 1985), but can be limited by competition, predation or substrate morphology; therefore, very large individuals are more likely to have irregular shapes. Field observations at our study sites suggested that most *C. tenuis* were less than 20 cm diameter and broadly circular. These observations concur with previous studies; González-Rivero et al. (2013) report a size class structure

for *C. tenuis* on fore-reefs (5 – 15 m) in Belize which was dominated by small individuals – 46.1% <10 cm^2 (≈ 3.5 cm diameter). Additionally, López-Victoria and Zea (2005) report that most *C. tenuis* individuals were in the 16 – 45 cm size class category on shallow (3 – 6 m) reefs from Isle del Rosario, Columbia. This suggests that *C. tenuis* populations on coral reefs are dominated by small individuals and that the area expanded by gallery-forming sponges can typically be described mathematically using an expanding circle as a model. This approach has been successfully employed by González-Rivero (2012) to model the growth of *C. tenuis* and is also employed here for all gallery-forming species. Published lateral expansion rates of some excavating sponge species are displayed in Table 5.1. These data are from non-manipulated individuals in fore-reef habitats and thus integrate the effects of predation, competition and substrate relief. Species specific expansion rates were used to calculate the area expanded and then combined with a mean substrate density and the mean % of substrate eroded beneath *C. tenuis*. Bioerosion (kg $CaCO_3$ yr^{-1}) was estimated for each individual sponge and then summed for all of the sponges recorded within each transect. Average substrate density on Caribbean coral reefs was taken as 1.7 g cm^{-3} (Perry et al. 2012), based on a meta-data assessment of 22 coral species from 27 separate studies. Equation 2 describes the calculation of bioerosion for an individual gallery-forming excavating sponge:

Eq. 2 Bioerosion = area expanded * % substrate eroded * substrate density

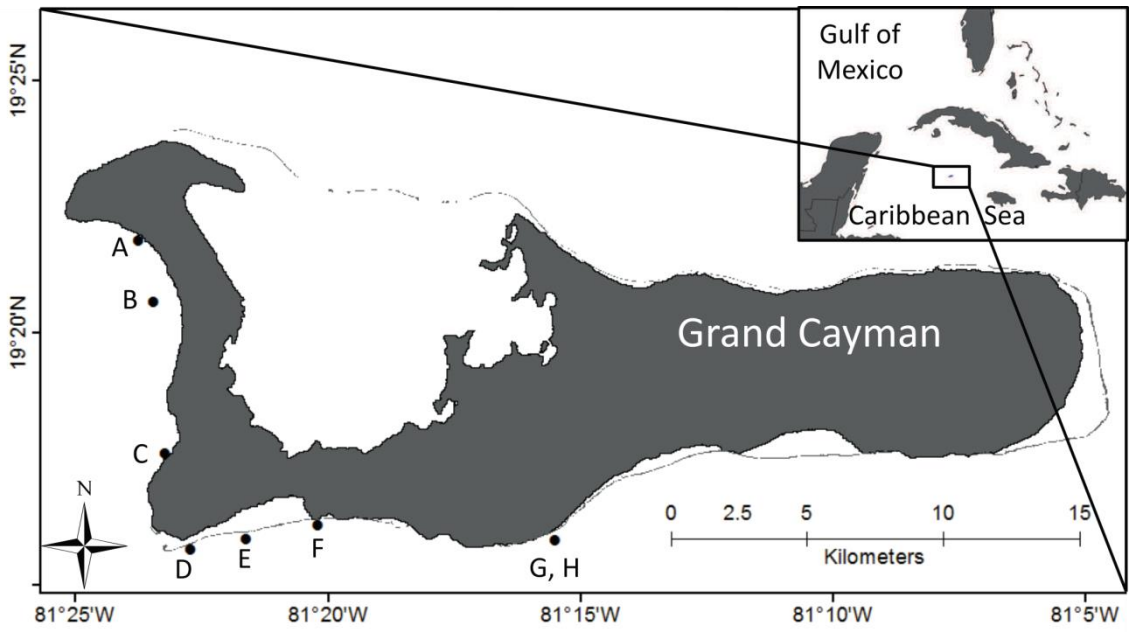

Figure 5.2 Map of Grand Cayman, showing its location in the Caribbean and the surveyed sites; A – Cemetery (~ 2 m), B – Killer Puffer (~ 10 m), C – Eden Rock (~ 9 m), D – Pallas (~ 3 m), E – Bullwinkle (~ 9 m), F – Prospect (~ 15 m), G – Manse PR (~ 6 m) and H – Manse OR (~ 12 m).

5.3.3 *Surveying excavating sponge communities on Grand Cayman coral reefs*

Census surveys were designed so that the abundance of each excavating sponge species would contribute to the total bioerosion estimate. Three 10 m transects were surveyed for bioeroding sponge species at 8 sites (2 – 15 m; Figure 5.2) around Grand Cayman. Most of the sites were located in *Orbicella* reef (OR) habitat, but two were in *Acropora palmata* reef (PR) habitat – Cemetery and Manse PR. Transects were laid perpendicular to shore on adjacent fore-reef spurs. Along each transect a 0.5 m^2 quadrat was alternated between sides of the transect line in a checkerboard fashion, to survey sponge tissue cover. This provided a total planar area of 5 m^2 per transect. While recording data, one of three different approaches was required depending on the species being observed. Despite this, a single observer could complete all three transects for a site within a single dive. The first approach was used for sponge species which excavate tissue galleries (*e.g. C. tenuis*, *C. aprica* etc.) – the areas of individuals within each quadrat were recorded. The second approach was used for *S. brevitubulatum*, a cavity-forming sponge which only exhibits the α-growth-form – fistules within quadrats were individually measured as previously described. Finally, the third approach was used for *C. delitrix*, a cavity-forming sponge which exhibits the α, β and γ growth forms – cover was

measured by estimating the papillar zone (*sensu* Calcinai et al. 2011) *i.e.* the area surrounding fistules and/or tissue from the same sponge. In the field this can sometimes be subjective. Whenever there was a doubt, it was assumed that *C. delitrix* tissue portions within 10 cm of one another belonged to the same sponge, following (Chaves-Fonnegra and Zea 2011). Percent cover by species was determined and used to calculate bioerosion by the cavity-formers; *C. delitrix* – Equation 3, *S. brevitubulatum* – Equation 4 (described in Results). Bioerosion by the gallery-formers was calculated on a per sponge basis using Equation 2.

Eq. 3: Bioerosion (kg m^{-2} yr^{-1}) = 0.0237 * *C. delitrix* % cover (Perry *et al.* 2012)

Table 5.1 Published lateral expansion rates for tissue gallery-forming clionaid sponge species. All data are from non-manipulated sponges in natural settings.

Species (growth form)	**Substrate**	**Lateral advance (cm/yr)**	**References**
Cliona tenuis (β)	Short algal turf (<10mm)	3.4	González-Rivero et al. 2012
	Live coral tissue	4.3	López-Victoria et al. 2006
	Turf algae	2.4	
	Coralline algae	4.4	
Cliona caribbaea (β)	Hardgrounds	4.0	Acker and Risk 1985
	Live coral tissue	5.5	
	Live coral tissue	1.8	López-Victoria et al. 2006
	Macroalgae	0.9	
	Live coral	7.3 (median)	Rützler 2002
Cliona aprica (α, β)	Live coral tissue	1.3	López-Victoria et al. 2006

5.4 Results

5.4.1 *Bioerosion by Siphonodictyon brevitubulatum*

The volume of *S. brevitubulatum* tissue within 25 dead *Orbicella annularis* coral heads, and therefore the quantity of substrate eroded, ranged from 0.79 – 46.88 % (Table 5.2). An additional coral head was so eroded that it collapsed before the sawing process and could not be included in the results, clearly demonstrating the capacity of sponge erosion to weaken coral framework. The volume of substrate eroded from the 25 coral heads was significantly proportional to the percentage of area covered by fistules on the coral heads ($F = 450.6$, $p < 0.001$). The linear regression yielded a high correlation coefficient ($r^2 = 0.95$) indicating a very strong relationship: % volume of substrate eroded = 11.328 * % cover of fistules.

One of the coral heads investigated had over twice the sponge percent cover and tissue volume of any of the other coral heads. This data point greatly influenced the observed relationship above 1.5% fistule cover. However, since the assumptions of linear regression were rigorously tested (including an assessment of whether the relationship changed as the predictor increased – Breusch-Pagan test: $BP = 1.589$, $p > 0.05$) I have confidence in the strength of this relationship. Substituting this relationship into Equation 1 yields Equation 4:

Eq. 4: *S. brevitubulatum* bioerosion (kg m^{-2} yr^{-1}) = 0.721 * % cover of fistules

This equation can thus be used to estimate bioerosion by *S. brevitubulatum* using visual census surveys of the inhalant and exhalant fistules. The relationship is illustrated in Figure 5.3 and is forced through the origin to allow field survey use *i.e.* 0% fistule cover is assumed to equal 0 kg $CaCO_3$ m^{-2} yr^{-1} erosion.

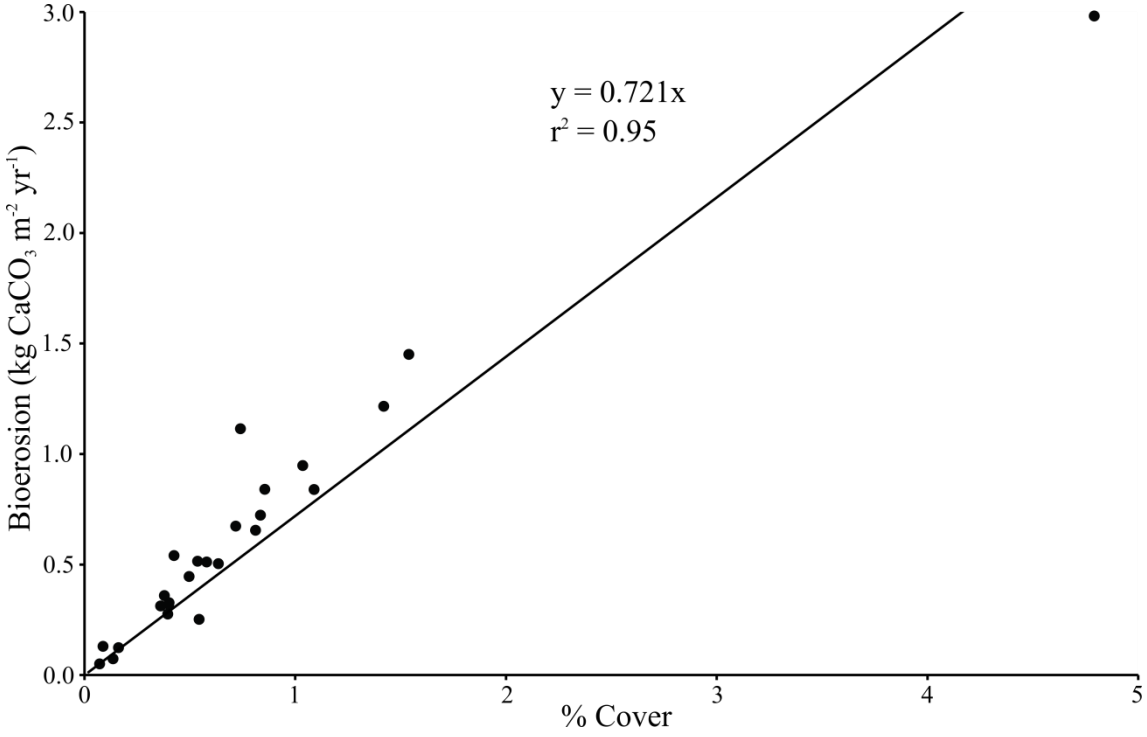

Figure 5.3 Bioerosion by *Siphonodictyon brevitubulatum* relative to the percentage cover of inhalant and exhalant fistules, derived from 25 dead *Orbicella annularis* coral heads.

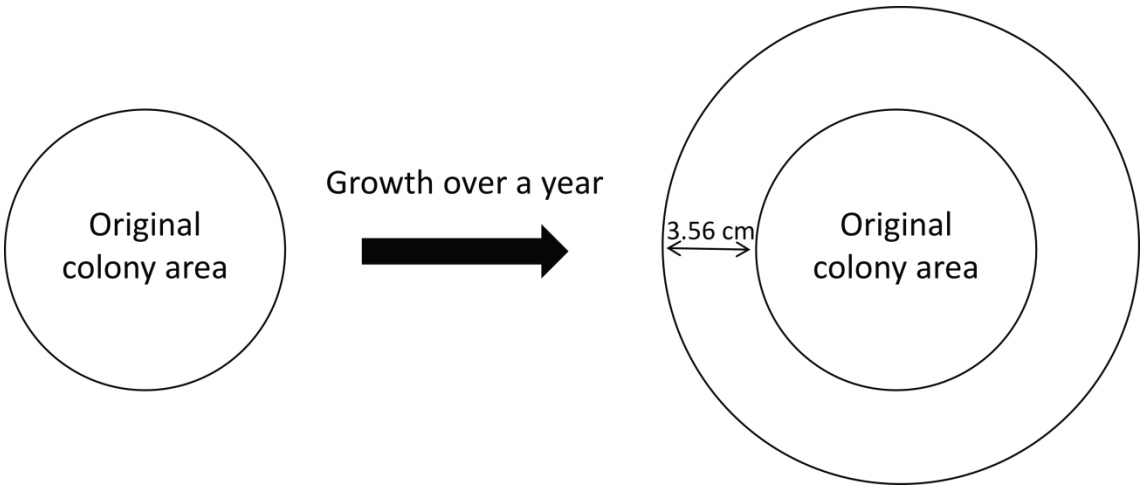

Figure 5.4 A depiction of the circular expansion growth model for *Cliona tenuis*, using an annual lateral expansion rate of 3.56 cm.

Table 5.2 Bioerosion by *Siphonodictyon brevitubulatum* within 25 *Orbicella annularis* coral heads.

Coral Head	Coral head volume (ml)	% Papillae cover	% Volume eroded
1	830	0.58	8.04
2	500	4.79	46.88
3	750	1.42	19.12
4	475	0.16	1.94
5	1450	1.54	22.81
6	250	0.72	10.59
7	1200	0.64	7.92
8	1050	0.09	2.04
9	325	0.43	8.50
10	800	0.40	4.34
11	900	0.07	0.79
12	600	0.36	4.91
13	500	0.14	1.16
14	1300	0.54	8.09
15	875	0.38	5.65
16	550	0.40	5.14
17	850	0.50	7.00
18	1100	0.40	5.02
19	200	0.74	17.52
20	1075	1.09	13.19
21	750	1.04	14.90
22	2800	0.54	3.96
23	1050	0.86	13.21
24	1275	0.84	11.37
25	475	0.81	10.30

5.4.2 *Bioerosion by Cliona tenuis*

The depth of tissue penetration for 20 *C. tenuis* individuals was relatively consistent within individual cores (Figure 5.1f). The maximum depth of penetration ranged from 0.9 to 1.4 cm (Table 5.3) and the mean was 0.98 cm (SD = 0.12). On average 20.56% (16.0% – 28.7%, SD = 3.16) of the substrate beneath *C. tenuis*, down to a depth of 1.4 cm, was excavated and filled with sponge tissue. This mean and the maximum penetration depth are inserted into equation 2 to allow the prediction of the quantity of substrate that will likely be eroded by an individual *C. tenuis* sponge over a year. Assuming a circular expansion model (Figure 5.4), the area expanded by any sponge over a year can be calculated using the lateral expansion rates presented in Table 5.1. Here I use a mean lateral expansion rate of 3.56 cm yr^{-1}, based on data from two studies (López-Victoria et al. 2006, González-Rivero et al. 2012). As an example, I calculate the area that a 10 cm^2 sponge (radius = 1.784 cm) would expand into over the course of a year and then bioerosion (kg $CaCO_3$ yr^{-1}) can be calculated using equation 2:

Bioerosion by a 10 cm^2 *C. tenuis* individual over 1 year

= area expanded * (20.56% * 1.4 cm) * 1.7 g cm^{-3}

= (new area – original area) * 0.489 g cm^{-2}

= $((\pi*(3.56+1.784)^2) – 10\ cm^2) * 0.489$ g cm^{-2}

= 39 g $CaCO_3$ yr^{-1}

= 0.039 kg $CaCO_3$ yr^{-1}

Table 5.3 The maximum depth of tissue penetration for *Cliona tenuis* sponges along with estimates of the substrate eroded beneath each sponge, to a depth of 1.4 cm.

Core no.	Max tissue penetration (cm)	Mean % Excavated
1	1.00	21.12
2	1.15	19.06
3	1.19	20.28
4	1.23	22.00
5	1.02	21.12
6	1.00	19.85
7	1.14	22.15
8	1.40	28.70
9	1.08	22.20
10	1.09	26.60
11	0.95	21.27
12	0.91	20.29
13	1.24	17.20
14	1.19	19.30
15	1.09	16.29
16	1.03	23.03
17	1.04	17.88
18	0.94	15.99
19	0.90	17.63
20	1.10	19.24

5.4.3 *Bioerosion by sponge populations on Grand Cayman coral reefs*

A total of six excavating sponge species were observed across all of the investigated sites – *S. brevitubulatum*, *C. delitrix*, *C. aprica*, *C. tenuis*, *C. caribbaea* and *C. varians*. *C. varians* was the rarest, with only four individuals observed during all surveys and these were found at just two sites. While *C. delitrix* and *C. tenuis* were ubiquitous, the remaining three species were only absent from surveys on Cemetery Reef which was very shallow (~ 2 m). Benthic cover by the six observed excavating sponge species was low at all sites and ranged from 0.26% at Manse OR (~ 12 m) to 2.56% at Pallas (~ 3 m), with a mean substrate cover (+/- SE) across all sites of 1.24 +/- 0.3%. *C. tenuis* was the most abundant species at the four shallowest sites; Cemetery, Pallas, Manse PR and Bullwinkle (Table 5.4). On deeper reefs both *C. caribbaea* and *C. aprica* tended to be more common and each became the dominant species at two sites. The cavity-forming sponges contributed very little to the visible cover by excavating sponges at all sites and this was particularly true of *S. brevitubulatum*, which did not cover greater than 0.015% of the substrate at any site (Table 5.4).

A similar trend to that observed for excavating sponge cover was observed for bioerosion at each site with *C. tenuis* being the dominant bioeroder at the four shallowest sites (Table 5.4). Eden Rock was marginally deeper than Bullwinkle and at this site *C. caribbaea* was the most important excavating sponge, followed closely be *C. aprica* and then *C. tenuis*. At Killer Puffer, *C. caribbaea* was again the most important excavating sponge. *C. aprica* contributed most to sponge bioerosion at the two deepest sites, but also had the least variable bioerosion rates of any species, ranging from 0.016 to 0.035 kg $CaCO_3$ m^{-2} yr^{-1} across all sites where it was observed (Table 5.4). *C. delitrix* and *S. brevitubulatum* contributed little to total sponge bioerosion at most sites; however, *S. brevitubulatum* was the second biggest contributor to bioerosion at Prospect making up 31% of the total (Table 5.4). The percent cover by *S. brevitubulatum* at this site was 12 times lower than that of *C. caribbaea*, the next biggest contributor to bioerosion at Prospect. This shows that the visible cover by excavating sponges is not always indicative of bioerosion when comparing cavity and gallery-forming species.

Table 5.4 The percentage cover and bioerosion by 6 species of excavating sponge recorded at 8 reef sites on the south and west coasts of Grand Cayman. Dashes indicate a species was not recorded.

	Cliona aprica	***Cliona caribbaea***	***Cliona tenuis***	***Cliona varians***	***Cliona delitrix***	***Siphonodictyon brevitubulatum***
% Cover						
Cemetery	-	-	0.250	0.038	0.033	-
Pallas	0.172	0.001	2.242	-	0.144	0.003
Manse PR	0.162	0.020	1.220	-	0.028	0.009
Bullwinkle	0.088	0.117	2.116	0.016	0.016	0.010
Eden Rock	0.446	0.328	0.138	-	0.016	0.005
Killer Puffer	0.465	0.824	0.149	-	0.238	0.005
Manse OR	0.160	0.028	0.049	-	0.018	0.009
Prospect	0.137	0.187	0.015	-	0.009	0.015
Bioerosion (kg $CaCO_3$ m^{-2} yr^{-1})						
Cemetery	-	-	0.030	0.005	0.001	-
Pallas	0.028	0.002	0.113	-	0.005	0.003
Manse PR	0.027	0.003	0.047	-	0.001	0.011
Bullwinkle	0.016	0.009	0.132	0.004	0.001	0.011
Eden Rock	0.035	0.043	0.019	-	0.001	0.008
Killer Puffer	0.020	0.081	0.023	-	0.011	0.007
Manse OR	0.025	0.007	0.005	-	0.001	0.008
Prospect	0.024	0.013	0.006	-	0.0003	0.019

The relative contributions to substrate cover and bioerosion by cavity-formers (*C. delitrix* and *S. brevitubulatum*) and gallery-formers (*C. aprica*, *C. caribbaea*, *C. tenuis* and *C. varians*) are presented in Figure 5.5. Bioeroding sponge cover was dominated by the gallery-formers and these species did not contribute less than 86% to the total at any site (Figure 5.5a). Bioerosion by the gallery-formers was also much higher than that estimated for the cavity-formers at all sites. However, there was an obvious decrease in the contributions of gallery-formers to total bioerosion with depth (Figure 5.5b). At Prospect (~ 15 m) the cavity-forming sponges contributed just 5% to the total substrate cover by bioeroding sponges but 31% of total estimated bioerosion.

Total sponge bioerosion varied considerably between sites and ranged from 0.036 to 0.172 kg $CaCO_3$ m^{-2} yr^{-1} (Figure 5.6). Mean sponge bioerosion (+/- SE) was 0.100 +/- 0.020 kg CaCO3 m^{-2} yr^{-1}. In general higher bioerosion was found on sites with higher excavating sponge cover, however, the order of sites from highest to lowest was not mirrored by sponge cover. Bullwinkle had the most bioerosion of any site, but did not have the highest percent cover of excavating sponges. Similarly, Cemetery had the lowest bioerosion of any site but Manse OR had the lowest excavating sponge cover.

In addition to illustrating total bioerosion, Figure 5.6 also compares bioerosion by the gallery-forming sponges to that which would have been measured using the original method of Perry et al. (2012). Across all sites bioerosion by the gallery-formers was consistently higher (1.7 – 5 times) when estimated using the methodology presented here. The largest differences were observed on sites where total bioerosion was low – Cemetery, Manse OR and Prospect. A similar comparison between the methods for cavity-forming sponges could not be made because of differences in how data needed to be collected for *S. brevitubulatum*.

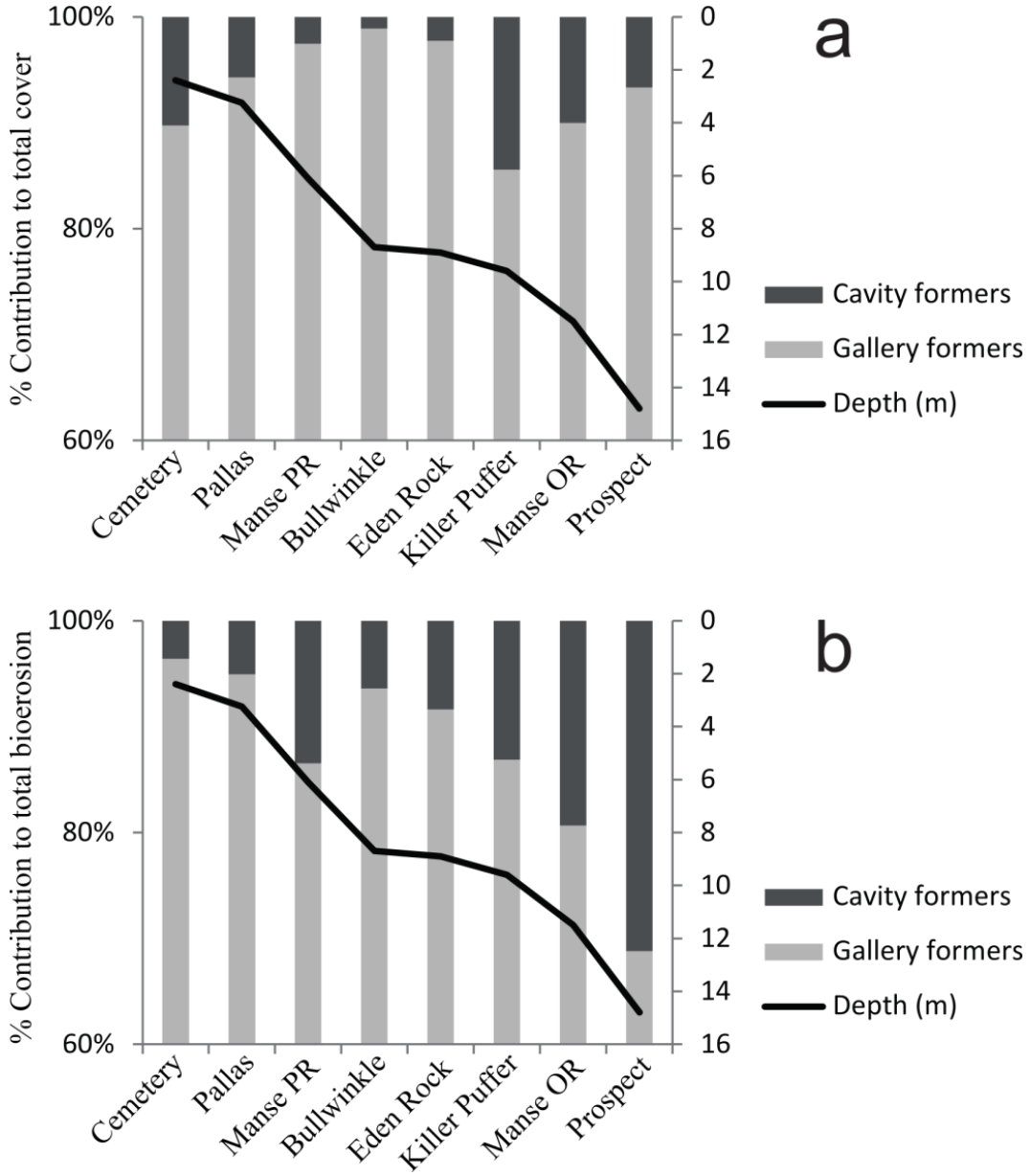

Figure 5.5 Contributions of cavity- (*Siphonodictyon brevitubulatum* and *Cliona delitrix*) and gallery- (*C. aprica, C. caribbaea, C. tenuis* and *C. varians*) forming species to **a** the total percentage cover of the substrate and **b** total bioerosion, by excavating sponges at 8 reef sites around Grand Cayman.

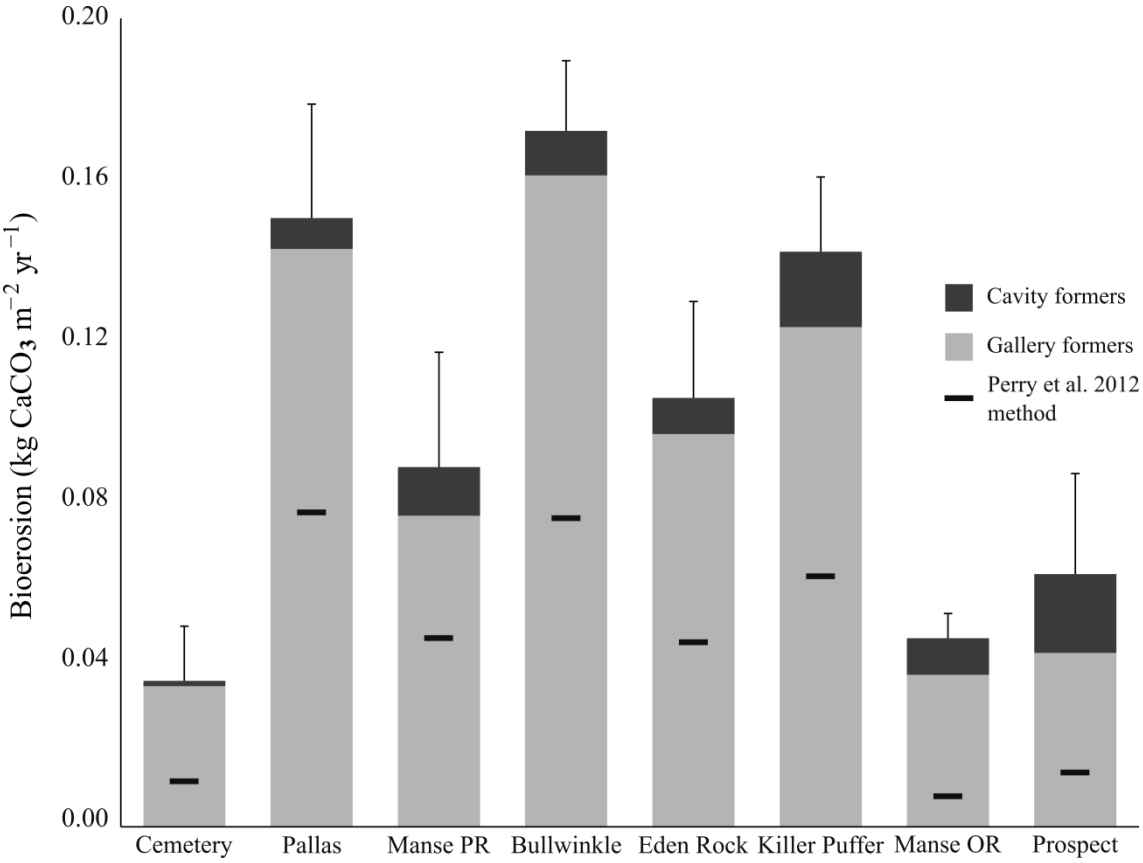

Figure 5.6 Bioerosion (kg $CaCO_3$ m^{-2} yr^{-1}) by sponge populations on Grand Cayman reefs. Each column refers to the mean total bioerosion at each reef site. Site means are reported plus their standard errors. Dark grey portions reflect the contribution of cavity-forming sponges (*Cliona. delitrix* and *Siphonodictyon brevitubulatum*) to the total and light grey portions reflect the contribution of the gallery-forming sponges (e.g. *C. tenuis*). Black bars represent the contribution of gallery-forming sponges that would have been measured using the method of Perry et al. (2012). Differences in data collection methods prevented a similar comparison for the cavity-formers.

5.5 Discussion

Here I have determined bioerosion rates for two excavating sponge species (*C. tenuis* and *S. brevitubulatum*) and developed new approaches to sponge census surveys which cater for species specific growth-forms and differences in the mode of substrate excavation. In combination with the approach developed for *C. delitrix* (Perry et al. 2012), this allows the presentation of an improved methodology for monitoring sponge erosion on Caribbean coral reefs. The approach developed for *C. tenuis* estimated bioerosion at 0.489 g $CaCO_3$ cm^{-2} of tissue and compares favourably with previous estimates for other β-form sponges which excavate tissue galleries *e.g. C. caribbaea* in Belize – 0.39 g CaCO3 cm^{-2} of tissue (Rützler 2002). However, it should be noted that this author considered *Cliona aprica* and the then undescribed *C. tenuis* (Zea and Weil 2003) as morphological variations of *C. caribbaea* (Rützler 2002, Zea and Weil 2003). Acker and Risk (1985) reported that 20% of the substrate was eroded down to 1 cm beneath *C. caribbaea* individuals (a lighter coloured variant of *C. caribbaea* was also described, which was probably *C. tenuis*) from the west coast of Grand Cayman and this figure compares well with that estimated here for *C. tenuis* (20.56% down to 1.4 cm). Despite differences in methodologies, locations and species investigated, the three studies present broadly comparable figures and provide confidence in the data generated here for *C. tenuis*.

To estimate total sponge bioerosion on Grand Cayman reefs, it was assumed that bioerosion beneath *C. tenuis* was broadly equivalent to that for other Caribbean gallery-forming species and that any differences in the rate of bioerosion could be explained by species specific expansion rates. This assumption is necessary, because of the lack of data available for other Caribbean species, but there is some evidence to support it. Both Rützler (2002) and Acker and Risk (1985) found similar erosion beneath *C. caribbaea* to that which we report for *C. tenuis*. Additionally, the maximum and mean depths of penetration of sponge tissue into the substratum are also broadly similar for gallery-forming species: *C. tenuis* max = 1.4 cm, mean = 0.96 cm – this study; *C. caribbaea* (and probably *C. tenuis*) max = 1.4 cm, mean = 0.9 cm – Acker and Risk (1985); *C. tenuis*, *C. caribbaea* and *C. aprica* max = 1.5 cm –

López-Victoria *et al.* (2003); *C. orientalis* mean = 1.3 cm – Schönberg (2001). It may be that the depth to which tissue can penetrate the substratum and the quantity of substrate eroded by gallery-forming excavating sponges is relatively uniform across species. However, Calcinai et al. (2007) recorded a maximum depth of penetration of 2 cm for *C. albimarginata* in coral blocks and it may be that some Indo-Pacific species bore further into the substrate.

Nevertheless, this assumption can be assessed further by comparing the results of studies which measured bioerosion by other gallery-forming species to that which would be estimated using the approach developed here. Schönberg (2002) investigated bioerosion by *C. orientalis*, a Pacific bioeroding sponge which has similar growth (β) and excavation strategies (tissue galleries) to *C. tenuis*. After exposure to small disks (3.5 cm diameter) containing *C. orientalis*, blocks cut from different coral species were eroded at rates ranging from 3.4 – 10.3 kg $CaCO_3$ m^{-2} of tissue yr^{-1}. The large range was related to coral density with more dense coral substrates having greater erosion – *Porites* blocks (density approx. 1.6 g cm^{-3}) were eroded at a rate of 9.7 kg $CaCO_3$ m^{-2} of tissue yr^{-1}. Other studies have also found that density is an important environmental factor for sponge bioerosion (*e.g.* Calcinai et al. 2007). Using the method proposed here, a hypothetical *C. tenuis* sponge of 3.5 cm diameter would generate an erosion rate of 4.4 kg $CaCO_3$ m^{-2} of tissue yr^{-1} (based on the final area of the sponge), using an expansion rate of 3.56 cm (Table 5.1) and a substrate density of 1.7 g cm^{-3}. This estimate is just less than half the bioerosion rate measured for *C. orientalis*. However, the coral blocks used in the *C. orientalis* study had been cleaned prior to sponge attachment and so each individual was likely to have benefitted from a completely flat area to expand into, devoid of competitors. Competition, particularly by macroalgae, and reef morphology are key controls on the lateral expansion rates of *C. tenuis* (López-Victoria and Zea 2005, González-Rivero et al. 2012) and probably all gallery-forming sponges. Hence the erosion rate estimated here for a small *C. tenuis* individual may be more realistic for natural settings.

The approach developed for *S. brevitubulatum* draws attention to the damaging affect this species can have on coral heads. In particular our data show that the presence of even relatively small numbers of fistules can be indicative of high rates of bioerosion. However, most benthic survey methods would not record

fistules as they are often too small (<1 cm diameter). Hence reef monitoring programs which do not include dedicated surveys for the bioeroding sponges are likely to greatly underestimate the presence of *S. brevitubulatum* and other α-growth-form species, if they are recorded at all. The structural complexity of reef habitats in the Caribbean has been decreasing since at least the 1960s (Alvarez-Filip et al. 2009). While the agents or mechanisms underlying this net destruction of habitat include damage by storms and visually obvious bioeroding taxa (e.g. parrotfish), against a background of decreasing habitat construction by corals (Perry et al. 2014), cryptic excavating sponges may have contributed significantly to the overall decline, unnoticed.

Results indicate distinct habitat preferences for *C. tenuis* and *C. caribbaea* and suggest that the make-up of excavating sponge communities on coral reefs changes with depth (Table 5.4). This has also been found for reefs in Colombia (López-Victoria and Zea 2005). It is likely that excavating sponge communities become increasingly dominated by cavity-forming species as light attenuation decreases the influence of the symbiotic gallery-formers at greater depths. Although there was no clear evidence for an increase in bioerosion by the cavity-formers with depth, the relative contributions of these species (which are cryptic except for mature individuals of some species) to total sponge bioerosion clearly increased (Figure 5.5). The space occupied by these species causes a disproportionately high level of bioerosion in comparison to gallery-formers. Therefore, comparisons of the substrate covered by bioeroding sponge communities at different depths may incorrectly suggest higher levels of total bioerosion for shallow reefs where gallery-formers dominate. Hence, the monitoring of sponge erosion on coral reefs must incorporate the growth and excavation strategies of different species by assessing abundance and bioerosion appropriately, as attempted here. By focusing on the excavation strategy bioeroding sponges can be divided into two types, cavity and gallery-formers, which can determine the approach to estimating bioerosion for any species. Focusing on the growth form (α, β, γ) allows the selection of a suitable census protocol. In Table 5.5 different census methodologies and approaches to estimating bioerosion are allocated to combinations of sponge growth form and excavation strategy. Additionally, an excel spreadsheet was developed that will calculate bioerosion by different sponge species from census data collected

using the approaches described here. This spreadsheet is available online at the *ReefBudget* website (http://geography.exeter.ac.uk/reefbudget/) or as electronic supplementary material with the published paper (DOI: 10.1007/s00338-016-1442-z)

Table 5.5 Selection of appropriate census survey protocols and equations for estimating bioerosion by excavating sponge species based on their growth form and excavation strategies.

	α-growth-form	**β-growth-form**	**γ-growth-form**
Gallery-formers	*C. tenuis* approach – Equation 2 Measure tissue area using the papillar zone	*C. tenuis* approach – Equation 2 Measure sponge area	*C. tenuis* approach – Equation 2 Measure sponge area
Cavity-formers	*S. brevitubulatum* approach – Equation 4 Measure papillae area	*C. delitrix* approach – Equation 3 Measure tissue area using the papillar zone	*C. delitrix* approach – Equation 3 Measure tissue area using the papillar zone

5.5.1 *Monitoring bioerosion by sponge communities*

Methodologies that can aid surveys of endolithic sponges and generate estimates for bioerosion are urgently needed within reef monitoring programmes (Schönberg 2015). Here the census based approach of Perry et al. (2012) has been expanded to account for the main growth forms and excavation strategies that exist for bioeroding sponges, thus providing a basis for estimating sponge community bioerosion on Caribbean coral reefs. The approach also has the potential to be adapted for the Indo-Pacific region. Mean bioerosion by sponge communities ranged from 0.036 to 0.172 kg $CaCO_3$ m^{-2} yr^{-1} on the sites investigated. This is comparable to bioerosion rates measured in other Caribbean and Atlantic studies; (*e.g.* 0.256 kg m^{-2} yr^{-1} in Bermuda; Rützler 1975) and also to those for macroboring communities in the Indo-Pacific (*e.g.* 0.040 – 0.197 kg m^{-2} yr^{-1} on the mid – outer shelf of the Great Barrier Reef;

Tribollet & Golubic 2005). While our results broadly agree with studies from other areas, the methods used may be limited by a lack of species specific data. Given our present level of understanding of the growth and excavation rates of bioeroding sponge species, more research is clearly required to expand the list of species for which data are available and also to develop our understanding of how habitat, water quality and climate change may affect bioerosion by sponges.

The approaches described here are straight forward, relatively quick, and replicable over different spatial and temporal scales. They do not require destructive coral sampling or substrate removal and can generate instant, meaningful results on sponge abundance and bioerosion, while additionally having the potential to be used by surveyors after a little training. Furthermore, all of these advantages are desirable for a sponge bioerosion assessment protocol which can fit into current benthic monitoring regimes (Schönberg 2015). The adoption of these approaches by monitoring agencies would create a framework for the provision of data which is relevant to both coral reef management and to developing our understanding of how bioeroding sponge populations may be influencing reef structure and carbonate budgets.

Bioerosion on Grand Cayman coral reefs and hardgrounds

6.1 Abstract

Bioerosion is a critically important, but little studied, function on coral reefs and contributes to habitat maintenance, sediment generation and over time reef growth and geomorphology. On Caribbean reefs the main agents of bioerosion are parrotfish, urchins, sponges and various microendolithic taxa. Here, the contributions of these taxonomic groups to bioerosion are assessed at 24 sites on Grand Cayman, within *Acropora palmata* reef (1 – 8 m), *Orbicella* reef (8 – 15 m) and hardground (4 – 7 m) habitats. The effects of wave energy and depth on bioerosion are considered along with the effects of an unfished marine protected area which encompasses most of the sheltered west coast. Mean total bioerosion was 1.32, 2.27 and 2.28 kg $CaCO_3$ m^{-2} yr^{-1} within hardgrounds, *Acropora palmata* reef and *Orbicella* reef habitats respectively. Total bioerosion was not influenced by depth or wave energy. Parrotfish dominated bioerosion at all sites except one, contributing 29 – 86 % of total bioerosion. Micro-endolithic communities were the next most important contributors to bioerosion (10.6–37.1%) at most sites, followed by sponges (1.7 – 9.7%). Urchins were minor contributors to total bioerosion, except at two *Acropora palmata* reef sites (Cemetery and Pallas SB) where they were responsible for 50% and 23%. Parrotfish biomass was significantly related to both total bioerosion and parrotfish bioerosion. The stoplight parrotfish (*Sparisoma viride*) contributed most to parrotfish bioerosion at all sites (mean 0.79 kg $CaCO_3$ m^{-2} yr^{-1}). The effect of the marine protected area was only apparent within *Orbicella* reef habitat. Parrotfish biomass was significantly higher for *Orbicella* reef habitat within the marine protected area, raising important questions about bioerosion on recovering reefs and whether too many parrotfish can be detrimental.

6.2 Introduction

The destruction of coral reef framework by organisms is an integral part of coral reef systems. This process (bioerosion; sensu Neumann 1966) also operates on coral rubble (Holmes et al. 2000) and other carbonate producing organisms e.g. bivalves (Akpan and Farrow 1985), but here I focus on the bioerosion of coral reef framework. Within coral reef systems, bioerosion operates in association with carbonate production and various physical forces to produce the physical structures that exist in different environments (e.g. fore-reef, back reef, lagoon, hardground and beach environments). The geomorphology of reef systems is as much a consequence of calcium carbonate framework destruction as it is framework production (Hubbard et al. 1990). Hence, bioerosion is an important metric to measure. Our understanding of coral reefs often focuses on reefs as constructional entities, and therefore bioerosion may be considered negatively. However the evolution of reef systems has always occurred with carbonate production and bioerosion operating synergistically; both are integral to the functioning and health of coral reef systems.

The consequences of bioerosion include the weakening of coral framework (Goreau and Hartman 1963, Scott and Risk 1988, Bak 1994, Schönberg 2002), the development of micro-habitats (Hutchings 1986), the generation of sediment (Fütterer 1974, Chazottes et al. 2004, Perry et al. 2015a) and the removal of epilithic and shallow endolithic communities from grazed substrate (Chazottes et al. 1995, Bruggemann et al. 1996). Previous studies have identified urchins (e.g. Ogden 1977; Scoffin et al. 1980; Bak 1990), parrotfish (e.g. Bellwood 1995; Bruggemann et al. 1996; Alwany et al. 2009), macro-endolithic (e.g. (Neumann 1966, Chazottes et al. 1995, Perry 1998) and micro-endolithic organisms (e.g. Vogel et al. 2000; Tribollet 2008) as important bioeroding groups.

Bioerosion by reef species changes from one habitat to another as environmental regimes and the availability of suitable substrate change and impact their populations (Perry 1998, Peyrot-Clausade et al. 2000, Vogel et al. 2000). Additionally, anthropogenic activities may impact bioeroder populations and therefore bioerosion rates. For instance, nutrient enrichment of coral reefs,

from sewage or agricultural runoff, often leads to an increase in bioerosion (Rose and Risk 1985, Holmes 2000, Chazottes et al. 2002, Carreiro-Silva et al. 2012). Additionally, fishing may reduce bioerosion due to parrotfish loss (Carreiro-Silva and McClanahan 2001, Mumby et al. 2006) or paradoxically increase it in some situations, due to the success of urchins released from predation (Carreiro-Silva and McClanahan 2001). Ecological controls are also important considerations for estimating bioerosion. For both parrotfish and urchins, size and species are important controls on the rate of bioerosion (Scoffin et al. 1980, Bruggemann et al. 1996, Griffin et al. 2003). Differences in jaw structure and subsequently feeding mode allows parrotfish species to be described as 'excavators', 'scrapers' (Bellwood and Choat 1990) or 'browsers' (Bellwood 1994). Excavators are far more effective bioeroders than both scrapers and browsers and for all three types larger individuals erode more with each bite (Bellwood 1995, Bruggemann et al. 1996, Lokrantz et al. 2008). Fishing is widely recognised to reduce the biomass and size structure of reef fish communities (Roberts 1995, Mumby et al. 2006, Ong and Holland 2010). Hence, fishing will probably have an effect on the provision of functions associated with bioerosion by parrotfish.

Size dependent control on bioerosion also occurs with sea urchins (Scoffin et al. 1980, Griffin et al. 2003). *Diadema antillarum* is the largest sea urchin on Caribbean reef systems and up until 1984, this urchin was often the most important bioeroder on coral reefs (Ogden 1977; Scoffin et al. 1980 – 4.6 and 5.3 G respectively, where 1 G = 1 kg $CaCO_3$ m^{-2} yr^{-1}). Bioerosion estimates as high as 9.7 G were reported for *D. antillarum* on a Barbados reef (Hunter 1977). This species was most abundant on shallow reef habitats but was recorded down to 36 m on a fore-reef slope in Curacao (Bak et al. 1984). However, during 1983/1984 an unknown pathogen spread throughout the Caribbean killing most of these urchins (>93% Lessios et al. 1984). *D. antillarum* populations have not yet recovered (Lessios 2005, 2016). It is possible that *D. antillarum* populations had been inflated prior to 1983, due to decreases in predation by fish predators as fishing has been shown to influence urchin populations on reefs in east Africa (Carreiro-Silva and McClanahan 2001), however, it is certain that the mass mortality of *D. antillarum* urchins, has led to

a reduction in bioerosion related functions on Caribbean reefs (Perry et al. 2014).

Macro- and micro-endolithic boring organisms tend to be filter feeders (e.g. *Siphonodictyon brevitubulatum*) or phototrophs (e.g. *Ostreobium quekettii*) and hence environmental factors that directly affect their populations include water quality and light availability. Several studies have shown that increasing nutrients increases populations of macroboring fauna (Rose and Risk 1985, Holmes 2000) and there is evidence to indicate that this is also true for boring micro-organisms (Chazottes et al. 2002). In the Caribbean, macroboring communities are dominated by sponges in fore-reef environments (Perry 1998) and therefore sponges alone provide conservative estimates for bioerosion by macroborers (Perry et al. 2012). The rates of bioerosion by micro-endolithic organisms have been shown to decrease with depth (Vogel et al. 2000) and therefore, light availability. Succession is also an important factor in dictating bioerosion by micro-endolithic communities. Mature communities are dominated by the chlorophyte *Ostreobium quekettii* (Vogel et al. 2000, Tribollet 2008, Grange et al. 2015), which penetrates the substrate to 4.1 mm (Tribollet 2008, Grange et al. 2015) and may require the presence of early successional stages to colonise new substrate (Vogel et al. 2000, Grange et al. 2015). Hence, the relationship between microbioerosion, environment and herbivory may be very complex.

In general, total bioerosion may decrease with depth (Hubbard 2009, Weinstein et al. 2014) and therefore from *Acropora palmata* reef habitats to *Orbicella* reef habitats on Grand Cayman. However, few studies have investigated this in detail and our understanding of how bioerosion changes in relation to populations of the relevant species, depth, and habitat type is limited. Despite this, many studies identify external grazers as the dominant bioeroding taxa within shallow reef habitats (Scoffin et al. 1980, Chazottes et al. 1995, Perry et al. 2014) and a reduction in their influence with depth (Kiene and Hutchings 1994, Bruggemann et al. 1996, Weinstein et al. 2014). In contrast, bioerosion by sponges may increase with depth on deep water mesophotic reef systems (>25 m, Weinstein et al. 2014).

Here, the contributions of populations of each of the aforementioned groups to total bioerosion are assessed on hardgrounds (4 – 7 m), *Acropora palmata* reef (1 – 8 m), and *Orbicella* reef (8 – 15 m) habitats in wave exposed and sheltered environments on Grand Cayman. Data for a single stump and boulder site is also considered. It is expected that total bioerosion will be different within different habitats and that the marine protected area on the sheltered west coast may have higher rates of bioerosion due to the protection of parrotfish. Mean total bioerosion is calculated for each habitat type, so that carbonate budgets can be calculated in Chapter 7.

Null hypothesis 1: Total bioerosion does not vary between different habitat types or exposure regimes.

Null hypothesis 2: Individual species contribute uniformly to total bioerosion within coral reef and hardground habitats.

Null hypothesis 3: The presence of a marine protected area on the sheltered west coast does not affect the rates of bioerosion within habitat types.

Specific objectives:

1. To estimate the population density and size distributions of individual parrotfish and urchin species within *Acropora palmata* reef, *Orbicella* reef and hardground habitats.

2. To quantify the population of excavating sponge species within *Acropora palmata* reef, *Orbicella* reef and hardground habitats by estimating visible tissue cover for each species.

3. To estimate the contributions of individual species of parrotfish, urchins and sponges to total bioerosion within *Acropora palmata* reef, *Orbicella* reef and hardground habitats.

4. To estimate the contributions of micro-endolithic organisms to total bioerosion within *Acropora palmata* reef, *Orbicella* reef and hardground habitats using estimates of available substrate taken from benthic transects.

5. To estimate mean total bioerosion within *Acropora palmata* reef, *Orbicella* reef and hardground habitats.

6. To compare total bioerosion within similar habitat types exposed to different wave energy regimes.

7. To compare parrotfish bioerosion inside and outside of the marine protected area on Grand Cayman

6.3 Methodology

Bioerosion by parrotfish, urchins, sponges and micro-endolithic organisms was estimated for 24 sites on Grand Cayman. Site selection is described in Chapter 2, but in brief, sites were chosen to reflect changes in exposure to wave energy within different habitat types, which occur across a depth range from 1 – 15 m. The methods used to estimate bioerosion for each of the four groups of bioeroding taxa were based on those developed by Perry et al. (2012) and augmented with a new approach for sponges described in Chapter 5.

6.3.1 *Parrotfish*

Eight to ten 30 * 4 m transects were surveyed to census for parrotfish at all sites. Transects were laid haphazardly in the area surrounding benthic community transects (see Chapter 4) and surveyed between 11 am and 5 pm; these being the reported hours of maximum feeding intensity (Bruggemann et al. 1994a). Divers were absent from the surveyed areas for at least 15 minutes prior to each survey. The sexual phase (juvenile, initial or terminal) of each parrotfish was recorded and fork lengths were estimated and assigned to a size class; 5 – 14 cm, 15 – 24 cm etc. Parrotfish smaller than 5 cm were not recorded and those larger than 44 cm were estimated to the nearest 10cm.

Biomass was measured using the formula:

$$W = aL^b$$

where, W = mass (g)

L = fork length (cm)

a and b are species specific constants chosen based on Marks and Klomp (2003), but originating from Bohnsack and Harper (1988). Data for *Scarus vetula* is not available and therefore a and b constants for *Sparisoma viride* were used, following Marks and Klomp (2003).

Bioerosion was calculated for each fish based on length and sexual phase (Perry et al. 2012), summed for transects and reported in kg $CaCO_3$ m^{-2} yr^{-1}.

6.3.2 *Urchins*

Urchins were recorded along each of the benthic community transects assessed (Chapter 4), by examining the substrate 1 m either side of the transect line. Each individual was identified to species and its test size estimated (0 – 2 cm, 2 – 4 cm, etc.). Bioerosion was then calculated for each urchin using one of two equations (Perry et al. 2012), depending on the species and summed for each transect:

Diadema antillarum:

$$y = 0.0029x^{1.6624}$$

Other species:

$$y = 0.0007x^{1.7309}$$

where, y = bioerosion rate (g/urchin/day)

x = urchin test size (mm)

6.3.3 *Sponges*

Sponge erosion was assessed using census surveys of excavating sponge communities along the benthic transects described in Chapter 4. For each 10 m transect sponge tissue cover was assessed within 0.5 m^2 quadrats, which were alternated between sides of the transect line in a checkerboard fashion. This provided a total planar area of 5 m^2 per transect. Data were recorded using one of three approaches, depending on the species, and these are described in detail in Chapter 5. However, these approaches to estimating sponge bioerosion were developed during the course of the present study and therefore it was not possible to apply them to all of the data collected for one species – *Siphonodictyon brevitubulatum*. Specifically, data collected for *S. brevitubulatum* before 2013 (8 sites) could not be used to estimate bioerosion using the new methodology and therefore the method of Perry et al. (2012) was employed. The eight sites include two *Acropora palmata* reef sites (Boggy Sands and Pallas), five *Orbicella* reef sites (Anchor, Don Fosters, Pallas, Spotts and Babylon) and one hardground site (Don Fosters). Data collected after 2013 (16 sites) could not be applied to the Perry et al. (2012) method. Differences between data collection techniques for both methods are discussed in more detail in Chapter 5. However, it was not possible to compare the results for both methods at any site, because enough survey time was not available to use both data collection approaches.

6.3.4 *Micro-endoliths*

Bioerosion by micro-endolithic organisms was estimated by applying an erosion rate (0.278 kg $CaCO_3$ m^{-2} yr^{-1}) to the percentage of substrate available to them; this excluded only sand. The structural complexity of the site was then incorporated by multiplying by rugosity. The bioerosion rate was calculated from mean rates of microbioerosion collected at 8 fore-reef sites by 3 studies (Chazottes et al. 1995, Vogel et al. 2000, Tribollet and Golubic 2005). Rates were selected for the mean if they were from a unique site and a mature (≥ 6 months) micro-endolithic community (Table 6.1).

6.3.5 *Statistical analysis*

Habitat types were classified as per Chapter 4 and this meant that one site (Don Fosters hardground) was excluded from habitat level analyses for hardgrounds, although data for this site is presented in the results. Total bioerosion within habitat types could only be assessed statistically using site level data because parrotfish transects were more numerous and occurred over a larger area than the benthic community transects. A two way analysis of variance was used to test total bioerosion for the effects of habitat type and exposure level (sheltered vs exposed). Total bioerosion was tested for the assumptions of normality and homogeneity of variance using Shapiro–Wilk and Fligner–Kileen tests respectively. Pairwise comparisons, using the Tukey – Kramer adjustment (Dunnett 1980) for unequal sample sizes, were employed to test which habitat types were different from one another.

Table 6.1 Selected bioerosion rates from mature micro-endolithic communities at fore-reef sites. GBR – Great Barrier Reef.

Site	**Microbioerosion rate (kg $CaCO_3$ m^{-2} yr^{-1})**	**Exposure (years)**	**Reference**
Moorea, Central Pacific	0.180	0.5 – 2	Chazottes et al. 1995
Snapper Island, GBR	0.077	3	Tribollet and Golubic 2005
Low Isles, GBR	0.180	3	Tribollet and Golubic 2005
Lizard Island, GBR	0.297	3	Tribollet and Golubic 2005
Harrier Reef, GBR	0.473	3	Tribollet and Golubic 2005
Ribbon Reef, GBR	0.320	3	Tribollet and Golubic 2005
Osprey Reef, GBR	0.430	3	Tribollet and Golubic 2005
Lee Stocking Island, Bahamas	0.270	0.5	Vogel et al. 2000

Linear models were used to investigate relationships with bioerosion for both parrotfish abundance and biomass. Assumptions of normality and homogeneity of variance were tested as before. The effect of parrotfish biomass on bioerosion within habitat type/marine protected area combinations (there were six) was further investigated using transect data. Kruskal-Wallis rank sum tests with Nemanyi pairwise comparisons were required because the data was not normally distributed. Levels associated with marine protected area designation (Fished/Unfished) and exposure (exposed/sheltered) are essentially the same because all sheltered sites lie within a marine protected area and all exposed sites are outside. Hence ‘Fished’ is equivalent to ‘Exposed’ and ‘Unfished’ is equivalent to ‘Sheltered’.

All analysis was undertaken in the R statistical environment (R Development Core Team 2011).

6.4 Results

Total bioerosion at all sites ranged from 0.756 G at Boggy Sands hardground to 3.804 G at Don Fosters *Orbicella* reef. Linear regression models suggested that the natural environmental regimes of depth and wave energy did not influence total bioerosion on Grand Cayman: depth - F = 0.1848, df = 22, p = 0.672; ln wave energy index – F = 1.67, df = 22, p = 0.210. However, it may be that the effects of depth and wave energy (if any) are different within different types of habitat.

6.4.1 *Bioerosion at the habitat scale*

There were significant differences between the mean bioerosion rates for habitat types (F = 4.074, df = 2, p = 0.034, Figure 6.1). On *Acropora palmata* reef habitat the mean rate of bioerosion (+/- SE) was 2.27 +/- 0.26 G and very similar to that on *Orbicella* reef habitat (2.28 +/- 0.26 G). They were not significantly different. Hardground sites had a mean bioerosion rate of 1.32 +/- 0.21 G, which was significantly different to *Orbicella* reef sites but not to *Acropora palmata* reef sites, based on Tukey-Kramer pairwise comparisons (t = 2.657, p = 0.039 for OR vs HG and t = 2.350, p = 0.073 for PR vs HG). Total bioerosion was 1.562 G at the stump and boulder site on Pallas reef (Figure 6.2a) and 2.708 G at the Don Fosters hardground site (Figure 6.2c). However, this site had an atypical benthic community for hardgrounds (Chapter 4) and was not included in habitat comparisons. Table 6.2 displays mean bioerosion for the three main habitats investigated on exposed and sheltered shores of Grand Cayman.

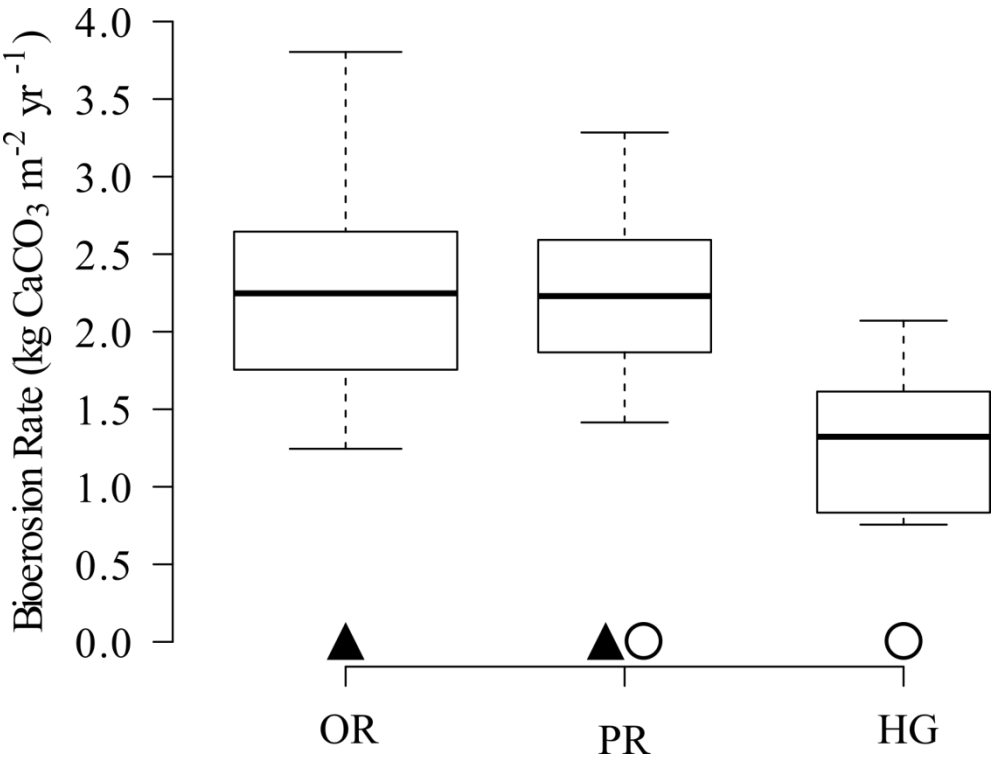

Figure 6.1 Boxplot of bioerosion within habitat types. Triangles and circles denote significant differences based on Tukey-Kramer pairwise comparisons. OR – *Orbicella* reef, PR – *Acropora palmata* reef, HG – Hardground.

Table 6.2 Mean bioerosion within habitat types on exposed and sheltered shores of Grand Cayman. HG – Hardground, SB – stump and boulder, PR – *Acropora palmata* reef, OR – *Orbicella reef*. Figures in kg $CaCO_3$ m^{-2} yr^{-1}.

	HG		SB		Sheltered PR		Exposed PR		Sheltered OR		Exposed OR	
Micro-endoliths	0.279 0.004	+/-	0.352 0.018	+/-	0.371 0.016	+/-	0.366 0.01	+/-	0.449 0.03	+/-	0.352 0.02	+/-
Sponges	0.049 0.009	+/-	0.151 0.023	+/-	0.046 0.010	+/-	0.120 0.02	+/-	0.138 0.01	+/-	0.054 0.01	+/-
Urchins	0.018 0.013	+/-	0.364 0.072	+/-	0.552 0.382	+/-	0.028 0.02	+/-	0.045 0.01	+/-	0.007 0.003	+/-
Parrotfish	0.975 0.219	+/-	0.695 0.134	+/-	1.148 0.605	+/-	1.833 0.40	+/-	2.166 0.28	+/-	1.352 0.25	+/-
Total	1.321 0.209	+/-	1.562 0.070	+/-	2.116 0.25	+/-	2.346 0.395	+/-	2.797 0.31	+/-	1.764 0.26	+/-

6.4.2 *Intra habitat variation*

Cumulative bioerosion by each of the four taxa investigated (parrotfish, urchins, sponges and micro-endoliths) is depicted in Figure 6.2 for each site. Mean total bioerosion ranged from 1.415 G to 3.284 G at *Acropora palmata* reef sites (Figure 6.2a) and there were no obvious trends with either depth or exposure. However, urchins were clearly more important to total bioerosion at sites less than 4 m depth (Boggy Sands and Cemetery). This was also evident at the Pallas stump and boulder site where urchins contributed 23 % to total bioerosion and were the second most important taxonomic group (Table 6.2). Within *Orbicella* reef habitat (Figure 6.2b) sheltered sites had generally higher rates of total bioerosion than exposed ones, although this was not the case for all. Armchair (a sheltered site) had lower bioerosion than two of the five exposed sites and Spotts (an exposed site) had the third highest rate of total bioerosion measured for sites within *Orbicella* reef habitat. However, it is interesting to note that this site has the lowest wave energy index of any site on the south coast (Chapter 2). Despite this, the effect of exposure level was not found to be significant in a two way analysis of variance for total bioerosion (habitat interacted with exposure level, $F = 0.579$, $p = 0.457$ for Exposure level). Change in total bioerosion measured for sites within *Orbicella* reef habitat was clearly related to bioerosion by parrotfish, which contributed 64 – 83 % of total bioerosion at these sites.

Total bioerosion measured for hardground habitat ranged from 0.756 – 2.071 G (Table 6.3). As in the other habitat types, parrotfish dominated bioerosion contributing between 52 and 85% of the total. There was only one wave exposed site (Prospect) and although bioerosion was low here (0.833 G) it was within the range recorded at other hardground sites (Figure 6.2c) and hence assessments of the effect of exposure level are difficult. There were no depth related trends.

Table 6.3 Percent contribution of excavating organisms to total bioerosion (kg $CaCO_3$ m^{-2} yr^{-1}) at 24 sites around Grand Cayman.* The hardground habitat at Don Fosters was not considered similar to the other hardground sites. SB – stump and boulder.

	Bioerosion (kg $CaCO_3$ m^{-2} yr^{-1})	Relative % contributions by taxonomic groups			
Acropora palmata reef		Parrotfish	Urchins	Sponges	Micro-endoliths
Boggy Sands	2.365	74.1	7.2	2.4	16.3
Cemetery	1.867	29.1	50.0	1.9	19.0
Pallas	2.094	71.6	4.0	5.8	18.6
Bullwinkle	2.592	80.1	0.1	6.6	13.2
Prospect	3.284	85.6	0.7	3.1	10.6
Manse	1.415	66.6	0.1	5.9	27.4
Pallas (SB)	1.562	44.5	23.3	9.7	22.5
Orbicella reef					
Anchor	3.060	79.5	0.8	6.0	13.7
Killer Puffer	2.570	76.3	2.3	5.5	15.9
Eden Rock	2.630	74.6	1.3	4.0	20.1
Don Fosters	3.804	81.0	2.4	3.8	12.8
Armchair	1.919	72.7	0.8	5.9	20.6
Pallas	1.755	80.0	-	1.7	18.3
Prospect	1.251	63.9	1.0	5.0	30.1
Spotts	2.645	83.2	0.3	1.8	14.7
Manse	1.245	70.5	1.0	3.8	24.7
Babylon	1.925	76.9	0.1	4.2	18.8
Hardground					
Boggy Sands	0.756	52.9	0.9	9.1	37.1
Anchor	1.092	68.5	0.1	7.1	24.3
Killer Puffer	2.071	84.6	0.2	1.7	13.5
Eden Rock	1.614	78.9	0.7	3.5	16.9
Armchair	1.553	79.7	-	1.9	18.4
Prospect	0.833	52.2	9.7	2.7	35.4
Don Fosters*	2.708	79.8	0.6	7.5	12.1

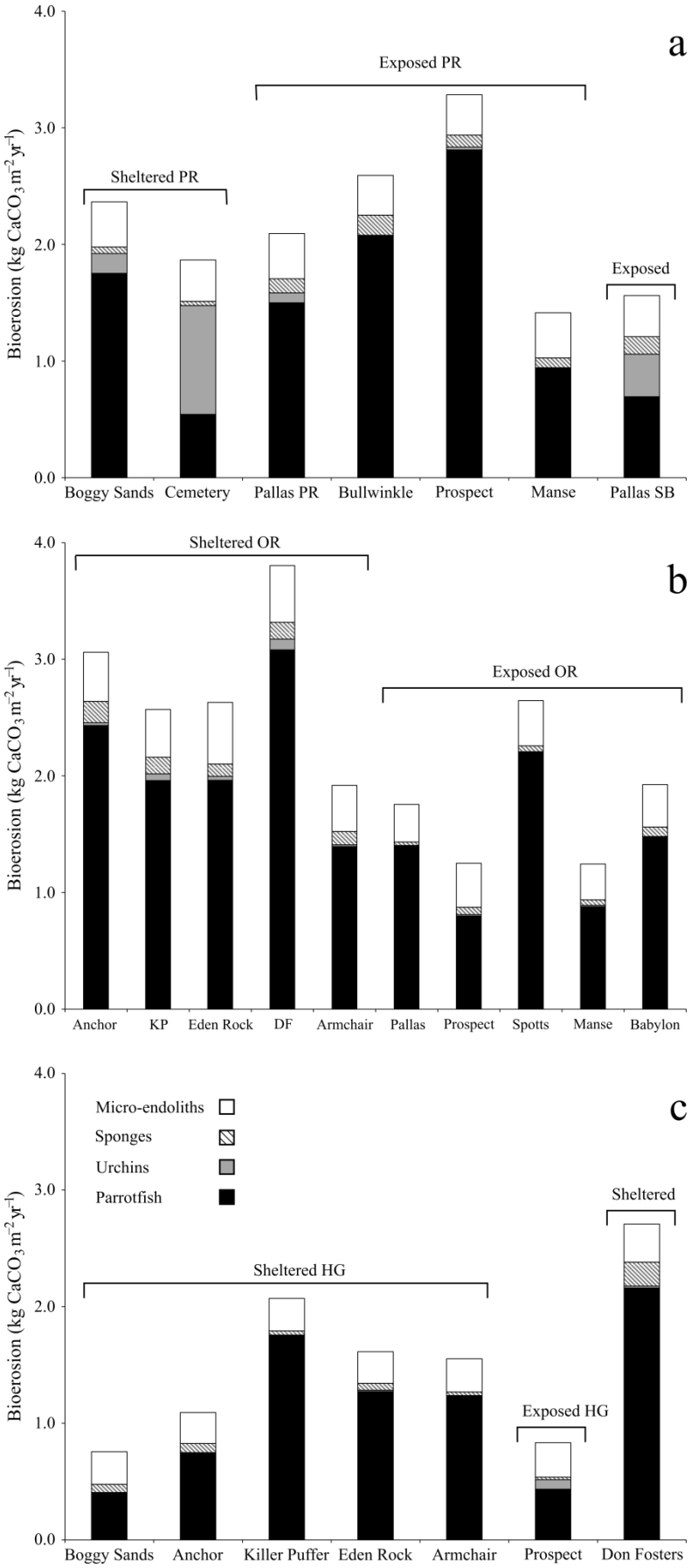

Figure 6.2 Cumulative bioerosion at coral reef and hardground sites. a) *Acropora palmata* reef (PR), stump and boulder (SB). b) *Orbicella* reef (OR) c) Hardground (HG), Don Fosters was not considered similar to other HG habitats.

6.4.3 *Bioerosion by micro-endoliths*

Micro-endoliths contributed an estimated 10.6 – 37.1 % of total bioerosion (Table 6.3) across all sites and were an important group within the bioeroding communities investigated. Mean bioerosion (+/- SE) was 0.368 +/- 0.01 G within *Acropora palmata* reef habitat, 0.400 +/- 0.02 G within *Orbicella* reef habitat and 0.279 +/- 0.01 G within hardground habitat. Microbioerosion at individual sites ranged from 0.265 G at Anchor hardground to 0.528 G at Eden Rock *Orbicella* reef. The differences between the sites were almost solely due to structural complexity, as bioerosion was calculated by multiplying a standard rate for microbioerosion by rugosity and applying this figure to the area available to micro-endoliths.

6.4.4 *Bioerosion by sponges*

A total of six excavating sponge species were recorded during all surveys; *S. brevitubulatum*, *Cliona delitrix*, *Cliona aprica*, *Cliona tenuis*, *Cliona caribbaea* and *Cliona varians*. Each of these species was recorded in each habitat and their contribution to sponge bioerosion was discussed in Chapter 5 for a subset of reef sites. Here, I describe how total sponge bioerosion relates to that for the other three groups investigated. Sponges were less important to bioerosion than both parrotfish and micro-endoliths at all sites (Table 6.3). Their contributions to total bioerosion ranged from 0.022 G (2.7 %) at Prospect hardground to 0.204 G (7.5 %) at Don Fosters hardground. In relation to the other bioeroding groups, sponges contributed between 1.7 and 9.7 % to total bioerosion across all sites (Table 6.3) and hence they were occasionally, locally important.

Mean bioerosion was 0.095 +/- 0.02 G within *Acropora palmata* reef habitat, 0.096 +/- 0.02 G within *Orbicella* reef habitat and 0.049 +/- 0.01 G within hardground habitat. Relative to the urchins, sponge bioerosion was higher at 20 of the 24 sites investigated. Of the four sites where sponges contributed less to total bioerosion than urchins, three were the shallowest sites surveyed (Boggy Sands: 1 – 2 m, Cemetery: 1 – 4 m and Pallas SB: 2 – 4 m). However, urchin bioerosion at these three sites ranged from 0.170 G to 0.933 G and it was the increase in urchin densities rather than a decrease in sponge bioerosion that

resulted in a change in the order of bioeroding group importance. The fourth site was the exposed hardground habitat at Prospect (6 – 8 m) and here sponge bioerosion was the lowest of any site (0.022 G, Figure 6.2).

As with total bioerosion, habitat differences in mean sponge bioerosion suggested that hardground sites had less sponge bioerosion than both *Acropora palmata* and *Orbicella* reef habitats. Within both coral reef habitat types sponge bioerosion was similar, however, exposure level masked differences between these habitat types (Figure 6.3). Mean sponge bioerosion was 0.046 +/- 0.01 G on sheltered *Acropora palmata* reef sites but almost three times higher at 0.120 +/- 0.02 G on exposed *Acropora palmata* reef sites. On deeper *Orbicella* reef sites this relationship was reversed; sheltered transects had mean sponge bioerosion of 0.138 +/- 0.01 G which was over 2.5 times the mean for exposed sites (0.054 +/- 0.01 G).

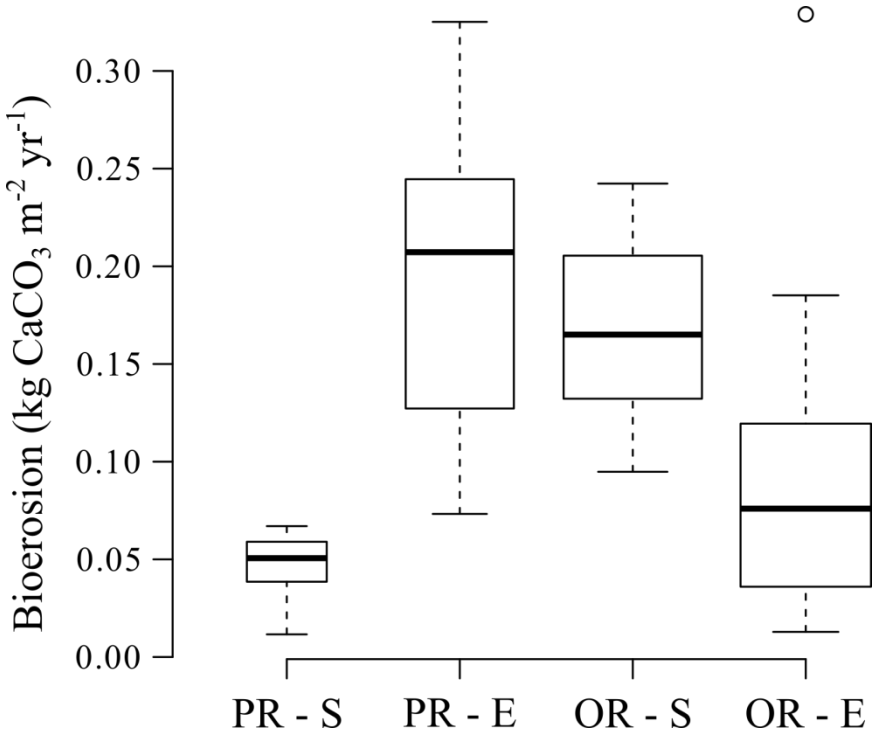

Figure 6.3 Sponge bioerosion on transects within coral reef habitat types under different wave exposure regimes. PR – *Acropora palmata* reef, OR – *Orbicella* reef, S – Sheltered, E – Exposed.

6.4.5 *Bioerosion by sea urchins*

Sea urchins were generally of minor importance in terms of their contributions to bioerosion on the reefs and hardgrounds of Grand Cayman. Four species were recorded at all sites – *Echinometra viridis* (18 sites), *Diadema antillarum* (15 sites), *Echinometra lucunter* (8 sites), and *Eucidaris tribuloides* (4 sites). Most sites had low abundances of all species, but this was particularly true for *E. tribuloides*; a total of 9 individuals were recorded for all 83 transects. No species was restricted to a particular habitat type, but most observations tended to be clumped within specific sites and abundances varied widely over short distances. Prospect, on the south coast, is a good example of the apparently stochastic distribution of urchins. Here the hardground site was landward of the reef at about 7 m and had relatively high densities of urchins (3.68 m^{-2}; mostly *E. lucunter* but a few *E. viridis*). However, the adjoining *Acropora palmata* reef habitat was also at approximately 7 m and had low densities of only one species (0.03 *D. antillarum* m^{-2}). A little deeper and seaward within the Prospect *Orbicella* reef habitat, urchin density was 0.07 m^{-2} and composed of two species – *D. antillarum* and *E. viridis*.

Very high abundances (11.65 m^{-2}) of sea urchins were recorded at the Pallas stump and boulder site; all were *E. lucunter*, except for 1 *E. viridis*. At this site, urchins contributed 23% (0.364 G) to total bioerosion but most of these urchins had a test size within the 0–2 cm size class and hence the impact of an individual was low. At Cemetery, urchin densities were much reduced in comparison (0.85 m^{-2}), however, bioerosion was estimated to be 0.933 G (50% of total bioerosion) and this was almost completely due to *D. antillarum* which had abundances of 0.7 m^{-2}; the modal test size was 6 – 8 cm. Elsewhere urchin bioerosion was of less importance and the third highest rates were recorded at Boggy Sands *Acropora palmata* reef – 0.17 G or 7.2% of total bioerosion. At depths below 6 m, urchins only contributed a maximum of 0.081 G to total bioerosion and this was usually 0.1 – 2.4% of the total bioerosion at the particular site, although for Prospect hardground (6 – 8 m) this amounted to 9.7% of the total bioerosion (Table 6.3).

6.4.6 *Bioerosion by parrotfish*

Parrotfish dominated bioerosion at all sites with the exception of Cemetery (Table 6.3), contributing 29.1 – 85.6 % to total bioerosion at all sites. Greater than half of the total estimated bioerosion was attributed to parrotfish, at 22 of the 24 sites. Hence, variability in bioerosion between sites was almost completely controlled by parrotfish. A total of nine species were recorded, but no single species occurred at all sites. The abundance of parrotfish species at each site is displayed in Table 6.5. The midnight parrotfish (*Scarus coelestinus*) was only recorded at two sites, Pallas *Acropora palmata* reef and Don Fosters *Orbicella* reef. This was also true of the rainbow parrotfish (*Scarus guacamaia*) which was recorded at Cemetery reef and Killer Puffer hardground. Across all sites *Scarus iseri* was the most commonly recorded parrotfish, having over twice the abundance of the next most common species – *Sparisoma aurofrenatum* and *Scarus taeniopterus* (Table 6.5). This order of decreasing abundance (*Scarus iseri* > *Sparisoma aurofrenatum* > *Scarus taeniopterus*) was consistent within coral reef habitats (*Orbicella* reef and *Acropora palmata* reef). In hardground habitat *Scarus iseri* was the most common parrotfish followed by *Sparisoma chrysopterum*, *Scarus taeniopterus* and then *Sparisoma aurofrenatum*. However, *Sparisoma chrysopterum* was generally recorded in low abundances for other habitat types. On hardgrounds parrotfish were usually observed feeding or moving in large groups (*pers obs*) and this behaviour may be related to the lack of structural complexity (and hence reduced cover) within these sites. The stoplight parrotfish (*Sparisoma viride*) was absent from only two sites (Table 6.5) and while it was generally common, it occurred in lower numbers than the three most common species. *Scarus vetula* and *Scarus rubripinne* were both commonly observed, but in relatively low abundances.

Parrotfish abundance was significantly related to both total bioerosion ($F = 9.744$, $df = 22$, $p = 0.005$) and that bioerosion due to parrotfish alone ($F = 11.58$, $df = 22$, $p = 0.003$). The relationships are displayed in Figure 6.4a, and the r^2 values were low – 0.31 and 0.34 for total bioerosion and parrotfish bioerosion respectively. The biomass of parrotfish at each site was also significantly related to both total bioerosion ($F = 38.65$, $df = 22$, $p < 0.001$) and parrotfish bioerosion ($F = 61.05$, $df = 22$, $p < 0.001$) at each site (Figure 6.4b). Here the r^2 values were higher – 0.64 and 0.74 for total bioerosion and parrotfish bioerosion

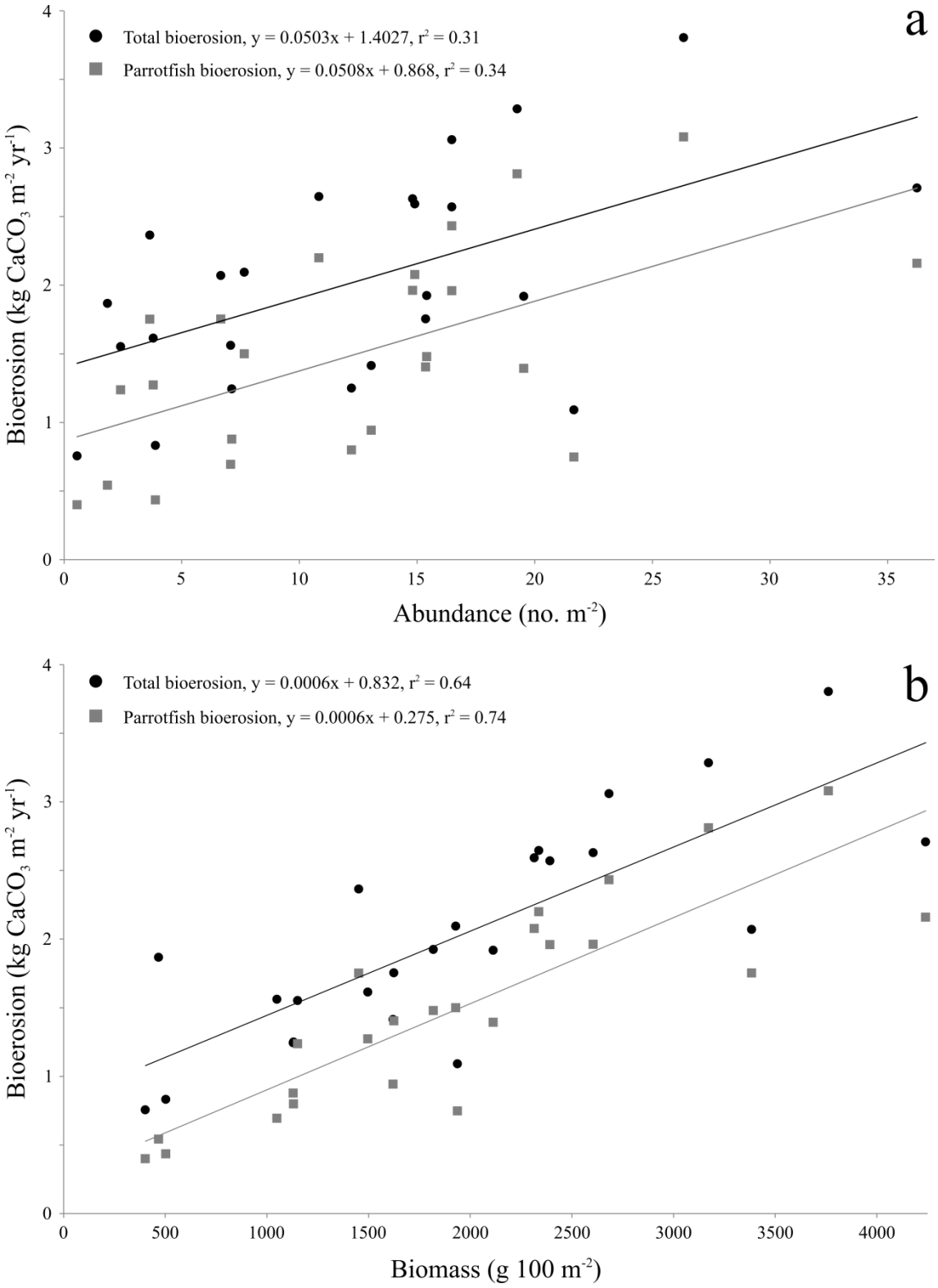

Figure 6.4 Relationships between total bioerosion and parrotfish bioerosion for a) parrotfish abundance and b) parrotfish biomass at 24 sites on Grand Cayman.

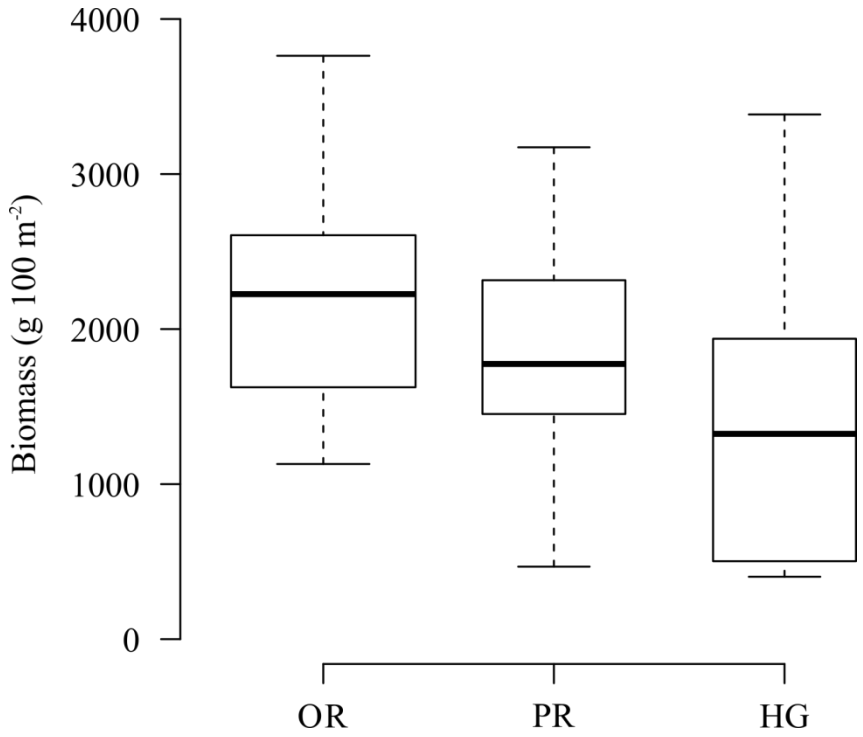

Figure 6.5 Parrotfish biomass within habitat types for 24 sites on Grand Cayman. OR – *Orbicella* reef, PR – *Acropora palmata* reef, HG – hardground.

respectively. This suggests that biomass is a much better predictor of bioerosion than abundance. Both abundance and biomass show parallel relationships with parrotfish bioerosion and total bioerosion (Figure 6.4). The slopes for each relationship were almost exactly the same for both abundance (~0.05) and biomass (~0.0006) and this suggests that total bioerosion was heavily influenced by the contributions of parrotfish at each site.

The biomass of parrotfish estimated for all sites ranged from 403 – 4240 g 100 m^{-2}; the minimum and maximum means were estimated for Boggy Sands hardground and Don Fosters hardground respectively. There was a clear trend of decreasing biomass with habitat type; *Orbicella* reef > *Acropora palmata* reef > hardground (Figure 6.5). It should be noted that two sites (Don Fosters hardground and Pallas stump and boulder) were excluded from this assessment because they were not considered typical of the three habitat types. However, any differences between the mean biomass estimates for habitat types were not significant (df = 2, F = 1.061, p = 0.366).

Fish biomass is commonly influenced by fishing pressure and 12 of the 22 sites examined here were within the marine protected area (MPA) on the west coast (Chapter 2, Figure 2.1), where fishing is prohibited. The effect of MPA was tested using ANOVA but not found to be significant ($df = 1$, $F = 1.466$, $p = 0.2435$). However, an interaction between habitat type and MPA was significant ($df = 2$, $F = 4.767$, $p = 0.024$) and this was investigated further using data at the transect level because the number of sites within the six habitat type/MPA combinations was low. Kruskal-Wallis rank sum tests showed a significant effect for habitat type (chi sq = 19.831, $df = 2$, $p < 0.001$) but not for MPA (chi sq. = 0.215, $df = 1$, $p = 0.643$). Transects within habitat type and fishing regime (inside/outside MPA) combinations were then considered separately. A Kruskal-Wallis rank sum test for the six combinations reported significant differences (Chi sq. = 57.271, $df = 5$, $p < 0.001$) and the results of post hoc Nemenyi pairwise comparisons are displayed in Table 6.5 along with the mean biomass for each. The general trend of decreasing biomass from *Orbicella* reef to *Acropora palmata* reef to hardground illustrated in Figure 6.5 is evident from the data in Table 6.5. Additionally, fished habitats tended to have lower biomass than unfished ones. However, *Acropora palmata* reef transects outside of the MPA had higher mean parrotfish biomass than those inside the MPA. The reasons for this juxtaposition between fished and unfished *Acropora palmata* reef transects are unclear. However, benthic communities were also different between *Acropora palmata* reef sites inside and outside of the MPA (see Chapter 4) and this may be a factor. Unfished *Orbicella* reef transects had significantly higher mean biomass than any of the other habitat/fishing regime combinations, except for *Acropora palmata* reef fished transects, which was lower but not found to be significantly lower using the rank sum test. Overall, the results suggest that parrotfish biomass is affected by both fishing and habitat type and therefore these also have an effect on total rates of reef bioerosion.

The bioerosion due to parrotfish was completely dominated by species from the genus *Sparisoma*, but mostly by *Sparisoma viride* (Figure 6.6). Mean bioerosion by *S. viride* at all sites was 0.79 G and this was more than 2.5 times the mean bioerosion due to the next most important species – *S. aurofrenatum*. Mean bioerosion by *S. chrysopterum* (0.15 G) and *S. rubripinne* (0.13 G) was far higher than that for any of the *Scarus* species (Figure 6.6). These trends in

bioerosion were mostly replicated within each habitat type. *S. viride* contributed most to parrotfish bioerosion on hardgrounds (0.46 G), *Orbicella* reefs (0.98 G) and *Acropora palmata* reefs (0.86 G), however, the order of importance of the other species changed with habitat type. On hardgrounds *S. chrysopterum* was almost as important as *S. viride* contributing 0.45 G to the total mean bioerosion within those sites. The other species were minor contributors. Within *Orbicella* reef habitat *S. aurofrenatum* (0.45 G) was the second biggest contributor to bioerosion, followed by *S. rubripinne* (0.11 G). Both these species contribute 0.28 G to bioerosion within *Acropora palmata* reef habitat and other species added little to bioerosion within both reef habitat types.

Table 6.4 Parrotfish biomass within habitat types exposed to different fishing regimes and the results of post hoc Nemenyi comparisons. OR – *Orbicella* reef, PR – *Acropora palmata* reef, HG – Hardground, ns – no significant difference.

	OR Unfished	PR Fished	HG Unfished	OR Fished	PR Unfished	HG Fished
Biomass (g $100m^{-2}$)	2734 +/- 170	2251 +/- 181	1675 +/- 355	1620 +/- 183	931 +/- 302	503 +/- 137
no. of transects	46	31	45	45	17	9
PR Fished	ns	-				
HG Unfished	$\chi^2 = 26.47$ $p < 0.001$	$\chi^2 = 11.60$ $p = 0.041$	-			
OR Fished	$\chi^2 = 17.80$ $p = 0.003$	ns	ns	-		
PR Unfished	$\chi^2 = 27.15$ $p < 0.001$	$\chi^2 = 15.57$ $p = 0.008$	ns	ns	-	
HG Fished	$\chi^2 = 24.80$ $p < 0.001$	$\chi^2 = 16.12$ $p = 0.007$	ns	ns	ns	-

The effects of fishing are considered in Figure 6.6. Within hardground and *Orbicella* reef habitat types fishing reduced the total bioerosion due to parrotfish. Hardgrounds only had one site exposed to fishing pressure and therefore these results should be considered cautiously for this habitat type. However, parrotfish bioerosion was much reduced at the single fished hardground site, where the contributions of two large bodied species, *S. viride* and *S. chrysopterum*, were greatly reduced. Within *Orbicella* reef habitat, the reduction in bioerosion was due to *S. viride* which contributed much less quantitatively (1.33 vs 0.62 G; Figure 6.6) to bioerosion. The percent contribution of *S. viride* to total parrotfish bioerosion was also reduced but not by the same magnitude (62% unfished vs 42% fished). Bioerosion by the small bodied species *S. aurofrenatum* was much less affected by fishing (0.48 G – unfished vs 0.42G - fished). Within *Acropora palmata* reef habitat, parrotfish bioerosion was reduced at unfished sites, but it is not clear why this was so.

Table 6.5 Parrotfish abundance (no. 100 m^{-2}) on Grand Cayman. Dark grey = fished. Light grey = unfished. PR – *Acropora palmata* reef, SB – stump and boulder, OR – *Orbicella* reef, HG – hardground. * Don Fosters HG was not considered similar habitat to other hardground sites.

Site	Habitat	*Scarus vetula*	*Scarus taeniopterus*	*Scarus iseri*	*Sparisoma viride*	*Sparisoma aurofrenatum*	*Sparisoma rubripinne*	*Sparisoma chrysopterum*
Boggy Sands	PR	0.31	0.00	0.10	1.67	0.31	0.94	0.31
Cemetery	PR	0.00	0.00	0.28	0.74	0.46	0.28	0.00
Pallas PR	PR	0.00	2.58	1.67	0.83	1.92	0.42	0.17
Bullwinkle	PR	0.93	3.24	4.63	2.59	3.15	0.37	0.00
Prospect	PR	0.46	2.50	7.69	3.33	4.91	0.37	0.00
Manse	PR	1.11	3.06	5.46	1.85	1.48	0.09	0.00
Pallas SB	SB	0.21	3.33	1.04	0.00	1.88	0.52	0.10
Anchor	OR	1.11	1.67	4.17	2.50	2.22	0.00	0.00
Killer Puffer	OR	1.48	4.26	4.44	2.59	3.52	0.00	0.19
Eden Rock	OR	0.93	3.06	3.61	4.26	2.87	0.00	0.09
Don Fosters	OR	1.67	7.75	6.83	4.58	4.92	0.00	0.50
Armchair	OR	0.00	6.20	7.59	1.20	3.98	0.09	0.46
Pallas	OR	1.76	0.00	3.98	4.35	4.81	0.28	0.19
Prospect	OR	0.00	1.02	6.57	1.20	3.33	0.09	0.00
Spotts	OR	0.33	0.42	4.17	2.42	2.25	0.83	0.42
Manse	OR	0.09	1.20	2.22	0.65	2.78	0.19	0.00
Babylon	OR	0.42	3.75	5.83	1.67	3.44	0.21	0.10
Boggy Sands	HG	0.00	0.00	0.00	0.28	0.00	0.00	0.28
Anchor	HG	0.74	2.13	15.83	0.74	2.13	0.00	0.09
Killer Puffer	HG	0.65	1.67	1.48	0.37	0.37	0.00	2.04
Eden Rock	HG	0.19	1.39	0.37	1.11	0.19	0.00	0.56
Armchair	HG	0.00	0.00	0.00	0.00	0.00	0.00	2.41
Prospect	HG	0.00	0.09	1.48	0.09	1.94	0.19	0.09
Don Fosters*	HG	0.75	5.42	24.75	2.00	3.17	0.08	0.08

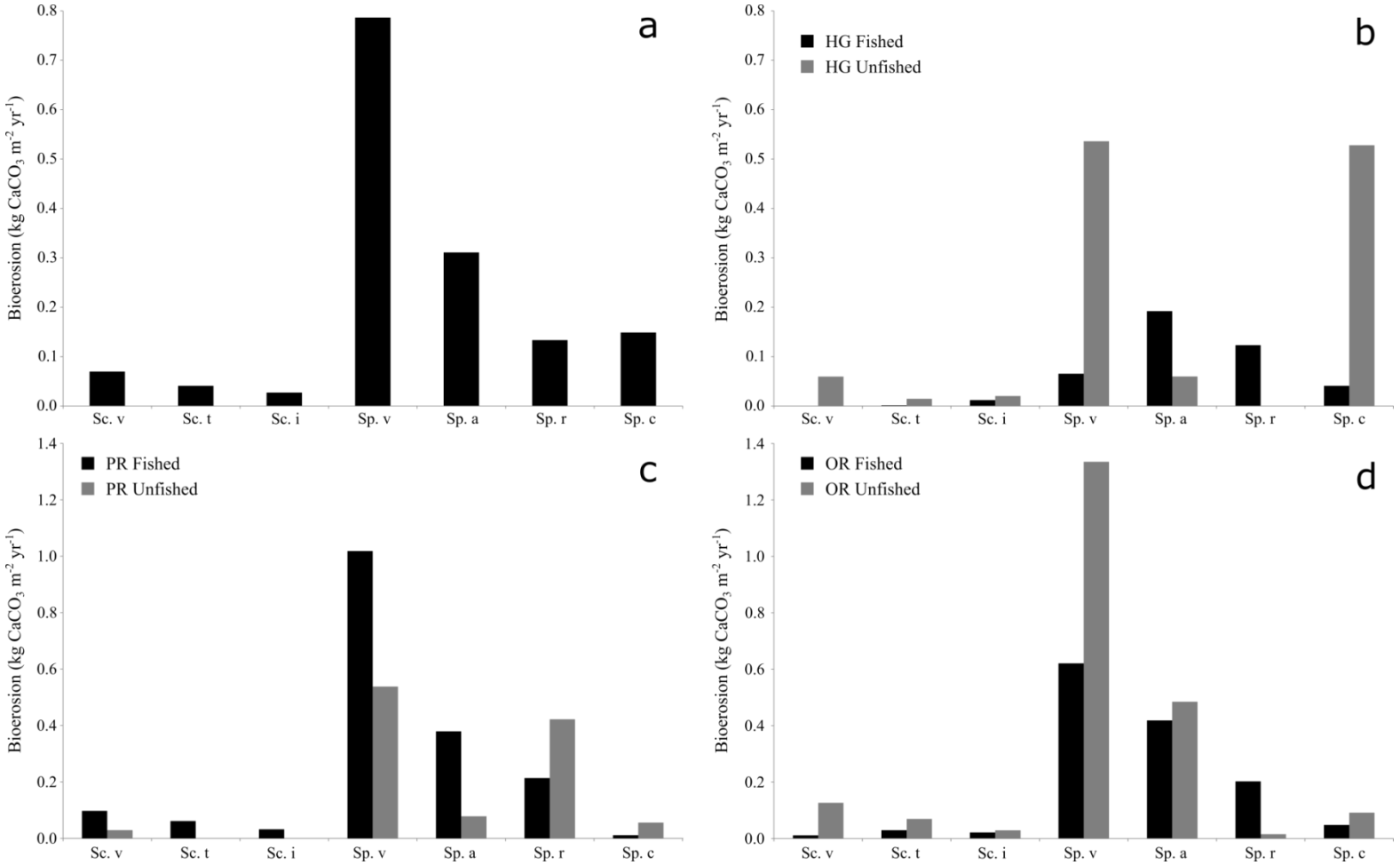

Figure 6.6 Bioerosion due to parrotfish species across all sites and within individual habitats. a – all sites, b – Hardgrounds (HG), c – *Acropora palmata* reef (PR), d - *Orbicella* reef (OR). Species: Sc. v – *Scarus vetula*, Sc. t – *Scarus taeniopterus*, Sc. i – *Scarus iseri*, Sp. v – *Sparisoma viride*, Sp. a – *Sparisoma aurofrenatum*, Sp. r – *Sparisoma rubripinne*, Sp. c – *Sparisoma chrysopterum*.

6.5 Discussion

6.5.1 *Bioerosion by endolithic organisms*

Estimations of bioerosion by micro-organisms varied from 10.6 – 37.1% of the total bioerosion at all sites, demonstrating the importance of these endolithic organisms to bioerosion on coral reefs. Habitat means are displayed in Table 6.2. The same basic rate of bioerosion was applied to transects within each habitat and therefore differences between habitats are controlled by the structural complexity measured on each transect along with an estimate of the area available to micro-endoliths. Hence, comparisons between the habitats do not reflect any actual differences in the rates of bioerosion by these organisms that might exist for different habitat types. Changes in the bioerosion rates by microorganisms from one environment to another probably occur but are poorly constrained generally. Vogel et al. (2000) report different micro-bioerosion rates on sheltered (0.52 G, 6 m) and exposed (0.27 G, 2 m) coasts of Lee Stocking Island, Bahamas. The same study also showed a decrease in micro-bioerosion with depth (0.135 G at 30 m, exposed). Nutrient enrichment may also alter micro-bioerosion rates, however, studies have found differing or unclear responses (Kiene 1997, Chazottes et al. 2002, Carreiro-Silva et al. 2012). Conversely, microbioerosion rates may be limited in certain environments – Tribollet (2008) suggested that turbidity, sedimentation and low grazing pressure can limit the development of micro-endolithic communities. Reductions in light availability due to sedimentation, turbidity and algal shading (from low grazing rates) may limit the light compensation depth (where photosynthesis = respiration) within reef substrata and therefore decrease penetration by autotrophic micro-organisms. Early stage (<6 months) micro-endolithic communities on shallow fore-reefs are dominated by cyanobacteria and chlorophytes (Vogel et al. 2000), and subsequently by a single chlorophyte species *Ostreobium quekettii* in mature communities (Chazottes et al. 1995, Vogel et al. 2000, Tribollet 2008). Hence, light availability is a key control on micro-bioerosion.

The effect of grazing pressure may be more complex. Some grazing organisms also cause bioerosion when feeding (Scoffin et al. 1980) and therefore much of the already micro-bioeroded substrate is also removed when these organisms feed. The light compensation depth for micro-endolithic communities migrates

deeper as the upper layers of substrate are removed by herbivore bioerosion and micro-endolithic communities respond by migrating similarly (Chazottes et al. 2002, Tribollet 2008). Most microbioerosion experiments using coral blocks only measure the residual microbioerosion (sensu Chazottes et al. 1995) after grazing (e.g. Vogel et al. 2000, Chazottes et al. 2002, Tribollet and Golubic 2005). The microbioerosion rate used here comes from such studies. Bioerosion by grazers reduces the measured microbioerosion rate by reducing the established micro-endolithic community (Grange et al. 2015). Low grazing rates (<0.5 G, Tribollet 2008) would allow the development of mature communities, but reduce the depth to which they could penetrate the substratum due to shading by macroalgae. Intense grazing rates would remove micro-endolithic communities before they could mature (Chazottes et al. 2002). Hence, the contributions of both micro-bioerosion and herbivore bioerosion to total bioerosion will vary depending on complex interactions between the two groups. For parrotfish and urchins, bioerosion is dependent on species and size (Bruggemann et al. 1996, Scoffin et al. 1980). Hence, more effective bioeroding grazers like *Sparisoma viride* and *Diadema antillarum*, in the Caribbean, would have a greater influence on the measured rates of microbioerosion in block experiments. It is unknown how parrotfish and urchin populations may affect microbioerosion within the habitat types investigated here.

For the purposes of understanding total bioerosion in a particular habitat or at specific sites, it is not important how much bioerosion is attributed to parrotfish or micro-endolithic communities, but rather only the sum of their contributions need be correct. However, moderate grazing may exacerbate the total bioerosion from both groups; regular cropping of micro-endolithic communities may stimulate rapid migration into the substratum, but encourage maximal abundances in upper substrate layers, which would reduce substrate density (Bruggemann et al. 1996; 21% of upper 0.3 mm of substrate removed by micro-endolithic communities) and ultimately facilitate bioerosion by herbivores (Chazottes et al. 2002). The bioerosion rates suggested here for micro-endolithic communities within hardgrounds, *Acropora palmata* reef and *Orbicella* reef habitats may be reasonable approximations for the correct values. However, it is clear that micro-endolithic communities are affected by many factors which have the potential to alter their rates of bioerosion. Key

areas of research required to address the unknowns include the effects of herbivory and exposure regimes.

Sponge bioerosion within reef habitats is also discussed in detail in Chapter 5 however, it is clear that these organisms can be significant contributors to total bioerosion on coral reefs and hardgrounds. Highest sponge bioerosion (0.204 G) was recorded at Don Fosters within a sheltered hardground habitat. Although this only accounted for 7.5% of the total bioerosion at this site, it is not a negligible quantity and in general sponge bioerosion was more important than bioerosion by sea urchins. Other studies have reported similar rates of sponge bioerosion to those reported here (e.g. 0.256 G on fore-reef environments in Bermuda – Rützler 1975). Studies that have investigated macrobioerosion on Indo – Pacific reefs report that bivalves and worms are often more important than sponges (Pari et al. 1998, e.g. Tribollet and Golubic 2005). The figures presented here for sponge bioerosion provide a conservative estimate for total macrobioerosion and have a similar range of values to those reported for the Indo-Pacific region (0.040 – 0.387 G, Tribollet and Golubic 2005; 0.02 – 0.14 G, Pari et al. 1998).

Environmental conditions can affect both sponge bioerosion and microbioerosion on coral reefs. Various studies have shown that nutrient enrichment can increase bioerosion by these endolithic communities (e.g. sponges – Rose & Risk 1985; Pari et al. 1998; Holmes 2000; Ward-Paige et al. 2005 and micro-endoliths – Carreiro-Silva et al. 2012). For Grand Cayman, nutrient enrichment of the surrounding waters may not be a major issue. Agriculture is minimal, there are no rivers and the island's population is relatively small (58,238 in 2014, source: Cayman Islands Economics and Statistics Office) in comparison to many other areas of the Caribbean. Additionally, a combination of the narrow shelf and wind driven waves may allow coastal water to mix well with the Caribbean Sea (Rigby and Roberts 1976), ensuring good water quality for most of the island. Water residence time along the sheltered west coast may be longer in certain areas than on more exposed coasts and therefore nutrient enrichment may affect localised areas. The Cayman Islands Department of Environment only monitor nutrients regularly in Georgetown harbour and so there are no data available for the reefs investigated here. However, I have personally observed a layer of black

sediment typical of anoxic environments within hardground habitat on the south-west coast. The lowest average wave energies were calculated for this area (Figure 2.3) and therefore water residence times may be greater for reefs at Eden Rock, Don Fosters and Armchair than at other shallow sites. Any nutrient enrichment in these areas may have a stronger influence on reef ecology, than at other sites where water mixing is perhaps greater. Although speculative, it is possible that tourism is having an impact on the levels of nutrients available to marine organisms (Baker et al. 2013) and promoting the growth of excavating sponges and/or micro-endoliths. 1.99 million people visited Grand Cayman in 2014 (source: Cayman Islands Economics and Statistics Office) and the only dump on the island is a landfill site in the western peninsula. Sewage and waste from such a large number of people may boost microbioerosion and/or macrobioerosion, beyond the rates reported here, via effluent release off the coast or through submarine groundwater discharge in areas where this may occur (Mioche and Cuet 1999, Ward-Paige et al. 2005, Paytan et al. 2006).

One sedimentary consequence of bioerosion by sponges in coral reef systems is the generation of fine carbonate sediments, in the form of small (mostly <125 micron) “chips” (Warburton 1958). This may be an important function for coral reef systems as many of the released chips can end up as fine sediments on beaches or in lagoons (Fütterer 1974). Most sponge species probably use a combination of chemical and mechanical methods to erode reef substrate (Zundelevich et al. 2007) and the proportion of calcium carbonate dissolved to chips produced is likely to be species specific (Nava and Carballo 2008). Estimations for this ratio for Caribbean species are limited but include 2-3% dissolution for *Cliona lampa* (Rützler and Rieger 1973). However, more recent studies suggest much higher dissolution rates for some species: *Pione* sp*., Red Sea* – 75% (Zundelevich et al. 2007), *Cliona vermifera*, Mexican Pacific – 28.7%, *Cliona flavifodina*, Mexican Pacific – 11.8 % (Nava and Carballo 2008). Hence, I cannot estimate the quantity of carbonate chips that would be produced by sponge erosion on Grand Cayman reefs with any confidence. However, sponge produced carbonate chips may not be an important contributor to sediment regimes within the Grand Cayman reef system. Acker and Risk (1985) suggest that the ultimate fate of sponge produced sediment is

off shelf transport on Grand Cayman, although their study area was restricted to a single site, which was located 0.5 km south of the site at Don Fosters.

6.5.2 *Bioerosion by grazing organisms*

Grazing by herbivores provides a number of ecosystem functions to coral reef systems (reviewed in Harborne et al. 2006). Bioerosion is one of those functions and on Grand Cayman reefs and hardgrounds it is currently provided by parrotfish (Figure 6.2). Urchins were locally important at shallow sites but only superseded parrotfish at one (Cemetery). Mean bioerosion by parrotfish within habitat types and exposure regimes was more than double that for any of the other bioeroding groups investigated (Table 6.2). Hence, variations in total bioerosion were almost always due to variations in parrotfish abundance and biomass (Figure 6.4). Only a handful of studies have attempted to estimate bioerosion by parrotfishes and the figures estimated here lie within the range reported for other Caribbean sites. Parrotfish bioerosion was reported as 0.061 G on a fringing reef in Barbados (Frydl and Stearn 1978) and ranged from 0.069 – 7.62 G on a sheltered reef system in Bonaire (Bruggemann et al. 1996), although for that particular study only *Scarus vetula* and *Sparisoma viride* were considered. Perry et al. (2014) assessed parrotfish bioerosion within the same habitats considered here using the same methods at various Caribbean sites. Mean parrotfish bioerosion was 1.56 G on hardground sites (n = 2 sites; from Grand Cayman and Bonaire). However one site was Don Fosters which is also reported here, but not included in the habitat mean (Table 6.2). On *Acropora palmata* reef sites mean parrotfish bioerosion was 1.76 G (n = 5 sites; Grand Cayman = 1, Belize = 3 and Bonaire = 1) and on *Orbicella* reef sites mean parrotfish bioerosion was 1.65 G (n = 6 sites; Grand Cayman = 2, Belize = 3 and Bonaire = 1). It should be noted that Grand Cayman sites in that study are also reported here. Despite the overlap in data, parrotfish bioerosion on Grand Cayman is fairly similar to the rates reported for the rest of the Caribbean.

Fished reef sites are commonly reported to have smaller parrotfish biomass than unfished ones (Mumby et al. 2006, O'Farrell et al. 2015). Additionally, studies show that parrotfish biomass decreases with depth (Bruggemann et al. 1996, Van Rooij et al. 1996, Nemeth and Appeldoorn 2009) and therefore

parrotfish bioerosion would be expected to decrease from *Acropora palmata* reef habitat to *Orbicella* reef habitat. Perry et al. (2012) report a decrease in mean parrotfish bioerosion from 5 to 10 m at Caribbean sites. However, a decrease did not occur on the sheltered coast of Grand Cayman which lies within the marine protected area, but did occur in the fished areas outside of the MPA on the south coast (Table 6.2). This result may have to do with the small size or isolated nature of the two patch reefs surveyed at 1 – 4 m on the sheltered coast. Larger parrotfish species tend to have larger territories (Mumby and Wabnitz 2002) and contiguous reef may be preferential habitat. Parrotfish range widely within contiguous reef but avoid moving over sand and rubble for large (>20 m) distances (*Sparisoma viride* – Chapman & Kramer 2000, *Scarus iseri* – Ogden & Buckman 1973). Hence isolation or small size of habitat area may reduce the populations of parrotfish and therefore comparisons between fished and unfished reef sites on Grand Cayman may only be appropriate within *Orbicella* reef habitat. Comparisons for hardgrounds may also be inappropriate because only one fished site was surveyed, and it is unlikely that this single site provides a good representation of all fished hardground areas. The biomass of parrotfish on *Orbicella* reef sites within the MPA was significantly higher than on *Orbicella* reef sites outside the MPA (Table 6.4). Although, sites inside and outside of the MPA are exposed to different wave energy regimes, *Orbicella* reef sites have similar benthic communities (Chapter 4) and therefore the differences in parrotfish biomass are probably due to fishing. Hence, fishing causes a reduction in bioerosion due to parrotfish and because total bioerosion is dominated by the contributions of parrotfish, fishing reduces this important function on Grand Cayman *Orbicella* reefs. Parrotfish bioerosion was 0.814 G less within fished *Orbicella* reef sites (Table 6.2) and this is 32% of what total bioerosion would be on fished *Orbicella* reef habitat if parrotfish biomass was similar to that in unfished areas.

Bioerosion by parrotfishes was dominated by a single species – *Sparisoma viride* (Figure 6.6). In all habitats this species contributed most to parrotfish bioerosion (51%) and was therefore the single most important species to total bioerosion. Fishing decreased the bioerosion function provided by *Sparisoma viride* and other parrotfish but there was no evidence that the loss was replaced by other organisms at fished sites. Functional redundancy may be generally

limited on coral reefs (Bellwood et al. 2003) and certainly for Grand Cayman *Sparisoma viride* is not functionally redundant. This species is the only *Sparisoma* species classed as an excavator; the others are classed as browsers (Bonaldo et al. 2014) and therefore they may not be as effective bioeroders as *S. viride*. The bioerosion calculations used here treat all *Sparisoma* species as *S. viride*, but use a species specific bite rate (Mumby et al. 2006). This is necessary because data only exist on erosion with each bite for two species in the Caribbean – *Scarus vetula* and *Sparisoma viride* (Bruggemann et al. 1996). Hence, bioerosion by large browsers such as *S. chrysopterum* and *S. rubripinne* may be overestimated. These two species were minor contributors to bioerosion at coral reef sites (Figure 6.6) and so any errors are probably small. However, bioerosion by *S. chrysopterum* matched that by *S. viride* within hardground habitats (Figure 6.6) and it may be that total bioerosion is overestimated here for hardgrounds. *S. chrysopterum* contributed 34% to total bioerosion within hardground habitat. It should also be noted that other fish species contribute to bioerosion that are not considered here, partly because there are no data available and partly because these species are probably very minor contributors; Glynn et al. (1972) estimated bioerosion by pufferfish (*Arothron meleagris*) to be 0.030 G. However, this narrative identifies a large knowledge gap in our understanding of bioerosion by Caribbean fish species, other than *S. vetula* and *S. viride* and even for these species as data only exist for Bonaire. More research on bioerosion rates by parrotfish species is clearly required.

Urchin bioerosion was only important at a few shallow reef sites on Grand Cayman. Previous studies have reported high bioerosion rates for urchins; 9.7 G – *Diadema antillarum*, Barbados (Hunter 1977), 4.6 G – *D. antillarum*, US Virgin Islands (Ogden 1977), 3.9 G – *Echinometra lucunter*, US Virgin Islands (Ogden 1977). However, on Grand Cayman the maximum bioerosion rate recorded for urchins was just 0.933 G, at Cemetery where *D. antillarum* were relatively abundant. Due to their large size *D. antillarum* urchins are generally more important than other urchin species in terms of bioerosion (Scoffin et al. 1980, Perry et al. 2012). After the *D. antillarum* die off in the 1980s (Lessios et al. 1984, Bak et al. 1984) bioerosion by this species decreased markedly - 0.17 G Hubbard et al. 1990, 0.11 G for *Acropora palmata* reef habitat (Perry et al.

2014), 0.20 G for *Acropora palmata* reef habitat (this study). Populations have not recovered to pre-decline levels (Lessios 2005) and therefore the function provided by these organisms has not recovered. In the same time parrotfish abundances have fallen and therefore the Caribbean has seen a large drop in total bioerosion by herbivorous organisms.

6.5.3 *Bioerosion as an ecosystem function on Grand Cayman and implications for coral reefs in the Caribbean*

Our understanding of the ecosystem functions associated with bioerosion is limited by a lack of published studies which examine the consequences of bioerosion by different species or the impact of the quantities of substrate degraded to sediment. On Grand Cayman, bioerosion is dominated by external grazers and mostly by parrotfish. In the Caribbean context, bioerosion by herbivores has decreased since the 1970s (Perry et al. 2014) and perhaps even well before this time (Jackson 1997). Fishing pressure has removed much of the former influence of parrotfish (Mumby 2006) and disease curtailed the rising influence of *Diadema antillarum* (Lessios 1984). The ecosystem functions associated with the feeding methods of parrotfish and urchins have therefore been affected.

Bioerosion contributes to the function of sediment generation within coral reef systems and while bioeroding sponges, parrotfish and sea urchins all contribute it is the parrotfish that currently dominate this function on Grand Cayman (Table 6.2) and across the Caribbean (Perry et al. 2014). The sediment generated can contribute to reef growth (Hubbard et al. 1990), island growth (Perry et al. 2015a) or stores of sediment (Morgan and Kench 2014) in lagoons (Fütterer 1974), on beaches (Perry et al. 2015a) and in other sedimentary environments. On Grand Cayman lagoons form important sediment stores (Rigby et al. 1976, Li et al. 1998, Beanish and Jones 2002) but there is also a sand plain circumnavigating the island (Rigby and Roberts 1976) between shallow terrace and shelf edge reefs. Sediment transport regimes on Grand Cayman are predominantly from east to west (Rigby and Roberts 1976, Beanish and Jones 2002) in response to wind generated currents. Large stores exist in the sand plain along the west coast and much sediment is lost off shelf (Rigby and

Roberts 1976, Acker and Rick 1985) as storage areas have filled over time. Interestingly, the fringing reef on the shallow terrace of the south coast often joins with the deeper shelf edge reef through spur formations (Rigby and Roberts 1976) which link up in some areas. This happens rarely on the sheltered west coast, which may be a result of sediment accumulation (Rigby et al. 1976, Roberts 1983). Periodically, increased wave energy can remobilise the stored sediment and during storm events huge quantities of sediment can be moved or lost off the shelf edge. A consequence of storms coming from the north-west is often the remobilisation of sediment stored on Seven Mile beach – a hub for the tourist industry on Grand Cayman. Over time development for tourism has exacerbated the loss of sediment from seven mile beach during storms (Seymour 2000, Turner et al. 2013), leading to costly beach replenishment programs. The natural system of sustained replenishment through sediment production by reef and lagoon associated organisms (Johns and Moore 1988, Li et al. 1997) along with sediment generated through bioerosion (Morgan and Kench 2014, Perry et al. 2015a) is still in place and will replenish lost sediments over time. However, the sources of sediment are dependent on the health of the coral reefs and lagoons that surround the entire island. *Orbicella* reef on the south coast generates 0.814 G less sediment through parrotfish bioerosion than *Orbicella* reef habitats on the west coast. It is likely that this is due to fishing. If trends in parrotfish biomass identified here for fished *Orbicella* reefs are replicated through the extent of fished reefs which constitute the majority of the coastline then huge quantities of calcium carbonate framework are not being converted to sediment. Hence, fishing may be reducing the quantities of sediment supplied to stores in lagoons and on the sediment plain. On the west coast, this would directly affect the ability of the reef system to replenish Seven Mile beach. It may be possible to quantify the effect of fishing on beach replenishment by tracking sediment movement and linking this to generation by parrotfish. Specific species may be more important than others, not just in their ability to erode but also in where they choose to defecate.

Certainly this is also a concern for coral reefs in the wider Caribbean where many reefs are overfished. The impact of fishing, an anthropogenic disturbance regime, alters reef ecosystem function by reducing the quantities of sediment

generated through bioerosion and therefore environments which may rely upon a source of sediment to endure in the long term, particularly after a storm event, may be threatened. Many such areas may have access to sediment stores which may need to become depleted before the consequences of parrotfish removal can be observed. Any time lag would depend on the size of the store, the reduction of sediment input to the store and how often sediment is remobilised from within the store. Hence, it would be site specific.

In addition to generating large quantities of sediment, bioeroding herbivores like *D. antillarum* and *S. viride* also contribute to the control of algal populations on coral reefs (Ogden et al. 1973, Steneck 1988, Bruggemann et al. 1994b, Williams et al. 2001). Burkepile and Hay (2008) showed that different species of parrotfish played different roles in the suppression of macroalgal species such that several were needed to control algal populations. The same division of functional roles may operate between urchins and parrotfish in terms of creating the right environment for the settlement and growth of corals.

If this were true, recovery on Caribbean reefs may be dependent on healthy populations of both *D. antillarum* and various parrotfish. A recovery in *D. antillarum* populations has begun in some areas of the Caribbean but numbers are still relatively low (Lessios 2016). Urchin bites tend to be relatively shallow (Steneck 1986) and their grazing intensive within a small area (Ogden et al. 1973). Parrotfish utilise larger areas (Bruggemann et al. 1994, Mumby and Wabnitz 2002) and bite size is deeper; for both sets of herbivores bioerosion is size dependent (Scoffin et al. 1980, Bruggemann et al. 1996) and this may mean important ecosystem functions rely on large adults of particular species (Lokrantz et al. 2008, Bonaldo et al. 2014). Crustose coralline algae with thicker thalli cope better with parrotfish bites and those with thinner thalli cope better with urchin bites (Steneck 1986). Hence, herbivore communities may select for certain coralline species (O Leary et al. 2012). Coral species have been shown to preferentially recruit to some species of coralline algae (Morse and Morse 1996, O Leary et al. 2012) and therefore herbivore communities may have an indirect effect on coral recruitment for those species that preferentially recruit to coralline algae. Since, parrotfish dominate bioerosion on Caribbean coral reefs, one effect of fishing may be to reduce the intensity of grazing, which would affect coralline algae communities allowing progression from early successional

stages to more mature communities with thicker thalli (Adey and Vassar 1976, Steneck 1986) more often. Hence, the reduction in bioerosion by parrotfish from fishing on Grand Cayman may affect coral recruitment and this could be tested by examining the recruitment rates of coral species inside and outside of the marine protected area. However, it should be noted that the large decrease in live coral cover over the past 40 years may have reduced the intensity of grazing below a critical level, as the area covered by epilithic algae communities would have increased during this time.

6.6 Conclusions

Bioerosion on Grand Cayman is dominated by parrotfish and in particular by a single species, *S. viride*. Fishing reduced total bioerosion by 32% within *Orbicella* reef habitat and therefore the ecosystem functions provided by parrotfish bioerosion in this habitat have also decreased. It is likely that fishing has also decreased bioerosion within *Acropora palmata* reef and hardground habitats.

An ecosystem based approach to reef management may be best placed to consider the links between ecology, geomorphology and long term health of the coral reef system on Grand Cayman. To aid this, studies are required which investigate the links between individual species, their ecosystem functions and carbonate cycling within the wider coral reef system.

The carbonate framework budget: a synthesis of carbonate production and bioerosion

In this chapter I will revisit the research objectives described in Chapter 1, and briefly describe how the content in each of the proceeding chapters relates to each objective. To amalgamate the results, I present a carbonate framework budget for each of the three habitat types investigated (hardground, *Acropora palmata* reef, *Orbicella* reef) but also for the single stump and boulder site. I then discuss how habitats types on Grand Cayman relate to the carbonate budget states of reefs globally and conclude by discussing some of the applications of carbonate budgets to coral reef management.

7.1 Revisiting the thesis: research objectives and synopsis

A key theoretical assumption underpinning the methodology employed in this thesis is that the calcification and bioerosion rates used for each species are suitable within the sites investigated. Data on coral growth and density is plentiful for many Caribbean species; the synthesis of both over a year yields a calcification rate. However, there are very little data available for the calcification rates of calcareous encruster communities. Hence my first research objective sought to quantify a calcification rate for these communities on Grand Cayman within hardgrounds, *Acropora palmata* reef and *Orbicella* reef habitats. Chapter 3 presents the data associated with this experiment and improves the confidence in carbonate production estimates for each habitat. Additionally, calcification by encruster communities was investigated to a depth of 30 m and therefore this chapter significantly adds to the available data for the Caribbean. Calcification rates were much higher on the exposed south coast than on the sheltered west coast. The underlying causes of this difference may include undertow which might decrease water residence times and therefore increase the availability of essential nutrients and/or elements. A similar increase in

calcification rate was recorded by Roik et al. (2016) as exposure increased along a cross-shelf gradient in the central Red Sea. Although the Red Sea study did not compare similar habitats, it seems likely that increases in calcification by calcareous encruster communities in response to increasing exposure are a general phenomenon. Future carbonate production studies should take reef setting into account when considering an appropriate calcification rate for calcareous encruster communities.

Research objective 2 sought to improve the bioerosion rates available for excavating sponge species, which are the most important macroborers within Caribbean fore-reef habitats (Perry 1998). Chapter 5 describes two experiments to estimate bioerosion rates for two common excavating sponges, *Siphonodictyon brevitubulatum* and *Cliona tenuis*. Both experiments showed conclusively that bioerosion was linearly related to the visible tissue area of both species. For *Siphonodictyon brevitubulatum*, an α-growth-form sponge, larger fisutles at the surface indicated larger erosion cavities within coral heads. For *Cliona tenuis*, a β-growth-form sponge, visible tissue corresponds well with the excavated area beneath the sponge and the quantity of material eroded was similar across colonies. The evidence presented in Chapter 5 strongly suggests that sponges with different growth and excavation strategies have different relationships between the area of visible tissue and bioerosion rate. Hence, the original *ReefBudget* protocol (Perry et al. 2012) is only appropriate for a single species, *Cliona delitrix*, and a new approach to estimating sponge bioerosion was developed (objective 3). As a result, estimations of bioerosion by sponge populations on Grand Cayman were much improved and it is hoped that these methods can aid the monitoring of sponge bioerosion on Caribbean reefs into the future.

Chapters 4 and 6 estimate carbonate framework production and bioerosion (research objective 5) within three distinct habitats on Grand Cayman: hardgrounds, *Acropora palmata* reef and *Orbicella* reef. They also provide data for a single site within a stump and boulder habitat. Together these habitat types cover most of the submarine area on Grand Cayman to a depth of approximately 15 m (DaCosta-Cottam et al. 2009). They are also common habitat types throughout Caribbean reef systems. On Grand Cayman sand habitats are the only other significant contributor to submarine area along the

two stretches of coast investigated (west – 12 km, south – 14 km), exclusive of South Sound lagoon on the South coast. The results detailed in Chapters 4 and 6 describe the variation in carbonate framework production and bioerosion that occurs within *Acropora palmata* reef, *Orbicella* reef and hardground habitats on wave exposed and sheltered shorelines of Grand Cayman. Hence, they provide good estimates of the mean quantities of carbonate framework produced and biologically eroded and an important dataset relevant to understanding carbonate budget dynamics in the Caribbean.

Detailed census surveys in each habitat provided information on the biological drivers of both carbonate production and bioerosion (research objective 4). This information is essential for an ecosystems based approach to reef management, as it provides quantitative data on the providers of ecological functions. On Grand Cayman, bioerosion is dominated by parrotfish and in particular by the stoplight parrotfish, *S. viride*. Hence, this important ecosystem function is very dependent on a single species and this knowledge suggests the necessity of developing a specific management plan for *S. viride*. The biomass of parrotfish was significantly higher within *Orbicella* reef inside the marine protected area on the west coast, than in fished areas on the south coast. This raises important questions on the effects of protecting bioeroding parrotfish (particularly excavating species like *S. viride*) on recovering coral reefs. Do they help or hinder the recovery process? Future research into the functional roles of *S. viride* should target the costs of erosion by this species versus benefits from their role in controlling macroalgae and excavating sponges and in clearing space for coral settlement.

Carbonate production on Grand Cayman is relatively low in comparison to other Caribbean reefs at similar depths. Additionally, the morphology of coral structures produced on Grand Cayman reefs has most likely changed in synergy with anthropogenically induced changes to coral assemblages and is different within different habitats. Carbonate production was higher in *Orbicella* reef habitat than in *Acropora palmata* reef habitat, which is a reversal of a natural biophysical relationship; carbonate production should decrease with depth. Hence, there has been a change in the focal point for carbonate framework production on Grand Cayman reefs from shallow (<8 m) to deeper (8

– 15 m) reef locations which may have consequences for the geomorphology of the entire reef system, if this new status quo remains.

Chapter 3 identified higher calcification rates for calcareous encruster communities on the exposed south coast than on the sheltered west coast. Consequently, the benthic surveys described in Chapter 4 could recognise calcareous encrusters as major carbonate producers within exposed *Acropora palmata* reef habitat. If this calcification trend is a model for the Caribbean in general, it has important implications for reef management because calcareous encruster communities, but particularly coralline algae, are important in the maintenance of reef structures. In the wake of a major coral killing disturbance event, exposed habitats may be more resilient to habitat loss by physical and biological erosion than their sheltered counterparts, because coralline algae can grow more quickly.

The effects of wave energy on both carbonate production and bioerosion were also investigated in Chapters 4 and 6. This natural disturbance regime had an obvious structuring effect on benthic communities (Chapter 4) but had no clear effect on the rates of carbonate production and bioerosion for similar habitats on sheltered and exposed coasts. However, it is likely that wave energy regimes above a certain threshold (not reached at the sites investigated here) would reduce carbonate production (Chollett and Mumby 2012, Hamylton et al. 2013).

7.2 Carbonate framework budgets for coral reef habitats on Grand Cayman

As described in Chapter 1, a reef carbonate budget is the sum of gross carbonate production from corals and calcareous encrusters, as well as sediment produced within or imported into the reef, less that lost through biological or physical erosion, dissolution or sediment export (Chave et al. 1972). The carbonate budget concept can be applied to specific taxa or specific carbonate production and erosion processes e.g. Neumann and Land (1975) used a sediment focused carbonate budget to investigate sediment production and loss within the bight of Abaco, Bahamas. The concept can also be used to

investigate a variety of spatial areas and previous studies have investigated specific sites e.g. Bellairs reef, Barbados (≈ 0.02 km^2 Stearn et al. 1977, Scoffin et al. 1980) or larger spatial areas e.g. Kailua Bay, Hawaii (≈ 10 km^2, Harney and Fletcher 2003). However, studies assessing both carbonate production and bioerosion, using a census based approach, have historically investigated small study areas because of the quantity of survey work required (e.g. 0.025 km^2 at Uva, Panama – Eakin 1996; 0.32 km^2 at Vabbinfaru, Maldives – Morgan 2014) or have compared sites within different environmental regimes (e.g. Mallela and Perry 2007). Here, I have focused on habitat types and assessed carbonate framework production and bioerosion at 24 sites within an area of approximately 12.25 km^2 (*pers comm* J. Olynik, Cayman Islands Department of Environment). My study has investigated the natural variation of carbonate budget dynamics both between and within distinct habitat types, exposed to different wave energy regimes. Hence my study examined the dynamics of carbonate framework production and bioerosion at a level of detail similar to previous studies, but over a much larger spatial area.

7.2.1 *Habitat carbonate budgets*

Carbonate framework production was highest within *Orbicella* reef habitat (3.54 G) and although the mean for sheltered sites (3.87 G) was higher than that for exposed sites (3.21 G), there were no significant differences between the two exposure regimes. Both exposed and sheltered *Acropora palmata* reef habitats had the next highest rates of carbonate framework production (Table 7.1). Despite having different benthic communities, *Acropora palmata* reef habitats in different exposure regimes both produced 2.65 G. Only one stump and boulder site was investigated, but it had carbonate production rates of 1.61 G. On hardgrounds, mean carbonate framework production was unsurprisingly low (0.38 G). The biological erosion of carbonate framework was highest within sheltered *Orbicella* reef habitat (2.8 G) and significantly higher than that for exposed *Orbicella* habitat which was 1.76 G. It is likely that fishing contributes to the measured differences, because sheltered sites are within a marine protected area where fishing is banned. Bioerosion was similar within exposed and sheltered *Acropora palmata* reef habitats and on hardgrounds it was measured at 1.32 G (Table 7.1).

Net carbonate framework production or an estimate for the accumulation of 'in-place' reef framework is displayed in Table 7.1, for each habitat and exposure regime, along with similar estimates for other areas of the world. For reef frameworks, 'in-place' accumulation requires a positive carbonate budget and therefore net negative budget figures are indicative of a coral reef undergoing structural collapse (Eakin 2001). Only hardground habitat had a net negative budget figure (- 0.94 G) and this is expected since these habitats are broadly flat and show no evidence of 'in-place' framework accumulation. Hence, hardgrounds on Grand Cayman have a bioerosion-dominated framework production state (*sensu* Kleypas et al. 2001). At first glance Table 7.1 suggests that the net rates of carbonate production on Grand Cayman reefs are similar to estimates for other areas, however, many previous studies have investigated budgets on the scale of a whole reef, which have areas covering a range of net production states. This study has focused on specific habitats.

The stump and boulder site at Pallas reef (2–4 m) had very low rates of carbonate production and similar rates of bioerosion. Hence, this site had net production rates of + 0.05 G and signifies a reef that is in stasis with essentially no net addition or loss of carbonate framework. Coralline algae populations in this area are probably responsible for the maintenance of the relict *A. palmata* structures, many of which remain in place. However, physical erosion was not quantified and it is highly likely that this habitat is actually net erosional. Morgan (2014) estimated net carbonate production of + 13.3 G at 1 m on the Vabbinfaru reef platform in Male atoll, Maldives, which illustrates the naturally high net carbonate production rates of healthy shallow reef systems.

Both sheltered and exposed *Acropora palmata* reef habitats had similar rates of net production, at + 0.53 and + 0.30 G respectively. Although these habitats may be production-dominated (*sensu* Kleypas et al. 2001) the quantities are so low that they are essentially in a period of stasis with little or no net accumulation of framework. Again, physical erosion was not quantified and therefore, these habitats may also be net erosional. Mean net carbonate framework production was estimated to be much higher (+ 1.5 G) at 5 m within 4 sites from Belize and Bonaire (Perry et al. 2013).

Table 7.1 A calcium carbonate framework budget for distinct reef habitats on Grand Cayman along with net production estimates from other studies. Values for bioerosion are negative to indicate the removal of framework. SB – stump and boulder, PR – *Acropora palmata* reef, OR – *Orbicella* reef. Units in kg $CaCO_3$ m^{-2} yr^{-1}. Potential accretion in mm yr^{-1}.

Habitat	**Framework production**	**Framework bioerosion**	**Framework accumulation**	**Potential accretion**
SB	+1.61	-1.56	+0.05	0.33
Sheltered PR	+2.65	-2.12	+0.53	0.55
Exposed PR	+2.65	-2.35	+0.30	0.41
Sheltered OR	+3.87	-2.80	+1.07	0.85
Exposed OR	+3.21	-1.76	+1.45	0.90
Hardgrounds	+0.38	-1.32	- 0.94	–

Other estimations for net carbonate production

Location	**Habitat/Scale**	**Net Production**	**Study**
Bellairs reef, Barbados	whole reef	+4.48	Scoffin et al. 1980
Cane Bay, St. Croix	whole reef	+0.91	Hubbard et al. 1990
Uva Island, Panama, 1982	whole reef	+0.34	Eakin 1996
Uva Island, Panama, 1983	whole reef	- 0.19	Eakin 1996
Kailua Bay, Hawaii	whole reef	+0.89	Harney and Fletcher 2003
Rio Bueno, Jamaica	turbid reef	+1.24	Mallela and Perry 2007
Rio Bueno, Jamaica	whole reef	+1.90	Mallela and Perry 2007
4 sites, Caribbean	fore-reef, 5 m	+1.52	Perry et al 2013
Various sites, Caribbean	fore-reef, 10 m	+3.15	Perry et al. 2013
Vabbinfaru, Maldives	fore-reef, 1 m	+13.3	Morgan 2014
Various sites, Chagos	fore-reef, 10 m	+3.70	Perry et al. 2015b

The rates of net production on *Orbicella* reef habitat were much higher than other reef habitats on Grand Cayman, for both sheltered and exposed coasts. Although mean carbonate framework production was not significantly different between coasts, the rates of bioerosion were and hence, they are reported separately in Table 7.1. Net carbonate production was 1.07 G and 1.45 G in sheltered and exposed *Orbicella* reef habitats respectively. However, these

figures are much lower than estimates for other reef sites at similar depths (approximately 10 m): +3.15 G in Bonaire and Belize (Perry et al. 2013), + 3.70 G in the Chagos archipelago (Perry et al. 2015b). Hence, Grand Cayman reefs have subdued levels of net carbonate production over the depth range investigated.

7.2.2 *Reef growth and accretion estimates*

Measurable rates of reef growth (accretion) occur over very long periods of time and are therefore difficult to estimate from census based carbonate budget data, which provide a snapshot of carbonate dynamics at a specific point in time. However, I will attempt to do so here following the method of Perry et al. (2013), and suggest that the figures reported in Table 7.1 are reasonable estimates of the potential accretion (mm yr^{-1}) that would occur if carbonate budget dynamics remain the same over the next few centuries. Accretion is calculated as follows:

1. A portion of bioeroded framework is added to the estimates for net carbonate framework production; this is a measure of infilling due to bioeroded sediment (excludes dissolution by microborers) and a figure of 50% was calculated by Hubbard et al. (1990) for reefs at Cane Bay, St. Croix. Only 50% of bioerosion due to parrotfish is included as these fish may defecate randomly over the reef area, including in sediment repositories such as grooves. Subsequent remobilisation of this sediment by wave energy is likely to result in its export to lagoons or the sand plain circumnavigating the island. Off shelf transport is also likely (Rigby et al. 1976, Beanish and Jones 2002). It should be noted that the sediment produced by organisms like *Halimeda* spp. is not included, because there is currently a poor understanding of the quantities of sediment produced by their populations on coral reefs. However, *Halimeda* species had low benthic cover at all reef sites (0.9 +/- 0.2%) and may not be important in the habitats investigated.

2. Carbonate accumulation (kg $CaCO_3$ m^{-2} yr^{-1}) can be converted to potential accretion rates (mm yr^{-1}) using carbonate density (2.89 g cm^{-3}) and framework porosity (Kinsey and Hopley 1991). A framework porosity of 30% is assumed for Grand Cayman reefs as they are currently dominated by massive,

sub-massive and encrusting morphology coral assemblages. This suggests a density of 2.023 g cm^{-3} for accreting framework.

Hence,

(Net production + infilled sediment) / density = accretion potential

Estimates for accretion ranged from 0.3 – 0.9 mm yr^{-1} for Grand Cayman reefs, with highest rates occurring in *Orbicella* reef habitat. A model of reef accretion controlled by ephemeral storm events has been suggested by Blanchon et al. (1997) for the south coast of Grand Cayman. This suggests that storm generated rubble or carbonate framework export and import will be important to the accretion occurring within different reef habitats over long time periods. Evidence from cores suggest that the underling reef matrix of the reef crest and stump and boulder habitats is detrital in origin and composed of successive layers of a coral-cobble rudstone capped by coralline algae crusts. Hence, this area of the reef is progressively built up over time during major storm events (>5 m waves, Blanchon et al. 1997) by the destruction of coral stands both within the area and in the adjacent *Acropora palmata* reef habitat. Blanchon et al. (1997) suggested that the recurrence of hurricanes sufficiently powerful to cause major accretionary events is every 20 – 95 years and that this would provide sufficient time for the regeneration of the living coral communities.

Spurs in the *Acropora palmata* reef habitat have accreted differently; in-place framework growth by *Acropora* spp., *Orbicella* spp., and to a lesser degree other corals is evident from cores, with minor contributions from coralline algae crusts and infilling by sediment and coral rubble (Blanchon et al. 1997). Hence, this habitat must evade complete destruction by major hurricanes, although a portion of the carbonate framework produced within the habitat must be exported to adjacent habitats. Therefore, this habitat may have been an important source of larvae from surviving *A. palmata* adults, after major disturbance events caused by hurricanes and it is worrying that there are so few currently alive. Many of the *Orbicella* reef habitats (8–15 m) may occur below the wave base of even the most powerful storms and while they may avoid complete destruction, partial mortality from coral pruning, physical abrasion by rubble and sediment scour is unavoidable (Highsmith et al. 1980, Woodley et al. 1981, Edmunds and Witman 1991). Hence, at least some export of carbonate

framework to sand channels or adjacent habitats would take place. However, *Acropora palmata* reef habitat is separated from *Orbicella* reef habitat, along the south coast, by changes in slope which can be abrupt (up to 10 m relief; Blanchon and Jones 1995). Therefore the transport of large quantities of storm generated rubble may be impeded by steep slopes or buttress formations and may not progress further inshore. *Orbicella* reef habitats on the south coast of Grand Cayman have not been cored and therefore it is difficult to speculate on the composition of the underlying reef matrix. However, it seems likely that there would be a combination of both detrital and in-place framework. Therefore, it seems likely that carbonate framework production within *Acropora palmata* reef habitat supplements reef accretion within both stump and boulder and reef crest habitats, on the south coast. However, past accretion has occurred predominantly due to stands of *A. palmata* within both *Acropora palmata* reef habitat and the stump and boulder zone. Populations of this species are presently very low and this may mean that reef growth has stalled.

Global mean sea level is projected to increase by 26 cm – 82 cm by 2100 (IPCC 2014), with a mean projection of 47 cm by 2100 under emissions scenario RCP4.5 (relative to mean sea level from 1986 – 2005). Assuming, this change occurs over 100 years the rate of sea level rise would be 4.7 mm yr^{-1} which is in stark contrast to estimated sea level rise in the Caribbean over the past 2000 years (0.9 mm yr-1, Toscano & Macintyre 2003) and also the estimates for accretion on Grand Cayman reefs in Table 7.1. Additionally, Krasting et al. (2016) suggest that Atlantic regions may experience faster rates of sea level rise than the global average. Hence, actively accreting reef crest habitats will be essential for Caribbean reefs to keep pace with sea level rise and continue protecting coastal areas from wave energy. However, reef building taxa on many Caribbean reefs have suffered population declines. On Grand Cayman, accretion is estimated to be about an order of magnitude lower than conservative (RCP 4.5) estimates for global sea level rise. Wave exposed coasts will be affected most by changes in sea level.

7.3 Applications of carbonate budgets to reef management

A key benefit of census based carbonate budgets to the management of coral reefs is in the quantification of functional roles for species in terms of their contributions to carbonate production and bioerosion. This data can be used to develop a better understanding of how the functional roles of species contribute to the overall functioning of reef systems. For example while parrotfish are becoming more widely protected across the Caribbean to ensure ecological functions (Mumby et al. 2006), Kuffner and Toth (2016) point out that their role as bioeroders damages the existing physical structure and high rates of bioerosion may not be desirable everywhere. On Grand Cayman the marine protected area supports a higher biomass of parrotfish and the rates of erosion by *S. viride* are over twice that outside of the marine protected area within *Orbicella* reef habitat (Figure 6.6). This is an important finding and it is hoped that it may initiate a debate into the use of no fish zones in reef management. However, it is important to understand that higher bioerosion is not necessarily detrimental to coral reefs. The functional roles of individual species need to be considered and a single species may have several. Parrotfish are predominantly herbivorous and different species target different algal taxa providing different functions on coral reefs (O Leary and McClanahan 2010, Bonaldo et al. 2014). Bioerosion by excavating species is likely to be beneficial to the overall health of reef systems. However, there may be a biomass:substrate area ratio for individual species, which when exceeded causes more harm than good. It is suggested that the management of Caribbean coral reefs would benefit from an increased understanding of the functional roles of *S. viride* in relation to the available reef surface area (includes structural complexity) and how changes in biomass affect structural complexity, coral settlement and algal species. Additionally, the importance of *D. antillarum* should not be discounted and the reduction in ecological function caused by the mass die off in 1983/4 needs to be investigated.

Net rates of carbonate framework production can inform assessments of reef health (Perry et al. 2008) and provide a quantitative measure of functional performance. Net negative estimates are indicative of functional collapse (Eakin 1996) and net positives describe the rate of net habitat construction. Coral

cover is generally used as an important indicator of reef health and while useful, conclusions based on this descriptor can be misleading; percent live coral cover may conceal changes to the coral assemblage (Green et al. 2008) or colony sizes (Elahi and Edmunds 2007) which have important implications for future resilience.

This study provides evidence for a decrease in functionality associated with carbonate production and bioerosion on Grand Cayman coral reefs. The shallowest reef habitats (< 8 m) have been affected most and are now degraded versions of what they once were. Stump and boulder habitats are most likely net erosional when physical processes are considered, although it should be noted that only three transects were investigated. They have benthic communities consistent with hardground habitats and are now essentially algal reefs, which will lose their remaining structural complexity over time. It is likely that *Acropora palmata* reef habitats are experiencing a period of budgetary stasis; carbonate budgets were slightly net positive, but physical erosion may reduce this even to net erosional states. In addition to providing habitat for reef organisms, shallow reef habitats form important breakwaters that dissipate wave energy and protect coastal areas from erosion. Decreasing structural complexity has reduced this ecosystem service and rising sea levels will reduce it further as shallow reefs on Grand Cayman currently have little ability to accrete or build reef structures (Table 7.1). Carbonate budgets can help identify coastal areas most in danger from sea level rise and should be performed on the remainder of the south coast and along the north coast of Grand Cayman.

Orbicella reef habitats still provide many of the functions associated with carbonate production and bioerosion, although perhaps much reduced. These habitats may accrete slowly (0.9 mm yr^{-1}, dependent on physical export) and although habitat construction is diminished, it may be sufficient to maintain current reef communities. On Grand Cayman the marine protected area has maintained parrotfish biomass above that in comparable fished areas, but perhaps not at pre-coral decline levels. Do contemporary reefs have a reduced carrying capacity? The coral assemblage has changed and the combination of less carbonate production and less complex habitat constructors (fewer branched corals) make it likely that *Orbicella* reef habitat on Grand Cayman can no longer sustain the biomass of life it once could. This is an important

consideration in measuring the success of marine protected areas. Carbonate budgets, by measuring habitat construction can help develop an understanding of the carrying capacity of reef sites.

The marine protected area on Grand Cayman was implemented in 1986 and since then, coral reef degradation has occurred equally both inside and outside (this study), although it has been effective in maintaining higher fish biomass (McCoy et al. 2009, this study). Hence, protecting reef fish is not enough to halt/reverse the decline of coral reef systems in the Caribbean (Russ et al. 2015). Kennedy et al. (2013) recommended both local and global action. An ecosystems based approach to reef management in combination with research into the functional roles of species may be best placed to allow the recovery of reefs alongside economic development and the continued use of ecosystem services (World Bank 2010, Martin and Watson 2016).

Future research suggestions

- A next step in understanding carbonate dynamics on coral reefs is the development of methodologies which would allow the calculation of sediment budgets through census studies. Aspects of this, in terms of bioerosion have already been developed, however there are still large knowledge gaps, particularly in the contributions of carbonate sediment producers such as *Halimeda* spp.
- Sediment transport studies are an important aspect of the sediment budget as they inform on the pathways, sources and sinks of carbonate sediment within coral reef systems.
- There is also a role for coring studies in understanding how specific reefs have been constructed during the Holocene and their rates of accretion in relation to sea-level rise. We might expect a similar character of growth (the relation of in-place:detrital carbonate accumulation) at similar rates of sea level rise for a specific area.
- Additionally wave propagation studies will provide information on how wave energy affects coastal zones in the lee of fringing or barrier reefs and subsequent modelling may be used to constrain potential effects of sea level rise.

- Ocean acidification may well decrease calcification rates on coral reefs and therefore it is important to monitor calcification of both corals and encruster communities as sea water pH decreases.
- The functional roles of herbivores are key to understanding recovery processes on Caribbean coral reefs. Investigations into herbivore biomass, species functional roles and reef complexity or surface area would allow reef managers to begin to link population sizes with an estimated functional performance. Modelling studies may be best placed to understand the effects of changing herbivore populations on recovery dynamics.

Management suggestions for Grand Cayman

- Categorise functionally important species and develop specific management plans for their populations on Grand Cayman which link abundance with specific ecosystem functions. Suggested species are:
    - *Sparisoma viride*
    - *Diadema antillarum*
    - *Acropora palmata*
    - *Acropora cervicornis*
    - *Orbicella annularis*
    - *Orbicella faveolata*
- Use sediment transport studies to constrain sediment pathways, sources, sinks and off reef export.
- Carbonate budget studies of the shelf edge reefs around Grand Cayman.
- Carbonate budget studies along the North Coast.
- Existing habitat maps for Grand Cayman do not identify reef habitat types, but instead designate all as ‘Spur and Groove’. This study has demonstrated clearly that carbonate production and bioerosion vary significantly between habitat types and identifying the area extent of each habitat type (stump and boulder, *Acropora palmata* reef, *Orbicella* reef) would allow the combination of budget dynamics with spatial analyses. This spatial approach may be particularly useful in characterising coastal areas most susceptible to sea level rise.

- Coring studies may be useful in identifying the pace and character of reef accretion during the Holocene within habitat types, which could be combined with contemporary carbonate budget studies to model predicted reef accretion over the next century.
- Models of wave energy propagation across the shelf could be used to understand the effects of sea-level rise and storm surge along vulnerable coastal areas. This approach may be particularly valuable if combined with an understanding of how reef structural complexity dissipates wave energy. Estimations of the value of reef recovery to coastal protection could then be provided to policy makers and the general public.
- Assessments of water chemistry focusing on parameters that affect calcification (e.g. pH, aragonite and calcite saturation states, dissolved inorganic carbon, respiration) in association with calcification rate studies for both corals and coralline algae.

Appendices

Appendix A – Calcification rates

Table A.1 Calcification rates used for taxa within *Acropora palmata* reef, stump and boulder and hardground habitats. Mean extension and density rates sourced from published Caribbean data, available online: http://geography.exeter.ac.uk/reefbudget/datasets/

Taxon	Mean Extension rate (cm/yr)	Mean Density (g/cm^3)	Mean Calcification ($g/cm^2/yr$)
Acropora cervicornis	11.560	1.955	22.600
Acropora palmata	0.600	1.814	1.088
Acropora prolifera	0.700	1.8845	1.319
Agaricia agaricites	0.254	1.825	0.464
Agaricia fragilis	0.254	1.849	0.470
Agaricia grahamae	0.254	1.849	0.470
Agaricia humilis	0.254	1.849	0.470
Agaricia lamarcki	0.254	1.849	0.470
Agaricia tenuifolia	0.254	1.849	0.470
Agaricia undata	0.254	1.849	0.470
Crustose coralline algae			0.056
Colpophyllia natans	0.809	0.783	0.633
Dichoenia stokesii	0.504	2.300	1.159
Diploria clivosa	0.441	1.403	0.619
Diploria labyrinthiformis	0.386	1.605	0.620
Diploria strigosa	0.495	1.200	0.594
Dendrogyra cylindrus	0.504	1.544	0.778
Eusmilia fastigiata	0.700	1.300	0.910
Favia fragum	0.500	1.544	0.772
Isophyllastrea rigida	0.388	1.544	0.599
Isophyllia sinuosa	0.388	1.544	0.599
Leptoceris cucullata	0.254	2.025	0.514
Manicina areolata	0.504	1.544	0.778
Macroalgae/CCA			0.056
Madracis carmabi	2.140	1.64	3.510
Madracis decactis	2.140	1.64	3.510
Madracis formosa	2.140	1.64	3.510
Madracis mirabilis	1.880	1.64	3.083
Madracis pharensis	2.140	1.64	3.510
Madracis senaria	2.140	1.64	3.510
Meandrina danae	0.115	1.900	0.219

Meandrina meandrites	0.115	1.900	0.219
Millepora alcicornis	0.515	2.270	1.169
Millepora complanata	1.960	2.270	4.449
Orbicella annularis	0.882	1.576	1.390
Montastraea cavernosa	0.645	1.670	1.077
Orbicella faveolata	0.842	1.390	1.170
Orbicella franksi	0.498	1.820	0.906
Mussa angulosa	0.504	1.544	0.778
Mycetophyllia aliciae	0.504	1.544	0.778
Mycetophyllia danaana	0.504	1.544	0.778
Mycetophyllia ferox	0.504	1.544	0.778
Mycetophyllia lamarckiana	0.504	1.544	0.778
Mycetophyllia reesii	0.504	1.544	0.778
Other calcareous encrusters			0.056
Peysonellid algae			0.056
Porites astreoides	0.447	1.558	0.696
Porites branneri	0.447	1.558	0.696
Porites colonensis	0.447	1.558	0.696
Porites divaricata	2.623	1.115	2.925
Porites furcata	3.195	1.050	3.355
Porites porites	2.050	1.180	2.419
Scolymia spp.	0.504	1.544	0.778
Siderastrea radians	0.201	1.605	0.323
Siderastrea siderea	0.479	1.605	0.769
Solenastrea bournoni	0.504	1.544	0.778
Stephanocoenia intersepta	0.500	1.544	0.772
Stylaster roseus	1.238	2.270	2.810

Table A.2 Calcification rates for taxa within *Orbicella* reef habitat. Mean extension and density rates sourced from published Caribbean data, available online: http://geography.exeter.ac.uk/reefbudget/datasets/

Taxon	Mean Extension rate (cm/yr)	Mean Density (g/cm^3)	Mean Calcification ($g/cm^2/yr$)
Acropora cervicornis	12.308	1.955	24.062
Acropora palmata	0.600	1.814	1.088
Acropora prolifera	0.700	1.8845	1.319
Agaricia spp.	0.232	1.879	0.436
Agaricia agaricites	0.232	1.823	0.423
Agaricia fragilis	0.232	1.879	0.436
Agaricia grahamae	0.232	1.879	0.436
Agaricia humilis	0.232	1.879	0.436
Agaricia lamarcki	0.232	1.879	0.436
Agaricia tenuifolia	0.232	1.879	0.436
Agaricia undata	0.232	1.879	0.436
Crustose coralline algae			0.019
Colpophyllia natans	0.598	0.783	0.468
Dichoenia stokesii	0.200	2.300	0.460
Diploria spp.	0.553	1.420	0.785
Diploria clivosa	0.479	1.420	0.679
Diploria labyrinthiformis	0.511	1.640	0.838
Diploria strigosa	0.668	1.200	0.802
Dendrogyra cylindrus	0.769	1.568	1.206
Eusmilia fastigiata	0.700	1.300	0.910
Favia fragum	0.500	1.568	0.784
Hard Coral (branching)	5.387	1.493	8.043
Hard Coral (encrusting)	0.572	1.568	0.897
Hard Coral (massive)	0.511	1.568	0.801
Hard Coral (platy/foliose)	0.213	1.901	0.405
Isophyllastrea rigida	0.511	1.568	0.801
Isophyllia sinuosa	0.511	1.568	0.801
Leptoceris cucullata	0.232	2.025	0.470
Manicina areolata	0.842	1.568	1.320
Macroalgae/CCA			0.019
Madracis spp.	2.140	1.660	3.552
Madracis carmabi	2.140	1.660	3.552
Madracis decactis	2.140	1.660	3.552
Madracis formosa	2.140	1.660	3.552
Madracis mirabilis	1.880	1.660	3.121
Madracis pharensis	2.140	1.660	3.552
Madracis senaria	2.140	1.660	3.552
Meandrina spp.	0.115	1.900	0.219
Meandrina danae	0.115	1.900	0.219
Meandrina meandrites	0.115	1.900	0.219
Millepora alcicornis	0.515	2.270	1.169
Millepora complanata	1.960	2.270	4.449

Montastraea spp.	0.723	1.646	1.190
Montastraea annularis	0.888	1.664	1.478
Montastraea cavernosa	0.512	1.670	0.855
Montastraea faveolata	0.771	1.358	1.047
Montastraea franksi	0.511	1.820	0.930
Mussa angulosa	0.511	1.568	0.801
Mycetophyllia spp.	0.511	1.568	0.801
Mycetophyllia aliciae	0.511	1.568	0.801
Mycetophyllia danaana	0.511	1.568	0.801
Mycetophyllia ferox	0.511	1.568	0.801
Mycetophyllia lamarckiana	0.511	1.568	0.801
Mycetophyllia reesii	0.511	1.568	0.801
Other calcareous encrusters			0.019
Peysonellid algae			0.019
Porites astreoides	0.332	1.343	0.446
Porites branneri	0.332	1.343	0.446
Porites colonensis	0.332	1.343	0.446
Porites divaricata	3.398	1.115	3.788
Porites furcata	3.195	1.050	3.355
Porites porites	3.600	1.180	4.248
Scolymia spp.	0.511	1.568	0.801
Siderastrea radians	0.200	1.600	0.320
Siderastrea siderea	0.527	1.600	0.843
Solenastrea bournoni	0.511	1.568	0.801
Stephanocoenia intersepta	0.500	1.568	0.784
Stylaster roseus	1.238	2.270	2.810

Appendix B – Data underpinning Figure 4.2

Table B.1 Data for construction of the dendrogram in Figure 4.2. Numbers 1–83 correspond to individual transects, which are described in Table B.2

Begin	Column 2	Column 3
30+83 -> 84 at 95.03	11+105 -> 111 at 84.35	76+96 -> 138 at 78.48
29+84 -> 85 at 92.41	93+102 -> 112 at 84.24	16+130 -> 139 at 78.29
17+18 -> 86 at 91.92	22+24 -> 113 at 84.03	63+128 -> 140 at 77.86
35+40 -> 87 at 91.33	4+99 -> 114 at 83.9	49+50 -> 141 at 77.42
81+85 -> 88 at 91.32	47+110 -> 115 at 83.72	112+140 -> 142 at 76.85
33+80 -> 89 at 90.77	36+109 -> 116 at 83.63	118+137 -> 143 at 76.23
6+32 -> 90 at 90.27	71+75 -> 117 at 83.56	21+126 -> 144 at 75.9
2+65 -> 91 at 89.52	66+68 -> 118 at 83.54	10+111 -> 145 at 75.77
1+3 -> 92 at 88.97	97+104 -> 119 at 83.02	67+127 -> 146 at 75.64
41+91 -> 93 at 88.82	14+15 -> 120 at 82.94	143+146 -> 147 at 75.29
88+89 -> 94 at 88.64	82+115 -> 121 at 82.9	120+133 -> 148 at 75.11
55+69 -> 95 at 88.15	58+103 -> 122 at 82.52	25+135 -> 149 at 74.64
38+43 -> 96 at 87.81	79+100 -> 123 at 82.44	53+136 -> 150 at 74.48
44+77 -> 97 at 87.72	101+108 -> 124 at 81.78	139+141 -> 151 at 74.37
28+94 -> 98 at 87.63	23+113 -> 125 at 81.45	134+147 -> 152 at 73.55
37+39 -> 99 at 87.41	62+107 -> 126 at 81.43	34+142 -> 153 at 73.47
9+90 -> 100 at 87.15	54+117 -> 127 at 81.38	52+150 -> 154 at 73.14
56+59 -> 101 at 86.82	42+116 -> 128 at 81.27	144+153 -> 155 at 72.78
64+92 -> 102 at 86.16	114+119 -> 129 at 81.15	72+148 -> 156 at 71.77
57+95 -> 103 at 86.14	51+86 -> 130 at 80.91	145+155 -> 157 at 70.8
5+45 -> 104 at 86.07	27+125 -> 131 at 80.8	138+154 -> 158 at 70.25
12+73 -> 105 at 85.93	123+129 -> 132 at 80.66	151+152 -> 159 at 70.11
31+98 -> 106 at 85.8	19+20 -> 133 at 80.24	48+159 -> 160 at 69.13
60+61 -> 107 at 85.35	122+124 -> 134 at 80.03	158+160 -> 161 at 68.95
7+8 -> 108 at 85.31	26+131 -> 135 at 79.75	156+157 -> 162 at 66.34
74+87 -> 109 at 84.79	46+70 -> 136 at 79.48	149+161 -> 163 at 65.31
78+106 -> 110 at 84.66	121+132 -> 137 at 78.93	13+162 -> 164 at 58.53
go to column 2	go to column 3	163+164 -> 165 at 56.71

Table B.2 Transect ID. HG – Hardground, FRS – fore-reef slope, PR – Acropora palmata reef, OSG – Orbicella spur and groove, SB – stump and boulder.

Code	Location	Habitat	Code	Location	Habitat
1	Armchair	HG	43	Killer Puffer	OSG
2	Armchair	HG	44	Killer Puffer	OSG
3	Armchair	HG	45	Killer Puffer	OSG
4	Armchair	FRS	46	Manse	OSG
5	Armchair	FRS	47	Manse	OSG
6	Armchair	FRS	48	Manse	OSG
7	Babylon	FRS	49	Manse	PR
8	Babylon	FRS	50	Manse	PR
9	Babylon	FRS	51	Manse	PR
10	Boggy Sands	HG	52	Pallas	OSG
11	Boggy Sands	HG	53	Pallas	OSG
12	Boggy Sands	HG	54	Pallas	OSG
13	Boggy Sands	PR	55	Pallas	PR
14	Boggy Sands	PR	56	Pallas	PR
15	Boggy Sands	PR	57	Pallas	PR
16	Bullwinkle	PR	58	Pallas	PR
17	Bullwinkle	PR	59	Pallas	PR
18	Bullwinkle	PR	60	Pallas	SB
19	Cemetery	PR	61	Pallas	SB
20	Cemetery	PR	62	Pallas	SB
21	Cemetery	PR	63	Prospect	HG
22	Don Fosters	HG	64	Prospect	HG
23	Don Fosters	HG	65	Prospect	HG
24	Don Fosters	HG	66	Prospect	OSG
25	Don Fosters	HG	67	Prospect	OSG
26	Don Fosters	HG	68	Prospect	OSG
27	Don Fosters	HG	69	Prospect	PR
28	Don Fosters	OSG	70	Prospect	PR
29	Don Fosters	OSG	71	Prospect	PR
30	Don Fosters	OSG	72	Anchor	HG
31	Don Fosters	OSG	73	Anchor	HG
32	Don Fosters	OSG	74	Anchor	HG
33	Don Fosters	OSG	75	Anchor	OSG
34	Eden Rock	HG	76	Anchor	OSG
35	Eden Rock	HG	77	Anchor	OSG
36	Eden Rock	HG	78	Spotts	OSG
37	Eden Rock	OSG	79	Spotts	OSG
38	Eden Rock	OSG	80	Spotts	OSG
39	Eden Rock	OSG	81	Spotts	OSG
40	Killer Puffer	HG	82	Spotts	OSG
41	Killer Puffer	HG	83	Spotts	OSG
42	Killer Puffer	HG			

Appendix C – Data underpinning Figure 4.3

Table C.1 Data underpinning the MDS plot in Figure 4.3. Transect ID in Table B.2

Transect	x	y	Transect	x	y
1	1.01	-0.25	43	-0.01	0.67
2	1.4	-0.38	44	-0.07	0.23
3	1.36	-0.31	45	-0.29	0.31
4	-0.52	0	46	-0.57	0.57
5	-0.12	0.22	47	-0.47	0.07
6	-0.44	0.17	48	-0.92	0.83
7	-1.05	0.02	49	-0.62	-0.46
8	-1.15	-0.31	50	-0.16	-0.66
9	-0.86	0.32	51	-0.53	-0.18
10	2.04	0.16	52	-0.52	0.97
11	2.09	-0.24	53	-0.01	-0.44
12	1.7	-0.02	54	-0.01	0.48
13	1.58	1.34	55	-0.85	-0.37
14	1.02	1.12	56	-1.01	-0.32
15	1.38	0.58	57	-0.89	-0.2
16	-0.4	-0.14	58	-1.02	-0.13
17	-0.25	-0.63	59	-0.76	-0.33
18	-0.4	-0.68	60	0.83	-0.2
19	0.81	0.9	61	0.88	-0.51
20	0.87	0.43	62	0.84	-0.62
21	0.46	-0.51	63	0.58	-0.05
22	-0.15	-0.92	64	1.3	-0.18
23	-0.72	-0.98	65	1.1	-0.16
24	-0.28	-0.91	66	-0.45	0.37
25	-0.36	-1.58	67	-1.1	0.57
26	-0.54	-0.41	68	-0.44	0.54
27	-0.28	-0.85	69	-0.91	-0.49
28	-1.03	0.17	70	0.04	0.07
29	-0.88	0.14	71	-0.29	0.44
30	-0.8	0.03	72	1.16	0.42
31	-0.81	0.06	73	1.25	-0.58
32	-0.47	0.24	74	0.63	0.09
33	-0.64	0.11	75	-0.33	0.65
34	1.61	-0.64	76	0.36	0.5
35	0.75	-0.25	77	-0.21	0.47
36	0.55	0.04	78	-0.65	0.2
37	-0.3	0.15	79	-0.78	0.5
38	0.06	0.7	80	-0.93	0.1
39	-0.14	0.12	81	-0.96	0.07
40	0.51	-0.21	82	-1.26	0.23
41	1.46	-0.32	83	-0.71	0.08
42	0.72	-0.03			

Appendix D – Coral Reefs article

Reference:

Murphy, G. N., Perry, C.T., Chin, P., and McCoy, C. 2016 New approaches to quantifying bioerosion by sponge populations with applications to the coral reefs of Grand Cayman. Coral Reefs. doi:10.1007/s00338-016-1442-z

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REPORT

New approaches to quantifying bioerosion by endolithic sponge populations: applications to the coral reefs of Grand Cayman

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Abstract Bioerosion is a critical process on coral reefs, influencing reef structural integrity and complexity and generating significant amounts of sediment. Excavating sponges are important bioeroders, especially in the Caribbean where sponges dominate macroborer communities. However, the contribution of bioeroding sponge communities to total bioerosion on coral reefs is not well understood; census surveys are rarely employed by monitoring agencies, and there is little data on the erosion rates of different species. Here, we investigated bioerosion by two Caribbean sponge species with different growth forms (*Siphonodictyon brevitubulatum*—α-form and *Cliona tenuis*—β-form). We also described new approaches to estimating bioerosion by sponge communities. By categorising the growth form of different species, we applied newly developed bioerosion rates, along with a previously published rate for *C. delitrix*, to census surveys and use these to estimate bioerosion by sponge communities on Grand Cayman reefs. Results indicate distinct habitat preferences for the two most abundant sponge species, *C. tenuis* and *C. caribbaea*. Mean sponge bioerosion across eight sites was 0.1 kg $CaCO_3$ m^{-2} yr^{-1}. Visible cover by α-growth-form excavating sponges caused a disproportionately high level of bioerosion in comparison with cover by β-growth-form species. Therefore, it is important to consider growth forms and excavation strategies when assessing bioerosion by sponge communities. Our present level of understanding of bioerosion by sponge species is limited, and more research is clearly required. However, the approaches described here can generate instant, meaningful results on sponge abundance and bioerosion and would complement many current benthic monitoring regimes. Furthermore, they create a framework for the provision of data, which is relevant to both coral reef management and to developing our understanding of how bioeroding sponge populations influence reef structure and carbonate budgets.

Keywords Bioerosion · *Cliona tenuis* · *Siphonodictyon brevitubulatum* · Caribbean · Excavating sponge

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Introduction

The biological erosion of hard substrates (bioerosion; sensu Neumann 1966) occurs through the feeding and excavating activities of a range of external grazers, including various parrotfish (Bruggemann et al. 1996), urchins (Bak 1994) and both macro- and micro-endolithic taxa (reviewed in Hutchings 2011). On coral reefs, bioerosion is a critical process that can influence reef structural integrity and complexity (Goreau and Hartman 1963; Scott and Risk 1988) while generating significant amounts of sediment (Fütterer 1974). The sediment produced is often important as a contributor to reef framework accretion (Hubbard et al. 1998) and also as a source of reef island sediment (Perry et al. 2015). Bioerosion is also a key determinant of

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carbonate budgetary states on coral reefs (i.e., the balance between calcium carbonate production and erosion; Perry et al. 2008, 2014a). Rates of bioerosion greatly in excess of carbonate production have been measured at some reef sites, resulting in net erosional carbonate budgets (e.g., −6.9 kg $CaCO_3$ m^{-2} yr^{-1}; Edinger et al. 2000). Although their contribution to total bioerosion may often be less than external grazers, endolithic macroboring taxa can be responsible for a significant proportion of bioerosion occurring on coral reefs (e.g., 1.2 kg $CaCO_3$ m^{-2} yr^{-1}; Tribollet and Golubic 2005). In the Caribbean, most macroboring communities are volumetrically dominated by bioeroding sponges, particularly in fore-reef habitats where sponges commonly contribute over 90% of substrate removal (MacGeachy and Stearn 1976; Scoffin et al. 1980; Perry 1998).

Despite the importance of sponges to reef bioerosion, species-specific erosion rate data are limited (e.g., Schönberg 2002) and only a few studies have attempted to investigate the relative contributions of sponge species to total bioerosion on coral reefs (e.g., Perry et al. 2014a). However, there is a growing consensus that understanding sponge bioerosion is vitally important to the management of coral reef systems, particularly from the perspective of understanding carbonate budget dynamics (Perry et al. 2008). It has been widely reported that reefs affected by nutrient enrichment support larger sponge populations (Rose and Risk 1985; Holmes 2000; Ward-Paige et al. 2005), which inevitably leads to increased sponge bioerosion on reefs affected by agricultural run-off, sewage or other sources of nutrients. Additionally, ocean acidification is likely to increase the rates at which endolithic sponge species erode (Fang et al. 2013; Wisshak et al. 2014; DeCarlo et al. 2015). Hence, a major concern for the management of coral reefs must be that atmospheric changes, which influence ocean pH and temperature, in association with localised anthropogenic influences, will increase bioerosion while simultaneously decreasing the ability of coral reef communities to calcify. Such a scenario would push reefs towards negative carbonate budget states (Perry et al. 2014b), threatening reef growth (Perry et al. 2013) and potentially leading to catastrophic habitat loss (Eakin 2001). Hence, there is an urgent need to better understand how sponge populations contribute to overall bioerosion and how the rates and patterns of bioerosion are changing on coral reefs, while integrating this knowledge into monitoring and management efforts.

Recent attempts to investigate bioerosion by sponge populations have involved methods that relate the percentage cover of bioeroding sponge tissue to erosion rates (e.g., Perry et al. 2012 for the Caribbean and Calcinai et al. 2011 in the Adriatic). In the Caribbean, Rose and Risk (1985) correlated the visible presence of bioeroding sponge tissue with a predicted bioerosion rate. Published data on the relationship between the rate of bioerosion by macroborers and the volume of substrate removed (Scoffin et al. 1980; Chazottes et al. 1995; Tribollet and Golubic 2005) was used with data relating the volume of substrate excavated by *Cliona delitrix*, a common Caribbean sponge, to the visible tissue area on the surface of individual coral heads. While this approach provided an initial step towards understanding and monitoring population level bioerosion, it is not clear how suitable this relationship is for species other than *C. delitrix*. Typically, bioeroding sponges have three growth forms (α, β or γ; Vosmaer 1931) and different species can grow in only one form or change forms as they mature. A species will typically erode either large single cavities (Fig. 1c) or a series of small interconnected chambers (galleries; Fig. 1f). In the α-form, only the inhalant and exhalant fistules are visible and most of the tissue is hidden. In the β-form, the sponge encrusts the substratum above excavated galleries or cavities. γ-form sponges become massive, overgrowing the surrounding substratum. It is thus reasonable to hypothesise that the relationship between the area occupied by visible tissue and the volume of internally eroded substrate is likely to be inherently different for species with different growth forms (α, β or γ) and endolithic chambers (galleries or cavities). However, these relationships are at present poorly understood.

We investigated the relationship between excavated substrate and visible tissue area for two common Caribbean sponge species, *C. tenuis* Zea and Weil (2003) and *Siphonodictyon brevitubulatum* Pang (1973). Both species exhibit different growth forms to *C. delitrix*. *Siphonodictyon brevitubulatum* only grows in the α-form and individual sponges excavate a single cavity (Pang 1973) that contains the vast majority of tissue. Water exchange occurs through bright yellow inhalant and exhalant fistules, which are the only visible evidence of the sponge's presence within the substratum (Fig. 1a–c). *Cliona tenuis* is a brown, encrusting, β-growth-form sponge (Fig. 1d–f) that hosts endosymbiotic dinoflagellates (*Symbiodinium* spp.) and prefers shallow windward habitats (Zea and Weil 2003; López-Victoria and Zea 2005). This species excavates tissue galleries within the substratum and the visible area of epilithic tissue corresponds closely to the area of substrate excavated (López-Victoria et al. 2003). Our aim was, therefore, to expand the potential of using census-based sponge cover data to estimate rates of bioerosion at the growth form/species level and thus to improve our understanding of the impact of bioeroding sponge populations on coral reef carbonate budgets. We applied these newly developed approaches to estimating sponge bioerosion on Grand Cayman coral reefs using census surveys of individual sponge species.

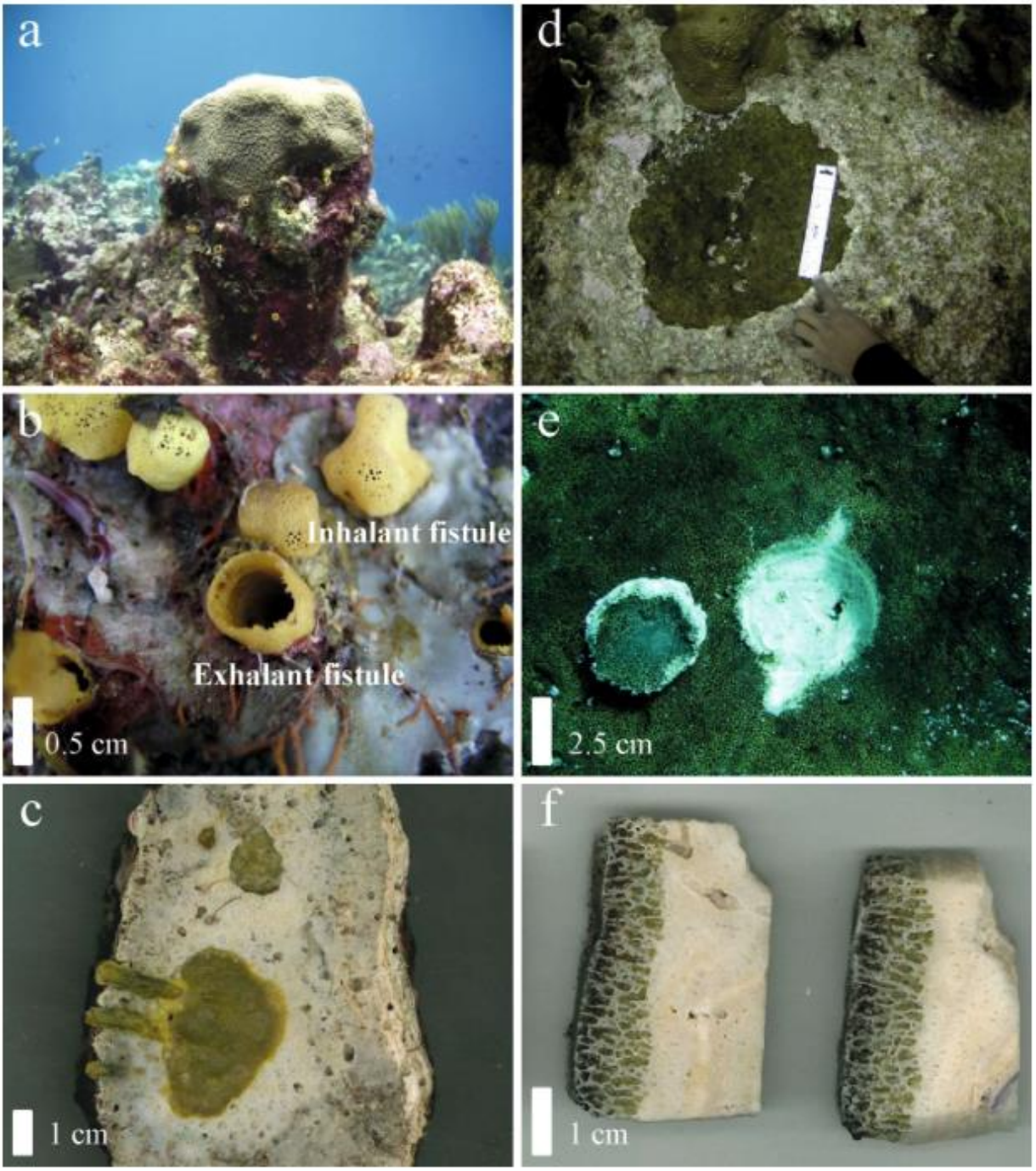

Fig. 1 Bioeroding sponge images showing visible tissue and endolithic structures. **a** Bright yellow fistules indicating the presence of *Siphonodictyon brevitubulatum* (α-growth-form) below the living portion of an *Orbicella annularis* colony. **b** Close-up of the inhalant and exhalant fistules of *S. brevitubulatum*. **c** Slab cut from an infested coral head illustrating the large cavities generated by *S. brevitubulatum* and fistules, which link the colony to the surface. **d** Roughly circular colony of *Cliona tenuis* (β-growth-form). **e** 5 cm core taken from *C. tenuis*. **f** Slabbed core from a *C. tenuis* individual illustrating the green tissue galleries that exist beneath the surface

Methods

Two different methods were used to calculate the relationship between visible sponge tissue at the substrate surface and the volume of substrate eroded. The method of Rose and Risk (1985) was adapted for use with *S. brevitubulatum*, while the method used for *C. tenuis* was based on an assessment of erosion in slabs cut from short cores of the coral substrate beneath the sponge. Both relationships were then used along with existing published data to estimate total sponge bioerosion at eight reef sites in Grand Cayman, northern Caribbean.

Calculation of a rate of bioerosion for *Siphonodictyon brevitubulatum*

Dead *Orbicella annularis* coral heads ($n = 25$, volume range 250–2800 cm^3) infested with *S. brevitubulatum* were removed from fore-reef spur and groove habitats at depths between 6 and 14 m, on the west and south coasts of Grand Cayman. After the removal, the coral heads were kept in sea water prior to an analysis of the number and dimensions of *S. brevitubulatum* fistules. Exhalant fistules had approximately circular oscula, and so the maximum dimension was used as a proxy for diameter. Inhalant fistules were irregularly shaped, and therefore, the maximum lengths and widths were recorded. Height was not recorded for either fistule type. Coral head volumes were estimated using water displacement (Rose and Risk 1985), and the surface area of each (excluding the base) was also measured by using tissue paper to conform to the coral head shape. After sponge fistule measurements were obtained, coral heads were cut into slabs [mean thickness = 1.53 cm, standard deviation (SD) = 0.35] using a wet saw and returned to fresh water to avoid desiccation. Slabs were then gently washed with water and blotted dry. Each slab was colour scanned at 600 dpi using a Ricoh Aficio MP C4500 multifunctional printer. A portion of *S. brevitubulatum* tissue was taken from each coral head to confirm species identity using spicule morphology (Schönberg and Beuck 2007).

The percentage cover of sponge tissue on the scanned images of both sides of each slab was measured by tracing around visible sponge tissue using ImageJ software (Rasband 1997–2014) with the Livewire plugin. Sponge tissue volume within each slab was calculated by multiplying mean cover by slab volume (mean slab area × slab thickness). Sponge tissue volumes were summed for each coral head and the percentage volume of sponge tissue within the coral head calculated, using the sum of all slab volumes. In this way, the percentage volume of sponge tissue within each coral head (i.e., the substrate removed through sponge erosion) was calculated so that it could be related to the area covered by fistules at the surface. Correlation was checked for significance using simple linear regression in the R statistical environment (R Development Team 2012) and the assumptions of linear regression verified using plots of the residuals and a Breusch–Pagan test.

Data generated from previous macroborer studies (Caribbean: Scoffin et al. 1980; Indo-Pacific: Chazottes et al. 1995; Tribollet and Golubic 2005) suggest that there is a strong linear relationship between the rate of bioerosion and the volume of substrate removed by macroborers. Equation 1 (Perry et al. 2012) describes this relationship:

$$\text{Bioerosion}\left(\text{kg m}^{-2}\,\text{yr}^{-1}\right) = 0.0636 \times \%\ \text{substrate volume removed} \quad (1)$$

Here, we calculated a relationship between the percentage cover of *S. brevitubulatum* fistules on the surface of coral heads and the volume of substrate removed from those coral heads. To calculate the rate of bioerosion (kg $CaCO_3$ m^{-2} yr^{-1}) by *S. brevitubulatum* on coral reefs, we substituted our newly developed relationship into Eq. 1 (see "Results").

Calculation of a rate of bioerosion for *Cliona tenuis*

The growth and erosional strategies of *C. tenuis* (and other β-form species) are so different to those of α-form species like *S. brevitubulatum* that a different method for extrapolating a relationship between visible tissue and bioerosion is required. Short 5-cm-diameter cores (recovered using a carpenter's brace and hole saw) were used to assess chamber development and depth of substrate erosion by *C. tenuis* ($n = 20$ cores taken from the centre of individual sponges). All cores were recovered in situ using SCUBA at a depth of approximately 5 m on the south coast of Grand Cayman. The underlying coral species was not considered during sponge selection because their identity was usually not possible to determine visually. Additional cores were recovered from across the tissue/substrate boundary to investigate the consistency of boring across the sponge; these cores revealed a rapid transition from the average boring depth to unbored substrate (G. Murphy pers. obs.). Tissue samples taken in situ from individual sponges were frozen upon returning to the lab. Subsequently, six tissue samples were randomly selected to confirm sponge species by spicule analysis (Rützler 1974; Zea and Weil 2003). Each core was left in fresh water overnight and subsequently cut into vertical slabs approximately 1 cm thick (Fig. 1f). Slab sides were scanned and investigated as described for *S. brevitubulatum*. The maximum depth of penetration of sponge tissue was recorded for each image and the highest value (1.4 cm) used in assessments of

tissue cover. A 1.4-cm-depth polygon was drawn around the area of each slab image. Lateral slab edges and any damaged or crumbling areas were avoided as tissue retention may have been affected by the coring or sawing processes. Sponge tissue was traced within this polygon and an average percentage cover was calculated from the cut slabs taken from each core. An overall mean was then calculated. This was assumed to be equivalent to the mean percentage of substrate eroded beneath *C. tenuis*, down to a standardised depth of 1.4 cm.

To calculate a rate of bioerosion for *C. tenuis*, the growth and boring strategies of gallery-forming sponges must be considered. These sponges excavate downwards forming tissue-filled chambers, which connect to an encrusting surface layer (Fig. 1d–f). López-Victoria et al. (2003) reported that *C. tenuis* and other gallery-forming species do not continue downward excavation once maximum penetration has been achieved, and therefore, only lateral expansion was considered in the calculation of a bioerosion rate. The expansion of an individual sponge is typically uniform in all directions (Acker and Risk 1985), but can be limited by competition, predation or substrate morphology; therefore, very large individuals are more likely to have irregular shapes. Field observations at our study sites suggested that most *C. tenuis* were less than 20 cm diameter and broadly circular. These observations concur with previous studies. González-Rivero et al. (2013) reported a size class structure for *C. tenuis* on fore-reefs (5–15 m) in Belize that was dominated by small individuals; 46.1% of individuals were <10 cm^2 (≈3.5 cm diameter). Additionally, López-Victoria and Zea (2005) reported that most *C. tenuis* individuals were in the 16–45 cm size class category on shallow (3–6 m) reefs from Isle del Rosario, Columbia. This suggests that *C. tenuis* populations on coral reefs are dominated by small individuals and that the area expanded by gallery-forming sponges can typically be described mathematically using an expanding circle as a model. This approach has been successfully employed by Gonzalez-Rivero (2012) to model the growth of *C. tenuis* and is also employed here for all gallery-forming species. Published lateral expansion rates of some excavating sponge species are displayed in Table 1. These data are from non-manipulated individuals in fore-reef habitats and thus integrate the effects of predation, competition and substrate relief. Species-specific expansion rates were used to calculate the area expanded and were then combined with a mean substrate density and the mean percentage of substrate eroded beneath *C. tenuis*. Bioerosion (kg $CaCO_3$ yr^{-1}) was estimated for each individual sponge and then summed for all of the sponges recorded within each transect. Average substrate density on Caribbean coral reefs was taken as 1.7 g cm^{-3} (Perry et al. 2012), based on a metadata assessment of 22 coral species from 27 separate studies. Equation 2 describes the calculation of bioerosion for an individual gallery-forming excavating sponge:

$$\text{Bioerosion} = \text{area expanded} \times \text{mean } \% \text{ substrate eroded} \times \text{substrate density}. \quad (2)$$

Surveying excavating sponge communities on Grand Cayman coral reefs

Census surveys were designed so that the abundance of each excavating sponge species would contribute to the total bioerosion estimate. Three 10-m transects were surveyed for bioeroding sponge species at eight sites around Grand Cayman (2–15 m depth; Fig. 2). Transects were laid perpendicular to shore on adjacent fore-reef spurs. Along each transect, we used a 0.5 m^2 quadrat to survey sponge tissue cover, alternating between sides of the transect line in a checkerboard fashion for a total planar area of 5 m^2 per transect. A single observer could complete all three transects for a site within a single dive. While recording data, one of three different approaches was required depending on the species being observed. The first approach was used for sponge species, which excavate tissue galleries (e.g., *C. tenuis*, *C. aprica*)—the areas of individuals within each quadrat were recorded. The second approach was used for *S. brevitubulatum*, a cavity-forming sponge, which only exhibits the α-growth form—fistules within quadrats were individually measured as previously described. The third approach was used for *C. delitrix*, a cavity-forming sponge, which exhibits the α-, β- and γ-growth forms—cover was measured by estimating the papillar zone (sensu Calcinai et al. 2011), the area surrounding fistules and/or tissue from the same sponge. In the field, this method can sometimes be subjective; however, following Chaves-Fonnegra and Zea (2011), we assumed that *C. delitrix* tissue portions within 10 cm of one another belonged to the same sponge. Percentage cover by species was determined and used to calculate bioerosion by the cavity formers (Eq. 3 for *C. delitrix* and Eq. 4 for *S. brevitubulatum)* (see "Results"). Bioerosion by the gallery formers was calculated on a per sponge basis using Eq. 2.

$$\text{Bioerosion}\left(\text{kg m}^{-2}\,\text{yr}^{-1}\right) = 0.0237 \times \textit{C. delitrix}\ \%\ \text{cover (Perry et al. 2012)}. \quad (3)$$

Results

Bioerosion by *Siphonodictyon brevitubulatum*

The volume of *S. brevitubulatum* tissue within 25 dead *Orbicella annularis* coral heads, and therefore the quantity of

Table 1 Published lateral expansion rates for tissue gallery-excavating clionaid sponge species

Species (growth form)	Substrate	Lateral advance (cm/yr^{-1})	References
Cliona tenuis (β)	Short algal turf (<10 mm)	3.4	Gonzalez-Rivero et al. (2012)
	Live coral tissue	4.3	López-Victoria et al. (2006)
	Turf algae	2.4	Ibid.
	Coralline algae	4.4	Ibid.
Cliona caribbaea (β)	Hard grounds	4.0	Acker and Risk (1985)
	Live coral tissue	5.5	Ibid.
	Live coral tissue	1.8	López-Victoria et al. (2006)
	Macroalgae	0.9	Ibid.
	Live coral	7.3 (median)	Rützler (2002)
Cliona aprica (α, β)	Live coral tissue	1.3	López-Victoria et al. (2006)

All data from non-manipulated sponges in natural settings

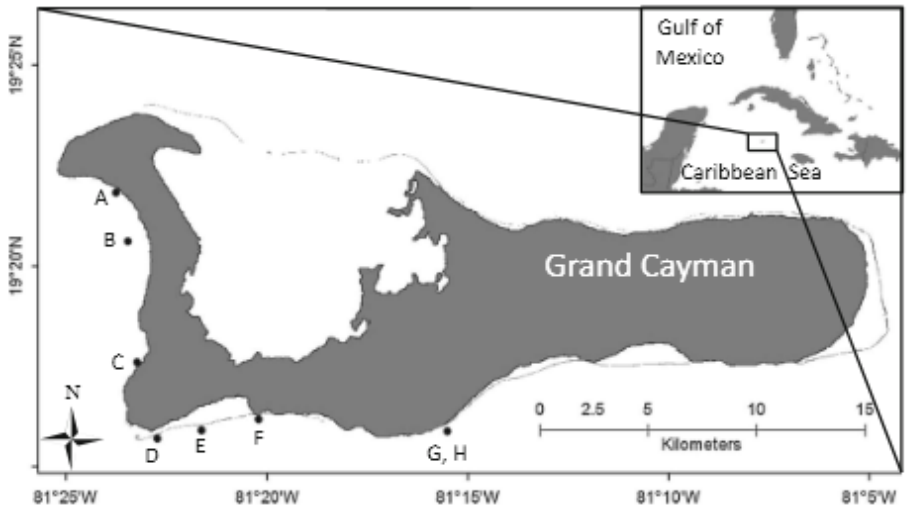

Fig. 2 Map of Grand Cayman, showing its location in the Caribbean and the surveyed sites; *A* Cemetery (depth ~2 m), *B* Killer Puffer (~10 m), *C* Eden Rock (~9 m), *D* Pallas (~3 m), *E* Bullwinkle (~9 m), *F* Prospect (~15 m), *G* Manse Shallow (~6 m) and *H* Manse Deep (~12 m)

substrate eroded, ranged from 0.79 to 46.88% (Electronic Supplementary Material, ESM Table S1). An additional coral head was so eroded that it collapsed before the sawing process and could not be included in the results, clearly demonstrating the capacity of sponge erosion to weaken coral framework. The volume of substrate eroded from the 25 coral heads was significantly proportional to the percentage of area covered by fistules on the coral heads ($F = 450.6, p < 0.001$). The linear regression yielded a high correlation coefficient ($r^2 = 0.95$) indicating a very strong relationship: % volume of substrate eroded = 11.328 × % cover of fistules.

We noted that one of the coral heads investigated had over twice the sponge percentage cover and tissue volume of any of the other coral heads. This data point greatly influenced the observed relationship above 1.5% fistule cover. However, since the assumptions of linear regression were rigorously tested (including an assessment of whether the relationship changed as the predictor increased; Breusch–Pagan test, BP = 1.589, $p > 0.05$), we have confidence in the strength of this relationship. Substituting this relationship into Eq. 1 yields Eq. 4:

$$S.\ brevitubulatum\ \text{bioerosion}\left(\text{kg m}^{-2}\,\text{yr}^{-1}\right) = 0.721 \times \%\ \text{cover of fistules} \quad (4)$$

This equation can thus be used to estimate bioerosion by *S. brevitubulatum* using visual census surveys of the inhalant and exhalant fistules. The relationship is illustrated in Fig. 3 and is forced through the origin to allow field survey use, i.e., 0% fistule cover is assumed to equal 0 kg $CaCO_3$ m^{-2} yr^{-1} erosion.

Bioerosion by *Cliona tenuis*

The depth of tissue penetration for 20 *C. tenuis* individuals was relatively consistent within individual cores (Fig. 1f). The maximum depth of penetration ranged from 0.9 to 1.4 cm (ESM Table 2), and the mean was 0.98 cm (SD = 0.12). On average, 20.56% (16.0–28.7%, SD = 3.16) of the substrate beneath *C. tenuis*, down to a depth of 1.4 cm, was excavated and filled with sponge tissue. This mean and the maximum penetration depth are inserted into Eq. 2 to allow the prediction of the quantity of substrate that will likely be eroded by an individual *C. tenuis* sponge over a year. Assuming a circular expansion model (Fig. 4), the area expanded by any sponge over a year can be calculated using the lateral expansion rates presented in Table 1. Here, we used a mean lateral expansion rate of 3.56 cm yr^{-1}, based on data from two studies (López-Victoria et al. 2006; González-Rivero et al. 2012). As an example, we calculated the area that a 10 cm^2 sponge (radius = 1.784 cm) would expand into over the course of a year and then bioerosion (g $CaCO_3$ yr^{-1}) can be calculated using Eq. 2:

Bioerosion by a 10 cm^2 *C. tenuis* individual over 1 yr

= area expanded × (20.56% × 1.4 cm) × 1.7 g cm^{-3}
= (new area − original area) × 0.489 g cm^{-2}
= ((π(3.56 + 1.784)^2) − 10 cm^2) × 0.489 g cm^{-2}
= 39 g $CaCO_3$ yr^{-1}.

Bioerosion by sponge populations on Grand Cayman coral reefs

A total of six excavating sponge species were observed across all of the investigated sites—*S. brevitubulatum*, *C. delitrix*, *C. aprica*, *C. tenuis*, *C. caribbaea* and *C. varians*. *Cliona varians* was the rarest, with only four individuals at two sites observed during all surveys. *Cliona delitrix* and *C. tenuis* were ubiquitous, and the remaining three species were only absent from surveys on Cemetery Reef, which was very shallow (~2 m). Benthic cover of the six observed excavating sponge species was low at all sites and ranged from 0.26% at Manse Deep (~12 m) to 2.56% at Pallas (~3 m), with a mean substrate cover (±SE) across all sites of 1.24 ± 0.3%. *Cliona tenuis* was the most abundant species at the four shallowest sites, Cemetery, Pallas, Manse Shallow and Bullwinkle (Table 2). On deeper reefs, both *C. caribbaea* and *C. aprica* tended to be more common and each formed the dominant species at two sites. The cavity-forming sponges contributed very little to the visible cover of excavating sponges at all sites, particularly *S. brevitubulatum*, which did not cover more than 0.015% of the substrate at any site (Table 2).

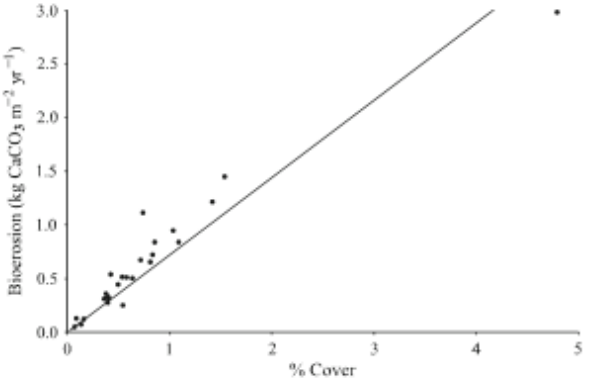

Fig. 3 Bioerosion by *Siphonodictyon brevitubulatum* relative to the percentage cover of inhalant and exhalant fistules derived from 25 dead *Orbicella annularis* coral heads

C. tenuis was the dominant bioeroder at the four shallowest sites (Table 2). Eden Rock was marginally deeper than Bullwinkle, and at this site, *C. caribbaea* was the most important excavating sponge, followed closely by *C. aprica* then *C. tenuis*. At Killer Puffer, *C. caribbaea* was also the most important excavating sponge. *Cliona aprica* contributed most to sponge bioerosion at the two deepest sites, but also had the least variable bioerosion rates of any species, ranging from 0.016 to 0.035 kg $CaCO_3$ m^{-2} yr^{-1} across all sites where it was observed (Table 2). *Cliona delitrix* and *S. brevitubulatum* contributed little to total sponge bioerosion at most sites; however, *S. brevitubulatum* was the second biggest contributor to bioerosion at Prospect making up 31% of the total (Table 2). The percent cover by *S. brevitubulatum* at this site was 12 times lower than that of *C. caribbaea*, the next biggest contributor to bioerosion at Prospect. This shows that the visible cover by excavating sponges is not always indicative of bioerosion by cavity- or gallery-forming species.

The relative contributions to substrate cover and bioerosion by cavity formers (*C. delitrix* and *S. brevitubulatum*) and gallery formers (*C. aprica*, *C. caribbaea*, *C. tenuis* and *C. varians*) are presented in Fig. 5. Bioeroding sponge cover was dominated by the gallery formers, which contributed more than 86% to the total cover of bioeroding sponges at all sites (Fig. 5a). Bioerosion by the gallery formers was also much higher than that estimated for the cavity formers at all sites. However, there was an obvious decrease in the contributions of gallery formers to total bioerosion with depth (Fig. 5b). At Prospect (~15 m), the cavity-forming sponges contributed just 5% to the total substrate cover by bioeroding sponges but 31% of total estimated bioerosion.

Total sponge bioerosion varied considerably among sites and ranged from 0.036 to 0.172 kg $CaCO_3$ m^{-2} yr^{-1} (Fig. 6). Mean sponge bioerosion (±SE) was 0.10 ± 0.02 kg

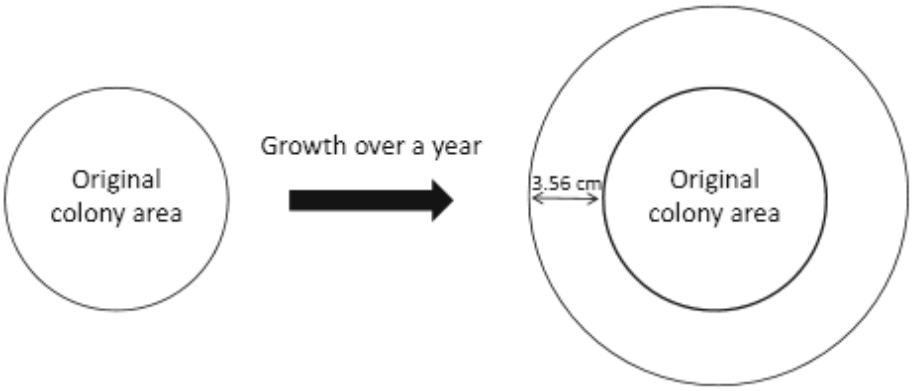

Fig. 4 A depiction of the circular expansion growth model for *Cliona tenuis*, using an annual lateral expansion rate of 3.56 cm yr^{-1}

Table 2 The percentage cover and bioerosion by six species of excavating sponge recorded at eight reef sites on the south and west coasts of Grand Cayman

	Cliona aprica	*Cliona caribbaea*	*Cliona tenuis*	*Cliona varians*	*Cliona delitrix*	*Siphonodictyon brevitubulatum*
% Cover						
Cemetery	–	–	0.250	0.038	0.033	–
Pallas	0.172	0.001	2.242	–	0.144	0.003
Manse Shallow	0.162	0.020	1.220	–	0.028	0.009
Bullwinkle	0.088	0.117	2.116	0.016	0.016	0.010
Eden Rock	0.446	0.328	0.138	–	0.016	0.005
Killer Puffer	0.465	0.824	0.149	–	0.238	0.005
Manse Deep	0.160	0.028	0.049	–	0.018	0.009
Prospect	0.137	0.187	0.015	–	0.009	0.015
Bioerosion (kg $CaCO_3$ m^{-2} yr^{-1})						
Cemetery	–	–	0.030	0.005	0.001	–
Pallas	0.028	0.002	0.113	–	0.005	0.003
Manse Shallow	0.027	0.003	0.047	–	0.001	0.011
Bullwinkle	0.016	0.009	0.132	0.004	0.001	0.011
Eden Rock	0.035	0.043	0.019	–	0.001	0.008
Killer Puffer	0.020	0.081	0.023	–	0.011	0.007
Manse Deep	0.025	0.007	0.005	–	0.001	0.008
Prospect	0.024	0.013	0.006	–	0.0003	0.019

Dashes indicate a species was not recorded

$CaCO_3$ m^{-2} yr^{-1}. In general, more bioerosion was found at sites with higher excavating sponge cover; however, the order of sites from highest to lowest was not mirrored by sponge cover. Bullwinkle had the most bioerosion of any site, but did not have the highest percentage cover of excavating sponges. Similarly, Cemetery had the lowest bioerosion of any site but Manse Deep had the lowest excavating sponge cover.

In addition to illustrating total bioerosion, Fig. 6 also compares bioerosion by the gallery-forming sponges using our method to rates using the method of Perry et al. (2012). Across all sites, calculated bioerosion by the gallery formers was consistently higher (1.7–5 times) using our method. The largest differences were observed at sites where total bioerosion was low—Cemetery, Manse Deep and Prospect. A similar comparison between the methods for cavity-forming sponges could not be made because of differences in data collection for *S. brevitubulatum*.

Discussion

We determined bioerosion rates for two excavating sponge species (*C. tenuis* and *S. brevitubulatum*) and developed new approaches to sponge census surveys, which cater for species-specific growth forms and differences in the mode of substrate excavation. In combination with the approach

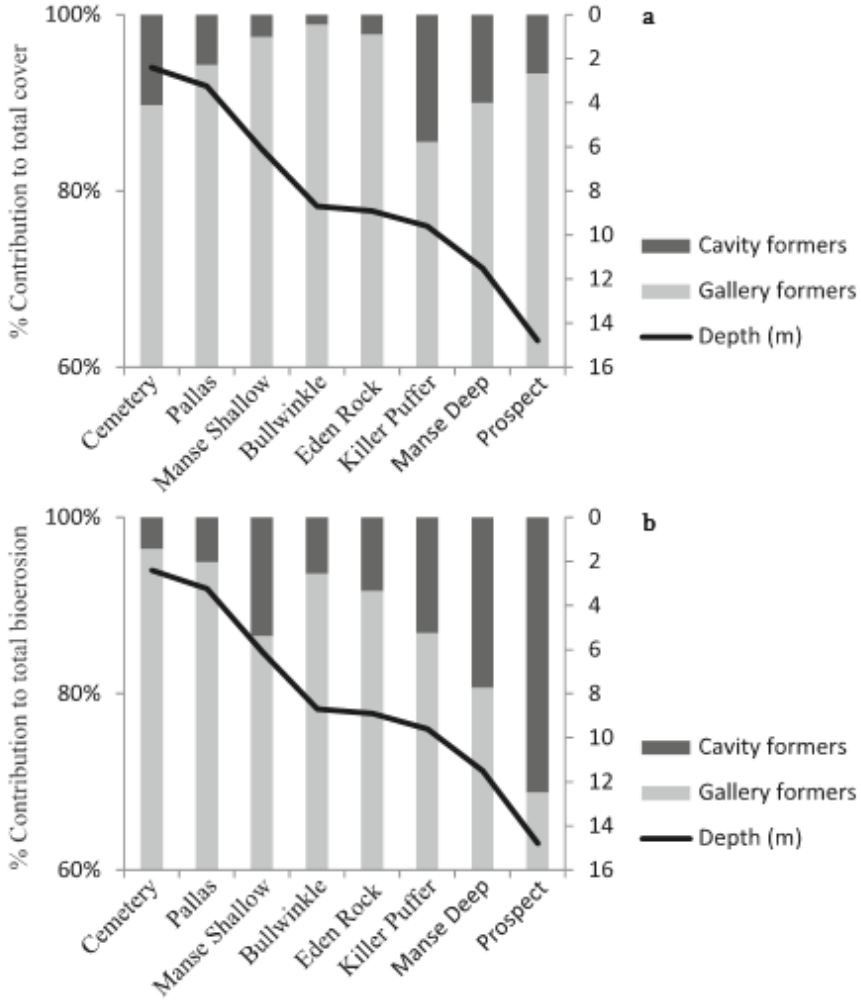

Fig. 5 Contributions of cavity-forming (*Siphonodictyon brevitubulatum* and *Cliona delitrix*) and gallery-forming (*C. aprica*, *C. caribbaea*, *C. tenuis* and *C. varians*) species to **a** the total percentage cover of the substrate and **b** total bioerosion, by excavating sponges at eight reef sites around Grand Cayman

developed for *C. delitrix* (Perry et al. 2012), this enables us to present an improved method for monitoring sponge erosion on Caribbean coral reefs. The approach developed for *C. tenuis* estimated bioerosion at 0.489 g $CaCO_3$ cm^{-2} of tissue and compares favourably with previous estimates for other β-form sponges, which excavate tissue galleries (e.g., *C. caribbaea* in Belize: 0.39 g $CaCO_3$ cm^{-2} of tissue; Rützler 2002). However, it should be noted that Rützler considered *C. aprica* and the then-undescribed *C. tenuis* as morphological variations of *C. caribbaea* (Rützler 2002; Zea and Weil 2003). Acker and Risk (1985) reported that 20% of the substrate was eroded down to 1 cm beneath *C. caribbaea* individuals (a lighter coloured variant of *C. caribbaea* was also described, which was probably *C. tenuis*) from the west coast of Grand Cayman and this figure compares well with that estimated here for *C. tenuis* (20.56% down to 1.4 cm). Despite differences in methods, locations and species investigated, the three studies present broadly comparable figures suggesting a high level of confidence in the data generated here for *C. tenuis*.

To estimate total sponge bioerosion on Grand Cayman reefs, we assumed that bioerosion beneath *C. tenuis* was broadly equivalent to that for other Caribbean gallery-forming species and that any differences in the rate of bioerosion could be explained by species-specific expansion rates. This assumption is necessary because of the lack of data on other Caribbean species, but there is some evidence to support it. Both Rützler (2002) and Acker and Risk (1985) found similar erosion beneath *C. caribbaea* to our findings for *C. tenuis*. Additionally, the maximum and mean depths of penetration of sponge tissue into the substratum are also broadly similar for gallery-forming species: *C. tenuis* max = 1.4 cm and mean = 0.96 cm, this study; *C. caribbaea* (and probably *C. tenuis*) max = 1.4 cm and mean = 0.9 cm, Acker and

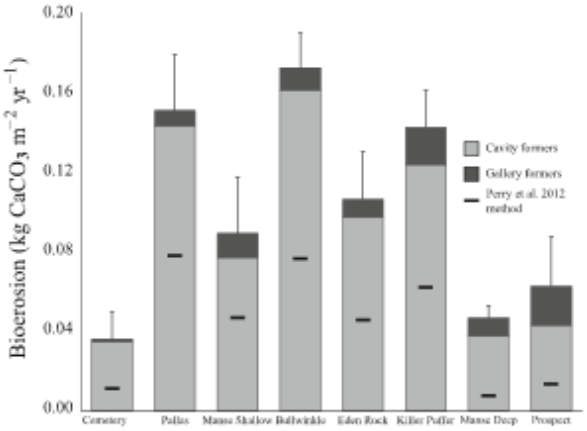

Fig. 6 Bioerosion (kg $CaCO_3$ m^{-2} yr^{-1}) by sponge populations on Grand Cayman reefs. Each column refers to the mean total bioerosion at each reef site. Site means are reported plus their *standard errors*. *Dark grey* portions reflect the contribution of cavity-forming sponges (*Cliona delitrix* and *Siphonodictyon brevitubulatum*) to the total and *light grey* portions reflect the contribution of the gallery-forming sponges (e.g. *C. tenuis*). *Black bars* represent the contribution of gallery-forming sponges that would have been measured using the method of Perry et al. (2012). Differences in data collection methods prevented a similar comparison for the cavity formers

Risk (1985); *C. tenuis*, *C. caribbaea* and *C. aprica* max = 1.5 cm, López-Victoria et al. (2003); *C. orientalis* mean = 1.3 cm, Schönberg (2001). It may be that the depth to which tissue can penetrate the substratum and the quantity of substrate eroded by gallery-forming excavating sponges is relatively uniform across species. However, Calcinai et al. (2007) recorded a maximum depth of penetration of 2 cm for *C. albimarginata* in coral blocks, and it may be that some Indo-Pacific species bore further into the substrate.

Nevertheless, our assumption can be assessed further by comparing the results of studies which measured bioerosion by other gallery-forming species to estimates for *C. tenuis*, using our approach. Schönberg (2002) investigated bioerosion by *C. orientalis*, a Pacific bioeroding sponge, which has similar growth (β) and excavation strategies (tissue galleries) to *C. tenuis*. After exposure to small discs (3.5 cm diameter) containing *C. orientalis*, blocks cut from different coral species were eroded at rates ranging from 3.4 to 10.3 kg $CaCO_3$ m^{-2} of tissue yr^{-1}. The large range was related to coral density with more dense coral substrates having greater erosion; *Porites* blocks (density approx. 1.6 g cm^{-3}) were eroded at a rate of 9.7 kg $CaCO_3$ m^{-2} of tissue yr^{-1}. Other studies have also found that density is an important environmental factor for sponge bioerosion (e.g., Calcinai et al. 2007). Our estimation for a hypothetical *C. tenuis* sponge of 3.5 cm diameter, using an expansion rate of 3.56 cm (Table 1) and a substrate density of 1.7 g cm^{-3}, would generate an erosion rate of 4.4 kg $CaCO_3$ m^{-2} of tissue yr^{-1}, based on the final area of the sponge. This estimate is within the range reported by Schönberg (2002) but less than half that recorded for *C. orientalis* in similarly dense substrate—Porites blocks. However, the coral blocks used in the *C. orientalis* study had been cleaned prior to sponge attachment, and so each individual was likely to have benefitted from a completely flat area devoid of competitors to expand into. Competition, particularly by macroalgae, and reef morphology are key controls on the lateral expansion rates of *C. tenuis* (López-Victoria and Zea 2005; González-Rivero et al. 2012) and probably all gallery-forming sponges. Hence, the erosion rate estimated here for a small *C. tenuis* individual may be more realistic for natural settings.

The approach developed for *S. brevitubulatum* draws attention to the damaging effect this species can have on coral heads. In particular, our data show that the presence of even relatively small numbers of fistules can be indicative of high rates of bioerosion. However, most benthic survey methods would not record fistules as they are often too small (<1 cm diameter). Hence, reef monitoring programmes that do not include dedicated surveys for bioeroding sponges are likely to greatly underestimate the presence of *S. brevitubulatum* and other α-growth-form species, if they are recorded at all. Reef structure has been flattening in the Caribbean since at least the 1960s (Alvarez-Filip et al. 2009) and while the agents of the physical destruction of reef complexity are likely to include storms and visually obvious bioeroding taxa such as parrotfishes, cryptic excavating sponges may have contributed markedly, unnoticed.

Our results indicate distinct habitat preferences for *C. tenuis* and *C. caribbaea* and suggest that the make-up of excavating sponge communities on reefs changes with depth (Table 2). This has also been found for reefs in Columbia (López-Victoria and Zea 2005). It is likely that excavating sponge communities in deeper reef habitats would become increasingly dominated by cavity-forming species as light attenuation decreases the influence of the symbiotic gallery formers. Although there was no clear evidence for an increase in bioerosion by cavity formers with depth, the relative contributions of these species (which are cryptic except for mature individuals of some species) to total sponge bioerosion clearly increased (Fig. 5). The space occupied by these species causes a disproportionately high level of bioerosion in comparison with gallery formers. Therefore, comparisons of the substrate covered by bioeroding sponge communities at different depths may incorrectly suggest higher levels of total bioerosion for shallow reefs where gallery formers dominate. Hence, the monitoring of sponge erosion on coral reefs must incorporate the growth and excavation strategies of different species by assessing abundance and bioerosion

Table 3 Selection of appropriate census survey protocols and equations for estimating bioerosion by excavating sponge species based on their growth form and excavation strategies

	α-Growth form	β-Growth form	γ-Growth form
Gallery formers	*C. tenuis* approach—Eq. 2 Measure tissue area using the papillar zone	*C. tenuis* approach—Eq. 2 Measure sponge area	*C. tenuis* approach—Eq. 2 Measure sponge area
Cavity formers	*S. brevitubulatum* approach—Eq. 4 Measure papillae area	*C. delitrix* approach—Eq. 3 Measure tissue area using the papillar zone	*C. delitrix* approach—Eq. 3 Measure tissue area using the papillar zone

appropriately, as we have attempted here. By focusing on excavation strategy, bioeroding sponges can be divided into two types, cavity and gallery formers, which can determine the approach to estimating bioerosion for any species. Focusing on the growth form (α, β, γ) allows the selection of a suitable census protocol. In Table 3, different census methodologies and approaches to estimating bioerosion are allocated to combinations of sponge growth form and excavation strategy. Additionally, we have included an excel spreadsheet with the ESM that will calculate bioerosion by different sponge species from census data collected using the approaches described here.

Monitoring bioerosion by sponge communities

Methods that can aid surveys of endolithic sponges and generate estimates for bioerosion are urgently needed within reef monitoring programmes (Schönberg 2015). Here, the census-based approach of Perry et al. (2012) has been expanded to account for the main growth forms and excavation strategies of bioeroding sponges, thus providing a basis for estimating sponge community bioerosion on Caribbean coral reefs. The approach also has the potential to be adapted for the Indo-Pacific region. Our data show that mean bioerosion by sponge communities ranged from 0.036 to 0.172 kg $CaCO_3$ m^{-2} yr^{-1} on Grand Cayman reefs. This is comparable to that measured in other Caribbean and Atlantic studies; (e.g., 0.256 kg m^{-2} yr^{-1} in Bermuda; Rützler 1975) and also to macroboring communities in the Indo-Pacific (e.g., 0.040–0.197 kg m^{-2} yr^{-1} on the mid- to outer shelf of the Great Barrier Reef; Tribollet and Golubic 2005). While our results broadly agree with studies from other areas, the methods used may be limited by a lack of species-specific data. Given our present level of understanding of the growth and excavation rates of bioeroding sponge species, more research is clearly required to expand the list of species for which data are available and also to develop our understanding of how habitat, water quality and climate change may affect bioerosion by sponges.

The approaches described here are straightforward, relatively quick and applicable over different spatial and temporal scales. They do not require destructive coral sampling or substrate removal and can generate instant, meaningful results on sponge abundance and bioerosion, while additionally having the potential to be used by surveyors after a little training. Furthermore, all of these advantages are desirable for a sponge bioerosion assessment protocol, which can fit into current benthic monitoring regimes (Schönberg 2015). The adoption of these approaches by monitoring agencies would create a framework for the provision of data that are relevant to both coral reef management and to developing our understanding of how bioeroding sponge populations may be influencing reef structure and carbonate budgets.

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References

Acker KL, Risk MJ (1985) Substrate destruction and sediment production by the boring sponge *Cliona caribbaea* on Grand Cayman Island. J Sediment Petrol 55:705–711

Alvarez-Filip L, Dulvy NK, Gill JA, Côté IM, Watkinson AR (2009) Flattening of Caribbean coral reefs: region-wide declines in architectural complexity. Proc R Soc Lond B Biol Sci 276:3019–3025

Bak R (1994) Sea urchin bioerosion on coral reefs: place in the carbonate budget and relevant variables. Coral Reefs 13:99–103

Bruggemann JH, vanKessel AM, vanRooij JM, Breeman AM (1996) Bioerosion and sediment ingestion by the Caribbean parrotfish *Scarus vetula* and *Sparisoma viride*: implications of fish size, feeding mode and habitat use. Mar Ecol Prog Ser 134:59–71

Calcinai B, Bavestrello G, Cuttone G, Cerrano C (2011) Excavating sponges from the Adriatic Sea: description of *Cliona adriatica* sp. nov.(Demospongiae: Clionaidae) and estimation of its boring activity. J Mar Biol Assoc U.K. 91:339–346

Calcinai B, Azzini F, Bavestrello G, Gaggero L, Cerrano C (2007) Excavating rates and boring pattern of *Cliona albimarginata* (Clionaidae, Demospongiae, Porifera) in different substrata. In: Custódio MR, Lobo-Hajdu G, Hajdu E, Muricy G (eds) Porifera

research: biodiversity, innovation and sustainability. Museu Nacional, Rio de Janeiro, pp 203–210

Chaves-Fonnegra A, Zea S (2011) Coral colonization by the encrusting excavating Caribbean sponge *Cliona delitrix*. Mar Ecol 32:162–173

Chazottes V, Campion-Alsumard TL, Peyrot-Clausade M (1995) Bioerosion rates on coral reefs: interactions between macrobor-ers, microborers and grazers (Moorea, French Polynesia). Palaeogeogr Palaeoclimatol Palaeoecol 113:189–198

DeCarlo TM, Cohen AL, Barkley HC, Cobban Q, Young C, Shamberger KE, Brainard RE, Golbuu Y (2015) Coral macro-bioerosion is accelerated by ocean acidification and nutrients. Geology 43:7–10

Eakin CM (2001) A tale of two ENSO events: carbonate budgets and the influence of two warming disturbances and intervening variability, Uva Island, Panama. Bull Mar Sci 69:171–186

Edinger EN, Limmon GV, Jompa J, Widjatmoko W, Heikoop JM, Risk MJ (2000) Normal coral growth rates on dying reefs: are coral growth rates good indicators of reef health? Mar Pollut Bull 40:404–425

Fang JK, Mello-Athayde MA, Schönberg CH, Kline DI, Hoegh-Guldberg O, Dove S (2013) Sponge biomass and bioerosion rates increase under ocean warming and acidification. Glob Chang Biol 19:3581–3591

Fütterer DK (1974) Significance of the boring sponge *Cliona* for the origin of fine grained material of carbonate sediments. J Sediment Petrol 44:79–84

Gonzalez-Rivero MA (2012) The ecology of bioeroding sponges on Caribbean coral reefs. Ph.D. thesis, University of Exeter, Exeter, UK, p 97

González-Rivero M, Ferrari R, Schönberg CH, Mumby PJ (2012) Impacts of macroalgal competition and parrotfish predation on the growth of a common bioeroding sponge. Mar Ecol Prog Ser 444:133–142

González-Rivero M, Ereskovsky AV, Schönberg CH, Ferrari R, Fromont J, Mumby PJ (2013) Life-history traits of a common Caribbean coral-excavating sponge, *Cliona tenuis* (Porifera: Hadromerida). Journal of Natural History 47:2815–2834

Goreau TF, Hartman WD (1963) Boring sponges as controlling factors in the formation and maintenance of coral reefs. In Sognnaes RF (ed.) Mechanisms of hard tissue destruction. American Association for the Advancement of Science, Issue 75, pp 25–54

Holmes KE (2000) Effects of eutrophication on bioeroding sponge communities with the description of new West Indian sponges, *Cliona* spp. (Porifera: Hadromerida: Clionidae). Invertebr Biol 119:125–138

Hubbard DK, Burke RB, Gill IP (1998) Where's the reef: the role of framework in the Holocene. Carbonates and Evaporites 13:3–9

Hutchings P (2011) Bioerosion. In: Hopley D (ed.) Encyclopedia of modern coral reefs. Springer, pp 139–156

López-Victoria M, Zea S (2005) Current trends of space occupation by encrusting excavating sponges on Colombian coral reefs. Mar Ecol 26:33–41

López-Victoria M, Zea S, Weil E (2003) New aspects on the biology of the encrusting excavating sponges *Cliona aprica*, *Cliona caribbaea* and *Cliona* sp. Bollettino dei musei e degli istituti biologici dell'Università di Genova 68:425–432

López-Victoria M, Zea S, Weil E (2006) Competition for space between encrusting excavating Caribbean sponges and other coral reef organisms. Mar Ecol Prog Ser 312:113–121

MacGeachy JK, Stearn CW (1976) Boring by macro-organisms in the coral *Montastrea annularis* on Barbados reefs. Internationale Revue der Gesamten Hydrobiologie und Hydrographie 61:715–745

Neumann AC (1966) Observations on coastal erosion in Bermuda and measurements of the boring rate of the sponge, *Cliona lampa*. Limnol Oceanogr 11:92–108

Pang RK (1973) The systematics of some Jamaican excavating sponges (Porifera). Peabody Museum of Natural History, Yale University

Perry C (1998) Macroborers within coral framework at Discovery Bay, north Jamaica: species distribution and abundance, and effects on coral preservation. Coral Reefs 17:277–287

Perry CT, Spencer T, Kench PS (2008) Carbonate budgets and reef production states: a geomorphic perspective on the ecological phase-shift concept. Coral Reefs 27:853–866

Perry CT, Kench PS, O'Leary MJ, Morgan KM, Januchowski-Hartley F (2015) Linking reef ecology to island building: parrotfish identified as major producers of island-building sediment in the Maldives. Geology 43:503–506

Perry CT, Edinger EN, Kench PS, Murphy GN, Smithers SG, Steneck RS, Mumby PJ (2012) Estimating rates of biologically driven coral reef framework production and erosion: a new census-based carbonate budget methodology and applications to the reefs of Bonaire. Coral Reefs 31:853–868

Perry CT, Murphy GN, Kench PS, Smithers SG, Edinger EN, Steneck RS, Mumby PJ (2013) Caribbean-wide decline in carbonate production threatens coral reef growth. Nat Commun 4:1402

Perry CT, Murphy GN, Kench PS, Edinger EN, Smithers SG, Steneck RS, Mumby PJ (2014a) Changing dynamics of Caribbean reef carbonate budgets: emergence of reef bioeroders as critical controls on present and future reef growth potential. Proc R Soc Lond B Biol Sci 281:2014–2018

Perry CT, Steneck RS, Murphy GN, Kench PS, Edinger EN, Smithers SG, Mumby PJ (2014b) Regional-scale dominance of non-framework building corals on Caribbean reefs affects carbonate production and future reef growth. Glob Chang Biol 21:1153–1164

R Development Core Team (2012) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Rasband WS (1997–2014) ImageJ. U.S. National Institutes of Health, Bethesda, Maryland, USA, http://imagej.nih.gov/ij/

Rose CS, Risk MJ (1985) Increase in *Cliona delitrix* infestation of *Montastrea cavernosa* heads on an organically polluted portion of the Grand Cayman fringing reef. Mar Ecol 6:345–363

Rützler K (1974) The burrowing sponges of Bermuda. Smithson Contrib Zool 165:1–32

Rützler K (1975) The role of burrowing sponges in bioerosion. Oecologia 19:203–216

Rützler K (2002) Impact of crustose clionid sponges on Caribbean reef corals. Acta Geologica Hispanica 37:61–72

Schönberg CHL (2001) Estimating the extent of endolithic tissue of a Great Barrier Reef clionid sponge. Senckenbergiana Maritima 31:29–39

Schönberg CHL (2002) Substrate effects on the bioeroding demosponge *Cliona orientalis* 1. Bioerosion rates. Mar Ecol 23:313–326

Schönberg CHL (2015) Monitoring bioeroding sponges: using rubble, quadrat, or intercept surveys? Biol Bull 228:137–155

Schönberg CHL, Beuck L (2007) Where Topsent went wrong: *Aka infesta* a.k.a. *Aka labyrinthica* (Demospongiae: Phloeodictyidae) and implications for other *Aka* spp. J Mar Biol Assoc U.K. 87:1459–1476

Scoffin TP, Stearn C, Boucher D, Frydl P, Hawkins C, Hunter I, MacGeachy J (1980) Calcium carbonate budget of a fringing reef on the west coast of Barbados: Part II, Erosion, sediments and internal structure. Bull Mar Sci 30:475–508

Scott P, Risk MJ (1988) The effect of *Lithophaga* (Bivalvia: Mytilidae) boreholes on the strength of the coral *Porites lobata*. Coral Reefs 7:145–151

Tribollet A, Golubic S (2005) Cross-shelf differences in the pattern and pace of bioerosion of experimental carbonate substrates exposed for 3 years on the northern Great Barrier Reef, Australia. Coral Reefs 24:422–434

Vosmaer GC (1931) The sponges of the Bay of Naples, Porifera incalcaria. Martinus Nijhoff, The Hague

Ward-Paige CA, Risk MJ, Sherwood OA, Jaap WC (2005) Clionid sponge surveys on the Florida Reef Tract suggest land-based nutrient inputs. Mar Pollut Bull 51:570–579

Wisshak M, Schönberg CHL, Form A, Freiwald A (2014) Sponge bioerosion accelerated by ocean acidification across species and latitudes? Helgol Mar Res 68:253–262

Zea S, Weil E (2003) Taxonomy of the Caribbean excavating sponge species complex *Cliona caribaea–C. aprica–C. langae* (Porifera, Hadromerida, Clionaidae). Caribb J Sci 39:348–370

References

Acker, K. L. and Risk, M. J. 1985. Substrate destruction and sediment production by the boring sponge *Cliona caribbaea* on Grand Cayman Island. *Journal of Sedimentary Research* **55**(5), pp. 705–711.

Adey, W. H. and Vassar, J. M. 1975. Colonization, succession and growth rates of tropical crustose coralline algae (Rhodophyta, Cryptonemiales)*. *Phycologia* **14**(2), pp. 55–69.

Akpan, E. B. and Farrow, G. E. 1985. Shell bioerosion in high-latitude low-energy environments: Firths of Clyde and Lorne, Scotland. *Marine Geology* **67**(1), pp. 139–150.

Albright, R.R., Langdon, C.C. and Anthony, K.K., 2013. Dynamics of seawater carbonate chemistry, production, and calcification of a coral reef flat, central Great Barrier Reef. *Biogeosciences*, **10**, pp. 6747–6758

Allemand, D., Ferrier-Pagès, C., Furla, P., Houlbrèque, F., Puverel, S., Reynaud, S., Tambutté, É., Tambutté, S. and Zoccola, D., 2004. Biomineralisation in reef-building corals: from molecular mechanisms to environmental control. *Comptes Rendus Palevol*, **3**(6), pp.453-467.

Alvarez-Filip, L., Dulvy, N. K., Gill, J. A., Côté, I. M., and Watkinson, A. R. 2009. Flattening of Caribbean coral reefs: region-wide declines in architectural complexity. *Proceedings of the Royal Society B: Biological Sciences* **276**, pp 3019–3025.

Alvarez-Filip, L., Dulvy, N. K., Côté, I. M., Watkinson, A. R. and Gill, J. A. 2011a. Coral identity underpins architectural complexity on Caribbean reefs. *Ecological Applications* **21**, pp 2223–2231.

Alvarez-Filip, L., Gill, J. A. and Dulvy, N. K. 2011b. Complex reef architecture supports more small-bodied fishes and longer food chains on Caribbean reefs. *Ecosphere* **2**(10), pp. 1–17.

Alvarez-Filip, L., Carricart-Ganivet, J. P., Horta-Puga, G. and Iglesias-Prieto, R.

2013. Shifts in coral-assemblage composition do not ensure persistence of reef functionality. *Scientific reports* **3**, p3486.

Alvarez-Filip, L., Paddack, M. J., Collen, B., Robertson, D. R. and Cote, I. M. 2015. Simplification of Caribbean reef-fish assemblages over decades of coral reef degradation. *PLoS ONE* 10(4), p.e0126004

Alwany, M. A., Thaler, E. and Stachowitsch, M. 2009. Parrotfish bioerosion on Egyptian Red Sea reefs. *Journal of Experimental Marine Biology and Ecology* **371**(2), pp. 170–176.

Anthony, K.R., Kline, D.I., Diaz-Pulido, G., Dove, S. and Hoegh-Guldberg, O., 2008. Ocean acidification causes bleaching and productivity loss in coral reef builders. *Proceedings of the National Academy of Sciences*, **105**(45), pp.17442-17446.

Appeldoorn, R. S., Aguilar-Perera, A., Bouwmeester, B. L. K., Dennis, G. D., Hill, R. L., Merten, W., Recksiek, C. W. and Williams, S. J. 2009. Movement of fishes (Grunts: Haemulidae) across the coral reef seascape: A review of scales, patterns and processes. *Caribbean Journal of Science* **45**, pp. 304–316.

Aronson, R. B. and Precht, W. F. 1997. Stasis, biological disturbance, and community structure of a Holocene coral reef. *Paleobiology* **23**(3), pp. 326–346.

Aronson, R. B. and Precht, W. F. 2001. White-band disease and the changing face of Caribbean coral reefs. *Hydrobiologia* **460**(1-3), pp. 25–38.

Aronson, R. B., Precht, W. F. and Macintyre, I. G. 1998. Extrinsic control of species replacement on a Holocene reef in Belize: The role of coral disease. *Coral Reefs* **17**(3), pp. 223–230.

Bak, R. P. M. 1976. The growth of coral colonies and the importance of crustose coralline algae and burrowing sponges in relation with carbonate accumulation. *Netherlands Journal of Sea Research* 10(3), pp. 285–337.

Bak, R. P. M. 1990. Patterns of echinoid bioerosion in two Pacific coral reef lagoons. *Marine Ecology Progress Series* **66**(26), pp. 267–272.

Bak, R. P. M. 1994. Sea urchin bioerosion on coral reefs: place in the carbonate budget and relevant variables. *Coral Reefs* **13**(2), pp. 99–103.

Bak, R. P. M., Carpay, M. and De Ruyter Van Steveninck, E. D. 1984. Densities of the sea urchin *Diadema antillarum* before and after mass mortalities on the coral reefs of Curacao. *Marine Ecology Progress Series* **17**(1), pp. 105–108.

Baker, A. C., Glynn, P. W. and Riegl, B. 2008. Climate change and coral reef bleaching: An ecological assessment of long-term impacts, recovery trends and future outlook. *Estuarine, Coastal and Shelf Science* **80**(4), pp. 435–471.

Baker, D. M., Rodríguez-Martínez, R. E. and Fogel, M. L. 2013. Tourism's nitrogen footprint on a Mesoamerican coral reef. *Coral Reefs* **32**(3), pp. 691–699.

Barkley, H. C., Cohen, A. L., Golbuu, Y., Starczak, V. R., DeCarlo, T. M. and Shamberger, K. E. F. 2015. Changes in coral reef communities across a natural gradient in seawater pH. *Science Advances* **1**(5), pp. 1–7.

Beanish, J. and Jones, B. 2002. Dynamic carbonate sedimentation in a shallow coastal lagoon: Case study of South Sound, Grand Cayman, British West Indies. *Journal of Coastal Research* **18**, pp. 254–266.

Bellwood, D. R. 1994. A phylogenetic study of the parrotfishes family Scaridae (Pisces: Labroidei), with a revision of genera. *Records of the Australian Museum* **20**, pp. 1–86.

Bellwood, D. R. 1995. Direct estimate of bioerosion by 2 parrotfish species, *Chlorurus gibbus* and *C. sordidus*, on the Great Barrier Reef, Australia. *Marine Biology* **121**(3), pp. 419–429.

Bellwood, D. R. and Choat, J. H. 1990. A functional analysis of grazing in parrotfishes (family Scaridae): the ecological implications. *Environmental Biology of Fishes* **28**(1-4), pp. 189–214.

Bellwood, D. R. Hoey, A. S. and Choat, J. H. 2003. Limited functional redundancy in high diversity systems: resilience and ecosystem function on

coral reefs. *Ecology Letters* **6**(4), pp. 281–285.

Blanchon, P. and Jones, B. 1995. Marine-planation terraces on the shelf around Grand Cayman: a result of stepped Holocene sea-level rise. *Journal of Coastal Research* **11**, pp. 1–33.

Blanchon, P. and Jones, B. 1997. Hurricane control on shelf-edge-reef architecture around Grand Cayman. *Sedimentology* **44**(3), pp. 479–506.

Blanchon, P., Jones, B. and Kalbfleisch, W. 1997. Anatomy of a fringing reef around Grand Cayman: Storm rubble, not coral framework. *Journal of Sedimentary Research* **67**(1), pp. 1–16.

Bohnsack, J. A. and Harper, D. E. 1988. Length-weight relationships of selected marine reef fishes from the southeastern United States and the Caribbean. *NOAA Technical Memorandum* NMFS-SEFC-215.

Bonaldo, R. M., Hoey, A. S. and Bellwood, D. R. 2014. The ecosystem roles of parrotfishes on tropical reefs. *Oceanography and Marine Biology: An Annual Review* **52**, pp. 81–132.

Bosence, D. W. J. 1984. Construction and preservation of two modern coralline algal reefs, St. Croix, Caribbean. *Palaeontology* **27**(3), pp. 549–574.

Bosence, D. W. J. 1989. Biogenic carbonate production in Florida Bay. *Bulletin of Marine Science* **44**(1), pp. 419–433.

Bosscher, H. 1992. Growth potential of coral reefs and carbonate platforms. Vrije University. Utrecht.

Bruckner, A. W. 2012. Factors contributing to the regional decline of *Montastraea annularis* (complex). In *Proceedings of the 12th International Coral Reef Symposium, Cairns, Australia, July*, pp. 9-13.

Bruckner, A. W. and Bruckner, R. J. 2006. The recent decline of *Montastraea annularis* (complex) coral populations in western Curacao: a cause for concern? *Revista de Biologia Tropical* **54**, pp. 45–58.

Bruckner, A. W. and Hill, R. L. 2009. Ten years of change to coral communities off Mona and Desecheo Islands, Puerto Rico, from disease and bleaching.

Diseases of Aquatic Organisms **87**(1-2), pp. 19–31.

Bruggemann, J. H., Begeman, J., Bosma, E. M., Verburg, P. and Breeman, A. M. 1994a. Foraging by the stoplight parrotfish *Sparisoma viride*. II. Intake and assimilation of food, protein, and energy. *Marine Ecology Progress Series* **106**, pp. 57–71.

Bruggemann, J. H., Kuyper, M. W. and Breeman, A. M. 1994b. Comparative analysis of foraging and habitat use by the sympatric Caribbean parrotfish *Scarus vetula* and *Sparisoma viride* (Scaridae). *Marine Ecology Progress Series* **112**(1), pp. 51–66.

Bruggemann, J. H., Van Oppen, M. J. and Breeman, A. M. 1994c. Foraging by the stoplight parrotfish *Sparisoma viride*. I. Food selection in different, socially determined habitats. *Marine Ecology Progress Series* 106, pp. 41–55.

Bruggemann, J. H., VanKessel, A. M., VanRooij, J. M. and Breeman, A. M. 1996. Bioerosion and sediment ingestion by the Caribbean parrotfish *Scarus vetula* and *Sparisoma viride*: Implications of fish size, feeding mode and habitat use. *Marine Ecology Progress Series* **134**, pp. 59–71.

Budd, A. F., Fukami, H., Smith, N. D. and Knowlton, N. 2012. Taxonomic classification of the reef coral family Mussidae (Cnidaria: Anthozoa: Scleractinia). *Zoological Journal of the Linnean Society* **166**(3), pp. 465–529.

Burke, L., Greenhalgh, S., Prager, D. and Cooper, E. 2008. Coastal capital: economic valuation of coral reefs in Tobago and St. Lucia.

Burkepile, D. E., and Hay, M. E. 2008. Herbivore species richness and feeding complementarity affect community structure and function on a coral reef. *Proceedings of the National Academy of Sciences* **105**(42), pp. 16201–16206.

Burman, S. G., Aronson, R. B. and Van Woesik, R. 2012. Biotic homogenization of coral assemblages along the Florida reef tract *Marine Ecology Progress Series* **467**, pp. 89–96.

Burton, F. J. 1994. Climate and tides of the Cayman Islands. In *The Cayman Islands: Natural History and Biogeography* (pp. 51–60). Kluwer Academic Publications.

Calcinai, B., Azzini, F., Bavestrello, G., Gaggero, L. and Cerrano, C. 2007. Excavating rates and boring pattern of *Cliona albimarginata* (Porifera: Clionaidae) in different substrata. *Porifera research: biodiversity, innovation and sustainability*. **28**, pp. 203–210.

Calcinai, B., Bavestrello, G., Cuttone, G. and Cerrano, C. 2011. Excavating sponges from the Adriatic Sea: description of *Cliona adriatica* sp. nov. (Demospongiae: Clionaidae) and estimation of its boring activity. *Journal of the Marine Biological Association of the United Kingdom* **91**(2), pp. 339–346.

Carreiro-Silva, M. and McClanahan, T. R. 2001. Echinoid bioerosion and herbivory on Kenyan coral reefs: The role of protection from fishing. *Journal of Experimental Marine Biology and Ecology* **262**(2), pp. 133–153.

Carreiro-Silva, M., Kiene, W. E., Golubic, S. and McClanahan, T. R. 2012. Phosphorus and nitrogen effects on microbial euendolithic communities and their bioerosion rates. *Marine Pollution Bulletin* **64**(3), pp. 602–613.

Ceccarelli, D. M., Richards, Z. T., Pratchett, M. S. and Cvitanovic, C. 2011. Rapid increase in coral cover on an isolated coral reef, the Ashmore Reef National Nature Reserve, north-western Australia. *Marine and Freshwater Research* **62**(10), pp. 1214–1220.

Chapman, M. R. and Kramer, D. L. 2000. Movements of fishes within and among fringing coral reefs in Barbados. *Environmental Biology of Fishes* **57**(1), pp. 11–24.

Chave, K. E., Smith, S. V. and Roy, K. J. 1972. Carbonate production by coral reefs. *Marine Geology* **12**(2), pp. 123–140.

Chaves-Fonnegra, A., and Zea, S. 2011. Coral colonization by the encrusting excavating Caribbean sponge *Cliona delitrix*. *Marine Ecology* **32**(2), pp. 162–173.

Chazottes, V., Le Campion-Alsumard, T. and Peyrot-Clausade, M. 1995. Bioerosion rates on coral reefs: Interactions between macroborers, microborers and grazers (Moorea, French Polynesia). *Palaeogeography, Palaeoclimatology, Palaeoecology* **113**, pp. 189–198.

Chazottes, V., Le Campion-Alsumard, T., Peyrot-Clausade, M. and Cuet, P. 2002. The effects of eutrophication-related alterations to coral reef communities on agents and rates of bioerosion (Reunion Island, Indian Ocean). *Coral Reefs* **21**(4), pp. 375–390.

Chazottes, V., Chevillotte, V. and Dufresne, A. 2004. Caractérisation de la production particulaire par l'oursin *Echinometra mathaei* sur les récifs Indo-Pacifiques: Influence des peuplements coralliens et implications sur la dynamique sédimentaire. *Geobios* **37**(1), pp. 13–22.

Chazottes, V., Cabioch, G., Golubic, S. and Radtke, G. 2009. Bathymetric zonation of modern microborers in dead coral substrates from New Caledonia—Implications for paleodepth reconstructions in Holocene corals. *Palaeogeography, Palaeoclimatology, Palaeoecology* **280**(3), pp. 456–468.

Constantz, B. and Weiner, S., 1988. Acidic macromolecules associated with the mineral phase of scleractinian coral skeletons. *Journal of Experimental Zoology Part A: Ecological Genetics and Physiology*, **248**(3), pp.253-258.

Chollett, I., and Mumby, P. J. 2012. Predicting the distribution of *Montastraea* reefs using wave exposure. *Coral Reefs* **31**(2), pp. 493–503.

Chornesky, E. A., and Peters, E. C. 1987. Sexual reproduction and colony growth in the scleractinian coral *Porites astreoides*. *The Biological Bulletin*, **172**(2), pp. 161–177.

Colin, P. L. 1992. Reproduction of the Nassau grouper, *Epinephelus striatus* (Pisces: Serranidae) and its relationship to environmental conditions. *Environmental Biology of Fishes* **34**(4), pp. 357–377.

Coralpedia. 2016. Coralpedia. http://coralpedia.bio.warwick.ac.uk/.

Crabbe, M. J. C. 2009. Scleractinian coral population size structures and growth rates indicate coral resilience on the fringing reefs of North Jamaica.

Marine Environmental Research **67**(4), pp. 189–198.

Crawley, M. J. 2007. The R Book (pp. 1-942). John Wiley and Sons.

DaCosta-Cottam, M., Olynik, J., Blumenthal, J., Godbeer, K., Gibb, J., Bothwell, J., Burton, F. J., Bradley, P. E., Band, A., Austin, T. J., Bush, P., Johnson, B., Hurlston, L., Bishop, L., McCoy, C., Parsons, G., Kirkconnell, J., Halford, S. and Ebanks-Petrie, G. 2009. Cayman Islands National Biodiversity Action Plan 2009.

Darling, E. S., Alvarez-Filip, L., Oliver, T. A., McClanahan, T. R. and Cote, I. M. 2012. Evaluating life-history strategies of reef corals from species traits. *Ecology Letters* 15(12), pp. 1378–1386.

Davis, G. E. 1977. Anchor damage to a coral reef on the coast of Florida. *Biological Conservation* **11**(1), pp. 29–34.

DeCarlo, T. M., Cohen, A. L., Barkley, H. C., Cobban, Q., Young, C., Shamberger, K. E., Brainard, R. E. and Golbuu. Y. 2015. Coral macrobioerosion is accelerated by ocean acidification and nutrients. *Geology* **43**(1), pp. 7–10.

Disalvo, L. H. 1969. Isolation of bacteria from the corallum of *Porites lobata* (Vaughn) and its possible significance. *Integrative and Comparative Biology* **9**(3), pp. 735–740.

Done, T. J. 1992. Phase shifts in coral reef communities and their ecological significance. *Hydrobiologia* **247**, pp. 121–132.

Donner, S. D., Skirving, W. J., Little, C. M., Oppenheimer, M. and Hoegh-Gulberg, O. 2005. Global assessment of coral bleaching and required rates of adaptation under climate change. *Global Change Biology* **11**(12), pp. 2251–2265.

Dullo, W. C. 2005. Coral growth and reef growth: A brief review. *Facies* **51**, pp. 33–48.

Dunnett, C. W. 1980. Pairwise multiple comparisons in the unequal variance case. *Journal of the American Statistical Association* **75**, pp. 796–800.

Eakin, C. M. 1996. Where have all the carbonates gone? A model comparison of calcium carbonate budgets before and after the 1982-1983 El Nino at Uva Island in the eastern Pacific. *Coral Reefs* **15**(2), pp. 109–119.

Eakin, C. M. 2001. A tale of two enso events: Carbonate budgets and the influence of two warming disturbances and intervening variability, Uva Island, Panama. *Bulletin of Marine Science* **69**(1), pp. 171–186.

Edinger, E. N., Limmon, G. V., Jompa, J., Widjatmoko, W., Heikoop, J. M. and Risk. M. J. 2000. Normal coral growth rates on dying reefs: Are coral growth rates good indicators of reef health? *Marine Pollution Bulletin* **40**(5), pp. 404–425.

Edmunds, P. J. and Witman, J. D. 1991. Effect of Hurricane Hugo on the primary framework of a reef along the south shore of St John, US Virgin Islands. *Marine Ecology Progress Series* **78**(2), pp. 201–204.

Emery, K. O. 1981. Low marine terraces of Grand Cayman Island. *Estuarine, Coastal and Shelf Science* **12**(5), pp. 569–578.

Eyre, B.D., Andersson, A.J. and Cyronak, T., 2014. Benthic coral reef calcium carbonate dissolution in an acidifying ocean. *Nature Climate Change*, **4**(11), pp.969-976.

Fabricius, K. E. 2005. Effects of terrestrial runoff on the ecology of corals and coral reefs: review and synthesis. *Marine Pollution Bulletin* **50**(2), pp. 125–146.

Fagerstrom, J. A. 1987. The evolution of reef communities. Wiley, New York.

Fang, J. K. H., Mello-Athayde, M. A., Schönberg, C. H. L., Kline, D. I., Hoegh-Guldberg, O. and Dove, S. 2013. Sponge biomass and bioerosion rates increase under ocean warming and acidification. *Global Change Biology* **19**(12), pp. 3581–3591.

Frisch, A.J., Cole, A.J., Hobbs, J.P.A., Rizzari, J.R. and Munkres, K.P., 2012. Effects of spearfishing on reef fish populations in a multi-use conservation area. *PLoS One*, **7**(12), p.e51938.

Frydl, P. and Stearn C. W. 1978. Rate of bioerosion by parrotfish in Barbados

reef environments. *Journal of Sedimentary Research* 48(4), pp. 1149–1157.

Fütterer, D. K. 1974. Significance of the boring sponge *Cliona* for the origin of fine grained material of carbonate sediments. *Journal of Sedimentary Research* **44**(1).

Gardner, T. A., Cote, I. M., Gill, J. A., Grant, A. and Watkinson, A. R. 2003. Long-term region-wide declines in Caribbean corals. *Science* **301**, pp. 958–960.

Gattuso, J.P., Allemand, D. and Frankignoulle, M., 1999. Photosynthesis and calcification at cellular, organismal and community levels in coral reefs: a review on interactions and control by carbonate chemistry. *American zoologist*, **39**, pp.160-183.

Geister, J. 1977. The influence of wave exposure on the ecological zonation of caribbean coral reefs. In *Proceedings of Third International Coral Reef Symposium, Miami, USA,* **2** , pp. 23–29.

Gischler, E. and Hudson, J. H. 2004. Holocene development of the Belize barrier reef. *Sedimentary Geology* **164**(3), pp. 223–236.

Gladfelter, E. H., Monahan, R. K. and Gladfelter, W. B. 1978. Growth rates of five reef-building corals in the Northeastern Caribbean. *Bulletin of Marine Science* 28(4), pp. 728–734.

Glynn, P. W. 1997. Bioerosion and coral-reef growth: a dynamic balance. In Life and Death of Coral Reefs. Chapman and Hall, New York, pp. 68-94.

Glynn, P. W., Stewart, R. H. and McCosker, J. E. 1972. Pacific coral reefs of Panama: structure, distribution and predators. *Geologische Rundschau*, **61**(2), pp. 484–519.

Goatley, C. H. and Bellwood, D. R. 2011. The roles of dimensionality, canopies and complexity in ecosystem monitoring. *PLoS ONE* **6**(11), p.e27307.

González-Rivero, M., Ferrari, R., Schönberg, C. H. and Mumby, P. J. 2012. Impacts of macroalgal competition and parrotfish predation on the growth of a common bioeroding sponge. *Marine Ecology Progress Series* **444**, pp.

133–142.

González-Rivero, M., Ereskovsky, A. V., Schönberg, C. H., Ferrari, R., Fromont, J. and Mumby, P. J. 2013. Life-history traits of a common Caribbean coral-excavating sponge, Cliona tenuis (Porifera: Hadromerida). *Journal of Natural History* **47**, pp. 2815–2834.

Goreau, T. F. 1959. The ecology of jamaican coral reefs I. Species composition and zonation. *Ecology* **40**(1):67–90.

Goreau, T. F., and W. D. Hartman. 1963. Boring sponges as controlling factors in the formation and maintenance of coral reefs. In *Mechanisms of Hard Tissue Destruction*. Publications of the American Association for the Advancement of Science **75**, pp. 25–54.

Graham, N. A. J. and Nash, K. L. 2013. The importance of structural complexity in coral reef ecosystems. *Coral Reefs* **32**(2), pp. 315–326.

Grange, J. S., Rybarczyk, H. and Tribollet, A. 2015. The three steps of the carbonate biogenic dissolution process by microborers in coral reefs (New Caledonia). *Environmental Science and Pollution Research* 22(18), pp. 13625–13637.

Gratwicke, B. and Speight, M. R. 2005. Effects of habitat complexity on Caribbean marine fish assemblages. *Marine Ecology Progress Series* **292**, pp. 301–310.

Green, D. H., Edmunds, P. J. and Carpenter, R. C. 2008. Increasing relative abundance of *Porites astreoides* on Caribbean reefs mediated by an overall decline in coral cover. *Marine Ecology Progress Series* **359**, pp. 1–10.

Greenstein, B. J., Curran, H. A. and Pandolfi, J. M. 1998. Shifting ecological baselines and the demise of *Acropora cervicornis* in the western North Atlantic and Caribbean Province: A Pleistocene perspective. *Coral Reefs* 17(3), pp. 249–261.

Griffin, S. P., García, R. P. and Weil, E. 2003. Bioerosion in coral reef communities in southwest Puerto Rico by the sea urchin Echinometra

viridis. *Marine Biology* **143**(1), pp. 79–84.

Hallock, P. 1981. Production of carbonate sediments by selected large benthic Foraminifera on two Pacific coral reefs. *Journal of Sedimentary Research* **51**(2), pp. 467–474.

Hallock, P., Cottey, T. L., Forward, L. B. and Halas, J. 1986. Population biology and sediment production of *Archaias angulatus* (Foraminifera) in Largo Sound, Florida. *The Journal of Foraminiferal Research* **16**(1), pp. 1–8.

Hamylton, S. M., Pescud, A., Leon, J. X. and Callaghan, D. P. 2013. A geospatial assessment of the relationship between reef flat community calcium carbonate production and wave energy. *Coral Reefs* **32**(4), pp. 1025–1039.

Harborne, A. R., Mumby, P. J., Micheli, F., Perry, C. T., Dahlgren, C. P., Holmes, K. E. and Brumbaugh, D. R. 2006. The functional value of Caribbean coral reef, seagrass and mangrove habitats to ecosystem processes. *Advances in Marine Biology* **50**, pp. 57–189.

Harney, J. N., Hallock, P., Fletcher III, C. H. and Richmond, B. M. 1999. Standing crop and sediment production of reef-dwelling foraminifera on O'ahu, Hawai'i. *Pacific Science* **53**(1), pp. 61–73.

Harrison, P. L., Babcock, R. C., Bull, G. D., Oliver, J. K., Wallace, C. C. and Willis, B. L. 1984. Mass spawning in tropical reef corals. *Science* **223**, pp. 1186–1189.

Hepburn, L. J., Blanchon, P., Murphy, G., Cousins, L. and Perry C. T. 2014. Community structure and palaeoecological implications of calcareous encrusters on artificial substrates across a Mexican Caribbean reef. *Coral Reefs* **34**(1), pp. 189–200.

Highsmith, R. C., Riggs, A. C. and D'Antonio, C. M. 1980. Survival of hurricane-generated coral fragments and a disturbance model of reef calcification/growth rates. *Oecologia* **46**(3), pp. 322–329.

Hillis, L. 1997. Coralgal reefs from a calcareous green alga perspective, and a first carbonate budget. In *Proceedings of the 8th International Coral Reef*

Symposium, Vol. **1**, pp. 761–766.

Hoegh-Guldberg, O., Mumby, P. J., Hooten, A. J., Steneck, R. S., Greenfield, P., Gomez, E., Harvell, C. D., Sale, P. F., Edwards, A. J., Caldeira, K., Knowlton, N., Eakin, C. M., Iglesias-Prieto, R., Muthiga, N., Bradbury, R. H., Dubi, A. and Hatziolos, M. E. 2007. Coral reefs under rapid climate change and ocean acidification. *Science* **318**, pp. 1737–1742.

Holmes, K. E. 2000. Effects of eutrophication on bioeroding sponge communities with the descrption of new West Indian sponges, *Cliona* spp. (Porifera: Hadromerida: Clionidae). *Invertebrate Biology* **119**(2), pp.125–138.

Holmes, K. E., Edinger, E. N., Limmon, G. V. and Risk. M. J. 2000. Bioerosion of live massive corals and branching coral rubble on Indonesian coral reefs. *Marine Pollution Bulletin* **40**(7), pp. 606–617.

Hubbard, D. K. 2009. Depth-related and species-related patterns of Holocene reef accretion in the Caribbean and western Atlantic: a critical assessment of existing models. *Perspectives in Carbonate Geology* **41**, pp. 1–18.

Hubbard, D. K., and Scaturo, D. 1985. Growth rates of seven species of scleractinean corals from Cane Bay and Salt River, St. Croix, USVI. *Bulletin of Marine Science* **36**(2), pp. 325–338.

Hubbard, D. K., Miller, A. I. and Scaturo, D. 1990. Production and cycling of calcium carbonate in a shelf-edge reef system (St-Croix, United States Virgin Islands): Applications to the nature of reef systems in the fossil record. *Journal of Sedimentary Petrology* **60**(3), pp. 335–360.

Hubbard, D. K., Burke, R. B. and Gill, I. P. 1998. Where's the reef: the role of framework in the Holocene. *Carbonates and Evaporites* **13**(1), pp. 3–9.

Hubbard, D. K., Gill, I. P. and Burke, R. B. 2013. Holocene reef building on eastern St. Croix, US Virgin Islands: Lang Bank revisited. *Coral Reefs* **32**(3), pp. 653–669.

Humann, P., and DeLoach, N. 1996. *Reef coral identification: Florida, Caribbean, Bahamas.* New World Publications, Jacksonville.

Hunter, I. G. 1977. Sediment production by *Diadema antillarum* on a Barbados fringing reef. In Proceedings of the 3rd International Coral Reef Symposium, Vol. 2, pp. 105–110.

Huston, M. 1985. Variation in coral growth rates with depth at Discovery Bay, Jamaica. *Coral Reefs* **4**(1), pp. 19–25.

Hutchings, P. A. 1986. Biological destruction of coral reefs - A review. *Coral Reefs* **4**(4), pp. 239–252.

Hutchings, P. A. 2011. Bioerosion. In Encyclopedia of Modern Coral Reefs, pp. 139–156. Springer Netherlands.

IPCC. 2014. Summary for Policymakers. Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change.

Jackson, J. B. C. 1997. Reefs since Columbus. *Coral Reefs* **16**(1), pp. 23–32.

Jackson, J. B. C., and Winston, J. E. 1982. Ecology of cryptic coral reef communities. I. Distribution and abundance of major groups of encrusting organisms. *Journal of Experimental Marine Biology and Ecology* **57**(2), pp. 135–147.

Jackson, J. B. C., Donovan, M. K., Cramer, K. L., Lam, V. and Lam, W. 2014. Status and Trends of Caribbean Coral Reefs : 1970-2012. Global Coral Reef Monitoring Network, IUCN, Gland, Switzerland.

Johns, H. D., and Moore, C. H. 1988. Reef to basin sediment transport using *Halimeda* as a sediment tracer, Grand Cayman Island, West Indies. *Coral Reefs* **6**(3), pp. 187–193.

Johnson, M. D., and Carpenter, R. C. 2012. Ocean acidification and warming decrease calcification in the crustose coralline alga *Hydrolithon onkodes* and increase susceptibility to grazing. *Journal of Experimental Marine Biology and Ecology* **434**, pp. 94–101.

Kendrick, B., Risk, M. J., Michaelides, J. and Bergman, K. 1982. Amphibious microborers: bioeroding fungi isolated from live corals. *Bulletin of Marine Science* **32**(4), pp. 862–867.

Kennedy, E. V., Perry, C. T., Halloran, P. R., Iglesias-Prieto, R., Schönberg, C. H. L., Wisshak, M., Form, A. U., Carricart-Ganivet, J. P., Fine, M., Eakin, C. M. and Mumby. P. J. 2013. Avoiding coral reef functional collapse requires local and global action. *Current Biology* **23**(10), pp. 912–918.

Kiene, W. E. 1988. A model of bioerosion on the Great Barrier Reef. In Proceedings of the 6th International Coral Reef Symposium. Vol. 3, pp. 449–454.

Kiene, W. E. 1997. Enriched nutrients and their impact on bioerosion: results from ENCORE. In Proceedings of the 8th International Coral Reef Symposium, Vol. 1, pp. 897–902.

Kiene, W. E., and Hutchings, P. A. 1994. Bioerosion experiments at Lizard Island, Great Barrier Reef. *Coral Reefs* **13**(2), pp. 91–98.

Kinsey, D. W. 1985. Metabolism, calcification and carbon production. I. Systems level studies. In *Proceedings of the 5th International Coral Reef Congress*, Vol. 4, pp. 505–526.

Kinsey, D., and Hopley, D. 1991. The significance of coral reefs as global carbon sinks - response to Greenhouse. *Palaeogeography, Palaeoclimatology, Palaeoecology* **89**(4), 363–377.

Kleypas, J. A., Buddemeier, R. W. and Gattuso, J. P. 2001. The future of coral reefs in an age of global change. *International Journal of Earth Sciences* 90(2), pp. 426–437.

Knowlton, N. 2001. The future of coral reefs. *Proceedings of the National Academy of Sciences* 98(10), pp. 5419–5425.

Krasting, J. P., Dunne, J. P., Stouffer, R. J. and Hallberg, R. W. 2016. Enhanced Atlantic sea-level rise relative to the Pacific under high carbon emission rates. *Nature Geoscience* **9**, pp. 210–214.

Kuffner, I. B., and Toth, L. T. 2016. A geological perspective on the degradation and conservation of western Atlantic coral reefs. *Conservation Biology* **30**(4), pp. 706–715.

Lakes Environmental. 2016. wrplot. http://www.weblakes.com/products/wrplot/.

Land, L. S. 1979. The fate of reef-derived sediment on the north Jamaican island slope. *Marine Geology* **29**(1), pp. 55–71.

Langdon, C. and Atkinson, M.J., 2005. Effect of elevated pCO_2 on photosynthesis and calcification of corals and interactions with seasonal change in temperature/irradiance and nutrient enrichment. *Journal of Geophysical Research*, **110**, C09S07, doi:10.1029/2004JC002576.

Lessios, H. A. 2005. *Diadema antillarum* populations in Panama twenty years following mass mortality. *Coral Reefs* 24(1), pp. 125–127.

Lessios, H. A. 2016. The great *Diadema antillarum* die-off: 30 years later. *Annual Review of Marine Science* **8**, pp. 267–283.

Lessios, H. A., Robertson, D. R. and Cubit. J. D. 1984. Spread of *Diadema* mass mortality through the Caribbean. *Science* **226**, pp. 335–337.

Li, C., Jones, B. and Blanchon. P. 1997. Lagoon-shelf sediment exchange by storms - evidence from foraminiferal assemblages, east coast of Grand Cayman, British West Indies. *Journal of Sedimentary Research* **67**(1), pp. 17–25.

Li, C., Jones, B. and Kalbfleisch, W. B. C. 1998. Carbonate sediment transport pathways based on foraminifera: Case study from Frank Sound, Grand Cayman, British West Indies. *Sedimentology* **45**(1), pp. 109–120.

Logan, A. 1981. Sessile invertebrate coelobite communities from shallow reef tunnels, Grand Cayman, B.W.I. In *Proceedings of the 4th International Coral Reef Symposium*, Vol. 2, pp. 735–744.

Lokrantz, J., Nyström, M., Thyresson, M. and Johansson, C. 2008. The non-linear relationship between body size and function in parrotfishes. *Coral Reefs* **27**(4), pp. 967–974.

López-Victoria, M., and Zea, S. 2005. Current trends of space occupation by encrusting excavating sponges on Colombian coral reefs. *Marine Ecology* 26(1), pp. 33–41.

López-Victoria, M., Zea, S. and Weil, E. 2003. New aspects on the biology of the encrusting excavating sponges *Cliona aprica*, *Cliona caribbaea* and

Cliona sp. *Boll. Mus. Ist. Biol. Univ. Genova* **68**, pp. 425–432.

López-Victoria, M., Zea, S. and Weil, E. 2006. Competition for space between encrusting excavating Caribbean sponges and other coral reef organisms. *Marine Ecology Progress Series* **312**, pp. 113–121.

MacGeachy, J. K. and Stearn, C. W. 1976. Boring by macro-organisms in the coral *Montastrea annularis* on Barbados reefs. *Internationale Revue der Gesamten Hydrobiologie und Hydrographie* **61**(6), pp. 715–745.

Macintyre, I. G., Burke, R. B., and Stuckenrath, R. 1981. Core holes in the outer fore reef off Carrie Bow Cay, Belize: a key to the Holocene history of the Belizean barrier reef complex. In *Proceedings of the 4th International Coral Reef Symposium*, Vol. 1, pp. 567–574.

Macintyre, I. G., Multer, H. G., Zankl, H. L., Hubbard, D. K., Weiss, M. P. and Stuckenrath, R. 1985. Growth and depositional facies of a windward reef complex (Nonsuch Bay, Antigua, WI). In Proceedings of the 5th International Coral Reef Symposium, Vol. 6, pp. 605–610.

Mallela, J. 2007. Coral reef encruster communities and carbonate production in cryptic and exposed coral reef habitats along a gradient of terrestrial disturbance. *Coral Reefs* **26**(4), pp. 775–785.

Mallela, J. 2013. Calcification by reef-building sclerobionts. *PloS One* **8**(3), p.e60010.

Mallela, J. and Perry, C. T. 2007. Calcium carbonate budgets for two coral reefs affected by different terrestrial runoff regimes, Rio Bueno, Jamaica. *Coral Reefs* **26**(1), pp. 129–145.

Marks, K. W., and Klomp, K. D. 2003. Fish biomass conversion equations. *Atoll Research Bulletin* **496**, pp. 625–630.

Martin, T. G. and Watson, J. E. M. 2016. Intact ecosystems provide best defence against climate change. *Nature Climate Change* **6**(2), pp. 122–124.

Martindale, W. 1992. Calcified epibionts as palaeoecological tools: examples from the Recent and Pleistocene reefs of Barbados. *Coral Reefs* **11**(3), pp.

167–177.

McClanahan, T. R. and Muthiga, N. A. 1988. Changes in Kenyan coral reef community structure and function due to exploitation. *Hydrobiologia* **166**(3), pp. 269–276.

McCoy, C. M. R., Dromard, C. R. and Turner, J. R. 2009. An evaluation of Grand Cayman MPA Performance : A comparative study of coral reef fish communities. In *Proceedings of the 62nd Gulf and Caribbean Fisheries Institute*, Cumana, Venezula

Meissner, K. J., Lippmann, T. and Gupta, A. S. 2012. Large-scale stress factors affecting coral reefs: open ocean sea surface temperature and surface seawater aragonite saturation over the next 400 years. *Coral Reefs* **31**(2), pp. 309–319.

Meyer, J. L. and Schultz, E. T. 1985. Tissue condition and growth rate of corals associated with schooling fish. *Limnology and Oceanography*, **30**(1), pp. 157–166.

Mioche, D. and Cuet, P. 1999. Metabolisme du carbone, des carbonates et des sels nutritifs en saison chaude, sur un recif frangeant soumis a une pression anthropique (ile de la Reunion, ocean Indien). *Comptes Rendus de l'Academie de Sciences - Serie IIa: Sciences de la Terre et des Planetes* **329**(1), pp. 53–59.

Moberg, F. and Folke, C. 1999. Ecological goods and services of coral reef ecosystems. *Ecological Economics* **29**(2), pp. 215–233.

Moberg, F. and Rönnbäck, P. 2003. Ecosystem services of the tropical seascape: interactions, substitutions and restoration. *Ocean & Coastal Management* **46**(1), pp. 27–46.

Moore, C. H. and Shedd, W. W. 1977. Effective rates of sponge bioerosion as a function of carbonate production. In *Proceedings of the 3rd International Coral Reef Symposium*, Vol. 2, pp. 499–505.

Morgan, K. M. 2014. A calcium carbonate budget of a Maldivian reef platform. Ph D Thesis, University of Auckland.

Morgan, K. M., and Kench, P. S. 2014. A detrital sediment budget of a Maldivian reef platform. *Geomorphology* **222**, pp. 122–131.

Morse, A. N. C. and Morse, D. E. 1996. Flypapers for coral and other planktonic larvae. *BioScience* **46**(4), pp.254–262.

Mumby, P. J. and Wabnitz, C. C. 2002. Spatial patterns of aggression, territory size, and harem size in five sympatric Caribbean parrotfish species. *Environmental Biology of Fishes* 63(3), pp. 265–279.

Mumby, P. J., Edwards, A. J., Arias-González, J. E., Lindeman, K. C., Blackwell, P. G., Gall, A., Gorczynska, M. I., Harborne, A. R., Pescod, C. L. and Renken, H. 2004. Mangroves enhance the biomass of coral reef fish communities in the Caribbean. *Nature* **427**, pp. 533–536.

Mumby, P. J., Dahlgren, C. P., Harborne, A. R., Kappel, C. V. Micheli, F., Brumbaugh, D. R., Holmes, K. E., Mendes, J. M., Broad, K., Sanchirico, J. N., Buch, K., Box, S., Stoffle, R. W. and Gill, A. B. 2006. Fishing, trophic cascades, and the process of grazing on coral reefs. *Science* **311**, pp. 98–101.

Nagelkerken, I. and Van der Velde, G. 2004. Relative importance of interlinked mangroves and seagrass beds as feeding habitats for juvenile reef fish on a Caribbean island. *Marine Ecology Progress Series* **274**, pp. 153–159.

Nagelkerken, I., Van der Velde, G., Gorissen, M. W., Meijer, G. J., Van't Hof, T. and Den Hartog, C. 2000. Importance of mangroves, seagrass beds and the shallow coral reef as a nursery for important coral reef fishes, using a visual census technique. *Estuarine, Coastal and Shelf Science* **51**(1), pp. 31–44.

Nava, H. and Carballo, J. L. 2008. Chemical and mechanical bioerosion of boring sponges from Mexican Pacific coral reefs. *Journal of Experimental Biology* **211**(17), pp. 2827–2831.

Nemeth, M. and Appeldoorn, R. S. 2009. The distribution of herbivorous coral reef fishes within fore-reef habitats: The role of depth, light and rugosity. *Caribbean Journal of Science* **45**(2), pp. 247–253.

Neumann, A. C. 1966. Observations on coastal erosion in Bermuda and measurements of the boring rate of the sponge, *Cliona lampa*. *Limnology and Oceanography* **11**(1), pp. 92–108.

Neumann, A. C. and Land, L. S. 1975. Lime mud deposition and calcareous algae in the Bight of Abaco, Bahamas; a budget. *Journal of Sedimentary Research* **45**(4), pp. 763–786.

Neumann, A. C. and Macintyre, I. 1985. Reef response to sea level rise: Keep-up, catch-up or give-up. In *Proceedings of the 5th International Coral Reef Symposium*. Tahiti, Vol 3, pp. 105–110.

Nystrom, M., Folke, C. and Moberg, F. 2000. Coral reef disturbance and resilience in a human-dominated environment. *Trends in Ecology and Evolution* **15**(10), pp. 413–417.

O'Farrell, S., Harborne, A. R., Bozec, Y. M., Luckhurst, B. E. and Mumby, P. J. 2015. Protection of functionally important parrotfishes increases their biomass but fails to deliver enhanced recruitment. *Marine Ecology Progress Series* **522**, pp. 245–254.

O'Leary, J. K., Potts, D. C., Braga, J. C. and McClanahan, T. R. 2012. Indirect consequences of fishing: Reduction of coralline algae suppresses juvenile coral abundance. *Coral Reefs* **31**(2), pp. 547–559.

Ogden, J. C. 1977. Carbonate sediment production by parrotfish and sea urchins on Caribbean reefs: reef biota. *Studies in Geology*, **4**, pp. 281–288.

Ogden, J. C. 1988. The influence of adjacent systems on the structure and function of coral reefs. In *Proceedings of the 6th International Coral Reef Symposium*. Vol. 1, pp. 123–129.

Ogden, J. C. Brown, R. A. and Salesky, N. 1973. Grazing by the echinoid *Diadema antillarum* Philippi: Formation of halos around West Indian patch reefs. *Science* **182**, pp. 715–717.

Ogden, J. C. and Buckman, N. S. 1973. Movements, foraging groups, and diurnal migrations of the striped parrotfish *Scarus croicensis* Bloch (Scaridae). *Ecology* **54**(3), pp. 589–596.

Ong, L. and Holland, K. N. 2010. Bioerosion of coral reefs by two Hawaiian parrotfishes: Species, size differences and fishery implications. *Marine Biology* **157**(6), pp. 1313–1323.

Osorno, A., Peyrot-Clausade, M. and Hutchings, P. A. 2005. Patterns and rates of erosion in dead Porites across the Great Barrier Reef (Australia) after 2 years and 4 years of exposure. *Coral Reefs* **24**(2), pp. 292–303.

Pang, R. K. 1973. The systematics of some Jamaican excavating sponges [Porifera]. *Postilla* **161**, pp. 1–75.

Pari, N., Peyrot-Clausade, M. and Hutchings, P. A. 1998. Bioerosion of experimental substrates on high islands and atoll lagoons (French Polynesia) during 5 years of exposure. *Marine Ecology Progress Series* **166**, pp. 119–130.

Paytan, A., Shellenbarger, G. G., Street, J. H., Gonneea, M. E., Davis, K., Young, M. B. and Moore, W. S. 2006. Submarine groundwater discharge: An important source of new inorganic nitrogen to coral reef ecosystems. *Limnology and Oceanography* 51(1), pp. 343–348.

Perry, C. T. 1998. Macroborers within coral framework at Discovery Bay, north Jamaica: species distribution and abundance, and effects on coral preservation. *Coral Reefs* **17**(3), pp. 277–287.

Perry, C. T., Spencer, T. and Kench, P. S. 2008. Carbonate budgets and reef production states: a geomorphic perspective on the ecological phase-shift concept. *Coral Reefs* **27**(4), pp. 853–866.

Perry, C. T., Edinger, E. N., Kench, P. S., Murphy, G. N., Smithers, S. G., Steneck, R. S. and Mumby, P. J. 2012. Estimating rates of biologically driven coral reef framework production and erosion: a new census-based carbonate budget methodology and applications to the reefs of Bonaire. *Coral Reefs* **31**(3), pp. 853–868.

Perry, C. T., Murphy, G. N., Kench, P. S., Smithers, S. G., Edinger, E. N., Steneck, R. S. and Mumby, P. J. 2013. Caribbean-wide decline in carbonate production threatens coral reef growth. *Nature communications* **4**, p. 1402.

Perry, C. T., Murphy, G. N., Kench, P. S., Edinger, E. N., Smithers, S. G., Steneck, R. S. and Mumby, P. J. 2014. Changing dynamics of Caribbean reef carbonate budgets: emergence of reef bioeroders as critical controls on present and future reef growth potential. *Proceedings of the Royal Society B: Biological Sciences* **281**, p. 20142018.

Perry, C. T., Kench, P. S., O'Leary, M. J., Morgan, K. M. and Januchowski-Hartley, F. 2015a. Linking reef ecology to island building: Parrotfish identified as major producers of island-building sediment in the Maldives. *Geology* **43**(6), pp. 503–506.

Perry, C. T., Murphy, G. N., Graham, N. A. J., Wilson, S. K., Januchowski-Hartley, F. A. and East, H. K. 2015b. Remote coral reefs can sustain high growth potential and may match future sea-level trends. *Scientific Reports* **5**, p. 18289.

Perry, C. T., Steneck, R. S., Murphy, G. N., Kench, P. S., Edinger, E. N., Smithers, S. G. and Mumby, P. J. 2015c. Regional-scale dominance of non-framework building corals on Caribbean reefs affects carbonate production and future reef growth. *Global Change Biology* **21**(3), pp. 1153–1164.

Peyrot-Clausade, M., Chabanet, P., Conand, C., Fontaine, M. F., Letourneur, Y. and Harmelin-Vivien, M. 2000. Sea urchin and fish bioerosion on La Reunion and Moorea reefs. *Bulletin of Marine Science* **66**(2), pp. 477–485.

Polunin, N. V. C. 2008. Aquatic ecosystems : trends and global prospects. Cambridge Univeristy Press, Cambridge.

R Development Core Team, R. 2011. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing.

Rasband, W. S. 2007. ImageJ. U.S. National Institutes of Health, Bethesda, Maryland, USA.

Rasser, M., and B. Riegl. 2002. Holocene coral reef rubble and its binding agents. *Coral Reefs* **21**(1), pp. 57–72.

Reyes-Nivia, C., Diaz-Pulido, G., Kline, D., Guldberg, O.H. and Dove, S., 2013.

Ocean acidification and warming scenarios increase microbioerosion of coral skeletons. *Global Change Biology*, **19**(6), pp.1919-1929.

Riegl, B. M., Bruckner, A. W., Rowlands, G. P., Purkis, S. J. and Renaud, P. 2012. Red Sea coral reef trajectories over 2 decades suggest increasing community homogenization and decline in coral size. *PloS One* **7**(5), p.e38396.

Rigby, J. K. and Roberts, H. H. 1976. Geology, Reefs and Marine Communities of Grand Cayman Island, British West Indies. In Geology Studies Special Publication No 4. Brigham Young University

Roberts, C. M. 1995. Effects of fishing on the ecosystem structure of coral reefs. *Conservation Biology* 9(5), pp. 988–995.

Roberts, C. M. 1997. Connectivity and management of Caribbean coral reefs. *Science* **278**, pp. 1454–1457.

Roberts, H. H. 1983. Shelf margin reef morphology: a clue to major off-shelf sediment transport routes, Grand Cayman Island, West Indies. *Atoll Research Bulletin* **263**, pp. 1–11.

Roberts, H. H. 1994. Reefs and Lagoons of Grand Cayman. In *Biogeography of the Cayman Islands*, pp. 75–104.

Rogers, C. S. 1990. Responses of coral reefs and reef organisms to sedimentation. *Marine Ecology Progress Series* **62**, pp. 185–202.

Rohweder, J., Rogala, J. T., Johnson, B. L., Anderson, D., Clark, S., Chamberlin, F. and Runyon, K. 2012. Application of wind fetch and wave models for habitat rehabilitation and enhancement projects. U.S. Geological Survey Report , p. 43.

Roik, A., Roder, C., Röthig, T. and Voolstra, C. R. 2016. Spatial and seasonal reef calcification in corals and calcareous crusts in the central Red Sea. *Coral Reefs* **35**(2), pp. 681–693.

Rose, C. S. and Risk, M. J. 1985. Increase in *Cliona delitrix* infestation of *Montastrea cavernosa* heads on an organically polluted portion of the Grand Cayman fringing reef. *Marine Ecology* **6**(4), pp. 345–363.

Russ, G. R., Questel, S. L. A., Rizzari, J. R. and Alcala, A. C. 2015. The parrotfish–coral relationship: refuting the ubiquity of a prevailing paradigm. *Marine Biology* **162**(10), pp. 2029–2045.

Rützler, K. 1974. The burrowing sponges of Bermuda. *Smithsonian Contributions to Zoology* **165**, pp. 1–32.

Rützler, K. 1975. The role of burrowing sponges in bioerosion. *Oecologia* **19**(3), pp. 203–216.

Rützler, K. 2002. Impact of crustose clionid sponges on Caribbean reef corals. *Acta Geologica Hispanica* **37**(1), pp. 61–72.

Rützler, K. and Rieger, G. 1973. Sponge burrowing: fine structure of *Cliona lampa* penetrating calcareous substrata. *Marine Biology* **21**, pp. 144–162.

Schönberg, C. H. L. 2001. Estimating the extent of endolithic tissue of a Great Barrier Reef clionid sponge. *Senckenbergiana Maritima* **31**(1), pp. 29–39.

Schönberg, C. H. L. 2002. Substrate effects on the bioeroding demosponge *Cliona orientalis*. 1. Bioerosion rates. *Marine Ecology* **23**(4), pp. 313–326.

Schönberg, C. H. L. 2015. Monitoring bioeroding sponges: using rubble, quadrat, or intercept surveys? *The Biological Bulletin* **228**(2), pp. 137–155.

Schönberg, C. H. L. and Beuck, L. 2007. Where Topsent went wrong: *Aka infesta* a.k.a. *Aka labyrinthica* (Demospongiae: Phloeodictyidae) and implications for other *Aka* spp. *Journal of the Marine Biological Association of the UK* **87**(6), pp. 1459–1476.

Scoffin, T. P., Stearn, C. W., Boucher, D., Frydl, P., Hawkins, C. M., Hunter, I. G. and MacGeachy, J. K. 1980. Calcium carbonate budget of a fringing reef on the west coast of Barbados: Part II, Erosion, sediments and internal structure. *Bulletin of Marine Science* **30**(2) pp. 475–508.

Scott, P. J. B. and Risk, M. J. 1988. The effect of *Lithophaga* (Bivalvia: Mytilidae) boreholes on the strength of the coral *Porites lobata*. *Coral Reefs* **7**(3), pp. 145–151.

Seymour, R. 2000. Seven Mile Beach: A natural history.

Sheppard, C. R. C. 2003. Predicted recurrences of mass coral mortality in the Indian Ocean. *Nature* **425**, pp. 294–297.

Sheppard, C., Dixon, D.J., Gourlay, M., Sheppard, A. and Payet, R., 2005. Coral mortality increases wave energy reaching shores protected by reef flats: examples from the Seychelles. *Estuarine, Coastal and Shelf Science*, **64**(2), pp. 223-234.

Sheppard, C. R. C., Harris, A. and Sheppard, A. L. S. 2008. Archipelago-wide coral recovery patterns since 1998 in the Chagos Archipelago, central Indian Ocean. *Marine Ecology Progress Series* **362** pp. 109–117.

Shinn, E. A. 1966. Coral growth-rate, an environmental indicator. *Journal of Paleontology* **40**, pp. 233–240.

Simpson, S. D., Radford, A. N., Nedelec, S. L., Ferrari, M. C. O., Chivers, D. P., McCormick, M. I. and Meekan, M. G. 2016. Anthropogenic noise increases fish mortality by predation. *Nature communications* **7**, 10544.

Smith, S. 1973. Carbon dioxide dynamics :A record of organic carbon production, respiration, and calcification in the Eniwetok reef flat community. *Limnology and Oceanography* **18**(1), pp. 106–120.

Smith, S. H. 1988. Cruise ships: A serious threat to coral reefs and associated organisms. *Ocean and Shoreline Management* **11**(3), pp. 231–248.

Spencer, T. 1985. Marine erosion rates and coastal morphology of reef limestones on Grand Cayman Island, West Indies. *Coral Reefs* **4**(2), pp. 59–70.

Stearn, C. W., Scoffin, T. P. and Martindale, W. 1977. Calcium-carbonate budget of a fringing reef on the west coast of Barbados .1. Zonation and Productivity. *Bulletin of Marine Science* **27**(3), pp. 479–510.

Steneck, R. S. 1986. The ecology of coralline algal crusts: convergent patterns and adaptative strategies. *Annual Review of Ecology and Systematics* **17**(1), pp. 273–303.

Steneck, R. S. 1988. Herbivory on coral reefs: A synthesis. In *Proceedings of the 6th International Coral Reef Symposium*, Vol. 1, pp. 37-49.

Steneck, R. S. and Adey, W. H. 1976. The role of environment in control of morphology in *Lithophyllum congestum*, a Caribbean algal ridge builder. *Botanica Marina* **19**(4), pp. 197–216.

Steneck, R. S., Arnold, S. N. and Mumby, P. J. 2014. Experiment mimics fishing on parrotfish: Insights on coral reef recovery and alternative attractors. *Marine Ecology Progress Series* **506**, pp. 115–127.

Steneck, R. S. and Dethier, M. N. 1994. A functional group approach to the structure of algal-dominated communities. *Oikos*, **69**(3), pp. 476–498.

Sutherland, K. P., Porter, J. W., Turner, J. W., Thomas, B. J., Looney, E. E., Luna, T. P., Meyers, M. K., Futch, J. C. and Lipp, E. K. 2010. Human sewage identified as likely source of white pox disease of the threatened Caribbean elkhorn coral, *Acropora palmata*. *Environmental Microbiology* **12**(5), pp. 1122–1131.

Tambutté, S., Holcomb, M., Ferrier-Pagès, C., Reynaud, S., Tambutté, É., Zoccola, D. and Allemand, D., 2011. Coral biomineralization: from the gene to the environment. *Journal of Experimental Marine Biology and Ecology*, **408**(1), pp.58-78.

Tongpenyai, B. and Jones, B. 1991. Application of image analysis for delineating modern carbonate facies changes through time: Grand Cayman, western Caribbean Sea. *Marine Geology* **96**(1), pp. 85–101.

Torres, J. L. and Morelock, J. 2002. Effect of terrigenous sediment influx on coral cover and linear extension rates of three Caribbean massive coral species. *Caribbean Journal of Science* **38**(3), pp. 222–229.

Toscano, M. A. and Macintyre, I. G. 2003. Corrected western Atlantic sea-level curve for the last 11,000 years based on calibrated ^{14}C dates from *Acropora palmata* framework and intertidal mangrove peat. *Coral Reefs* 22(3), pp. 257–270.

Tratalos, J. A. and Austin, T. J. 2001. Impacts of recreational SCUBA diving on coral communities of the Caribbean island of Grand Cayman. *Biological Conservation* **102**(1), pp. 67–75.

Tribollet, A. 2008. Dissolution of dead corals by euendolithic microorganisms across the northern Great Barrier Reef (Australia). *Microbial Ecology* **55**(4), pp. 569–580.

Tribollet, A. and Golubic, S. 2005. Cross-shelf differences in the pattern and pace of bioerosion of experimental carbonate substrates exposed for 3 years on the northern Great Barrier Reef, Australia. *Coral Reefs* **24**(3), pp. 422–434.

Tunnicliffe, V. 1983. Caribbean staghorn coral populations: pre-Hurricane Allen conditions in Discovery Bay, Jamaica. *Bulletin of Marine Science* **33**(1), pp. 132–151.

Turner, J. R., McCoy, C., Cottam, M., Olynik, J., Austin, T. J., Blumenthal, J., Bothwell, J., Burton, F. J., Bush, P., Chin, P., Dubock, O., Godbeer, K., Gibb, J., Hurlston, L., Johnson, B., Logan, A., Parsons, G. and Ebanks-Petrie, G. 2013. Biology and ecology of the coral reefs of the Cayman Islands. In *Coral Reefs of the United Kingdom Overseas Territories*. Springer.

Van Rooij, J. M., De Jong, E., Vaandrager, F. and Videler, J. J. 1996. Resource and habitat sharing by the stoplight parrotfish, Sparisoms viride, a Caribbean reef herbivore. *Environmental Biology of Fishes* **47**(1), pp. 81–91.

Vaughan, T. W. 1916. The results of investigations of the ecology of the Floridian and Bahaman shoal-water corals. *Proceedings of the National Academy of Sciences* **2**(2), pp. 95–100.

Vecsei, A. 2001. Fore-reef carbonate production: Development of a regional census-based method and first estimates. *Palaeogeography, Palaeoclimatology, Palaeoecology* **175**(1), pp. 185–200.

Veron, J.E.N., Hoegh-Guldberg, O., Lenton, T.M., Lough, J.M., Obura, D.O., Pearce-Kelly, P., Sheppard, C.R.C., Spalding, M., Stafford-Smith, M.G. and Rogers, A.D., 2009. The coral reef crisis: The critical importance of< 350ppm CO 2. *Marine pollution bulletin*, **58**(10), pp.1428-1436.

Vezina, J., Jones, B. and Ford, D. 1999. Sea-level highstands over the last

500,000 years: evidence from the Ironshore Formation on Grand Cayman, British West Indies. *Journal of Sedimentary Research* **69**(2), pp. 317–327.

Vogel, K., Gektidis, M., Golubic, S., Kiene, W. E. and Radtke, G. 2000. Experimental studies on microbial bioerosion at Lee Stocking Island, Bahamas and One Tree Island, Great Barrier Reef, Australia: Implications for paleoecological reconstructions. *Lethaia* **33**(3), pp. 190–204.

Vosmaer, G. C. J. 1931. *The sponges of the Bay of Naples, Porifera incalcaria*. The Hague, Martinus Nijhoff.

Warburton, F. E. 1958. The manner in which the sponge *Cliona* bores in calcareous objects. *Canadian Journal of Zoology* **36**(4), pp. 555–562.

Ward-Paige, C. A., Risk, M. J., Sherwood, O. A. and Jaap, W. C. 2005. Clionid sponge surveys on the Florida Reef Tract suggest land-based nutrient inputs. *Marine Pollution Bulletin* **51**(5), pp. 570–579.

Weinstein, D. K., Smith, T. B. and Klaus, J. S. 2014. Mesophotic bioerosion: Variability and structural impact on U.S. Virgin Island deep reefs. *Geomorphology* **222**, pp. 14–24.

Williams, I. D. and Polunin, N. V. C. 2001. Large-scale associations between macroalgal cover and grazer biomass on mid-depth reefs in the Caribbean. *Coral Reefs* **19**(4), pp. 358–366.

Williams, G. J., Gove, J. M., Eynaud, Y., Zgliczynski, B. J. and Sandin, S. A. 2015. Local human impacts decouple natural biophysical relationships on Pacific coral reefs. *Ecography* **38**(8), pp. 751–761.

Williams, S. M., Chollett, I., Roff, G., Cortes, J., Dryden, C. S. and Mumby, P. J. 2015. Hierarchical spatial patterns in Caribbean reef benthic assemblages. *Journal of Biogeography* **42**(7), pp. 1327–1335.

Wisshak, M., Schönberg, C. H. L., Form, A. and Freiwald, A. 2012. Ocean acidification accelerates reef bioerosion. *PloS One* **7**, p.e45124.

Wisshak, M., Schönberg, C. H. L., Form, A. and Freiwald, A. 2014. Sponge bioerosion accelerated by ocean acidification across species and latitudes? *Helgoland Marine Research* **68**(2), pp. 253–262.

Wood, S., Paris, C. B., Ridgwell, A. and Hendy, E. J. 2014. Modelling dispersal and connectivity of broadcast spawning corals at the global scale. *Global Ecology and Biogeography* **23**(1), pp. 1–11.

Woodley, J. D., Chornesky, E., Clifford, P. A., Jackson, J. B., Kaufman, L. S., Knowlton, N., Lang, J. C., Pearson, M. P., Porter, J. W., Rooney, M. C., Rylaarsdam, K. W., Tunnicliffe, V. J., Wahle, C. M., Wulff, J. L., Curtis, A. S., Dallmeyer, M. D., Jupp, B. P., Koehl, M. A., Neigel, J. and Sides, E. M. 1981. Hurricane Allen's impact on Jamaican coral reefs. *Science* **214**, pp. 749–755.

World Bank. 2010. *Convenient Solutions to an Inconvenient Truth - Ecosystem-Based Approaches to Climate Change*. The World Bank, Washington

Zea, S. and Weil, E. 2003. Taxonomy of the Caribbean excavating sponge species complex *Cliona caribbaea - C. aprica - C. langae* (Porifera, Hadromerida, Clionaidae). *Caribbean Journal of Science* **39**(3), pp. 348–370.

Zundelevich, A., Lazar, B. and Ilan, M. 2007. Chemical versus mechanical bioerosion of coral reefs by boring sponges-lessons from *Pione* cf. *vastifica*. *Journal of Experimental Biology* **210**(1), pp. 91–96.