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Accretion versus bioerosion on the Maputaland reefs in South Africa – The major processes

Submitted in fulfilment of the academic requirements for the degree of Master of Science in the Oceanographic Research Institute, affiliated with the School of Biological and Conservation Sciences, University of KwaZulu-Natal, Durban.

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As the candidates supervisor I have/have not approved this thesis/dissertation for submission.

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i. Abstract

The development of coral reefs is largely restricted to areas within the tropics where favourable conditions for both coral and reef growth prevail. There is, however, a continuum from these typical, accretive reefs in the tropics to marginal, non-accretive, coral-dominated reef communities which occur at higher latitudes. High-latitude reefs function similarly in many regards to their tropical counterparts and are regulated by similar processes to a varying degree. In this study, the major biological and physico-chemical processes were assessed which directly or indirectly prevent the continued persistence of reefal frameworks and thus hinder reef accretion on high-latitude reefs in the iSimangaliso Wetland Park. These reefs have a high diversity of hard and soft corals with significant reef coverage, yet little evidence of any biogenic accretion has been observed. The scleractinian coral, *Acropora austera*, is one of the few corals which may be responsible for reef framework production. It exhibits a gregarious growth pattern, forming large, monospecific stands with an interlocking framework characteristic of the early stages of reef accretion. The framebuilding potential of *A. austera* and the continued persistence of such frameworks were thus determined by *in situ* monitoring of coral growth, mortality, bioerosion and several physico-chemical parameters.

Growth rate and mortality of *A. austera* branches were measured at three sites of differing stand size and apparent age. This was achieved by repeated image analysis and by staining branches with the vital stain, Alizarin Red S. Both measures of growth yielded a similar linear extension rate of 24.5 mm/yr (n = 467), comparable to related species at similar latitudes. Mean branch mortality was as high as 50%, with clear differences manifested between each *A. austera* stand. Branch extension rates and branch mortality were inversely related between sites. Small, young stands exhibited significantly faster coral growth rates, lower mortality and a net increase in overall branch length over the study period, whilst the opposite was true of larger, more developed stands. In addition, bioerosion was determined at each site to assess its potential for carbonate removal and its destabilizing effect on reef frameworks. Bioerosion intensity was recorded as “percentage area damage” within cross-sections and “frequency of occurrence” of bioeroding organisms in coral rubble fragments (n = 120). The level of bioerosion was found to be substantial (up to 11.5% loss in weight of coral fragments over the 12-month study period) and was found to decrease significantly with a reduction in size of each *A. austera* stand.

Aragonite saturation state is considered a major factor that limits the geographical range of coral reefs globally. Although previously thought to be limiting in Maputaland, mean Ω_{Arag} values of 4.40±0.29 were measured on the reefs in summer and 4.33±0.21 in winter and thus would not have limited reef development. Past studies have noted the turbulence on South African east coast reefs and its adverse effect on reef development. This was corroborated in this study with the measurement of considerable sediment resuspension (0.17 g cm^{-2} day^{-1}) and regular damage to both living coral and the reef framework caused by large swells.

These results lead to the theory that *Acropora austera* stands senesce with increasing size and age. Although large coral frameworks are found on the Maputaland reefs, they do not persist in the long term. High rates of sediment resuspension prevent infilling of the interstitial spaces and eventual cementation, while high levels of bioerosion lead to framework instability over time. Rough seas further hamper accretion by physical removal of both living coral and the coral-derived framework, thus removing recent growth. This process is suspected to cause an imbalance in the carbonate budget of these marginal reefs, ultimately favoring carbonate removal over carbonate deposition.

Keywords: *Acropora austera*; Linear extension; Bioerosion; Aragonite; Water movement; Sedimentation; Reef framework; Accretion

ii. Preface

The experimental work described in this dissertation was carried out at the Oceanographic Research Institute, affiliated with the School of Biological and Conservation Sciences, University of KwaZulu-Natal, Durban, from March 2009 to December 2011, under the supervision of Professors MH Schleyer and Dr D Glassom.

These studies represent original work by the author and have not otherwise been submitted in any form for any degree or diploma to any tertiary institution. Where use has been made of the work of others it is duly acknowledged in the text.

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1. Chapter 1 - A review of high-latitude reef processes

1.1. Introduction to High-latitude reefs

The majority of coral reefs found around the globe are restricted to tropical latitudes. There are, however, a number of localities where significant coral communities dominate areas outside the tropics. Some extend considerably into high-latitude, sub-tropical or marginal habitats and in several of these areas, there is significant reef accretion (e.g.: Gulf of Aqaba, Red Sea, Heiss 1995). By contrast, most high-latitude reefs are non-accretive in nature and fail to form a stable reef framework (Veron 1992; Glynn 1993; Riegl *et al*. 1995; Riegl 1999). By the same token, coral-dominated reefs in the iSimangaliso Wetland Park of South Africa show little evidence of a stable reef framework and no indication of any cumulative reef accretion from historic records (Ramsay & Mason 1990; Riegl *et al*. 1995; Ramsay 1996).

The causal circumstances which lead to reef framework production are a subject still receiving attention, yet it is known that there are differing limits of environmental conditions required for coral growth as opposed to reef growth (Grigg 1982 a, b). The results of this inconsistency are coral communities which often occur across a much wider latitudinal range than coral reefs themselves (Grigg 1982 a, b; Eakin 1996; Reaka-Kudla *et al*. 1996; Harriott 1999; Guinotte *et al*. 2003). At high-latitude sites or in biogeographically isolated areas, rich yet non-accretive coral communities are common and often function in a similar ecological fashion to tropical reefs (For example, Oman (Glynn 1993); Northern Ryukus, Japan (Veron 1992); South Africa (Riegl *et al*. 1995); Arabian Gulf (Riegl 1999); Lord Howe Islands and Solitary Islands, Eastern Australia (Harriott 1992); Hawaii (Grigg 1982 a, b)). Several hypotheses suggesting possible reasons for the distinct lack of accretion in high-latitude reef systems include: reduced coral growth rates and elevated mortality at lower temperatures (Edmondson 1929; Stoddart 1969; Veron & Done 1979; Rosen 1988; Veron 1995; Edmunds 2005), an inability to compete with benthic organisms from temperate regions (Holmes *et al*. 1997), low aragonite saturation states (Kleypas *et al*. 1999 a; Feely *et al*. 2009), or lowered reproductive output and/or planular settlement at high latitudes (Veron 1974). However, more recent work suggests that successful coral reproduction and subsequent recruitment occurs at high latitudes (Harriott 1992; Kenyon 1992; Babcock *et al*. 1994; van Woesik 1995; Glassom *et al*. 2006; Wilson & Harrison 1997; Kruger & Schleyer 1998) and many hermatypic corals are able to survive at temperatures as low as 14˚C (Veron 1995).

In addition to a general decline in conditions deemed desirable for coral growth with increasing latitude (Grigg 1982 a, b), coral reef formation is largely determined by the destructive forces of physical, chemical and biological erosion (Tribollet and Golubic 2011). Chemical erosion is considered negligible (Scoffin *et al* 1980 in Tribollet and Golubic 2011) and thus is not included in this study. Erosion from physical disturbances such as storms, although often temporary events, can result in significant damage but often on a localized scale (Riegl 1995; 1999). Biological erosion, however, is often considered the main force of reef degradation (Tribollet and Golubic 2011), particularly in areas of increasing environmental or anthropogenic stress (Hutchings *et al* 2005). Bioerosional processes play a domineering role in reef biogeochemical cycles such as sediment production and recycling of dissolved Ca^{2+} and C (Tribollet and Golubic 2011).

Within the tropical belt, many accretive reefs have lost their frame building corals during episodic disturbances (Riegl 2001). Temperature anomalies, *Acanthaster planci* predation and physical disturbance by hurricanes (Highsmith *et al*. 1980; Rogers *et al*. 1982; Perry 2001) all serve to diminish reef framework production. Most tropical reefs do, however, display the ability to recover from such disturbances, entering a continuum of “shifting steady-state mosaics” which are primarily regulated by disturbances rather than coral growth rates (Done 1999). High-latitude, marginal reefs often do not have the same resilience and frequent disturbances may result in the “switch-off” of framework production, or may have prevented it from ever being switched-on (Buddemeier 1988; Riegl 2001). Here, the major processes which inhibit reef accretion at high-latitude, marginal sites are investigated with reference to the implications of forecasted effects of climate change on ocean chemistry and thus coral growth, survival and carbonate precipitation or removal.

1.2. Reef Marginality

Guinotte *et al.* (2003) discuss the complexities in defining marginality in coral reefs and coral community assemblages in terms of ecosystem function and the conditions which make a habitat marginal. They suggest three definitions by which coral reefs or coral communities may be considered marginal:

“1. In a purely statistical sense, identifying the subset of reef communities or conditions that are near the extreme of a particular suite of environmental variables or community conditions.

2. On the basis of proximity to an environmental condition known or reasonably assumed, based on physiological or biogeographic evidence, to place an absolute limit on the occurrence of reef communities or key classes of reef organisms.

3. In terms of organism and community condition (cover, composition, diversity, health) or metabolism. We address the interacting concepts of community and marginality below."

(Guinotte *et al.* 2003)

The coral-dominated reef communities of South Africa fit definitions two and three above. However, the grouping of reefs by the extent to which environmental conditions are limiting often reflects the low ends of their environmental distribution, being high-latitude reefs (Kleypas *et al*. 1999 b; Guinotte *et al*. 2003). Yet stressed reefs, well within the tropics, may too be experiencing marginal conditions for either coral growth or reef accretion.

Often high or low extremes of temperature, salinity, light availability, aragonite saturation states (Kleypas *et al.* 1999 b; Guinotte *et al*. 2003) and the frequency of disturbance events (Harriott 1999; Riegl 2001) can be shown to be stressful and thus potentially limiting for reef development. Thus, an indication of their spatial and temporal (duration and frequency) delimitation needs to be incorporated in discussions on marginality (Guinotte *et al*. 2003). As such, reefs that occur at high-latitude are often considered to be marginal on the basis of their proximity to one or more environmental conditions which are known to limit the distribution of reef communities, key classes of organisms or key reef processes (Guinotte *et al*. 2003). Yet, it may be argued that the high-latitude reefs of South Africa are not marginal in terms of reef community structure and condition (cover, composition, diversity, health) or metabolism (Riegl *et al*. 1995; Guinotte *et al*. 2003; Celliers & Schleyer 2008), but rather in terms of limiting environmental conditions and habitat availability. Under the current pressure of climate change, many reefs are in danger of becoming marginal as local conditions continue to decline from the "normal" environmental limits for either coral growth or reef development (Kleypas et al. 1999 b). As such, understanding marginality at high-latitude sites may provide valuable insight into future limits on coral reef development.

1.3. Mechanisms of reef accretion/degradation

Reef accretion is only possible where carbonate precipitation, through the growth of calcifying organisms and chemical cementing processes within the reef framework, exceeds that of carbonate removal (Grigg 1982 a, b; Highsmith *et al*. 1983). The initial stages depend on rates of skeletogenesis of the constituent frame-builders (Highsmith *et al*. 1983) and subsequent retention of calcium carbonate in the reef framework. However, counteracting reef growth are physical, chemical and biological destructive processes (Goreau 1959; Hein & Risk 1975; MacGeachy & Steam, 1976; Hatcher 1997) which, if recurrent or chronic, can result in reef framework inhibition by an imbalance in the reef carbonate budget, favouring removal rather than deposition (Riegl 2001).

1.3.1. Aragonite saturation state

Aragonite saturation state is given as the ratio of the ion activity product to the stoichiometric solubility product with respect to calcium carbonate. Saturation states of greater than 1 refer to super saturation and $CaCO_3$ precipitation can occur (Morse & Mackenzie 1990). Global sea surface waters are supersaturated with respect to all mineral phases (calcite, aragonite and high-magnesium calcite) but the degree of super saturation varies both temporally and spatially (Holland 1984; Kleypas *et al*. 1999 a). Higher saturation states in the tropics are primarily due to high water temperatures, whilst lower saturation states are generally found at higher latitudes or areas of deep-water upwelling (Kleypas *et al.* 1999 b).

Calcite and aragonite saturation states are primarily dependent on carbonate ion concentrations in sea surface waters, and, as such, are sensitive to changes in ocean pH. Under normal conditions, the pH of ocean surface water is 8.0 to 8.2 with bicarbonate [HCO_3^-] ion concentrations between 6 and 10 times that of the carbonate ion [CO_3^{2-}] concentration. However, when CO_2 dissolves in ocean water, the acid formed lowers the ocean pH so that some carbonate binds with hydrogen molecules to form bicarbonate, a process termed ocean acidification. Since Ca^{2+} is rarely limiting, aragonite saturation states are largely determined by the availability of carbonate, described below as calcium carbonate saturation state (Ώ) and defined as:

$$'\Omega = \frac{([Ca^{2+}][CO_3^{2-}])}{K_{sp}} \, ,$$

where K_{sp} is the stoichiometric solubility product for a particular mineral phase of $CaCO_3$ (Kleypas *et al*. 1999 a).

The interaction between CO_2 and $CaCO_3$ in seawater ($CO_2 + H_2O + CaCO_3 \leftrightarrow 2HCO_3^- + Ca^{2+}$) alters with the addition of $CO_{2[aq]}$, encouraging $CaCO_3$ dissolution, and the reciprocal when CO_2 is removed (Kleypas *et al*. 1999). For this reason, Kleypas *et al.* (1999 b) suggest the transition from coral-community to accretive reef to occur only where saturation states rise above 3.4, despite super saturation of such minerals in ocean waters

Reef accretion is thus controlled both temporally and spatially by changes in sea water chemistry as a result of increased levels of anthropogenic CO_2. This may significantly affect the ability of reef organisms to calcify (Houghton *et al*. 2001) and the ability of reefs to form stable frameworks (Kleypas *et al*. 2001; Guinotte *et al*. 2003). Corals and other calcifying organisms are dependent on calcium and carbonate ion concentrations in ocean waters to secrete $CaCO_3$ skeletons. Reductions in ion concentrations associated with ocean acidification as a result of elevated $CO_{2[aq]}$ will greatly hamper corals in their growth and ability to deposit reefal structure (Langdon 2003; Jokiel *et al.* 2007). Coral and calcareous algae calcification rates were shown to decline by 11 – 37 and 16 – 44 %, respectively when using laboratory experiments and modelling techniques to simulate double the present CO_2 concentrations (Gattuso *et al*. 1999; Kleypas *et al*. 1999 a; Langdon 2003; Marubini *et al*. 2003). Moreover, Kleypas *et al*. (1999 a, b) estimated that an average decline in reef calcification of 6 – 11 % has occurred from preindustrial CO_2 levels and a further reduction of 14 – 30 % is expected by the middle of the next century. In addition to lowered growth rates as a consequence of ocean acidification, it is suggested that calcifying organisms may also produce skeletons of lower density (Buddemeier *et al*. 2004). Thus, not only will reef-building species be hampered in their ability to compete for space on the reef (Buddemeier *et al*. 2004), but will be more susceptible to physical breakage and invasion from bioeroders (Torunski 1979; Lopez-Victoria *et al*. 2006; Calcinai *et al*. 2007).

1.3.2. Climate change

Under presently forecast changes in climate, Edmunds (2005), amongst others, predicts a strong positive relationship between increases in scleractinian calcification and temperature but, more importantly, a rapid reversal of this effect beyond a narrow temperature threshold. Additionally, sub-lethal increases in temperature are expected to alter coral population dynamics through elevated growth rates, thus favouring an increase in the relative abundance of larger colonies (Edmunds 2005). Altered coral growth rates with increased SSTs may accelerate the transition of colonies between size classes and thus alter population trajectories (Edmunds 2005). A rapid transition to larger demographic stages will have beneficial consequences, possibly resulting in enhanced reproductive output (Hall & Hughes 1996), the higher survival of new recruits (Jackson 1977), greater resistance to partial tissue recession (Hughes & Jackson 1985) and changes in coral community composition as corals inclined to eurythermal conditions will have a heightened competitive advantage (McClanahan & Maina 2003). The changing thermal regime will thus provide the latter species the possibility of range extension (Precht & Aronson 2004; Edmunds 2005). Although these species may experience extensions in their geographic range under the influence of global climate change (Guinotte *et al*. 2003) and attain a competitive advantage over stenothermal assemblages, most tropical reefs are expected to become marginal in nature in the near future (Guinotte *et al*. 2003). Coral-dominated reefs may cease accretion and succumb to increased erosion pressure with further ocean acidification (Buddemeier *et al*. 2004). However, field studies have documented calcification rates in *Porites* spp. which have increased rather than decreased over the past century (Lough & Barnes 1997 & 2000; Bessat & Buigues 2001), and changes in community structure on a high-latitude reef in South Africa are presently favouring Scleractinea growth over Alcyonacea (Schleyer & Celliers 2003). This suggests that corals and coral-dominated communities are currently responding to the initial influences of increased temperature over that of decreased carbonate ion concentrations (Schleyer & Celliers 2003). However, deleterious effects will be manifested should ocean temperatures exceed the bleaching threshold (Buddemeier *et al*. 2004; Crabbe 2008). It is anticipated that, under the divergent forces of increasing temperature and declining levels of aragonite saturation, reef development at marginal, high-latitude sites will be subject to expansions in range yet further diminished accretive ability (Kleypas *et al*. 1999 a, b; Schleyer & Celliers 2003).

1.3.3. Storm disturbance

Large scale disturbances such as storm swells are known to provide episodic control over physical reef structure and the development of benthic communities (Massel & Done 1993; Riegl 2001). The partial, complete, or catastrophic removal of coral colonies and reef substratum may clear space on the reef and result in higher coral recruitment and larval settlement (Highsmith 1982) thus, influencing reef biodiversity and facilitating community succession (Huston 1985; Wilkinson *&* Buddemeier 1994).

Mass mortality of corals is a naturally occurring phenomenon and should not necessarily result in a "switch-off" in reef framework development (Riegl 2001). Post-hurricane survival rates of branching coral fragments, as cited in Perry (2001), are often high (e.g.: Belize, 46%, Highsmith *et al*. 1980; St. Croix, 35-66%, Rogers *et al*. 1982) and can promote the continued local dominance by branching corals by increasing colony numbers and promoting colony dispersal (Perry 2001). Thus, reef communities should have the potential to rapidly return to pre-disturbance conditions, as was the case in shallow water reef environments dominated by acroporids in the Caribbean throughout the Pleistocene and Holocene periods (Jackson 1992; cited in Perry 2001). However, reef framework development may be locally inhibited by chronic disturbances where living corals and reef frameworks are repeatedly removed by frequent storm surges, resulting in lower reef coverage (Connell 1997; Hughes & Connell 1999; Riegl 2001). Furthermore, excessive wave-stress may stunt asexual reproduction of potential frame-building species, thus limiting rates of population turnover and their ability for post-disturbance recovery (Riegl 2001). Storm-generated coral rubble is highly mobile and, unless held in place by existing reef topography or a coral framework, may be rapidly exported and/or eroded into sediment before sufficient cementation by calcareous algae has taken place (Blanchon *et al.* 1997). For example, coral-dominated reefs in Dubai fail to form stable rubble accumulations as storm-generated coral fragments are small, mobile and, due to a flat reef topography, are quickly eroded or exported (Riegl 2001).

1.3.4. Water movement and light availability

Water movement and availability of light are considered the dominant factors that influence hermatypic coral growth and survival on a local scale (Kaandorp 1999). Reef morphology, depth and zonation are all largely determined by these important factors (Wilkinson and Buddemeier 1994). Water movement also has a profound influence in modulating physiological pathways at the level of individual corals (Sebens *et al*. 2003). Flow affects nutrient diffusion (Kaandorp *et al*. 1996; Kaandorp 1999) and the encounter rate of corals with food particles (Sebens *et al*. 1997). Likewise, water movement enhances photosynthetic rates of the symbiotic algae and increases respiration rates within coral tissues (Bruno *&* Edmunds 1998). Thus, reduced water movement may decrease coral metabolic rates and may lead to a loss of coral condition and slower growth rates in certain species (Bruno & Edmunds 1998).

Several authors have ascribed the morphological plasticity of corals to variations in light availability (Barnes 1973; Graus & Macintyre 1982) and water movement (Helmuth & Sebens 1993; Lesser *et al*. 1994; Kaandorp 1999). Yap *et al*. (1998) report faster growth of transplanted nubbins of a hermatypic coral at shallow depths with high light availability and higher water motion. Likewise, a simulation model of coral growth forms, supported by *in situ* observations and experimentation, yielded a gradient in the growth form of *Pocillopora damicornis* relative to water movement (Kaandorp *et al*. 1996; Kaandorp 1999). Coral colonies gradually changed from compact growth forms in turbulent environments, where water movement was optimal for nutrient supply and adsorption, to thin-branching morphologies in calm environments where diffusive processes became the dominant form of nutrient gathering (Kaandorp *et al*. 1996; Kaandorp 1999). In addition to nutrient adsorption and possibly prey capture (Helmuth & Sebens 1993), the authors suggested that, with increased water movement, there is an increased probability of structural damage which results in a compact growth form in coral colonies.

1.3.5. Bioerosion

There is a synergistic relationship between the primary producers in any bioeroder community, microbial epiliths and endoliths, and their grazers. Grazing of carbonate substratum hampers the stabilizing effect of calcifying benthic organisms so that the bioerosional process and subsequent breakage becomes progressive (Goreau & Hartman 1963; Torunski 1979). Should this process become dominant or unbalanced in terms of carbonate removal over deposition, reef accretion may not occur.

Bioerosive agents occupy a wide variety of taxonomic affiliations, with each group performing some function in coral reef development or degradation (Tribollet and Golubic 2011). External bioeroders, such as fishes of the family Scaridae, graze on carbonate structures in an effort to reach the epilithic and endolithic organisms living within. In this manner, large portions of coral-derived substratum can be removed relatively quickly (Goreau & Hartman 1963; Torunski 1979). Macroboring organisms also contribute to carbonate removal. These are organisms which actively penetrate into carbonate structures in search of food or shelter and thus perform a different function to external bioeroders (Tribollet and Golubic 2011).

Macroborers constitute the primary focus in the Bioerosion section of this study. They include foraminifera, sponges, bryozoans, polychaetes, sipunculids, bivalves and some crustaceans (Tribollet and Golubic 2011). Despite the wide diversity of organisms which contribute to bioerosion on coral reefs, a significant portion of such erosion is attributable to boring sponges alone (MacGeachy & Stearn 1976; Hudson 1977). The erosive action of these organisms penetrates the carbonate substratum, resulting in the excavation of an extensive network of tunnels and cavities and the subsequent degradation of the reef (Lopez-Victoria *et al*. 2006; Calcinai *et al.* 2007). Sponges remove carbonate by both chemical dissolution and mechanical etching of carbonate chips, which are expelled through their aquiferous system into the reef environment (Rutzler & Rieger 1973). Calcareous chip production can attain up to 22 kg $CaCO_3m^{-2}$ $year^{-1}$and contribute up to 40% of the sediment production on coral reefs (Neumann 1966; Rutzler and Rieger 1973; Futterer 1974; Rutzler 1975). Additionally, recent studies have revealed that this can involve a rate of chemical dissolution of carbonate three times higher than that of the mechanical etching and chip production process (Zundelevich *et al*. 2007). In an accretive reef system, this process would be outweighed by higher carbonate deposition from calcifying organisms, such as scleractinian corals and various coralline algae, fast physical compaction by wave action and chemical solidification from rain water input (Veron 2000; Done *et al*. 1996). Yet, under environmental or anthropogenic stress, or in marginal habitats, many reefs fail to accrete (Harriott 1999 – Lord Howe Islands; Riegl 2003 – Arabian Gulf; Hutchings *et al* 2005).

1.3.6. Sedimentation and eutrophication

High rates of sedimentation on coral reefs can have opposing effects for coral health and for reef accretion. In severe cases, excessive sedimentation has been linked to coral stress and subsequent bleaching (Riegl & Branch 1995; Meehan & Ostrander 1997), among other physiological responses. For example, lowered growth rates of both branching and non-branching hard corals have been shown to occur with increased levels of sedimentation associated with coastal development and increased land run-off on Indonesian reefs (Crabbe & Smith 2005). A secondary effect of sedimentation stress is a change in coral growth form, favouring vertical, upright growth to prevent accumulation of sediment on the colony surface (Crabbe & Smith 2005). An associated decrease in light availability further contributes to this alteration in growth pattern (Wellington 1982; Rogers 1990). Yet certain aspects of reef accretion are dependent on the reworking of imported and locally derived autochthonous sediments into permanent reef structure (Ramsay 1996). Infilling of the interstitial spaces within reef frameworks is a vital component to unconsolidated reef accretion, particularly where branching-coral assemblages are dominant (Veron 1995). Sediments created by both biological and physical erosion are not necessarily subtracted from reef carbonate budgets but may be retained within the framework and, if stable, can add significantly to reef development (Veron 1995; Perry 1999; Riegl 2001). However, continual resuspension of sediments, as is common in a high-energy environment, can have deleterious effects of reef health.

Increased suspended material may not only reduce light levels (Rogers 1990) and interfere with photosynthesis, but also hinder coral feeding (Bak 1978) and cause corals to expend energy on the removal of sediment particles (Storlazzi *et al*. 2011). Furthermore, toxic substances, such as dissolved heavy metals, may adhere to fine-grained sediments, thus assisting in their transport and accumulation on reef substrata (Saouter *et al*. 1993; Bastidas *et al*. 1999). Settlement of such sediments on corals can alter the microbial community within their surface mucosal layer and lead to a loss of health, hampered resistance to disease, and subsequent infection (Kuntz *et al*. 2005). In addition, nutrient loading of sea surface waters may enhance pathogen growth and thus rates of infection (Bruno *et al*. 2003; Smith *et al*. 2006). Rates of bioerosion have also been shown to increase along gradients of increased eutrophication and the associated environmental parameters (Chazottes *et al*. 1995). Eutrophication by the addition of nitrogen and phosphorous, often associated with increased sedimentation or land-based run-off, has the potential to increase growth rates and thus the efficacy of many bioeroding organisms (Pastorak & Bilyard 1985; Sammarco & Risk 1990; Edinger *et al*. 2000). Additionally, eutrophication can alter the pattern of dominance on coral reefs in favour of various forms of algae and heterotrophic invertebrates relative to reef-building corals (Rose & Risk 1985; Sammarco & Risk 1990) and thus facilitate a change in reef community structure (Smith *et al*. 2006; Chazottes *et al*. 1995). This may disrupt the equilibrium between deposition and erosion of carbonate and can result in physical reef loss and possibly the "turn-off" of reef framework development (Davies & Hutchings 1983; Kiene 1988; Peyrot-Clausade *et al*. 1995, 1999; Reaka-Kudla *et al*. 1996; Pari *et al*. 1998; Riegl 2001).

1.3.7. Coral growth and reef accretion

Growth rates of calcifying organisms do not necessarily equate to reef accretion (Buddemeier & Kinzie 1974), nor does species richness or coral cover by major frame-builders result in a permanent reef framework (Riegl 2001). Yet both are necessary precursors for reef expansion. The development of a reef framework results from a balance in environmental conditions that favour scleractinian growth under a no-disturbance scenario (Riegl 2001). Although corals are not the only calcifiers on coral reefs, they provide an essential framework for other benthic calcifiers to adhere to. Coral derived frameworks facilitate the accumulation of sediments and the eventual chemical cementation of the sum into a permanent reef structure (Stoddart 1969). Overall accretion results from a surplus in the reef carbonate budget whereby carbonate precipitation outweighs both physical and biological reef erosion and subsequent sediment export (Ramsay 1996; Glynn 1997). A concept discussed by Grigg (1982 a) and termed a "Darwin point" is described as a region where coral reefs are able to persist yet fail to accrete. He argues that, with a southward progression in latitude, calcium carbonate deposition is gradually offset by an increasing level of bioerosion (Grigg, 1982 a, b; Eakin 1996; Reaka-Kudla *et al*. 1996; Harriott 1999; Guinotte *et al*. 2003), and thus a transition from accretive reefs to non-accretive coral communities and an increase in marginality of reef habitat (Veron 1995; Guinotte *et al*. 2003). Concurrently, there is a reduction in coral growth rate (Harriott 1999; Table 1). Both factors are likely to contribute to hampered frame-building capacity and thus lowered accretion at high-latitude sites (Johannes *et al*. 1983).

Table 1: Published data on growth rates of *Acropora* spp. at different latitudes and temperatures in the southern hemisphere (adapted from Harriott, 1999).

Latitude	**Mean annual water temperature (˚C)**	**Coral species**	**Location**	**Linear extension (mm/y)**	**Reference**
13˚S	28	*A. formosa*	Samoa	185	Mayor 1924
15˚S	26	*A. elseyi*	Lizard Island	38	Oliver 1985
		A. florida		45	Oliver 1985
		A. formosa		71.3	Oliver 1985
		A. nobilis		41	Oliver 1985
		A. robusta		55	Oliver 1985
18˚S	25.5	*A. formosa*	Palm Island, GBR	80-120	Oliver *et al*. 1983
21˚S	26	*A. formosa*	Dampier Archipelago	100 - 137	Simpson 1988
27.5˚S	24.4	*A. austera*	Sodwana Bay	24.5	Present study
28˚S	21	*A. formosa*	Houtman Abrolhos	37 - 76	Harriott 1998
30˚S	20.5	*A. cytherea*	Solitary Islands	20.9	Harriott 1999
		A. robusta		22.4	Harriott 1999
		A. valida		23.6	Harriott 1999
31.5˚S	21.5	*A yongei*	Lord Howe Island	49.4	Harriott 1999
32˚S	21	*A. yongei*	Rottnest Island	63.9	Marsh 1992

1.4. South African Reefs

The coral-dominated reefs of Sodwana Bay are the central of three reef complexes in South Africa. The central reef complex consists of Two-, Four-, Seven-, and Nine-mile reefs (Figure 1; TMR, FMR, SMR and NMR, respectively). Their ecology and community structure have been comprehensively studied and described by Riegl 2001, Celliers & Schleyer 2003, Riegl 2003, Schleyer & Celliers 2003, Glassom *et al*. 2006, Celliers & Schleyer 2008, and Schleyer *et al.* 2008.

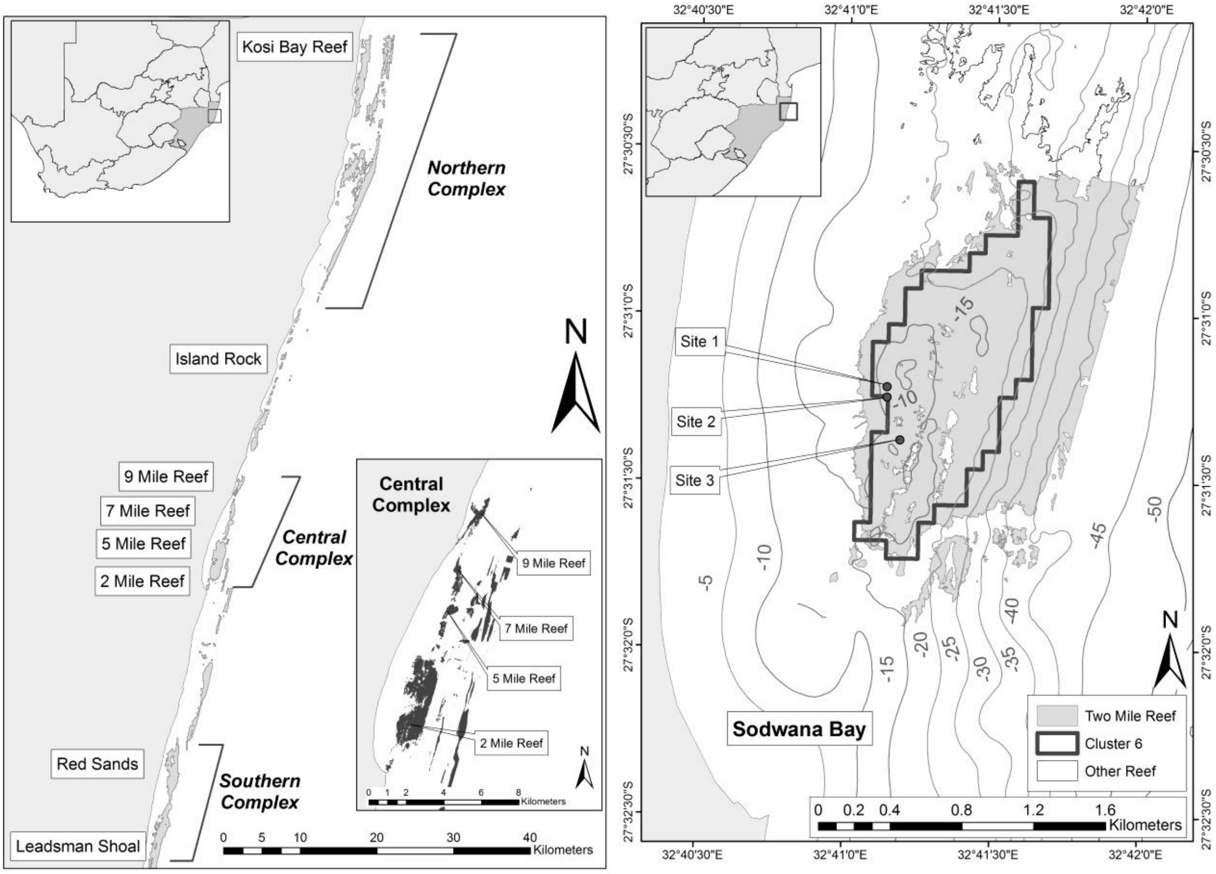

Figure 1: Seafloor map of the central reef complex at Sodwana Bay, South Africa, showing the study sites on Two-mile Reef.

Reefs on the north-eastern coast of South Africa constitute a diversity peak for coral communities south of the equator (Schleyer & Celliers 2003), with a notably high cover of scleractinian (26.9±15.0 %) and alcyonacean (32.0±11.9 %) species (Celliers & Schleyer 2008; Schleyer *et al*. 2008). The unique location of these reefs, representing the southernmost distribution of this fauna along the east African coast, results in a blend of both temperate and tropical marine organisms at Sodwana Bay and other local reefs. Lateral reef growth is prevented by a limited area of colonisable substratum (Ramsay 1996) whilst vertical reef growth appears non-existent. Assemblages of branching corals which hold the potential to build complex frameworks and thus contribute to vertical reef growth are found in varying densities on the reefs (Riegl 2001), yet no frameworks remain permanently.

There is a global trend of decreasing coral reproduction and subsequent planular settlement with increasing latitude (Hughes *et al.* 2002). Low latitudes exhibit high acroporid settlement which subsides with a relative increase in the numbers of pocilloporids at higher latitudes (Hughes *et al.* 2002). As such, coral settlement at Sodwana Bay is dominated by pocilloporids, regardless of site or season, comprising 86% of all coral settlement with a mere 9% of settlement being attributable to acroporid species (Glassom *et al.* 2006). However, this trend may be an artefact of experimental methods as faviids, poritids and other families which may contribute to reef development tend not to settle on artificial settlement tiles (Glassom *et al.* 2006). Although both acroporids and pocilloporids display some frame-building capacity, the coral-deposited carbonate reef structure at Sodwana Bay is minimal, with sandstone base-rock often only centimetres below the reef surface (Ramsay 1996; Riegl 2001).

Kleypas *et al*. (1999a) modelled the physical and chemical limitations for coral growth at different latitudes. It was estimated that South African reefs fall within acceptable limits for salinity, PO_4 and NO_3 but within the marginal limits for light penetration, temperature and aragonite saturation state (Schleyer & Celliers 2003). The above mentioned parameters dictate coral and reef distributions on a global scale whilst additional processes are thought to regulate development at the scale of individual reefs. Disturbances shape reef structure and influence benthic organism abundance and composition. Coral bleaching events have been observed but unlike the rest of the East Coast of Africa (Obura *et al*. 2000) only slight bleaching occurred at Sodwana Bay prior to and including the 1998 El Nino Southern Oscillation (ENSO) event (Schleyer *et al*. 1999; Celliers & Schleyer 2002). However, measureable bleaching was recorded in 2000 where protracted periods of elevated water temperature coincided with high levels of irradiance caused by exceptional water clarity (Celliers & Schleyer 2002). Again, slight bleaching was observed in early 2011 (pers. comm. local dive charters). A crown-of-thorns starfish (COTS; *Acanthaster planci*) outbreak occurred on the reefs during the 1990s (Celliers 2001). The persistence of COTS within the food-limited environment of these reefs caused significant reductions in hard coral cover over isolated areas, affecting coral community structure (Celliers 2001). Impacted areas entered post-disturbance, alternate stable-states (Celliers 2001). Perhaps the most active of all the disruptive processes occurring on the reefs of the iSimangaliso Wetland Park are frequent and high-energy storm surges (Riegl 2001). It is generally accepted that large-scale disturbance events such as storm surges or hurricanes play a definitive role in reef ecology and geomorphology (Stoddart 1969; Highsmith *et al*. 1980; Rogers *et al*. 1982; Riegl 2001).

Periodic and chronic disturbances, such as those mentioned above, coupled with the marginality in environmental conditions (i.e. aragonite saturation state, temperature, light availability) for reef growth has led to the current theory for the lack of reef development in the area (Kleypas *et al.* 1999 a, b; Riegl 2001; Schleyer & Celliers 2003). However, results obtained from a constant monitoring programme initiated on the Sodwana Bay reefs over the last decade have revealed conditions which currently favour scleractinian growth and calcification (Schleyer *&* Celliers 2003). Yet, if the predictions by Kleypas *et al*. (1999 a) hold true, hard coral cover will decrease as growth rates subside to diminished aragonite saturation states in the near future, further hampering accretive ability (Schleyer *&* Celliers 2003).

1.4.1. Frame-building coral assemblages in Sodwana Bay, South Africa

Several coral assemblages have previously been delimited in the Sodwana Bay reef complex (Riegl *et al*. 1995; Riegl 2001; Celliers *&* Schleyer 2008). Of these, it was only the *Acropora*-dominated assemblage (*A. clathrata*, *A glauca*, *A. branchi*, *A. tenuis* and *A. austera*) which showed frame-building potential (Riegl 2001), whereby large monospecific and potentially monoclonal stands develop to a sufficient size and density (i.e. interlocking) to classify as a reef framework. As such, *A. austera* was designated the focal species for this study, whereby its growth, mortality and the persistence of the underlying frameworks was monitored *in situ*.

1.5. Aims

In this study, it is postulated that the distinct lack of any cumulative biogenic accretion on South African reefs is a consequence of several interrelated processes. Limiting environmental parameters coupled with chronic stressors (i.e. excessive sedimentation and wave-generated surge) may result in reduced growth rates of frame-building corals. The persistence of frame-building coral populations is possibly negated by occasional failure in sexual reproduction and recruitment success, and chronic failure to reproduce asexually (Riegl 2001). Furthermore, periodic, large–scale disturbance from storm surges can uplift living coral cover along with the underlying reef framework revealing bare base-rock and thus, re-setting reef accretion to zero (Riegl 2001). Internal bioeroder communities weaken coral framework, adding to their susceptibility and facilitating the likelihood of physical damage (Torunski 1979; Lopez-Victoria *et al*. 2006; Calcinai *et al.* 2007). Bioeroders also reduce solid substratum to sediment and contribute significantly to sediment production on the reef (Scoffin *et al*. 1980; Hubbard *et al*. 1990). Should locally-generated autochthonous sediment be retained within the reefal framework and reworked into permanent structure, reef accretion would occur. Despite this no evidence of a permanent reef structure is observed at Sodwana Bay (Ramsay & Mason 1990; Ramsay 1996; Riegl 2001).

Therefore this study will investigate the mechanisms which prevent these reefs from forming permanent *in situ* frameworks in the presence of a rich coral fauna (Schleyer 2000; Glassom *et al*. 2006). This has relevance to our understanding of current coral reef dynamics at high-latitudes and may provide a model for the study of many of the stressors to which coral reefs are being subjected globally.

Several potentially limiting factors for reef development were assessed;

1. Aragonite saturation states were determined and compared to those stated in the literature,

2. Swell height data was collected from the nearest ADCP and temperature data from UTRs placed on the reef,

3. Rates of sedimentation were determined to assess the potential for sediment infilling of the reef interstitial spaces,

4. The level and severity of bioerosion and the quantity of $CaCO_3$ removed was measured and is suspected of weakening reef frameworks created by *Acropora austera*.

The growth, mortality and dynamics of large monospecific patches of the major frame-building coral, *Acropora austera,* was assessed by;

1. Repeated image analysis of quadrats within each of three sites,

2. Staining nubbins with the vital stain, Alizarin Red S,

3. Levels of water movement and sedimentation were compared between sites to detect potential differences.

2. Chapter 2- Introduction to methodology

2.1. Measuring growth

Measuring growth of branching corals in the field can be difficult, requiring individual branches to be monitored through time. A commonly used, non-invasive method of growth determination utilizes image analysis of photographs taken repeatedly of the same branches (Crabbe & Smith 2002; Crabbe & Smith 2005). However, growth estimates based solely on image analysis may introduce errors such as lens distortion or parallax in measuring the growth of branches not in a horizontal plane. Alternative methods are available, yet most also have limitations. Physical marking of colony branches with wire (Harriott 1999) or plastic cable-ties (Crabbe & Smith 2005) can damage coral polyps and may result in overgrowth by fouling organisms (attempted and abandoned in present study). Chemical marking with the vital stain, Alizarin Red S, has been used not only for corals (Harriott 1999), but also other calcifying organisms (Steller *et al*. 2007). Although a relatively easy and non-invasive technique, many authors report mixed results with low staining success (Blake & Maggs 2003; Harriott 1999; Present study). Here two methods of growth determination were employed for the hermatypic branching coral, *Acropora austera*, chemical staining with Alizarin Red S and photographic imaging.

2.2. Measuring bioerosion

Levels of micro and macro-bioerosion have been used as an integrated, holistic approach to evaluate coral reef health (McClanahan 1997; Edinger *et al*. 2000), yet methods of evaluating bioerosion rates and intensities differ substantially. The rate of bioerosion refers to the quantity of skeletal material removed over time, whilst the presence of bioeroding organisms and damage done by these organisms constitutes bioerosion intensity. Methods for the quantification of bioerosion rates are described by Zundelevich *et al*. (2007) and Nava & Carballo (2008) and require specialized and sensitive equipment. These, although yielding meaningful data, are generally inappropriate for rapid assessments on reefs. By contrast, measurements of bioerosion intensity by internal eroders have been achieved using a number of methods. Some authors have employed blocks of coral skeleton or calcite placed on the reef to quantify eroder invasion, eroder densities and net erosion over an extended time-frame (Kobluk & Risk 1977; Kiene & Hutchings 1994; Chalzottes *et al*. 1995; Pari *et al*. 1998; Tribollet *et al*. 2002). Measuring the area removed from cross-sections of branching corals or massive coral heads, of either dead rubble or living colonies, is a commonly applied method for the quantification of bioerosion intensity in modern reef assessments (e.g.: Holmes *et al*. 2000). This is often done using X-rays (Highsmith *et al*. 1983; Sammarco & Risk 1990) or photographs with subsequent image analysis (Risk *et al*. 1995). An inventory of bioeroders by species or eroder organism composition found within the coral skeleton is added to this methodology (Holmes *et al*. 2000; Nava & Carballo 2008). The use of these methods yields results which can be compared at various spatial and temporal scales to assess differences in reef ecosystem function, and may not only assist in categorizing reefs but also advance our understanding of the biogeographic and physiological limits to coral reef development within climatic and evolutionary time-scales (Guinotte *et al.* 2003).

2.3. Water movement

The use of dissolution rates from gypsum blocks as a non-dimensional index of water movement is a relatively simple and inexpensive technique for *in situ* measurements of water flow. This method was first introduced by Muus (1968) and Doty (1971) and termed “plaster balls” or, more commonly, the “clod card” technique. Subsequently, various forms of the gypsum-dissolution technique have been used for a large variety of physical-biological interactions in many disciplines (summarized by Porter *et al*. 2000). These initial studies have been supplemented by Jokiel (1978), Morrissey (1993) and Thompson & Glenn (1994) who investigated the effects of temperature, salinity and water volume on the rate of gypsum dissolution. In addition, the theory has been adapted to include materials such as dissimilar metals (McGehee 1997; Boizard & DeWreede 2006), orthorhombic forms of calcium sulphate (Barton & Wilde 1971), and sucrose candies (Shaughnessy 1996), among many others.

The gypsum-dissolution technique has previously been described as a method which ‘‘incorporates any water motion due to tidal as well as wind-wave effects in the same integrated measure’’ (Wildish & Kristmanson 1997) and thus provides either an absolute or, more importantly, a comparative measure of water motion. However, Porter *et al*. (2000) argue that the flow variables (e.g. current velocity, flow intensity, turbulence intensity, and water motion) are nonspecific, thus it is often not clear what gypsum-dissolution is measuring. They found gypsum-dissolution to be appropriate for steady flow and fluctuating flow regimes, but not so for a mixed flow environment. The relationship between rates of dissolution was found to be different in each flow environment and, most notably, the effects of steady flow and fluctuation intensity were not additive (Porter *et al*. 2000). Often a standardized calibration curve is created and used to translate a loss in weight of gypsum to water velocities. Creating such a curve requires immersion of similar blocks of gypsum in standing water or flowing water of known velocity within similar temperature and salinity ranges (Doty 1971; Jokiel 1978; Morrissey 1993; Thompson & Glenn 1994; Porter 2000). However, most authors attempting this technique report highly variable results and, consequently, a poor estimation of water velocity (Boizard & DeWreede 2006). Methods based on gypsum-dissolution have been used extensively as an index of water motion, yet have major limitations in that they provide no information regarding instantaneous flow, variable flow magnitudes or self-imposed hydrodynamic disturbances (Boizard & DeWreede 2006). However, once these limitations are taken into consideration, the method has proven useful for studies involving mass transfer, or nutrient delivery, or removal to and from organisms, and as a comparative index between study sites (Gerard 1982; Larned & Atkinson 1997; In: Boizard & DeWreede 2006). In the present study a variation of the gypsum dissolution technique was used as a method of comparative assessment of levels of water movement between several areas on the reef.

2.4. Sedimentation

Although various forms of sediment traps have been utilized since midway through the 20th century, it is only since the 1970s that modern variants have been used in shallow environments less than 40 m in depth (reviews in Bloesch & Burns 1980; Reynolds *et al*. 1980; Butman *et al*. 1986; Storlazzi *et al*. 2011). They have become increasingly popular as a comparative method to measure the effect of sedimentation on coral reefs and coral reef organisms (Rogers 1990; Holmes *et al*. 2000; Crabbe & Smith 2005 amongst many others), assessing the impact of land-use practices (Jordan *et al*. 2010) and as an effective tool in reef monitoring (Wilkinson *et al*. 2003).

Sediment traps are used to capture a representative sample of the net vertical flux of all sediment particles in the water column over a designated period. This provides (a) an integrated rate of particle supply and (b) an indication of particle properties and sediment composition over the time of deployment (Storlazzi *et al*. 2011). For these reasons, sediment traps have become a standard measurement tool and an important component of coral reef studies (Storlazzi *et al*. 2011).

Here, levels of sedimentation were assessed as an indication of a potential stressor to local corals and to provide insight into sediment resuspension within areas of reef framework and the implications for unconsolidated reef accretion.

3. Chapter 3 - Methods and materials

3.1. Study sites

The study was conducted at Sodwana Bay within the iSimangaliso Wetland Park on the north eastern coast of South Africa. The reefs are located between 27˚and 28˚S and comprise the central of three reef complexes (Riegl et. al. 1995; Schleyer 2000). They are the southernmost distribution of extensive coral-dominated benthic communities on the East African Coast (Schleyer 2000; Glassom *et al*. 2006). Sodwana Bay is a high-latitude, non-accretive reef community and considered marginal in nature, it has a persistent and significant coral community comprising of scleractinian corals (43 genera comprising 93 species) and an abundance of non-accretive species (11 genera of alcyonacea comprising 39 species with 1 species of Milleporina) (Riegl 2001; Schleyer & Celliers, 2003; Celliers & Schleyer 2007). However, these communities grow only as a thin veneer on a substratum consisting of fossilized Pleistocene beach-rock with the occasional aeolianite outcrop (Ramsay 1996).

In selecting study sites, preference was given to those located within TMR which had an established population of *Acropora austera*, forming large monospecific patches. Three sites were selected based on patch size and depth of the underlying coral framework. The size of each *A. austera* patch ranged from an estimated 6 m^2 up to 20 m^2. Other than the use of intrusive methods, the depth of any existing framework could not be directly measured without compromising its stability. For this reason an estimate of framework depth was used to rank sites. Site 1 was the largest with the deepest observable framework. Area coverage of the *A. austera* patch at site 1 was estimated to be >20 m^2 with interspersed colonies extending further. Framework depth to base-rock was 40 cm in areas where base-rock was visible and likely to be deeper in other areas (Figure 2a). Site 2 was observably smaller and less developed than site 1, with an overall size of 8 – 12 m^2 and framework depth of 30 cm and less where base-rock was visible (Figure 2b). Site 3 was the smallest and least developed of all sites. Total area cover was 6 – 8 m^2 with base-rock visible in most areas (Figure 2c). Study sites were all at a depth of 10 – 14 m depth and thus subject to similar irradiance levels.

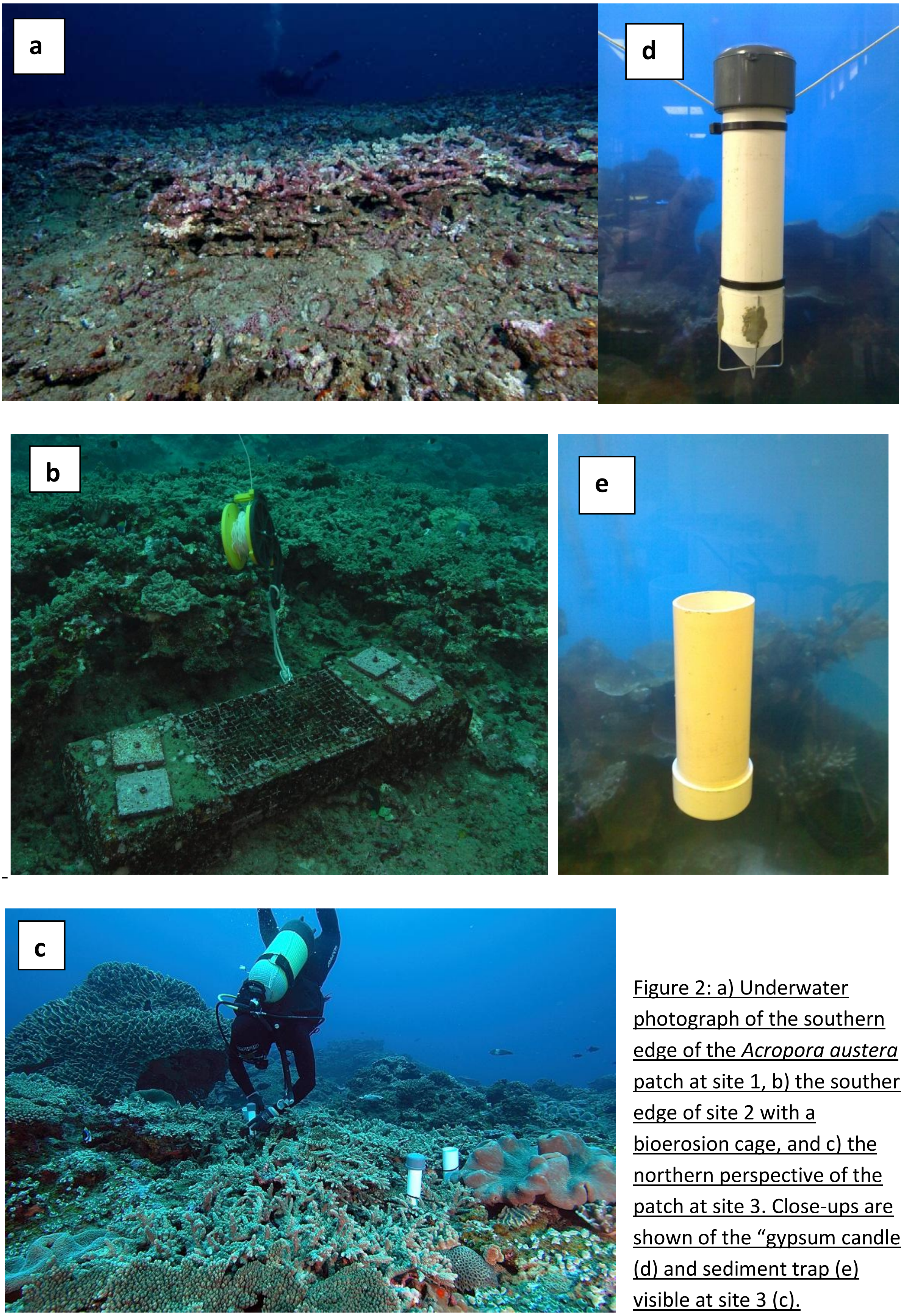

Figure 2: a) Underwater photograph of the southern edge of the *Acropora austera* patch at site 1, b) the southern edge of site 2 with a bioerosion cage, and c) the northern perspective of the patch at site 3. Close-ups are shown of the “gypsum candle” (d) and sediment trap (e) visible at site 3 (c).

Two-mile Reef lies 1.08 km offshore and is 2.14 km^2 in length. The water depth ranges from 6 – 10 m on the shallowest pinnacles to 24 – 27 m on the fore-reef (Celliers & Schleyer 2002). The reefs afford the coastline little protection from the substantial swells and storm surges which frequent the area (Southern African Data centre for Oceanography) The Agulhas Current passes southwards at a maximum velocity of up to 1.5 $m\ s^{-1}$ with its core situated just offshore to the continental shelf (Schumann 1988). Unconsolidated lithology in the region is predominantly quartzose shelf sand with a low carbonate content ranging from 4 to 13% (Ramsay 1996). Sediment reworking is common and highly active in depths less than 50 m due to the high-energy swell regime characteristic of the region (Ramsay 1996). Bioclastic sediments on this shelf are defined as having greater than 20% $CaCO_3$, of which the chief contributing components are molluscan fragments, foraminiferal tests, sclerites of soft corals and sea fans, echinoderm spines, bryozoan fragments, hard coral and calcareous algae remains, and spicules from sponges (Ramsay 1996).

3.2. Study species - Acropora austera (Dana 1846)

The genus *Acropora* is categorized as an important reef-building coral, particularly where the expected form of reef development is that of unconsolidated rubble accretion (Riegl 2001). *Acropora austera* is a common species of branching hard coral, and one of the few corals on the Maputaland reefs that form large monospecific stands with the potential to develop a complex, underlying framework. Although Buddemeier & Kinzie (1974) suggest no causal connection between coral growth and reef formation it is postulated that the persistence of a framework matrix, such as that created by *A. austera*, is a precursor to unconsolidated reef accretion (Veron 1995; Blanchon *et al.* 19979; Riegl 2001).

The coral dominated reefs of Sodwana Bay show 58.9±19.0 % total living cover with 26.9±15.0 % being hard corals, and 5.0±7.9 % of which were *Acropora* species (Celliers & Schleyer 2008). Furthermore, of the 29.0±7.8 % hard coral cover on TMR alone, only 2.7±2.4 % is attributable to *Acropora* species (Celliers & Schleyer 2008). *Acropora austera* generally has a caespitose to aborescent growth form with branches given off in all directions from a broad basal attachment (Riegl 1993). This species does, however, show great plasticity in growth form depending on local environmental conditions. On sheltered reefs, branching is broadly spaced with upward growing branches, whereas on exposed reefs, branches tend towards prostrate and sprawling forms (Riegl 1993). In these areas, however, the original branching pattern is barely discernable as colonies are frequently broken by rough seas (Riegl 1993). Instead they resemble a chaotic mass of broken and/or fused branches, perched on top of a framework of dead portions of the basal structure. As the growing tips extend, the underlying portion of the colony begins to be over-shaded and the living tissue recedes, leaving behind bare skeleton and adding to the underlying framework structure which may or may not still be attached to the base-rock.

3.3. Physico-chemical parameters

3.3.1. Aragonite saturation state at Sodwana Bay

Water samples for aragonite determinations were collected in summer (March 2010) and winter (September 2010). Measurements of salinity were done at the same time and locations as those for aragonite saturation states and were recorded using a hand held YSI ™ salinity meter. Samples were collected on the north, south, east and west corners and at the centre of each *Acropora austera* stand. Two samples were taken at each location, one directly above the coral substratum and a second 2 m above, using diver-operated Niskin bottles. The same sampling procedure was repeated at first light and at midday to assess diurnal effects on carbonate water chemistry. Water samples were drawn into labelled boro-silicate glass bottles without the introduction of gases and thereafter poisoned with 100-200 µl saturated $HgCl_2$ solution (50g/l) to stop any biological activity. These were then immediately sealed with ground-glass stoppers coated in Vaseline to prevent gas exchange with the atmosphere.

Determinations of carbonate saturations and aragonite saturation states were undertaken by the Council for Scientific and Industrial Research (CSIR), Stellenbosch.

3.3.2. Sea water temperature

Mean water temperatures for the study period were retrieved from a fixed temperature monitoring station located on the 18 m depth contour at NMR, Sodwana Bay. A pair of Hugrun underwater temperature recorders (UTRs) measured temperatures on the minute and recorded these as hourly means. Mean surface sea water temperatures over the study period were 24.45±1.74˚C with a summer and winter peak of 28.6˚C and 21.0˚C, respectively. Summer peak and winter trough temperatures lagged that of the atmospheric seasons by an average of one month. Moreover, several additional temperature troughs are recorded which are usually linked to upwelling events (Ramsay 1996).

3.3.3. Swell height data

Swell height data were obtained for the nearest ADCP at Richards Bay Harbour (154.5 km South), from the CSIR, Stellenbosch, and comprised data collected on behalf of the Transnet National Ports Authority (TNPA).

3.3.4. Water movement determinations

Novel devices termed "gypsum candles" (Figure 2d) were constructed to extend the immersion time of the gypsum dissolution determinations. These were constructed of 15 cm lengths of 35 mm diameter PVC pipe, inside which a precast 15 cm long cylindrical rod of plaster of Paris was inserted. The lower end of each pipe was caged with two 1.5 mm stainless steel cross bars to protect a 2 cm extension of the gypsum candle, thus exposing it to water movement and consequent erosion. The plaster of Paris candles had an 85 g lead weight placed on top within each device. This ensured a consistent downward force on each candle and prevented them from jamming. Finally, each device was capped with a PVC end-cap through which a 2mm hole was drilled to prevent a water lock from restricting the candle movement.

Gypsum candles were cast as 1 part plaster of Paris to 1 part distilled water. During the mixing process, powder was added to water, which facilitated an even consistency, and it was gently but thoroughly mixed until fully dissolved. The mixture was then carefully poured into two, 1 m long, 35 mm rigid PVC pipes. These took roughly 15 minutes to dry, during which each pipe was vibrated continuously to expel bubbles. A subsample of each cast was sectioned to check for bubbles and discarded if any were found. Thereafter, each 1 meter casting was cut into 15 cm rods and dried in an oven for 48 hours at 60˚C or until a constant weight was achieved. One end of each 15 cm piece was then shaped using a belt sander to create the "erosion edge" – a tapering point of 2 cm long.

Each gypsum candle was dried, weighed and measured both before and after immersion on the reef. A comparative index of water movement was calculated as:

$$WM = {\left(\frac{L_S - L_E}{L_S} X\, 100\right)}\Big/{T_{hr}},$$

where WM is the index of water movement, L_S the starting length of each gypsum candle, L_E the terminal Length and T_{hr} the immersion time in hours. Water movement is expressed as a percentage loss in candle length $hour^{-1}$. This results in a non-dimensional Index of water movement which is a product of all hydrodynamic forces, i.e. water motion, water movement and turbulence created by currents and swell-surges.

3.3.5. Sedimentation measurements

Sediment traps (Figure 2e) were constructed as simple tube traps (STT) with the purpose of providing an integrated rate of particle collection, regardless of composition, at the substratum level. White (1990) recommended they be constructed in a 3:1, height : diameter ratio. In this case, the traps were 50 mm diameter PVC pipes 150 mm in length. The lower end was sealed with a PVC end-cap whilst the trap opening was left unimpeded.

At the end of each sample period, STTs were sealed individually under water with a plastic sheet of polyethylene plastic over which a 50 mm diameter PVC end-cap was placed. This ensured a water-tight seal and prevented any loss of sediment during transport. The contents of each STT were filtered through individual sheets of pre-weighed, 3HW 240 mm filter paper and rinsed thoroughly with distilled water to remove any residual salts. These were then dried at 60˚C for a minimum of 24 hours or until a constant weight was achieved.

Rates of sedimentation were calculated as:

$$R_S = {\frac{W_S}{T_A}}\Big/{T_{hr}}\; X\, 24,$$

where R_s is the rate of sedimentation, W_s the weight of the sediment retained, T_A the area of the trap opening and T_{hr} the immersion time in hours. Rates of sedimentation are expressed as g dry weight cm^{-2} day^{-1}.

3.3.6. Sampling design

Sampling was carried out on a bimonthly basis between October 2009 and December 2010 to capture both *in situ* sedimentation and levels of water movement. Sediment traps and gypsum candles were placed in paired sample units (PSUs) consisting of one gypsum candle and one sediment trap each. PSUs were carefully placed within the monospecific *Acropora austera* stands in a nested experimental design and secured in place with plastic cable ties. Attachment to the reef was done to ensure the “erosion end” of each gypsum candle was located within the underlying reef framework matrix. Sediment traps were arranged such that the trap opening was as level with the coral reef surface as possible. Additional PSUs were attached to 45 cm tall stainless-steel bars attached to concrete moorings. These were situated around the edge of each A. *austera* stand and served the purpose of recording “off-patch” water movement and sedimentation. Immersion times varied according to sea conditions. Maximum time on the reef was 75.5 hours; however, on two occasions rough seas necessitated their removal after 23 and 25.2 hours of immersion. Field sampling was prevented where swell heights exceeded 4 m and was compounded by extended wave periods which resulted in strong surge, rendering underwater work impractical.

Table 2: Sample dates and duration for all methods used throughout the study.

Sample date	Aragonite saturation state	Sea water temperatures	Swell heights	Water movement	Sedimentation	*Acropora austera* branch extension rate (image analysis)	*Acropora austera* branch extension rate (Alizarin Red S stain)	Bioerosion rubble sections	Bioerosion cages
Oct 2009		Measured continuously	Measured continuously	30 Oct 2009	30 Oct 2009				Oct 2009 – Oct 2010
Nov 2009				26 Nov 2009	26 Nov 2009				
Dec 2009									
Jan 2010				27 Jan 2010	27 Jan 2010				
Feb 2010									
Mar 2010	11 Mar 2010			11 Mar 2010	11 Mar 2010	09 Mar 2010 – 21 Apr 2010		12 Mar 2010	
Apr 2010				22 Apr 2010	22 Apr 2010	21 Apr 2010 – 14 June 2010			
May 2010									
June 2010				14 June 2010	14 June 2010	14 June 2010 – 03 Sept 2010	14 June 2010 – 14 Dec 2010		
July 2010									
Aug 2010									
Sept 2010	5 Sept 2010			6 Sept 2010	6 Sept 2010	03 Sept 2010 – 18 Oct 2010		6 Sept 2010	
Oct 2010						18 Oct 2010 – 10 Dec 2010			
Nov 2010									
Dec 2010				11 Dec 2010	11 Dec 2010	10 Dec 2010 – 12 Feb 2011			
Jan 2011									
Feb 2011									

3.4. Acropora austera growth

3.4.1. Measurement of branch extension rates

Branch extension rates of *Acropora austera* were measured by photographic analysis. A total of 17 0.25 m^2 quadrats were randomly selected within the monospecific *Acropora austera* stands. These were each marked by securing a stainless steel gauge rod within the coral framework (Chapter 1) and revisited on a bimonthly basis over a 12-month period between March 2010 and February 2011. Mean branch extension rates were plotted at the beginning, end and mid-point of each sampling period (Chapter 4, figure 5). A maximum of ten *A. austera* nubbins were randomly selected in each quadrat and their growth followed over the study period. Coral tissue recession was recorded where individual nubbins remained in place but total length of living tissue decreased. Mortality was recorded where individual nubbins showed no visible sign of living tissue or were missing entirely. The number and time of nubbins measured per site are listed in Table 5 (Chapter 4.2). Underwater photographs of the quadrats were taken with a SEA&SEA 1G digital camera and wide angle conversion lens (Model no. 52116) mounted on a 0.25 m^2 stainless steel frame with two external SEA&SEA YS-27 DX strobes set on manual to optimise exposure and contrast. Images were taken at a height of 50 cm above the coral substratum.

A second method was used in which extension rates of marked branches, stained with the vital stain, Alizarin Red S (Crossland 1981; Oliver *et al* 1983; Harriott 1999), were measured after six months of *in situ* growth. Staining was accomplished in June 2010 when thirty healthy *Acropora austera* nubbins, ranging from 50 to 100 mm in length (living tissue), were brought to the surface and placed in an 80 l insulated cooler box with natural seawater. Efforts were taken to shade all nubbins in order to avoid light shock and temperature stress. Alizarin Red S was added to the water to make a solution of approximately 10 mg/l in which they were kept for 4 hours (Harriott 1999) before being returned to the reef and attached to the framework. Attachment was accomplished by securing the nubbins with plastic cable ties around their base and fastening this to the existing reef framework with additional cable ties. An additional 15 *Acropora austera* nubbins of similar size were used as controls. Stained nubbins and controls were marked with a plastic, numbered electrical tags and their position photographed to aid in relocation. All nubbins which could be relocated were collected in December 2010.

3.4.2. Image analysis of *in situ* coral nubbins for branch extension rates

The image analysis software ImageJ™ was used to orientate each image and measure branch length of the *Acropora austera* nubbins. Average extension rates per branch (n=142) were calculated by discounting negative values and mortalities. The remaining positive extension rates were then calculated for the 6 time periods by:

L_{T2}-L_{T1}/T(days)*365 = ER (mm/y) ,

where ER was the rate of branch extension, L the linear length at any given sample time and T the time interval in days between sampling periods. In addition to recording average extension rates, the overall percentage change in branch length was calculated as a cumulative value over time by:

$((L_{T2}/L_{T1})*100 – 100) + ((L_{T3}/L_{T2})*100 – 100) + ... + ((L_{Tx}/L_{Ty})*100 – 100) = APC$,

Where APC is the cumulative percentage change over the study period, L_T is the linear length at any given sample period. Cumulative percentage change in *A. austera* branch lengths was compared by site and sampling dates.

3.4.3. Reader error (APE and CV) for branch extension rates determined by image analysis

In order to identify possible error in the image analyses, estimates of reading precision were determined using average percentage error (APE) and coefficient of variation (CV) (Brower and Griffiths 2004). Thirty *Acropora austera* fragments were randomly selected from the image database and their length calculated. A minimum of three weeks later these fragments were re-measured and results compared for APE and CV.

3.4.4. Alizarin Red S stain

Stained fragments were sectioned longitudinally and evidence sought of a pink line indicating successful staining. Those which manifested an identifiable pink line were used in the analysis. The linear extension of each branch was measured from the stained point to the equivalent point on the edge of the skeleton. Annual growth rates in mm/y were calculated.

3.5. Bioerosion of reef framework

3.5.1. Collection of branching coral rubble

Rubble of the branching coral *Acropora austera* was collected at three sites on TMR, Sodwana Bay. Samples were taken from the underlying framework structure of monospecific *A. austera* stands on condition that each rubble piece was dead, an independent branch, and cylindrical in shape as this simplified later sectioning. Collections were made in both summer (September) and winter (March) to assess seasonal variation in bioerosion intensity. An average of 15 rubble pieces was collected at each site for each season, 90 pieces in total.

3.5.2. Sectioning coral rubble

Five cuts were made across the long axis of each piece of coral rubble using an otolith saw with a 1 mm diamond-edge blade. Following the methodology set out by Holmes *et al.* (2000), each cut was scored for the presence or absence of internal bioeroding organisms. A bioerosion score between 0 and 5 was assigned to each piece of rubble as one score for each cut containing a bioeroding organism. Thereafter each cut was photographed and, using the image analysis software ImageJ™, the surface area of each section and the percentage area damaged by bioeroding organisms was recorded. Internal damage by bioeroding organisms was only recorded where it resulted in a deformation of the natural internal structure of the coral skeleton. Results were compared for bioerosion score and percentage damage for each site and each season.

3.5.3. Bioerosion cages

Three “bioerosion cages” (Figure 2b) were placed at each site adjacent to the monospecific *A. austera* stands to achieve a crude estimate of macro-bioersion rate. Each cage was constructed of a 1 cm^2 stainless steel mesh cage with an internal volume of 0.2 m^3 and bordered at each end by a 30 kg concrete block. This added weight and ensured they did not move on the reef. The bioerosion cages were designed with the purpose of excluding large grazers such as parrotfish as only internal bioerosion was of interest.

During October 2009 several dozen pieces of *Acropora austera* rubble were collected at each site and brought to the surface. After being dabbed dry with paper towel, each piece was weighed. Time out of the water was minimized to prevent die-off of organisms within the rubble. An average of 3190.7 g of coral rubble was returned to each cage at the site of collection. Twelve months later, during October 2010, the contents of each cage was removed and reweighed. The net erosion per site was calculated by subtracting the weight at the end of the experiment from that at the beginning. A subsample of ten rubble pieces were removed from each cage and sectioned for bioerosion score and percentage area damaged by bioeroding organisms. Due to unavoidable inaccuracies and possible bias in measurements of wet weight of rubble fragments, results from this section were interpreted with caution.

4. Chapter 4 – Results

4.1. Physico-chemical parameters

Mean salinities of 32.73 and 32.19 were measured on the Sodwana Bay reefs respectively in March and November 2010, these values being lower than the range of 34.3 - 35.5 expected by Pearce (1973). Mean aragonite saturation states were calculated accordingly and did not differ significantly between March (summer) at 4.40±0.29 and November (winter) at 4.33±0.21 (Table 3; t=0.91, p>0.05, df=39).The mean aragonite saturation state over the study period was 4.36±0.25. No significant differences were observed between saturation states directly adjacent to the reef substratum and those measured within the water column (t=1.37, p>0.05, df=40). Likewise, water samples taken at both dawn and noon showed no significant difference in measured carbon parameters (t=1.17, p>0.05, df=32).

Table 3: Average concentrations (±standard deviations) of carbon system parameters at 0 m above the reef, 2 m above the reef, morning (7:00 am), noon (12:00 pm) (Inclusive of 0 m and 2 m measurements), summer (March) and winter (September) (inclusive of morning and noon measurements) on TMR, Sodwana Bay, South Africa.

Parameter	0m	2m	Morning	Noon	Summer	Winter	Average
Dissolved Inorganic Carbon (μmol kg^{-1})	2009.48 ± 19.30	2004.34 ± 22.94	2002.12 ± 20.15	2008.68 ± 22.33	1987.12 ± 12.01	2024.11 ± 7.48	2006.97 ± 21.05
Total alkalinity (μmol kg^{-1})	2386.73 ± 23.40	2391.18 ± 21.04	2382.33 ± 22.46	2399.12 ± 21.48	2373.33 ± 19.82	2402.35 ± 13.64	2388.90 ± 22.12
pH	8.22 ± 0.03	8.26 ± 0.06	8.22 ± 0.05	8.26 ± 0.05	8.25 ± 0.06	8.22 ± 0.04	8.238 ± 0.05
pCO_2 (μatm)	253.1 ± 22.75	231.91 ± 33.26	252.16 ± 26.8	228.74 ± 30.07	230.08 ± 33.11	255.01 ± 20.87	242.3 ± 30.25
HCO_3^- (μmol kgSW^{-1})	1727.48 ± 30.44	1706.69 ± 43.32	1727.11 ± 27.9	1702 ± 46.95	1690.96 ± 35.41	1743 ± 17.59	1743.9 ± 38.62
ΩCa	6.59 ± 0.33	6.85 ± 0.46	6.71 ± 0.45	6.84 ± 0.36	6.78 ± 0.48	6.66 ± 0.35	6.72 ± 0.42
ΩAr	4.29 ± 0.21	4.44 ± 0.27	4.35 ± 0.25	4.45 ± 0.23	4.40 ± 0.29	4.33 ± 0.21	4.36 ± 0.25
N	21	20	19	15	19	22	41

Mean swell heights for the period October 2009 to December 2010 were 2.41±0.60 m whilst mean swell heights recorded over the sample dates (Figure 3) were only slightly lower at 2.29±0.74 ($t=4.4$, $p>0.05$; SADCO). Few (4%) swells exceeded 4 m with only 1% exceeding 5 m in height. The majority of large swells occurred between May and December 2010.

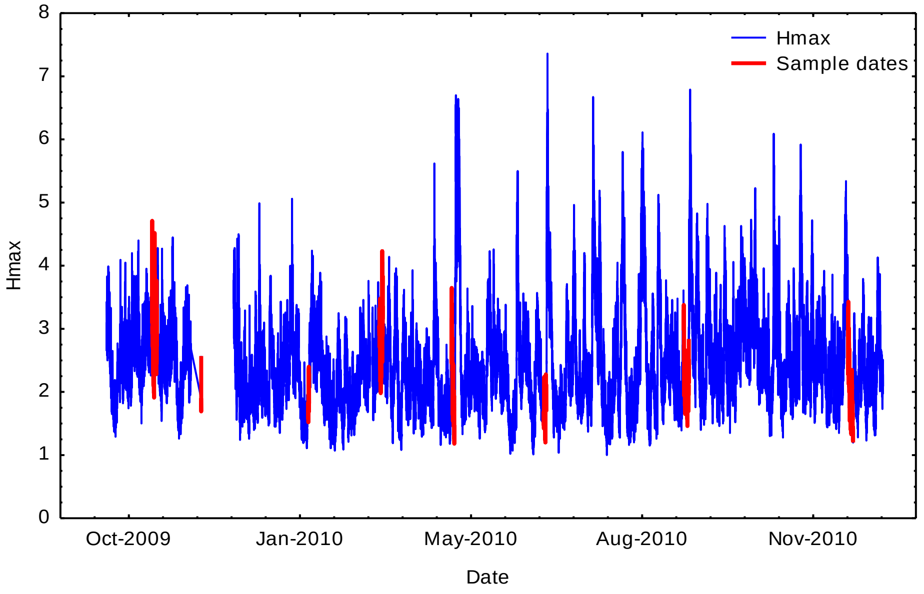

Figure 3: Maximum swell height data recorded at Richards Bay during October 2009 – February 2011. Sampling dates are represented in red. Data supplied by SADCO.

Mean swell heights were highly correlated under a Spearman Rank correlation test with measurements of water motion recorded during each sample period (Figure 4; $r_s=0.93$, $p<0.05$).

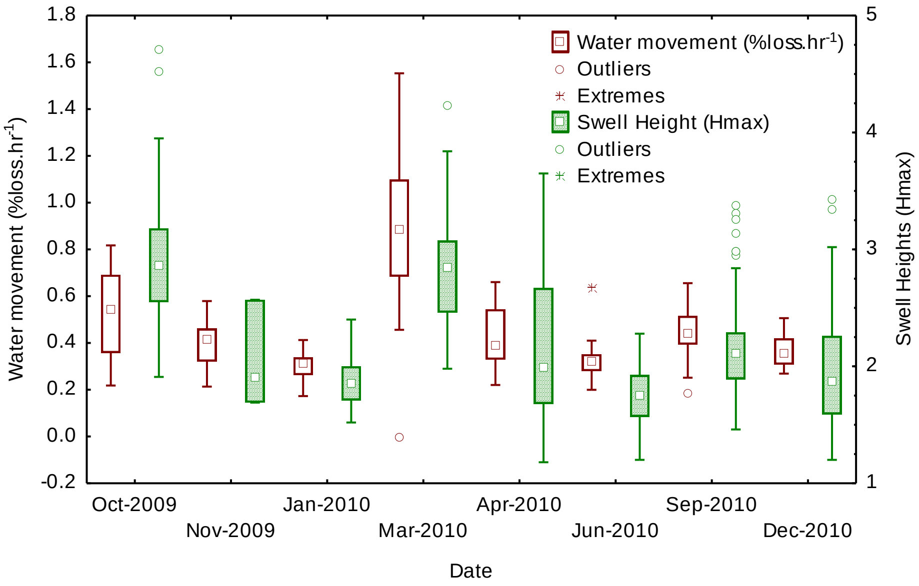

Figure 4: Box plots of swell heights (m) recorded in the Richards Bay area (200 km south) during October 2009 – February 2011 relative to measurements of water motion measured at Sodwana Bay over the same period.

Water movement measurements revealed significantly lower levels of flow within the basal framework matrix of each stand of *Acropora austera*, when compared to water flow over the reef (measured 45 cm above the reef substratum) (repeated measures ANOVA, F=4.8, $p<0.05$). Despite an observable reduction in framework complexity from site 1 to site 3, water movement indices within the reef frameworks differed significantly between sites (ANOVA, F=3.37, $p<0.05$). Water movement above the reef was similar among sites (ANOVA, F=1.56, $p>0.05$). Likewise, there was no difference in overall water motion between sites (ANOVA, F=2.28, $p>0.05$).

There were no significant differences in mean sedimentation rate between sites over the study period (Table 4; ANOVA, F=0.2, $p>0.05$) or between those recorded within the *Acropora austera* framework relative to those on the general reef substratum (ANOVA, F=2.44, $p>0.05$). This is due to a large standard deviation (SD) in the rate of sedimentation within groups. It is evident however, that the underlying framework structure created by *A. austera* does little in terms of trapping or retaining sediment.

Levels of water movement and rates of sedimentation were well correlated in a Spearman Rank correlation test (r_s=0.52, n=219, $p<0.05$). Levels of sedimentation varied little among sampling dates (ANOVA, F=33.8, $p<0.05$ and LSD a-posteriori; $p<0.001$) with the exception of March 2010 when relatively large swells occurred. This resulted in an approximately 32 times increase in sedimentation in March, from an average of 0.038 g cm^{-2} day^{-1} to 1.22 g cm^{-2} day^{-1}. This was acompanied by only a 2.3 times increase in water motion (ANOVA, F=30.55, $p<0.05$; a moderate increase in water motion thus resulted in considerable increases in the rate of sedimentation.

Table 4: Measurements of water motion (percentage loss in gypsum candle length hr^{-1}) and levels of sedimentation (g cm^{-2} day^{-1}) recorded at three sites on TMR, Sodwana Bay. "IP" are measurements recorded within the *Acropora austera* framework and "OP" are those recorded outside each coral patch (a-d indicate differences among groups indicated by an ANOVA, LSD a-posteriori analysis).

	Water motion (% loss hr^{-1})	**SD**	**n**	**Significance**	**Sedimentation (g cm^{-2} day^{-1})**	**SD**	**n**	**Significance**
Site 1	0.48	0.25	106	a	0.17	0.48	106	a
IP	0.45	0.19	82	b	0.12	0.29	82	b
OP	0.58	0.37	24	d	0.34	0.84	24	b
Site 2	0.37	0.19	45	a	0.13	0.28	44	a
IP	0.35	0.13	24	c	0.13	0.29	24	b
OP	0.40	0.23	21	d	0.12	0.28	20	b
Site 3	0.48	0.20	42	a	0.23	0.67	44	a
IP	0.41	0.19	20	b	0.13	0.38	20	b
OP	0.55	0.18	22	d	0.31	0.85	24	b
Total	0.45	0.23	193		0.17	0.49	194	

4.2. Growth and mortality of Acropora austera

Branch extension rates derived from image analysis of *Acropora austera* nubbins averaged 24.5±10.2 mm/y but varied widely between individual nubbins, ranging from 1.1 to 104.0 mm/y. Large variations in extension rates were observed between sample periods, ranging from 17.1 to 32.0 mm/y for the periods of September to October (late winter) and December to February (summer), respectively. Data for branch extension rates measured by image analysis are presented in Table 5.

Table 5: Extension of *Acropora austera* branches calculated from repeated image analysis at three sites on TMR, Sodwana Bay, South Africa

Site	Dates sampled	Days of growth	Mean extension (mm)	Extension per week (mm/week)	Annual extension (mm/y)	SD mean extension	N
Site 1	09 March 2010 – 21 April 2010	43	2.905	0.474	24.657	2.258	56
	21 April 2010 – 14 June 2010	54	2.531	0.329	17.110	2.725	62
	14 June 2010 – 03 Sept 2010	81	1.930	0.167	8.696	2.036	48
	03 Sept 2010 – 18 Oct 2010	45	2.230	0.348	18.085	2.553	32
	18 Oct 2010 – 10 Dec 2010	53	1.792	0.237	12.343	1.737	34
	10 Dec 2010 – 12 Feb 2011	64	3.569	0.391	20.357	2.139	26
Total	09 March 2010 – 12 Feb 2011	340	15.838	0.327	17.003	2.606	258
Site 2	09 March 2010 – 21 April 2010	43	4.138	0.676	35.127	2.318	27
	21 April 2010 – 14 June 2010	54	3.703	0.481	25.032	1.096	28
	14 June 2010 – 03 Sept 2010	81	4.964	0.430	22.367	2.431	28
	03 Sept 2010 – 18 Oct 2010	45	1.723	0.269	13.974	0.816	6
	18 Oct 2010 – 10 Dec 2010	53	4.437	0.588	30.559	1.652	12
	10 Dec 2010 – 12 Feb 2011	64	4.845	0.531	27.631	2.449	12
Total	09 March 2010 – 12 Feb 2011	340	25.206	0.520	27.060	8.247	113
Site 3	09 March 2010 – 21 April 2010	43	4.707	0.768	39.955	3.268	22
	21 April 2010 – 14 June 2010	54	5.831	0.758	39.411	3.261	30
	14 June 2010 – 03 Sept 2010	81	8.232	0.713	37.095	5.192	29
	03 Sept 2010 – 18 Oct 2010	45	-	-	-	-	-
	18 Oct 2010 – 10 Dec 2010	53	-	-	-	-	-
	10 Dec 2010 – 12 Feb 2011	64	9.758	1.070	55.650	7.242	15
Total	09 March 2010 – 12 Feb 2011	340	38.540	0.796	41.373	11.9	96
All Sites	09 March 2010 – 21 April 2010	43	3.600	0.588	30.554	2.606	105
	21 April 2010 – 14 June 2010	54	3.630	0.472	24.534	3.012	120
	14 June 2010 – 03 Sept 2010	81	4.479	0.388	20.185	4.202	105
	03 Sept 2010 – 18 Oct 2010	45	2.150	0.335	17.436	2.363	38
	18 Oct 2010 – 10 Dec 2010	53	2.482	0.329	17.095	2.063	46
	10 Dec 2010 – 12 Feb 2011	64	5.610	0.615	31.992	4.976	53
Grand total	09 March 2010 – 12 Feb 2011	340	22.772	0.470	24.446	10.166	467

A relationship between branch extension rate and mean water temperature was plotted for *Acropora austera*. Extension rates correlated positively with mean water temperature in a Spearman Rank correlation test (Figure 5; r_s=0.735, n=6, p<0.05). However, reduced winter growth rates persisted after the rise in SST in late spring. Coral growth rates increased when temperatures exceeded 22.9˚C (18 Oct – 13 Nov) to 24.8˚C (14 Nov – 10 Dec).

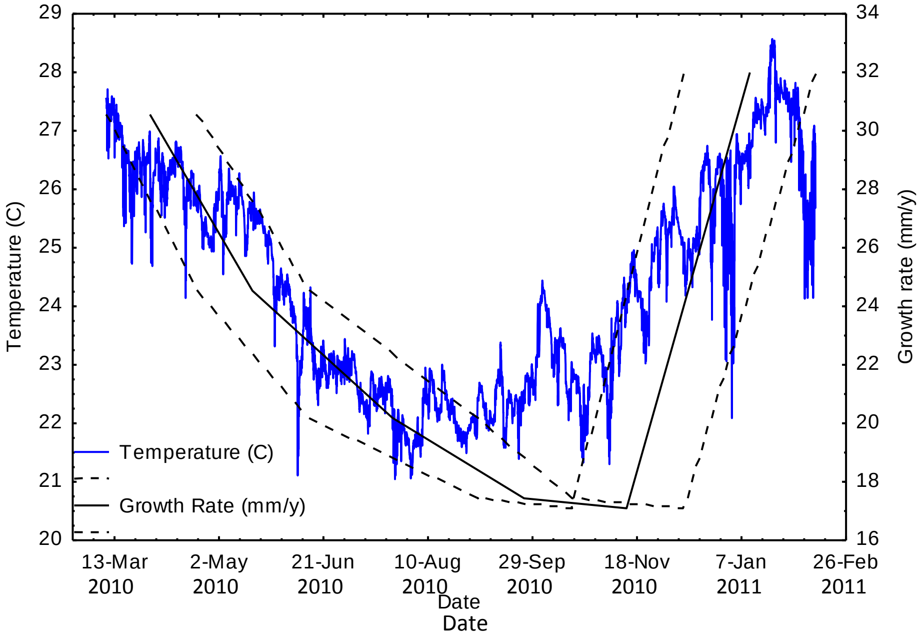

Figure 5: Relationship between mean water temperature and branch extension rates in *Acropora austera* on TMR, Sodwana Bay, South Africa. Dotted lines represent the branch extension rates at the start and end of each measurement period, and the solid line the extension rate at the midpoint of that period.

Clear differences were observed in branch extension rates between sites (Figure 6; repeated measures ANOVA, F=57.91, p<0.05). When analysed by an LSD a-posteriori test, site 1 yielded a significantly lower branch extension rate of 18.1± 14.8 mm/y (ANOVA LSD a-posteriori; p<0.001) when compared to sites 2 and 3 of 27.1±15.0 and41.4±27.8 mm/y, respectively.

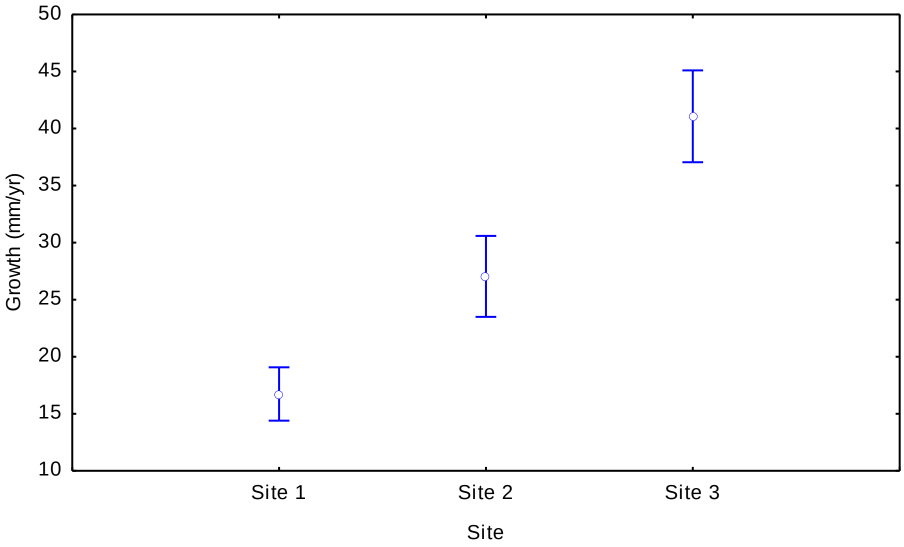

Figure 6: Branch extension rates of *Acropora austera* nubbins at three study sites on TMR, Sodwana Bay, South Africa

Acropora austera branch mortality, measured from photographs, was highest during spring and summer (Sept – Feb) when compared to that in autumn and winter (March – Aug) (Table 6; t=2.23, df=19, $p<0.05$). Seasonal storm frequency coupled with rough sea conditions coincided with high levels of mortality recorded over this period, when mortalities (June – Feb) were preceded by swell heights in excess of five meters. Exceptionally high mortalities were recorded in October 2010 due to large storm swells >6 m during September of the same year (SADCO).

Table 6: *Acropora austera* branch mortality (%) for each sample site and sampling date on TMR at Sodwana Bay

	09 March 2010	**21 April 2010**	**14 June 2010**	**03 September 2010**	**18 October 2010**	**10 December 2010**	**12 February 2011**	**Total**
Site 1	0	0	7.32	9.76	21.95	6.10	10.98	**56.10**
Site 2	0	0	0	0	56.67	0	0	**56.67**
Site 3	0	0	0	0	16.67	0	20	**36.67**
Total	**0**	**0**	**8.11**	**10.81**	**54.05**	**6.76**	**20.27**	

Growth dynamics of the *Acropora austera* stands were assessed by plotting the cumulative percentage change in branch length between sample periods, incorporating growth, tissue recession and fragment mortality (Figure 7).

Despite reduced winter growth, an increase in cumulative branch lengths of 39.3 % was observed from March to September 2010 when little mortality occurred. This resulted in a rate of increase of 0.21%/day for winter. Despite higher levels of mortality during summer, an increased growth rate resulted in a rate of increase in cumulative branch lengths of 0.33%/day between October 2010 and February 2011. The majority of reduction in total branch lengths is attributable to a single mass mortality event during October which coincides with large swells and resulted in a 67.7 % reduction from September to October 2010. Despite high mortalities over the 12-month study period, a significant increase in *A. austera* branch lengths of 29.7 % was still apparent at the end of the study (repeated measures ANOVA, $F=22.55$, $p<0.05$).

When analysed by an LSD a-posteriori test, a significantly lower cumulative per cent change in branch lengths of 3.6 % occurred at site 1 (repeated measures ANOVA, $F=23.67$, $p<0.05$ and LSD a-posteriori; $p<0.001$), compared to values of 22.5 % and 40.3 % at sites 2 and 3, respectively, over the 12-month study period. Conversely, sites 1 and 2 suffered approximately 56% total mortality, while site 3 exhibited notably less at 34%.

There were no significant differences between readings when testing for possible reader error originating from image analysis measurements ($t=1.01$, $n=30$. $p<0.05$). Both average percentage error (APE) and coefficient of variation (CV) were low at 1.2 and 1.4 respectively, indicating minimal reader error in branch extension rates derived from image analyses.

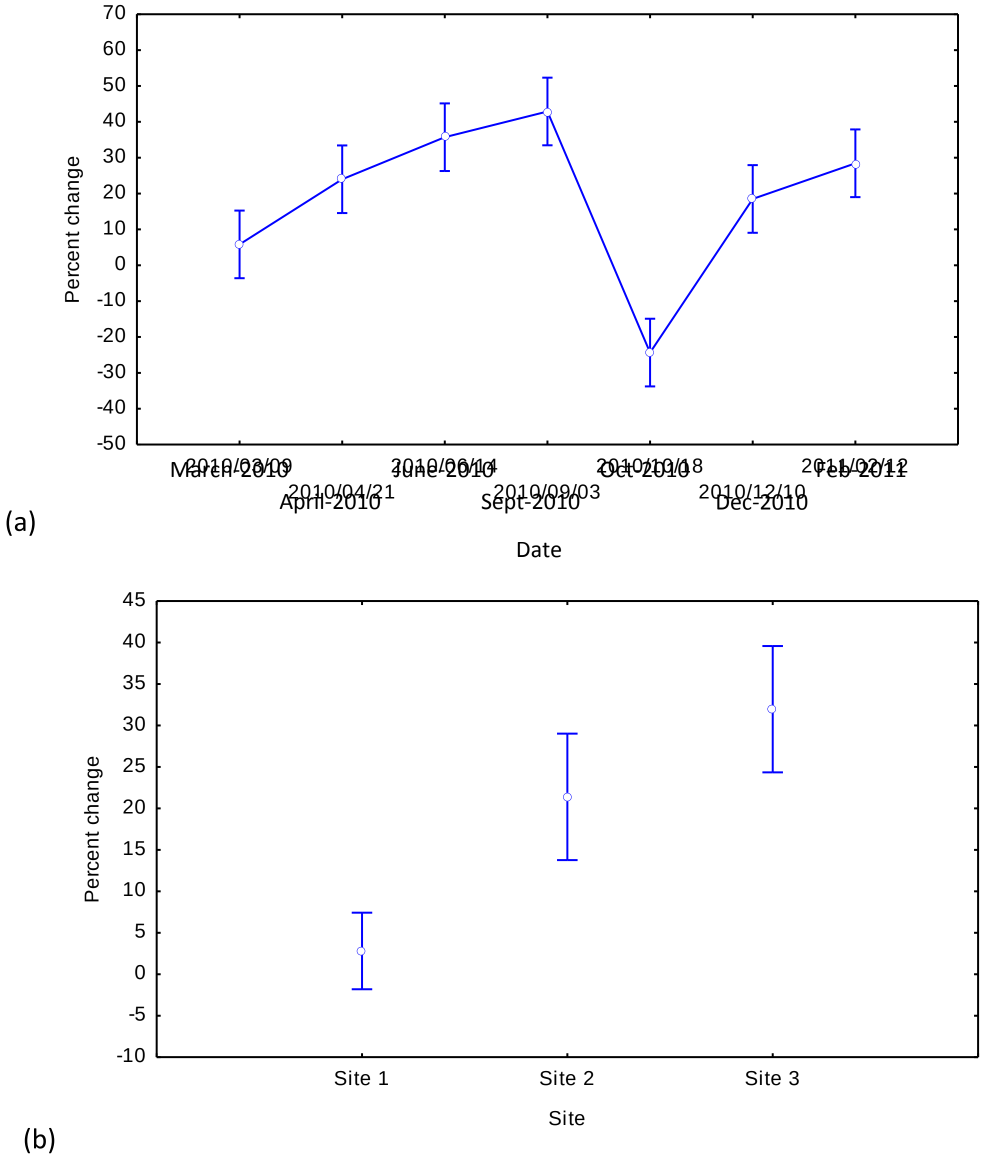

Figure 7: Cumulative percentage change (APC) in branch lengths of *Acropora austera.* a) Mean APC over time for the 12 month study period, and b) at three sites on TMR, Sodwana Bay, over

The number of nubbins stained, their mortality, subsequent recollection and the detection of successful staining is summarized in Table 6. High mortalities were exhibited in both the stained and control nubbins, resulting in the loss of 68 % of all nubbins. Additionally, only six of the nine surviving nubbins manifested evidence of a visible pink line. Growth rates derived from staining averaged 15.9±3.7 mm/y (Table 7), but no statistical analysis was performed on the data due to the low numbers of stained nubbins recovered at the end of the sample period. Branch extension rates of the surviving control nubbins averaged 23.6±7.9 mm/y and were not significantly different from the stained nubbins (t-test; t=0.9, n=5, p>0.05).

Table 7: Number of nubbins stained with Alizarin Red S, the number retrieved and the branch extension rates.

	Initial sample in June 2010	Nubbins collected in Dec 2010	Nubbins survived	Stained nubbins	mortality	Days of growth	Mean extension	Extension per week	Annual extension	SD
Stained	30	16	9	6	21	179	7.83	0.306	15.970	3.71
Control	15	8	5	-	10	179	11.55	0.452	23.552	7.929

4.3. Bioerosion of reef framework

Bioerosion intensity, recorded as the average bioerosion score for each *Acropora austera* rubble fragment, was shown to differ largely between sites (ANOVA, F=9.3, $p<0.05$). Although there was no correlation between bioerosion score and percentage area damaged within cross sections ($r^2=0.08$, $p>0.05$), both displayed a similar, significant decrease from Site 1 to Site 3 (Figure 7 a, b).

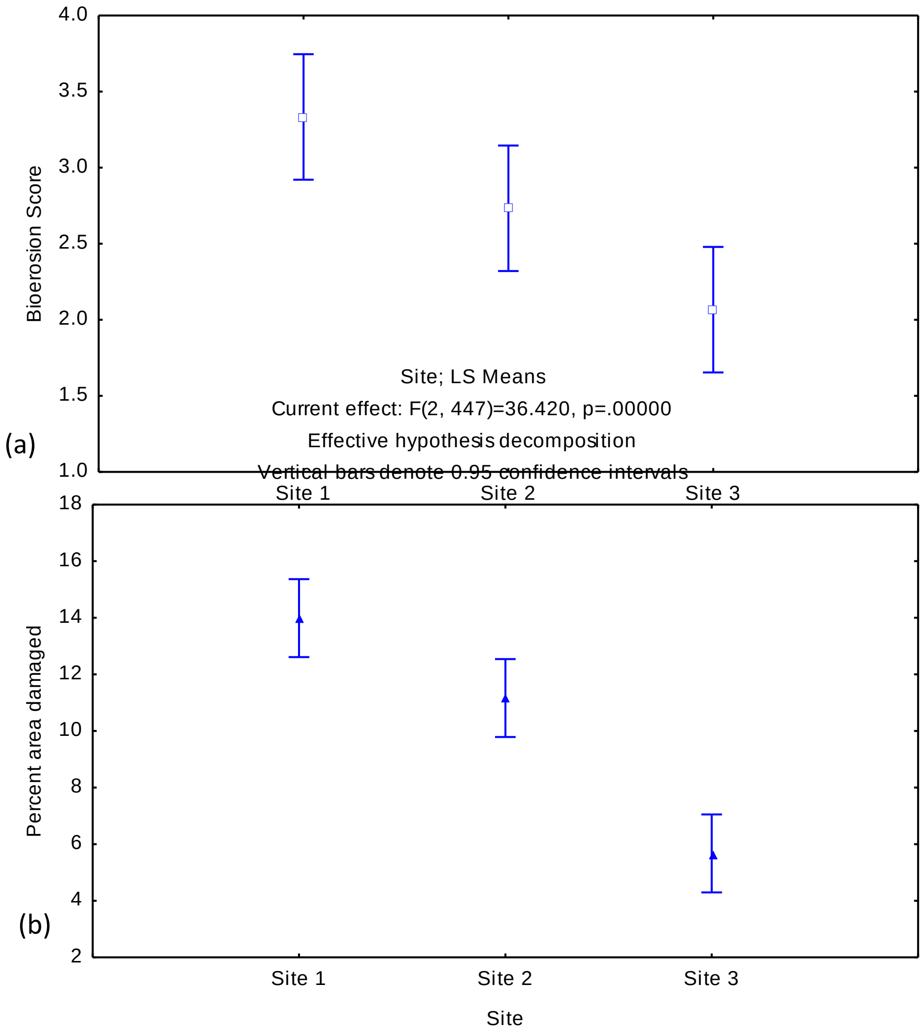

Figure 8: a) Average bioerosion score and b) percentage area damaged in *Acropora austera* rubble at three sites on TMR, Sodwana Bay, South Africa.

There were no significant differences in bioerosion score or percentage area damaged between measurements from *in situ* coral rubble and rubble from the "bioerosion cages" (t=0.86, p>0.05; t=0.92, p>0.05, respectively). As such it is concluded that the use of "bioerosion cages" did not affect the level of bioerosion intensity nor the damage done by bioeroders to coral rubble fragments.

Weight loss of *Acropora austera* rubble fragments placed in the "bioerosion cages" yielded a net decrease of 11.5 % in wet weight of coral rubble at site 1, notably higher than the 3.1 % decrease observed at site 3 (Table 8).

Table 8: Bioerosion score of *Acropora* austera rubble fragments and the percentage area damaged by bioeroders both *in situ* and in "bioerosion cages". N is the number of rubble pieces sampled, numbers in parenthesis are the total surface area of rubble sections measured in cm^2.

***In situ* coral rubble**							
	Bioerosion score	**SD**	**Percentage damage**	**SD**			**n**
Site 1	3.33	1.30	13.99	8.64			30 (300.2)
Site 2	2.73	1.17	11.16	9.37			30 (228.1)
Site 3	2.07	0.91	5.67	7.65			30 (240.2)
Bioerosion cage coral rubble							
	Bioerosion score	**SD**	**Percentage damage**	**SD**	**Rubble weight loss (g)**	**Rubble weight loss (%)**	**n**
Site 1	3.60	1.17	14.55	8.21	491.37	11.49	10 (93.6)
Site 2	2.70	1.16	9.12	7.82	393.04	10.39	10 (78.5)
Site 3	2.50	0.85	4.80	4.48	114.3	3.11	10 (82.8)

Seasonal variation in both percentage area damaged and bioerosion score for *in situ* coral rubble proved to be minimal and insignificant (ANOVA, F=0.07, p>0.05; F=1.04, p>0.05, respectively).

5. Chapter 5 –Discussion

5.1. Possible limits for coral reef development at Sodwana Bay, South Africa

5.5.1. Aragonite saturation state

Aragonite saturation states during this study were higher than expected by Kleypas *et al.* (1999) from extrapolating surface saturation states from GEOSECS ocean chemistry data (Takahashi *et al.* 1980). Saturation states were found to vary with latitude from 4.1 at the equator to 1.5 at the poles, with coral communities beginning to occur at saturation states of 3.1 (Kleypas *et al.* 1999). Feely *et al.* (2009) estimated saturation states for the Southern Indian Ocean where $Ώ_{arag}$ = 3.6±0.4, whereas Kleypas *et al.* 1999 estimated saturation states for the South African reefs at <3.5 (Kleypas *et al.* 1999; Schleyer & Celliers 2003). The transition from a coral dominated benthic community to an accretive coral reef is thought to occur were saturation states rise above 3.4 with few reefs occurring where saturation is lower (e.g.: Houtman Abrolhos reefs, Western Australia, Lord Howe Island, Southeast Australia) (Kleypas *et al.* 1999). However, mean aragonite saturation state for the Sodwana Bay reefs was 4.36±0.25 and, as such, was determined to be non-limiting for coral reef development.

The high aragonite saturation states found on the Sodwana Bay reefs may be linked to high levels of primary production and the associated effects on total dissolved inorganic carbon (DIC) and total alkalinity (TA). However, water samples taken at dawn and again at noon showed very little difference in saturation state. Elevated primary production during daylight hours would result in higher aragonite saturation states at noon, yet this was not the case. Other possible explanations for high saturation states include aspects of sediment production, import or uplifting. The majority of $CaCO_3$ sediments associated with coral reefs are derived from the mechanical and biological destruction of reef framework and reef-associated organisms (Scoffin 1987) with up to 34% of sediments found on Two-Mile Reef being bioclastic in origin (Ramsay 1996). High levels of bioerosion, substantial sediment resuspension and the presence of sediments with high carbonate content of 56 – 82% (Ramsay 1996) may all contribute to increased DIC levels and thus result in elevated aragonite saturation states.

5.5.2. SSTs and light availability

Other than saturation state, the most likely physical factors to place an absolute limit on reef development at these latitudes are light availability, water temperature (Kleypas *et al.* 1999) and physical disturbances. Temperature variations and limits imposed on the South African reefs are dealt with by Schleyer & Celliers 2003 whereby they documented a protracted increase is SSTs of 0.1˚C.decade since 1993. Although this increase in temperature on the marginal South African reefs does not reach hazardous levels for corals, protracted periods of elevated temperature coinciding with exceptional water clarity have been linked to coral bleaching in the area (Schleyer & Celliers 2003). However, aspects of irradiance and light availability at depth and its role as a limiting resource at Sodwana Bay will require further study.

5.5.3. Physical disturbance

The coral communities on TMR at Sodwana Bay are differentiated into several clusters by their community structure and species composition (Celliers & Schleyer 2008). For example, the reef gullies are typically occupied by high densities of plating hard corals such as *Acropora clathrata* and *A. hyacinthus*, whereas certain areas of the reef flat have higher numbers and greater area coverage of *Sinularia* and *Lobophytum* soft corals (Celliers & Schleyer 2008). Extending on this method of hierarchical separation of clusters Schleyer and Celliers (2005) created a Damage Potential index (DPI) for the northern reef complex within South Africa. They found that it was the *Acropora*-rich zones which had the highest DPI and were most at risk to physical breakage by natural or anthropogenic causes.

The differentiation in the coral community structure within the central reef complex of Sodwana Bay is likely a result of the interactive biological and oceanographic processes of recruitment, larval dispersal, temperature regimes, light availability, and water flow (Riegl 1993; Glassom *et al*. 2006; Celliers & Schleyer 2008). Disturbance events such as coral bleaching, SCUBA diver damage and persistent *Acanthaster planci* predation (Celliers & Schleyer 2008) further shape these communities and physical reef structure. Riegl (2001) adds to this by suggesting the primary modes of differentiation in coral community structure are along gradients of sedimentation and, for the most part, follow chronic disturbance events in the form of storm swells. The causal circumstances leading to differentiation in community structure on the coral reefs of Sodwana Bay are well documented

(Riegl 1993; Riegl 2001; Glassom *et al.* 2006; Celliers & Schleyer 2008), yet the processes which regulate the development and persistence of coral reef frameworks at this locality were still speculative. From results presented in this study, it is becoming more apparent that physical disturbances play a discerning role in regulating not only the occurrence and density of the *Acropora austera* patches on TMR, Sodwana Bay but also the long-term persistence of frameworks created by this coral.

5.5.4. Bioerosion and loss of reef framework

Although some coral mortality by tissue loss was observed and possibly linked to disease, most recorded mortalities occurred through loss of nubbins, branches or whole colonies. A common sight associated with the loss of fragments was a partial or complete removal of the underlying framework (Figure 9 a - e). A contributing factor in reef framework dislodgement is the level of bioerosion intensity (Stearn & Scoffin 1977; Macdonald & Perry 2003). Gradual erosion of the calcium carbonate skeleton by micro- and macro-borers can cause an extensive system of cavities and tunnels which negatively affects the structural integrity of the reef framework (López Victoria *et al.* 2006; Calcinai *et al.* 2007), thus making it susceptible to disturbance events such as storms or diver damage (Highsmith 1982). Chazottes *et al.* (1995) suggest a successional colonization of bioeroders over time with greatly increased damage after two years exposure. Moreover, Londoño-Cruz *et al.* (2003) report the susceptibility of exposed dead coral skeleton to invasion as opposed to living tissue. The growth pattern of the *Acropora austera* stands at Sodwana Bay is such that the corals leave behind an underlying framework of dead, exposed skeletal material with only the upper surfaces comprising the living colony. This growth pattern leads to an increased amount of substratum available for colonization over time and thus potentially increases susceptibility to physical damage (Nava & Carballo 2008) with age and framework complexity.

In the present study there was a clear relationship between the level of bioerosion, coral mortality and the loss of reef framework between each site sampled. The largest patch of *Acropora austera* (Site 1) showed the highest occurrence of bioeroders and the most damage done to the internal skeletal structure. This site also exhibited the highest branch mortality and lowest cumulative change in branch length over the study period; as a result of loss of the underlying framework and coral branches.

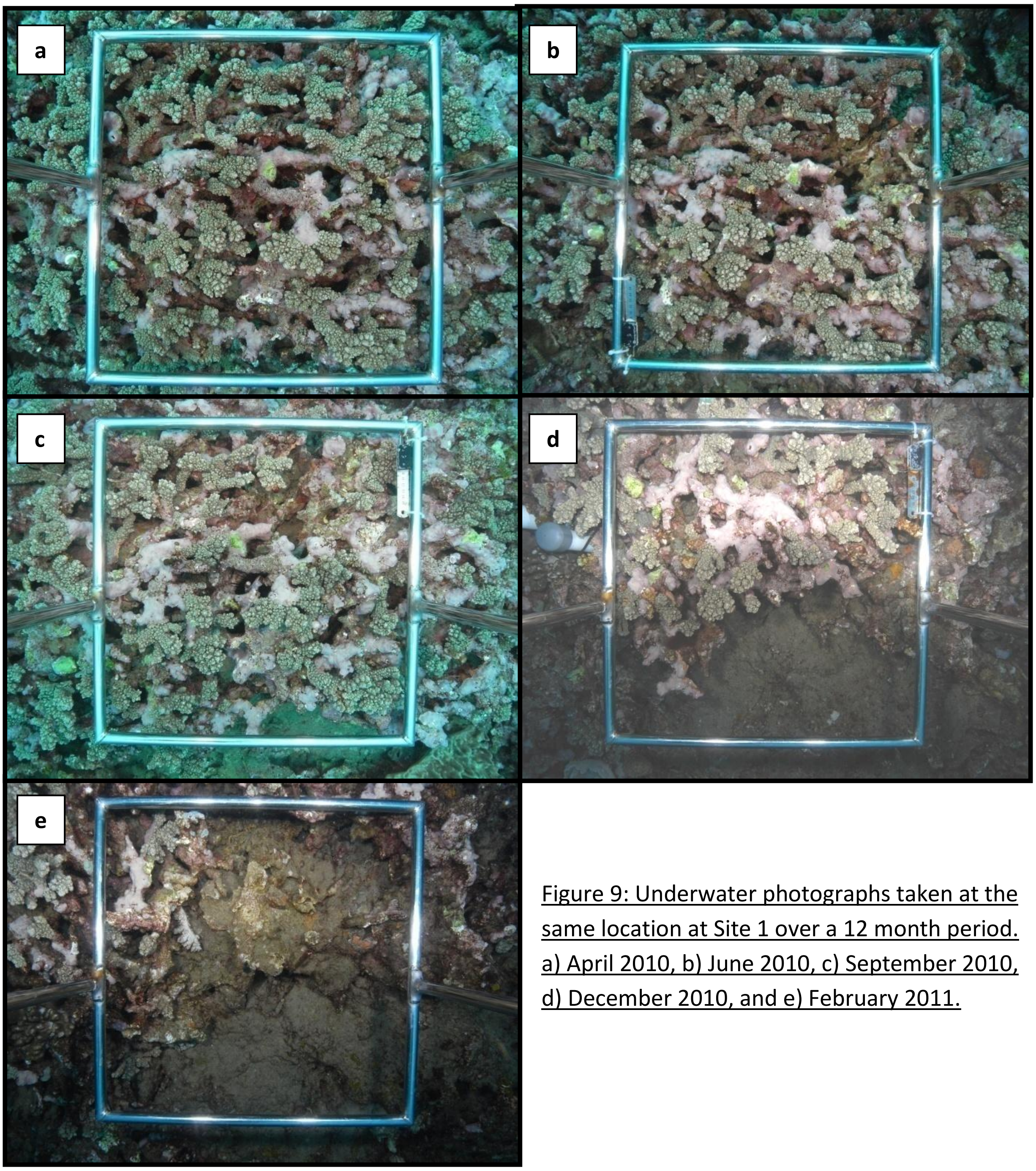

Figure 9: Underwater photographs taken at the same location at Site 1 over a 12 month period. a) April 2010, b) June 2010, c) September 2010, d) December 2010, and e) February 2011.

5.5.5. Water movement

Moderate levels of water movement are not expected to greatly hinder coral growth or frame-building potential as strong flow is required for the delivery/removal of food particles and waste products from the coral at an individual level (Helmuth & Sebens 1999). Likewise, under persistent flow, coral colonies form more compact colonies; this increases their resistance to breakage (Kaandorp *et al*. 1996; Kaandorp 1999). Levels of water movement recorded during this study showed no differences of relevance between sites suggesting all sites were similar in this regard.

5.5.6. Sedimentation

Compounding the effects of wave stress is the level of sedimentation as even moderate levels and the associated environmental variables (i.e.: reduced irradiance and nutrient loading) have been shown to have marked effects on coral function and thus coral growth. Crabbe & Smith (2005) assessed the impact of sedimentation on hermatypic coral growth on three reefs in Indonesia. They recorded modest amounts of sedimentation, ranging from 5 g dry weight m^{-2} day^{-1} to 20 g dry weight m^{-2} day^{-1} at a site of high anthropogenic input. Growth rates of both branching and non-branching corals were significantly less than reefs with little to no land run-off, with >50% reduction (species-dependent) in linear extension between their study sites. Likewise, the morphology of branching coral species manifested a clear preference for upright, vertical growth in the turbid environment (Crabbe & Smith 2005). At Sodwana Bay, the rates of sedimentation, recorded as net downward particle flux, regardless of particle composition, were shown to be several orders of magnitude larger than those reported for Indonesian reefs. Riegl (1993) recorded a maximum rate of sedimentation on the Sodwana Bay reefs of 1.8 kg m^{-2} hr^{-1}, equating to 43200 g m^{-2} day^{-1} in the sediment-rich gullies and 2.6 times less on the reef flat. While the present study yielded a mean sedimentation rate of 1721 g m^{-2} day^{-1}. However, this would be considerably lower (384 g m^{-2} day^{-1}) if the March 2010 sample is excluded from the analysis. Storm swells similar in size to and exceeding those experienced in March 2010 pose a considerable and frequent stress to corals when they not only are at risk of structural damage, but also burial by sediments. Even if conservative estimates of the rate of sedimentation are considered, this factor is still likely to hinder coral fitness and, as such, has been described as a major determinant of coral community structure on these and other reefs (Rogers 1990; Riegl 2001; Crabbe & Smith 2005). Although no difference in rates of sedimentation were detected between sites or between “in patch” and “off patch” measurements, a result likely due to high standard deviations, it is suspected that rates of sedimentation at specific locations will be highly dependent on the nearest source of sediment (gullies or sand traps) and swell conditions.

Unconsolidated reef accretion is assisted by sediment infilling of interstitial spaces and subsequent physical compacting or chemical cementation (Grigg 1982 a, b; Highsmith *et al*. 1983). However, rates of sedimentation were not significantly different between the “normal” reef substratum and *A. austera* frameworks, suggesting that sediments which settle within the framework are resuspended and do not add to framework stability by sediment infilling.

5.2. Acropora austera growth and reef accretion

There have been no studies reporting branch extension rates of *Acropora austera* at high-latitudes; however, branch extension rates of *A. austera* at Sodwana Bay were similar to *Acropora* species located at similar latitudes, yet less than half the rate of those located in the tropics (Table 1, chapter 1). This reduced growth rate at high latitudes, including Sodwana Bay is probably attributable to the low light penetration and temperature (Kleypas, *et al.* 1999).

It has been repeatedly illustrated that coral growth rates show a general decline with increasing latitude. Grigg (1982 a, b) reported a decrease in community calcification with latitudinal increase along the Hawaiian Archipelago, while both Crossland (1981) and Stimson (1996) recorded slower growth rates in *Pocillopora* and *Acropora* species at high-latitudes than their counterparts at tropical sites. Akin to such findings, Edmunds (2005) showed experimentally that three species of hard corals grew significantly slower at temperatures both higher and lower than their optimum. Alternatively there have been several instances where this trend has proved incorrect. Smith (1981), Marsh (1992) and Harriott (1998) studied the growth rates of *Porites* and branching *Acropora* corals at Houtman Abrolhos Islands, Perth, and Lord Howe Island, respectively, and found them similar to those in the tropics.

At Sodwana Bay, the branch extension rates of *Acropora austera* differed by 6.1 mm/y between summer and winter means. Water temperatures averaged 25.9˚C for the marine summer (November to April) and 23.1˚C for the marine winter period (May to October) but were highly variable. The decrease in growth rate from summer to winter is most likely linked to a concurrent decrease in water temperature and light availability, the latter predicted to be limiting at this latitude by Kleypas *et al.* (1999). Similarly, Harriott (1999) found large differences in growth rates of both branching and non-branching corals between seasons and attributed this to a simultaneous decrease in temperature and light availability from summer to winter. Through modelling the response of coral growth to future changes in SST's, Edmunds (2005) predicts that an increase in seawater temperatures nearing threshold levels will delay the timing of maximal coral growth, favouring brief periods of rapid growth in autumn and spring (235-343% stimulation), whilst depressing growth in the summer (15-33% inhibition). This constitutes a response which is not yet evident on the high-latitude reefs of South Africa as peak growth rates coincide with peak summer temperatures (January 2011). Interestingly, a lag is observed in the growth response of *A. austera* relative to a rise in temperature following the winter minimum. An increase in growth rate was only manifested where temperatures exceed roughly 23 - 25˚C. It is suggested that winter minimum temperatures at Sodwana Bay are below the optimal range for *A. austera* growth and result in prolonged lowered extension rates following winter. Similar results are reported by Edmunds (2005) and Gladfelter (1984) where growth rates of *Acropora cervicornis* in the Caribbean were greatly depressed by temperatures both above and below the corals sub-lethal range of 26 - 29˚C.

5.3. Acropora austera mortality and loss of stand structure

A large contributor to a lack of accretion on high-latitude reefs may not only be lowered rates of calcification relative to carbonate removal, but also the removal of coral skeletons during chronic and often severe storm swells. High coral mortality, averaging 48%, was observed over the study period and repeated in all three methods of growth determination. Mortality was shown to occur largely in summer, with the majority of all deaths between September 2010 and February 2011, coinciding with large storm swells in the Maputaland area (SADCO). Site 2 exhibited the highest mortality; this, however, was due to a single mass mortality event.

Net change in cumulative branch lengths over the study period was heavily influenced by mortality, where branch loss through breakage was the dominant cause. Despite moderate growth rates, net changes in branch length were minimal at the largest study site (site 1), yet increased by approximately 20% and 30% at sites 2 and 3 respectively. Frequent wave stress results in mass mortalities of potential frame-builders and, in particular, physical removal of framework structure revealing base-rock (Riegl 2001). Riegl (2001) argues that asexual reproduction by fragmentation of frame-building species is suppressed by wave stress, therefore framework development was thought only to be possible at depths greater than 18 meters. However, large, monospecific stands of the frame-building coral *Acropora austera* with complex underlying frameworks were observed at 10 – 14 meters depth and sampled in the present study. Furthermore, recent research has shown a high level of cloning in *Acropora austera* on Two-Mile Reef, particularly within large stands of this species (Montoya-Maya Unpublished). As such, it is apparent that wave stress does not prevent the formation of such coral stands at shallow depths, yet may hinder their continued persistence and thus their ability to contribute to permanent reef structure. Similar circumstances are observed in subtropical Australian reefs where a combination of significant levels of bioerosion and week attachments to the basal substrate results in a loss of skeletal material relative to calcification, particularly during severe weather conditions resulting in the failure of high-latitude reefs to accrete (Harriott 1999).

5.4. Climate change and reef marginality at high-latitude sites.

In an overview of their findings on the implications of increased sea surface temperatures (SST) and aragonite saturation states (Ω_{arag}), Guinotte *et al.* (2003) suggest all present-day reef habitats in the Pacific Ocean will become marginal within several decades. It is stressed, however, that this does not equate to the demise of corals (Kleypas *et al.* 1999 b) but rather a shift towards non-accretionary communities over reef-building scleractinians (Kleypas *et al*. 2001; Guinotte *et al*. 2003).

Controversy still surrounds the debate of the impact of rising atmospheric CO_2 on ocean carbonate system and thus coral reefs. It is largely unknown whether increased CO_2 will result in reduced calcification or the system will be buffered by dissolving existing carbonate reserves in the ocean (Guinotte *et al*. 2003). Future predictions on the implications of climate change and ocean acidification are often restricted to general assumptions of accepted standards of physical oceanography, temperature regimes and saturation states (Kleypas *et al.* 1999 a; Guinotte *et al.* 2003). However, predictions regarding impacts on smaller scales, for example coastal zone ecosystems or high-latitude reefs, are likely to be less accurate and may require study at the level of individual reefs (Guinotte *et al.* 2003). Furthermore, the behaviour of other extreme climatic and oceanic events in light of climate change, such as; the frequency, extent and duration of *El Niño* events, changes in ocean circulation, wave energy and storm intensity, and deep-ocean upwelling, need to be considered as they may be far less predictable than general ocean models (Guinotte *et al.* 2003). These periodic disturbances to coral reef ecosystems may be the dominant processes regulating coral community composition and reef growth at marginal locations (Guinotte *et al* 2003). At high-latitude and marginal sites, it is likely that these events and periodic stresses to reef-dwelling organisms will further limit reef development rather than any absolute limit on shifting environmental conditions in light of climate change (Harriott 1999; Riegl 2001; Guinotte *et al.* 2003). These periodic disturbances may have a greater role in regulating reef development under current and future climatic conditions than previously thought. As such, further research may be required to better understand the response of high-latitude reefs to disturbance events rather than predicted changes in ocean conditions.

5.5. Conclusion

The results of this study suggest that there are differing stages of development in each monospecific *Acropora austera* stand. This would be comparable with unpublished results of Montoya-Maya (pers. comm.) who is showing self-seeding in these coral stands. Of the three sites sampled, there were clear differences in coral growth rates, levels of mortality, framework depth (here assumed to be analogous to complexity) and net change in branch lengths over the study period. However, further research over a longer timeframe would elucidate such trends and provide further insight into the dynamics of these monospecific coral stands and their potential for reef accretion.

I hypothesize that these monospecific stands of *Acropora austera* are regulated by high summer mortalities and, in particular, mass mortality events arising from wave damage and facilitated by high levels of bioerosion. The results showed high growth rates and low mortality in young stands with little to no underlying framework and substantially higher mortality at sites that seemed to be older, with a deep, highly open framework. Mortality in the latter instance seemed to result predominantly from the collapse or removal of underlying framework structure. In addition, (presumably) younger *A. austera* stands (Sites 2 and 3) manifested a positive overall change in branch extension over time, as opposed to an older stand (Site 1) which yielded an effectively zero net percentage change at the end of the study period. This leads to the assumption that there is a maximum size for such monospecific coral stands where net growth is outweighed by loss through mortality due to collapse of the underlying framework structure before sufficient reef consolidation can occur. Under environmental circumstances in the Caribbean similar to those in South Africa, coral fragments broken by disturbance events quickly become incorporated into the reef structure by the binding effect of coralline algae and contribute significantly to reef accretion (Blanchon *et al.*

1997; Perry 1999). No such evidence for the permanent reincorporation of broken coral fragments into the reef structure was observed at Sodwana Bay. Collapsed areas in the coral stands either tended to erode further and expand, or were completely washed away during large storms. A similar relationship between disturbance by wave stress and reef development was seen in both Hawaii (Grigg 1998) and Lord Howe Island where evidence of reef accretion was observed only on the protected, leeward side of the island (Harriott 1999).

Although future predictions of elevated SSTs may provide a competitive advantage for a subset of corals due to increased growth rates and the opportunity expand their range, under temperature extremes (both above and below normal) corals may expel their symbiotic zooxanthellae and succumb to thermal-bleaching (Muller-Parker & D'Elia 1997; Lough 2000). Such a response by corals is often aggravated by high irradiance (Gleason &Wellington, 1993). Future predictions in SST from general circulation models (GCM) coupled with thermal limits for corals derived from various sources (summary in Crabbe 2008) indicate the frequency of bleaching events will rise rapidly. Such events are predicted to become annual in all oceans by 2040, and sooner in areas such as the Caribbean and Southeast Asia (Crabbe 2008). Increasing SSTs have been documented at Sodwana Bay over the past decade but they do not reach hazardous levels for any protracted period of time (Schleyer & Celliers 2003). Few instances of coral bleaching have been observed on these reefs, and their severity has been far less than that in the tropics and unlikely to pose a real threat at this latitude (Schleyer & Celliers 2003).

Future predictions on the reduction of aragonite saturation state in ocean waters indicate a gradual loss of carbonate accretion through reduced cementation and reef structure stabilization, and possibly slower coral growth rates (Kleypas *et al*. 2001; Guinotte *et al*. 2003; Schleyer & Celliers 2003). It has been suggested that this will result in fewer net accretionary reefs and community shifts towards more non-frame-building corals (Kleypas *et al*. 2001; Guinotte *et al*. 2003), leading them to resemble high-latitude, marginal reef systems such as those found off the Maputaland coastline of South Africa. However, aragonite saturation states were found to be non-limiting at this locality and yet these reefs fail to accrete.

This failure to accrete seems to result from a combination of high summer mortality and low winter growth rates which, when combined, limit framework development. Framework persistence is further limited by the export of $CaCO_3$ material through bioerosion, breakage and sediment resuspension. The results presented here suggest that seasonality is the primary cause that limits reef growth, and framework destructive processes are the primary factor that limit framework persistence. These processes regulate reef development, rather than any single environmental variable placing an absolute limit on accretion on the Maputaland reefs of South Africa.

The growth pattern of *Acropora austera*, one of the important reef-building corals on the Sodwana reefs, thus generates an essential framework necessary for reef growth. Yet, without sediment infilling and subsequent cementation by crustose coralline algae, these coral-derived frameworks do not remain stable and their large scale removal ensues. These findings suggest avenues for future research such as growth rates and the cementation potential of crustose coralline algae, further investigations on rates of bioerosion, and more refined measurement of sedimentation and sediment infilling.

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