

ECOPHYSIOLOGY OF INTERTIDAL CORALS ALONG THE EAST COAST OF SOUTH AFRICA: COPING IN MARGINAL HABITATS

by

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As the candidate's supervisor I have approved this dissertation for submission.

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Abstract

Coral survival in a time of climate change will depend largely on the ability to tolerate, acclimatise and adapt to changes in their natural environment. High-latitude intertidal corals along the east coast of South Africa withstand extreme temperature fluctuations, and endure highly marginal conditions for coral survival and growth. Intertidal corals have largely been ignored throughout years of coral research, yet they provide scope for understanding adaptation and acclimatisation in marginal conditions.

With focus on two scleractinian species occurring in rock pools, *Pocillopora verrucosa* and *Anomastrea irregularis*, the aim was to compare population size distributions and physiological responses (zooxanthellae density, chlorophyll a and lipid content) to season and latitude. Heterotrophy as a coping mechanism was also investigated. Five sites along the KwaZulu-Natal (KZN) coastline were sampled to determine latitudinal differences, from Sodwana Bay (27°S) to Munster (31°S), the southernmost point of coral distribution in this study.

Rock pools experience large temperature fluctuations over short time periods, emphasising the acute thermal stress endured by corals. At spring tide temperatures can fluctuate by more than 10°C over one tidal cycle. Temperatures in rock pools along the coast are a function of rock pool size and depth rather than latitude, with short-term fluctuations not seeming harmful to corals.

Coral population structure provides insight into the life history, juvenile input and mortality of these intertidal corals. High variability in size distributions between sites suggests that different disturbances are acting on intertidal coral populations and localised conditions are likely structuring these communities, nevertheless, populations seem relatively stable and likely to persist in these habitats.

Zooxanthellae density and lipid content decreased from summer to spring in *P. verrucosa*, whereas *A. irregularis* showed minimal seasonal patterns. Chlorophyll a was highest in winter in both species, possibly in response to low temperatures and light. Differences in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ between coral tissue and zooxanthellae suggest that heterotrophy contributes more to the metabolism of *A. irregularis* than *P. verrucosa*. Isotope signatures also reveal that corals at Sodwana Bay are either feeding less or comprise a different diet to those at other sites. Lipid utilisation and heterotrophy may comprise important energy sources in coping with marginal

conditions of the intertidal zone. Rock pools may thus constitute an important habitat for coral survival, growth and reproduction, allowing the southward extension of their range, which will be imperative during times of local and global environmental change.

Keywords

Pocillopora · *Anomastrea* · Marginal · Intertidal Rock Pool · Temperature · Physiology

Preface

The work described in this dissertation was carried out at the University of KwaZulu-Natal (UKZN). Field work was conducted at five sites along the east coast of South Africa from May 2012 - October 2013, under the supervision of Dr. David Glassom. This dissertation represents original work by the author and has not otherwise been submitted in any form for any degree or diploma to any tertiary institute.

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Declaration – Plagiarism

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Table of Contents

Abstract	i
Preface	iii
Declaration – Plagiarism	iv
Acknowledgments	v
Chapter 1: Introduction	1
1.1. Introduction	1
1.2. Background	1
1.3. Coral biology and symbiosis	3
1.4. Response to environmental stress	5
<i>1.4.1 Size frequency distributions</i>	5
<i>1.4.2 Coral physiology</i>	7
<i>1.4.3 Heterotrophy</i>	11
1.5. Marginal coral communities of South Africa	13
Chapter 2: Methods	16
2.1. Study site	16
2.2. Coral species selection	17
2.3. Site selection.....	18
2.4. Coral collection	19
2.5. Water temperature	20
2.6. Coral diversity survey	21
2.7. Population size distribution	21
2.8. Coral physiology	22
2.9. Coral surface area	23
2.10. Stable isotopes	23
2.11. Statistical analysis	24

Chapter 3: Results	26
3.1. Water temperature.....	26
3.2. Coral diversity	29
3.3. Size frequency distribution	30
3.4. Physiology: Effect of site, season and species	36
3.5. Stable isotopes	43
Chapter 4: Discussion	48
4.1. Water temperature	48
4.2. Coral diversity	50
4.3. Size frequency distribution	52
4.4. Physiology: Effect of site, season and species	55
4.4.1. <i>Zooxanthellae density</i>	55
4.4.2. <i>Chlorophyll a content</i>	57
4.4.3. <i>Total lipid content</i>	59
4.5. Heterotrophy.....	61
4.6. Overall discussion & summary.....	66
Chapter 5: Conclusion	67
References	71

Chapter 1

1.1. Introduction

Coral reefs worldwide are experiencing increased environmental pressures, exacerbated by the rate of climate change. Increasing sea surface temperatures due to global warming pose some of the main threats to coral reefs, in addition to other natural and anthropogenic stresses (Wittenberg and Hunte, 1992; Clark and Edwards, 1994; Treeck and Schuhmacker, 1997; Hughes *et al.*, 2003; Burt *et al.*, 2009). Temperature stress is recognised as the main contributor to coral bleaching, a global phenomenon posing a severe threat to coral reefs. It is predicted that mean global sea surface temperature is likely to increase by 1.5°C (at a conservative estimate based on minimum increases in CO₂) by the end of the 21st century (Meehl *et al.*, 2007). The ability to withstand these conditions and adapt to a changing environment is imperative for coral survival and persistence. Intertidal corals that can withstand marginal conditions are likely to show resilience to global climate change (Brown *et al.*, 1994; 1999; 2002; West and Salm, 2003).

Understanding physiological responses of intertidal corals to harsh conditions will help recognise the ability of other corals to acclimatise and adapt to increases in temperature and other physical factors, providing insight into resistance and resilience to climate change. Intertidal corals exemplify the ability to cope with harsh environmental conditions, and constitute a means to understand the fate of future coral populations. This provides the basis of this research, with a focus on the structure and function of intertidal coral populations, aiming to better understand their role in marginal environments.

1.2. Background

Coral reefs include some of the most diverse and productive ecosystems in the world, thriving in somewhat unproductive tropical oceans (Hoegh-Guldberg, 1999). Their distribution spans the tropical belt, characterised by warm, clear, oligotrophic waters. Regardless of low nutrient concentrations, high productivity of these ecosystems emphasises their importance in the tropical oceans, and the role they play in the global marine environment (Hoegh-Guldberg, 1999).

Subtidal coral reefs cover approximately 250 000km² of the earth's surface, and have played a vital role in shaping the marine environment over the past 200 million years (Hoegh-Guldberg, 1999; Veron, 2000). They provide a number of valuable environmental and economic services, adding to the value of their conservation and perpetuation of these species and coral reefs as a whole. These ecosystems support a high diversity of fish and other organisms allowing for the provision of resources and services such as coastal protection, fishing, tourism, and human livelihoods (Carte, 1996, Done *et al.* 1998; Hoegh-Guldeberg, 1999; Moberg and Folke, 1999).

Reef-building (hermatypic) corals are photosynthetic, calcifying organisms (Gattuso *et al.*, 1999; Hoegh-Guldebrg, 2007; Davy *et al.*, 2012). The growth of hermatypic corals provides the framework of coral reefs and the construction of these important bio-structures (Gattuso *et al.*, 1999). Calcification is the main process of skeleton formation, through the precipitation of calcium carbonate (CaCO₃) in the form of aragonite (Gattuso *et al.*, 1999). This process creates a variety of reef structures, including island atolls, barrier, fringing and patch reefs and intertidal reef flats. The diversity of reef form will also influence the degree of exposure and sensitivity to disturbance, and consequently to the impacts of climate change (Bellwood *et al.*, 2004). This can affect resistance and resilience of the reef as a whole, which affects the local coral communities.

Corals host symbiotic algae of the genus *Symbiodinium*, known as zooxanthellae, within their tissue. This symbiotic component is responsible for the photosynthetic capacity of corals (Muller-Parker and D'Elia, 1997; Muscatine, 1977; Muscatine and Porter, 1997). The majority of reef-building coral species live mutualistically with their endosymbiotic algae, restricting them to warm, clear, shallow waters where there is sufficient light penetration for photosynthesis (Stambler *et al.*, 1991; Muscatine and Porter, 1997; Kleypas *et al.*, 1999). However, they also function as secondary and tertiary consumers via heterotrophic feeding, and saprotrophs, taking up dissolved organic nutrients from surrounding seawater (Odum and Odum 1955; Stephens, 1962; Muscatine and Porter, 1977; Gattuso *et al.*, 1999). This functional diversity contributes to the success of corals and coral reef development.

Coral diversity is highest in the tropics, yet corals extend their range into subtropical habitats, where high-latitude coral-dominated communities persist (Harriott, 1999; Kleypas *et al.*, 1999;

Celliers and Schleyer, 2002; Riegl, 2003; Schleyer and Celliers, 2003; 2008). There is nonetheless a decline in coral richness and abundance in a poleward direction. Hoegh-Guldberg (1999) proposes a temperature range between 18°C and 30°C for optimal coral reef development. There is however speculation regarding the main drivers of coral growth, which will affect local reef development (Kleypas *et al.*, 1999). UV radiation and aragonite saturation could affect coral survival, growth and distribution (Gattusso *et al.*, 1999; Hoegh-Guldberg, 1999; Kleypas *et al.*, 1999). Biological factors such as competition and predation, and physical characteristics including salinity, nutrient concentration and turbidity or sedimentation also play a role (McClanahan and Obura, 1997; Brown *et al.*, 1999; Hoegh-Guldberg, 1999; Schleyer and Celliers, 2003; Sofonia and Anthony, 2008). Coral recruitment, reproduction, productivity and growth rates respond differently to latitude, emphasising the complexity of coral physiology and influences of the surrounding environment (Kleypas *et al.*, 1999). A combination of physical and biological factors thus contributes to the ecology of coral ecosystems, influencing their resilience to local and global environmental changes.

1.3. Coral Biology and Symbiosis

Scleractinian corals owe their success as reef builders in oligotrophic environments to the symbiotic relationship with zooxanthellae (Odum and Odum, 1955; Muscatine and Porter, 1977; Berkelmans and van Oppen, 2006; Mieog, 2009). Zooxanthellae are typically 8-12µm in diameter and occur at densities up to $1-2 \times 10^6 \text{ cm}^{-2}$. (Muller-Parker and D'Elia, 1997; Berkelmans and van Oppen, 2006) Densities vary among species of coral, and more importantly can change spatially and temporally. High variation in the response of zooxanthellae densities to the local environment emphasises the versatility of the coral-algal symbiotic relationship (Dustan, 1997; Stimson, 1997; Fagonee *et al.*, 1999; Fitt *et al.*, 2000; Costa *et al.*, 2005; Pillay *et al.*, 2005; Berkelmans and van Oppen, 2006; Suwa *et al.*, 2008). Zooxanthellae can contribute between 90 and 95% of the coral's energy requirements (Muscatine, 1990; Berkelmans and van Oppen, 2006), providing organic byproducts as a source of nutrition to the coral host (Muscatine and Porter, 1977; Muscatine, 1990). This autotrophic contribution is based on the highly efficient

transfer of organic material in the form of photosynthetic carbon (sugars) and amino acids to the corals, in exchange for protection and inorganic nutrients (ammonia and phosphates) from the host coral (Muscatine and Porter, 1977; Hoegh-Guldeberg, 1999). Carbon from zooxanthellae provides energy for important physiological functions including growth, reproduction and calcification, contributing to the fitness of corals. This tight nutrient cycling is fundamental to the high productivity of coral reefs worldwide (Hoegh-Guldeberg, 1999).

Zooxanthellae acquisition occurs in a variety of ways, during asexual or sexual reproduction of corals (Muller-Parker and D'Elia, 1997). Asexual budding results in a direct transfer of zooxanthellae to the new fragment/bud of coral. During sexual reproduction, zooxanthellae are either directly transferred via the parent or can be indirectly taken up from the immediate environment (Muller-Parker and D'Elia, 1997; Lewis *et al.*, 2004). Adult corals can also acquire symbionts from the external environment (Lewis *et al.*, 2004).

It was thought that zooxanthellae belong to one group or species (Muscatine, 1971). However, *Symbiodinium* is highly diverse and can be classified into eight groups or clades (A-H) based on ribosomal and chloroplast DNA sequences (Baker, 2003; Lewis *et al.*, 2004; Berkelmans and van Oppen, 2006; Suwa *et al.*, 2008; Mieog *et al.*, 2009). Symbionts associated with scleractinian corals come predominantly from clade A-D, and corals can associate with one or multiple clades of zooxanthellae at one time (Muller-Parker and D'Elia, 1997; Baker, 2003; Rowan and Knowlton, 2005; Berkelmans and Van Oppen, 2006; Ulstrup *et al.*, 2008; Mieog *et al.*, 2009). Recent studies investigated the response and acclimatisation of the host-algal combinations to environmental stressors, particularly light and temperature (Fabricius *et al.*, 2004; Berkelmans and Van Oppen, 2006; Robison and Warner, 2006; Suwa *et al.*, 2008; Mieog *et al.*, 2009; McGinley *et al.*, 2012). Clades show varying responses to environmental stressors, with Clade D frequently reflecting a higher temperature tolerance and stability than clade C (Rowan, 2004; Suwa *et al.*, 2008; Mieog *et al.*, 2009). Corals can also change the type of zooxanthellae within their tissue, which may explain variations in stress susceptibility between corals (Lewis *et al.*, 2004; Rowan, 2004; Suwa *et al.*, 2008).

Zooxanthellae play an important role in the fitness of their coral host. In addition to the primary function of nutrition, zooxanthellae indirectly play a role in other physiological processes. Photosynthesis and respiration are fundamental components of the energy budget and metabolism of corals (Coles and Jokiel, 1977). Carbon fixation through photosynthesis is the main source of energy that corals use to perform cellular and organism-level processes (Falkowski *et al.*, 1984; Gattuso, 1999). This is closely linked to calcification, the main mechanism of coral growth and reef development (Muscatine, 1971; Gattuso, 1999). Calcification is related to temperature and light, which also directly affects the photosynthetic rate of zooxanthellae (Howe and Marshall, 2001). These physiological processes are therefore closely linked, playing a pivotal role in the functioning of corals.

Muscatine (1971) suggested that zooxanthellae influence coral calcification and the presence of symbiotic algae increases calcification 3-4 fold during the day when symbionts are photosynthesising (Gattuso, 1999). The way in which these metabolic pathways are affected will influence the overall production and success of the corals in their environment. It is thus crucial to understand the way these processes interact with each other, and are influenced by the function and response of symbiotic zooxanthellae to local environmental conditions. This will subsequently affect the susceptibility of corals to stress and their ability to cope in marginal habitats.

1.4. Response to environmental stress

The intertidal zone is a highly dynamic, challenging benthic environment. It poses a variety of physical stresses including possible periodic aerial exposure, fluctuations in temperature and salinity, high solar radiation and strong wave action and sedimentation (Brown *et al.*, 1994; 1999; Anthony and Kerswell, 2007). Intertidal coral populations utilise an array of cellular, physiological and organism-level strategies to cope with these conditions. The response to physical and biological impacts will affect coral fitness and the status of the coral population.

1.4.1. Size frequency distributions

Population trends show signs of the responses to long term environmental stresses that are reflected in the proportion of different size classes (Bak and Meesters, 1998; Meesters *et al.*,

2001). Size distributions reveal the population state, reflecting processes that affect growth and mortality of individual colonies (Bak and Meesters, 1998). Stable populations have a balance between growth, survival/mortality and reproduction (Bak and Engel, 1979). The structure of a coral population reflects life history traits that will determine long term responses of the coral population (Bak and Meesters, 1998; Meesters *et al.*, 2001; de Baros and Pires, 2006; Crabbe *et al.*, 2009).

Coral population size structure can be related to processes such as recruitment and post-settlement survival (Edmunds, 2000; Miller *et al.*, 2000; Glassom and Chadwick, 2006; Cardini *et al.*, 2012). High recruitment of spawning species in particular, results in a large proportion of small colonies (Bak and Meesters, 1998; Vremeij and Bak, 2007). Recruit settlement rates and percentage of juvenile corals has been used to determine the state of coral reefs as a function of differential survivorship and growth rates (Glassom and Chadwick, 2006; Artzy-Randulp *et al.*, 2007; Goffredo *et al.*, 2008; Cardini *et al.*, 2012). There are however constraints to the ability to observe and measure the smallest corals present in each habitat. Juvenile corals less than 1cm in diameter are often undetectable, especially in the intertidal zone where there is high algae, sponge and zooanthid cover (Sink *et al.*, 2005). This needs to be considered when comparing coral size frequency distributions between species and habitats.

Population size structures are attributed to reef topography (i.e. depth, as a function of light intensity), sea surface temperatures, species specific growth rates, recruitment patterns, mortality rates, community composition and species density. Different life histories of coral species can influence the resistance and resilience to environmental perturbations. High reproductive output and larval settlement for example, will enable a fast turnover that can improve population recovery and adaptation to local conditions (Miller *et al.*, 2001; Glassom and Chadwick, 2006; Crabbe *et al.*, 2009). Post settlement survival and growth rates will also contribute to population success (Miller *et al.*, 2001; Glassom and Chadwick, 2006). Coral size frequencies can provide insight into long term responses to local environmental conditions, and important biological processes affecting the state of coral fitness.

1.4.2. Coral physiology

Coral fitness can be expressed in terms of growth, survival and reproduction (Anthony and Connolly, 2004; Mieog *et al.*, 2009). Physiological responses to environmental conditions will influence the coral's overall energy budget, affecting their ecological performance and fitness. This changes along an environmental gradient, creating a niche that structures the local coral assemblage (Anthony and Connolly, 2004; Mieog *et al.*, 2009). Physical factors including light, temperature, depth and turbidity have been used to quantify environmental tolerances and effectively determine niche boundaries. Photosynthesis (P) and respiration (R) and the ratio of P: R are used as a measure of coral function and response to environmental stress (Coles and Jokiel, 1977; Falkowski *et al.*, 1984; Edmunds and Davies, 1986) and to create coral energy budgets. Edmunds and Davies (1986) showed that 26% of photosynthetically produced energy is used for coral respiration and growth, 22% for algal respiration and growth, approximately 1% for reproduction and 45% was unaccounted for. Excess energy could contribute to stored reserves, periodically used when required (Edmunds and Davies, 1986). A decrease of P: R, as a sign of stress, to increasing water temperatures was shown in *Pocillopora damicornis*, *Montipora verrucosa*, *Porites compressa* and *Fungia scutarie* (Coles and Jokiel, 1977). Different responses of tropical and subtropical varieties of the same species emphasises the ability of corals to adapt to different ambient temperatures and cope with stress (Coles and Jokiel, 1977). Photosynthetic rates and efficiency will therefore influence these metabolic processes, ultimately contributing to the overall fitness of the coral.

Energy budgets in coral physiological studies are still commonly used to understand the response to various environmental factors. The relationship between photosynthesis and respiration can determine the efficiency of coral-algae symbiosis. Photosynthesis, respiration and other metabolic functions were modeled in relation to light penetration and turbidity (Anthony and Connolly, 2004). The change in respiration rate to turbidity was the main cause of differences of physiological niche boundaries in *Acropora valida* and *Turbinaria mesenterina*. Energy inputs and more importantly outputs can influence ecological niches and therefore the distribution of a species (Anthony and Connolly, 2004).

A more recent means of quantifying the response of the coral holobiont to environmental stress is through photobiology. This measures the photosynthetic output and efficiency of symbionts, including quantifying maximum quantum yield of photosystem II (PSII) which is the ratio of variable chlorophyll fluorescence to maximum chlorophyll fluorescence, F_v/F_m (Jones and Hoegh-Guldberg, 2001; Phillip and Fabricius, 2003; Ulsterp *et al.*, 2008; Mattan-Moorgawa *et al.*, 2012). The use of pulse-amplitude modulated fluorometry (PAM) to quantify photosynthetic stress in corals has proved highly useful in determining immediate responses to physical stressors such as light attenuation, temperature fluctuations and sedimentation (Jones and Hoegh-Guldberg, 2001; Phillip and Fabricius, 2003; Ulsterp *et al.*, 2008). This has also been used to quantify the photosynthetic responses of different zooxanthellae clades (Rowan, 2004; Ulsterp *et al.*, 2008). *Symbiodinium* clade C showed photoinhibition in response to increasing temperatures, and thermal sensitivity which could result in coral bleaching (Rowan, 2004). Hosting more than one type of symbiont with varying degrees of stress tolerance could be an important mechanism used to cope in marginal conditions. Within clade variation in thermal tolerance was found in *Symbiodinium*, with different functional responses observed among populations (Howells *et al.*, 2012). Within the same type of *Symbiodinium*, a distinctive response was observed in different thermal reef environments, suggesting the ability of adapt to local environmental conditions (Howells *et al.*, 2012). This adaptation and more importantly the pace of acclimatisation, could potentially allow corals to persist with increasing global sea surface temperatures (Howells *et al.*, 2012). This is important in a time of local and global environmental change.

Exposure to stressful environmental conditions can result in a breakdown of the symbiotic association of coral and zooxanthellae, leading to a phenomenon known as “coral bleaching” (Hoegh-Guldberg, 1999; Fitt *et al.*, 2001; Jokiel, 2004). This occurs when various physical stresses disrupt symbiosis leading to the degeneration or expulsion of the algae, resulting in a loss of pigment and colour of the coral tissue (Jokiel, 2004). The coral appears white as a result of the exposed skeleton (Fitt *et al.*, 2001; Jokiel, 2004). Coral bleaching has become a major threat to reefs worldwide. Increasing incidents of coral bleaching have been observed at a local, regional and global scale, often resulting in large-scale coral mortality (Glynn, 1993; Brown 1997; Hoegh-Guldberg, 1999). Increasing sea surface temperatures and thermal stress are

considered the main contributors to coral bleaching. However, bleaching can be caused by a variety of factors, including changes in salinity, solar radiation, sedimentation and aerial exposure. A combination of these is likely to be experienced in the intertidal zone (Brown *et al.*, 1994; 1999; Anthony and Kerswell, 2007).

The response of the holobiont to environmental factors can be shown by seasonal patterns of coral physiology. Pillay *et al.* (2005) found *Acropora millepora* zooxanthellae densities almost doubled with a decrease in water temperature and solar influx on the Great Barrier Reef. Similarly, zooxanthellae densities were highest during winter in corals collected from Hawaii (Stimpson, 1997), Mauritius (Fagoonee *et al.*, 1999) and the Bahamas (Fitt *et al.*, 2000). Coral tissue biomass reached a maximum during the spring, suggesting a lag time between these responses (Fitt *et al.*, 2000). Shallow water corals differed in symbiont density, pigment concentration and tissue biomass from those in deeper habitats. This further implies a relationship between light and temperature and zooxanthellae function (Fitt *et al.*, 2000). Despite some clear seasonal trends, symbiont density also showed high stochastic variability with periods of high and extreme low densities (Fagoonee *et al.*, 1999).

Sun altitude and azimuth were directly correlated to bleaching of intertidal *Gonastrea aspera* (Brown *et al.*, 1994). High light levels and often temperatures have resulted in zooxanthellae and host cell degeneration, followed by a reduction of zooxanthellae density at the onset of bleaching (Brown *et al.*, 1995; Le Tissier and Brown, 1996; Brown *et al.*, 1999). Changes in chlorophyll a, (Le Tissier and Brown, 1996; Brown *et al.*, 1999; Anthony and Hoegh-Guldberg, 2003; Stambler *et al.*, 2008), cell volume and zooxanthellae depth within the polyp are also affected by light and temperature (Stambler *et al.*, 2008). Microhabitats that differ in light and temperature are common in the intertidal zone, and can affect the physiological responses of corals. Lower photosynthetic and dark respiration rates were observed in corals in caves compared to open areas (Anthony and Hoegh-Guldberg, 2003). They also showed lower tissue and skeleton thickness and higher photosynthetic efficiency which could maximise light absorption per unit mass (Anthony and Hoegh-Guldberg, 2003).

Other cellular responses have also been used to monitor stress levels in corals. Thermal stress resulted in the production of reactive oxygen species in symbionts, associated with increased chlorophyll allomerisation and xanthophyll cycling (Lesser and Farrell, 2004; Takahashi *et al.*, 2004; Dove *et al.*, 2006; Kisten, 2013). Changes in protein levels and DNA damage is also observed as a cause of thermal and other physical stressors (Lesser and Ferrell, 2004; Dove *et al.*, 2006; Fitt *et al.*, 2009; Kisten, 2013; Mayfield *et al.*, 2013; Texeira *et al.*, 2013). Cellular and physiological responses in particular to thermal stress will affect the fitness of the coral in terms of growth, reproductive output and survival

The intertidal zone is characterised by the periodic exposure of the rocky habitat and biota to air (Brown *et al.*, 1994; Romaine, 1997; Texeira *et al.*, 2003). Corals may experience hypoxia which can negatively affect their metabolism and physiology. Romaine (1997) determined that maximum gross photosynthesis of corals was 3.6 times lower in air than water; however photoadaptation (*Ik*) did not differ between submerged and exposed colonies. Respiration rates did also not differ significantly between corals in water and air, however there was no calcification during periods of exposure (Romaine, '1997). An increase in the expression of molecular compounds heat shock cognate 70 (HSC70) and heat shock protein 70 (HSP70) also occurred during air exposure, which subsequently decreased during immersion (Texeira *et al.*, 2003; Carpenter *et al.*, 2010; Chow *et al.*, 2012). This suggests a cellular response that could allow corals to tolerate oxygen-limited conditions in the intertidal zone.

Corals are rich in lipids with *Pocillopora* containing approximately 30-40 % lipids per gram dry tissue weight (Stimpson, 1987). Lipids occur as structural molecules or can be stored within the endoderm of coral polyps, in reproductive eggs and cells and can be found within thylakoid membranes of symbiotic zooxanthellae (Patton *et al.*, 1977; Stimson, 1987; Tchernov *et al.*, 2004). When photosynthetically fixed carbon is not available, some corals rely on stored energy reserves such as lipids, carbohydrates or proteins (Anthony and Fabricius, 2000; Grottoli *et al.*, 2004; 2006; Rodrigues and Grottoli, 2007; Borell *et al.*, 2008). For example, the recovery of *Porites compressa* and *Montipora capitata* were tested after experimentally bleaching them. *P. compressa* used photosynthetically fixed energy for recovery of bleaching while *M. capitata* recovered faster using energy reserves and did not rely entirely on photosynthesis (Rodrigues

and Grottoli, 2007). Energy stores are also metabolised and synthesized differently and at different rates in different coral species. *P. compressa* first replenished lipids, carbohydrates and proteins while *M. capitata* recovered carbohydrates, proteins and lastly lipids (Rodrigues and Grottoli, 2007). The faster recovery rate of *M. capitata* was also attributed to heterotrophic feeding as a source of nutrition and energy during the recovery process (Rodrigues and Grottoli, 2007). These are both important mechanism of recovery and tolerance to stress.

During the 1998 increased sea surface temperature anomaly, widespread coral bleaching was observed. Using coral isotope analysis and global records of bleaching, extensive thermal stress and bleaching of corals during the 1998 warming event was shown in areas of high temperature variability (Thompson and van Woesik, 2009). These corals however showed reduced bleaching compared to other sites during the recent warming of 2005-2006, suggesting a selective pressure for those corals more tolerant to thermal stress (Thompson and van Woesik, 2009; Guest *et al.*, 2012). Previous exposure to high levels of solar radiation was also shown to improve tolerance to increased sea surface temperature (Dunne and Brown, 2001; Brown and Dunne, 2008). History of environmental stress and acclimatisation thus allows for increased tolerance and adaptability for future changes in the surrounding environment, resulting in a more tolerant coral community.

1.4.3. Heterotrophy

An important component of acclimatisation and adaptation includes the ability of corals to feed heterotrophically. Feeding may compensate for the loss of photosynthetic input by zooxanthellae. Exogenous food sources can affect protein levels, zooxanthellae densities, chlorophyll a concentrations and fatty acid and sterol compositions (Borell *et al.*, 2008; Treignier *et al.*, 2008; Houlbreque and Ferrier-Pages, 2009). Feeding affects photosynthesis and calcification rates and contributes to the metabolism and energy budget of corals (Borell *et al.*, 2008; Palardy *et al.*, 2008; Houlbreque and Ferrier-Pages, 2009; Hoogenboom *et al.*, 2010; Tremblay *et al.*, 2011).

Higher than expected contributions to the energy budget were observed, accounting for 46% of the daily metabolic carbon requirements of healthy corals, and 147% of bleached corals (Palardy *et al.*, 2008). Similar heterotrophic contributions were shown for the Mediterranean coral

Oculina pentagonica and tropical coral, *Turbinaria reniformis* (Tremblay *et al.*, 2011). Hoogenboom *et al.* (2010) found variation in heterotrophic feeding rates, related to differences in photosynthesis. The quantity and rate of feeding can change rapidly in response to surrounding conditions, and can alter the use of ingested energy, either for tissue biomass production, calcification or reproduction (Hoogenboom *et al.*, 2010). This can affect the success of the corals, emphasising the importance of feeding in adapting and acclimatising to environmental stress.

The ability of *M. capitata* to feed heterotrophically allowed a faster recovery rate from bleaching than *P. compressa* (Rodrigues and Grottoli, 2007). *P. compressa* relied on stored energy reserves while *M. capitata* used heterotrophy to maintain stored energy reserves (Rodrigues and Grottoli, 2007). Feeding contributed substantially to the energy budget of bleached corals and enhanced energy production, photosynthesis and growth in *Porites* spp and *Montipora capitata* (Palardy *et al.*, 2008). Feeding experiments of *Stylophora pistillata*, showed that fed corals contained higher concentrations of chlorophyll a, protein and had higher calcification rates than starved corals (Reynaud *et al.*, 2002). Thus heterotrophic feeding benefits coral physiology and may play an important role in adapting to stressful environmental conditions.

Stable isotope analysis is often used to determine the contribution of heterotrophy to the productivity and success of corals. In particular, carbon and nitrogen stable isotopes are used to determine carbon pathways and trophic relationships (Peterson and Fry, 1987). The ratio of $^{13}\text{C}:^{12}\text{C}$ can determine sources of organic intake, specifically diet, as the ratio of consumer tissue is assumed to be the same as the organic food source (DeNeiro and Epstein, 1978). $\delta^{13}\text{C}$ signatures can also measure carbon assimilation over a long period, in contrast to short-term physiological measurements (Goreau, 1977; DeNeiro and Epstein, 1978; Swart, 1983; Muscatine *et al.*, 1989). Carbon signatures can therefore be used to determine the contribution of allocthonous carbon (e.g. assimilated zooplankton) compared to that of photosynthetically produced carbon (Land *et al.*, 1975; DeNeiro and Epstein, 1978; Swart, 1983; Muscatine *et al.*, 1989). $\delta^{15}\text{N}$ signatures can also be used to determine the level of feeding within the trophic pyramid (Ferrier-Pages *et al.*, 2011), and it is suggested that coral host tissue should be enriched

in $\delta^{15}\text{N}$ by 1-3‰ compared to endosymbiotic zooxanthellae in the absence of heterotrophic feeding (Reynaud *et al.*, 2009).

Ferrier-Pages *et al.* (2011) compared $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in *Cladocora caespitosa* in summer and winter and found a decrease in the $\delta^{13}\text{C}$ from -17‰ (similar to the zooxanthellae) in the summer to -23‰ to -28‰ in the winter, suggesting a change from autotrophy to predominantly heterotrophic feeding (Ferrier-Pages *et al.*, 2011). A substantial $\delta^{15}\text{N}$ enrichment between the food source and the holobiont in winter also confirmed the contribution of heterotrophy during this time. Thus, *C. caespitosa* and possibly other corals in temperate habitats can derive a large proportion of their carbon requirements heterotrophically.

1.5. Marginal coral communities of South Africa

Accretion and development of coral reef structures declines at increasing latitudes. This is typified by corals on the east coast of South Africa, a pertinent example of high latitude reef systems (Schleyer, 2000; Riegl and Piller, 2003; Schleyer and Celliers, 2003b), which constitute the southern-most distribution of hermatypic coral-dominated communities in the western Indian Ocean (Riegl *et al.*, 1995; Schleyer and Celliers, 2003b). Predominantly, the subtidal reefs are located on the north coast of KwaZulu-Natal (KZN) (Fig. 1), in the Maputaland region, extending northwards into Mozambique. These reef systems are however not true coral reefs, but coral communities on a base of fossilised dune and beachrock (Ramsay, 1994; Riegl *et al.*, 1995). They comprise a high diversity of hard and soft coral species. In South Africa, 96 coral species have been documented consisting of 42 scleractinian genera, this being a conservative estimate (Riegl, 1996). The diversity is comparable to other high-latitude reef systems but lower than in the eastern Indian Ocean fringe (Riegl, 1996). Scleractinian diversity declines rapidly in the Southern parts of KZN. Approximately 10 species have been recorded on Aliwal Shoal (Riegl, 1996; Schleyer *et al.*, 2006), with only 2.3% hard coral cover (Schleyer *et al.*, 2006).

Kleypas *et al.* (1999) defined “marginal” environments as those that occur near or beyond the limits of natural coral distribution, based on physical factors including light, temperature and salinity. However, this definition is still debated. Guinotte *et al.* (2003) underline the fact that a coral community with a high diversity and large percentage cover of healthy scleractinian

species would be considered to be that of a non-marginal coral reef community. This does not always refer to the habitat in which this community exists, and marginality could exist with environmental conditions not conducive to coral survival and growth (Guinotte *et al.*, 2003). The Great Barrier Reef for example (Done, 1999) can experience high levels of dynamic stress and recovery, leading to areas of marginality, but overall this ecosystem would not be classified as a marginal coral reef environment (Guinotte *et al.*, 2003). Marginality must therefore be considered in terms of both the physical environment and coral community.

Coral reefs worldwide are being threatened with increasing marginality, as they change from healthy to poor-condition reefs due to natural and anthropogenic factors (Kleypas *et al.*, 1999; Wilson, 2000; Guinotte *et al.*, 2003; Perry and Larcomb, 2003). Kleypas *et al.* (1999b) found that temperature, light and aragonite saturation accounted for most of the variation observed in coral reef distribution. As these factors are altered through climate change, it is unclear how this will affect coral ecosystems worldwide (Guinotte *et al.*, 2003; Perry and Larcomb, 2003). It is predicted that almost all reef systems would become marginal in terms of aragonite saturation levels, and significant high-biodiversity areas will become marginal in terms of local sea surface temperatures (Guinotte *et al.*, 2003). This could also pose a significant threat to coral reefs around the world.

The high-latitude, non-accretive reef systems off the east coast of South Africa can be considered marginal reefs, in terms of light penetration, temperature and aragonite saturation (Kleypas *et al.* 1999; Schleyer and Celliers, 2003b). Perry and Larcombe (2003) add to the definition of Kleypas (1999), suggesting that ‘marginal’ environments are characterised by sub-optimal, fluctuating environments. ‘Fluctuating,’ is a pertinent description for coastal intertidal ecosystems. The intertidal environment presents extreme fluctuations of environmental conditions, often over short periods of time (Brown *et al.*, 1994; 2002; Anthony and Kerswell, 2007). All intertidal environments are thus marginal coral habitats. Corals in the intertidal zone, a highly dynamic environment, represent those that are able to tolerate harsh environmental conditions.

Research on marginal intertidal habitats may improve understanding of the biogeography of corals, and physiological niche limits (Guinotte *et al.*, 2003), thus providing an important means

of understanding coral functioning and ability to adapt in a changing environment. They are highly dynamic systems that undergo period air exposure and high solar radiation, wave activity and extreme temperature fluctuations (Anthony and Kerswell, 2007). Corals that are able to withstand such harsh conditions may provide a means to understand the mechanisms that are used to tolerate environmental extremes. These coral communities are also fundamental examples of species that can acclimatise to marginal conditions, and may play an important role in assuring the persistence of coral ecosystems worldwide in a critical time of global climate change.

The intertidal rocky shores of KZN are inhabited by a variety of scleractinian coral species. Corals have been observed as far south as Munster, approximately 12km from the southern border of KZN, at latitude 31° 04'S. Up to 15 coral species were observed in rock pools in the southern parts of KZN. Abundance is low for the majority of species, apart from a few common species that are abundant along the entire stretch of coastline. These include *Anomastrea irregularis*, *Pocillopora verrucosa* and *P. damicornis*. The aims of this study will thus be to determine aspects of coral physiology in an intertidal environment, providing insight into the adaptation and acclimatisation to local stresses in a marginal habitat:

1. Collect real-time temperature measurements of the intertidal rock pools.
2. Determine population size distributions of two intertidal coral species and compare them among latitudes.
3. Investigate selected physiological parameters of both species during each season and at different latitudes.
4. Estimate the contribution of heterotrophic feeding to the coral metabolism in coping with these marginal conditions.

Chapter 2: Methods

2.1. Study site

The east coast of South Africa exhibits a transition from the northern tropical and subtropical conditions to the cooler temperate conditions of the south. The oceanography of KwaZulu-Natal is influenced by the Agulhas current that runs along the continental shelf bringing with it warm water from the tropics. It constitutes the western boundary of a gyre that circulates in the south-west corner of the Indian Ocean (Jury, 1992). The current flows in a southward direction at $1\text{--}2\text{m.s}^{-1}$, guided by the narrow continental shelf (Jury, 1992; Ramsay, 1994; Hutchings *et al.*, 2002). Reversal currents do also occasionally occur, returning the current in a northward direction (Morris, 2009). Coral larvae are predicted to be transported in these currents, distributing planulae in a southward and northward direction (Morris, 2009; Macdonald *et al.*, 2011). The sea surface temperatures (SSTs) between November and March often exceed 24°C , which creates the warm, humid subtropical climate along most of the KwaZulu-Natal (KZN) coastline.

Rocky shore habitats are scattered among long stretches of sandy beach along the South African coastline (Branch and Branch, 1981). Coastal geomorphological structures on the east coast include rocky outcrops and cliffs, long rock ledges with a shoreward drop off, and areas of mixed elevation and isolated rock pools. Rock pools vary in size from 0.3-4m in diameter, or form larger gullies. Each rock pool varies in depth, shape and size, functioning as its own localised environment. If exposed at low tide during the day, water temperatures increase as the sun heats the pool, and cools again as the tide comes in and during the night. Some rock pools are more conducive to coral growth and survival than others, varying in terms of exposure and degree of physical and biological factors.

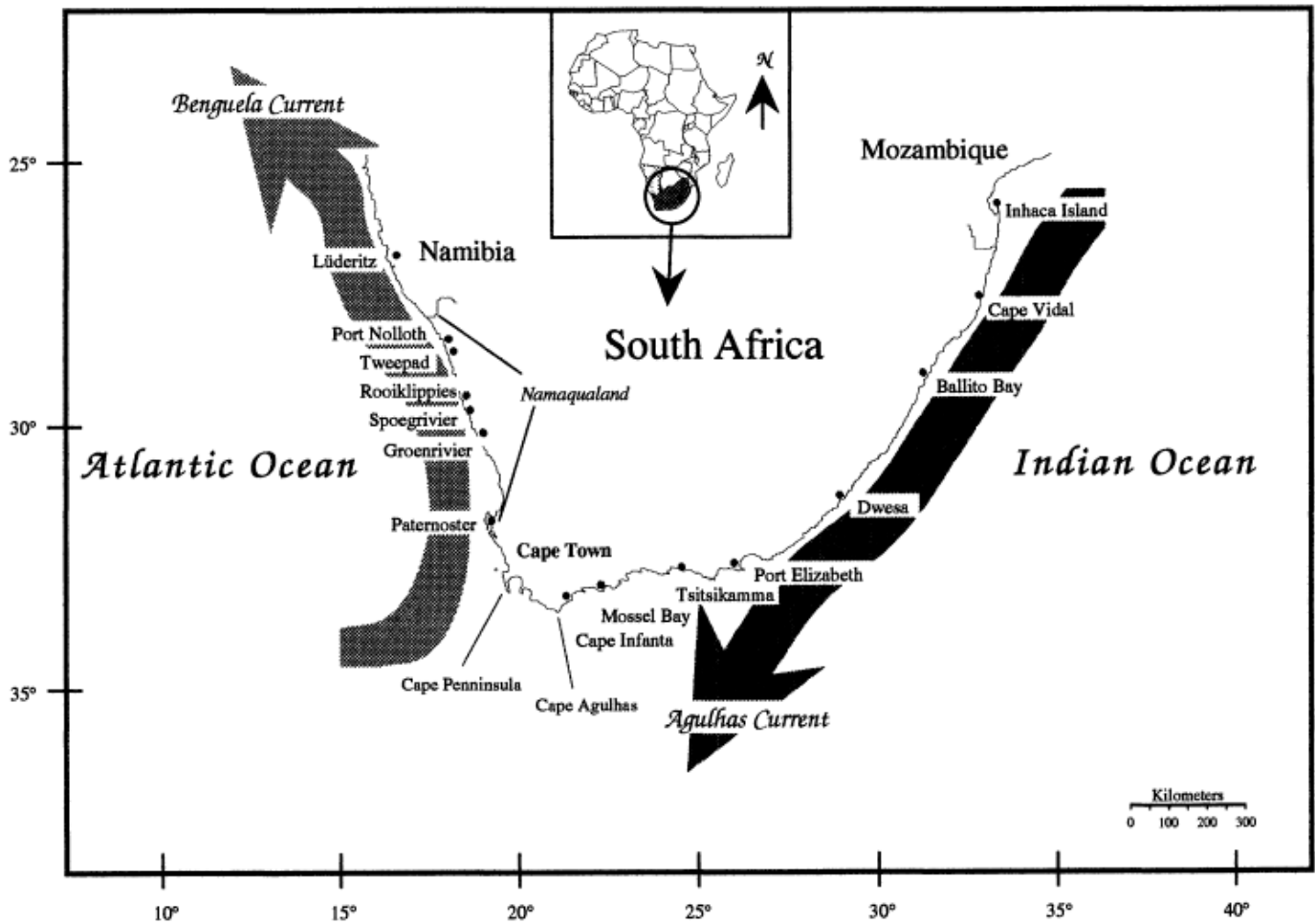


Fig. 1. The Southern African shoreline, south of 25°S, highlighting the southward flow of the Agulhas current in the south-west Indian Ocean (SWIO) (Bustamante and Branch, 1996).

2.2. Coral species selection

Despite some rock pools exhibiting a diversity of up to 10 coral species, abundances are often low, with sometimes only one representative of a species. Two species were however dominant in rock pools throughout most of the visited sites along the KZN coast. *Anomastrea irregularis* had the highest abundance and was the most common species in intertidal rock pools. *Pocillopora* were also common in rock pools, with lower abundances than *A. irregularis*.

Pocillopora includes some of the most widely distributed coral species, many of which occur at high latitudes, and form distinct geographic subspecies (Veron, 2000). Both *Pocillopora damicornis* and *Pocillopora verrucosa* were present in most rock pools, however *P. verrucosa* was chosen for this study as it was more abundant than *P. damicornis* at most intertidal sites.

This represented a branching species, while *A. irregularis* was chosen as massive coral. *A. irregularis* along the east coast of South Africa is relatively small, ranging from approximately 2-15cm in diameter. Smaller colonies tend to be flat, and become rounded as they increase in size. *A. irregularis* typically occurs in turbid environments, at the reef base or in intertidal pools (Veron, 2000), which explains their high abundance in the intertidal rock pools of KwaZulu-Natal.

2.3. Site selection

Site selection was predominantly based on availability of coral species and habitat type. Similarity of the rocky shore environment was important in order to reduce the effect of confounding factors. This includes the size of the intertidal area, degree of exposure to wave action (by the presence of a protective ledge), and the presence of isolated pools versus large gullies. To determine the effect of latitude on coral biology, five sites were chosen covering the coast of KZN (Fig. 2). The northern-most site was Jesser point at Sodwana Bay (27°S). Two central sites were chosen, Treasure Beach and Isipingo (29°S), and two southern sites including Park Rynie (30°S) and Munster (31°S). Within each site, rock pools of similar size and depth were chosen. Factors such as shading, light intensity and sedimentation were (as much as possible) kept constant between rock pools and between sites. Despite the predominance of *P. verrucosa* and *A. irregularis* in rock pools, the number of colonies present was still limiting at some sites. Site and rock pool choice was based on the availability of each species for sufficient replication.

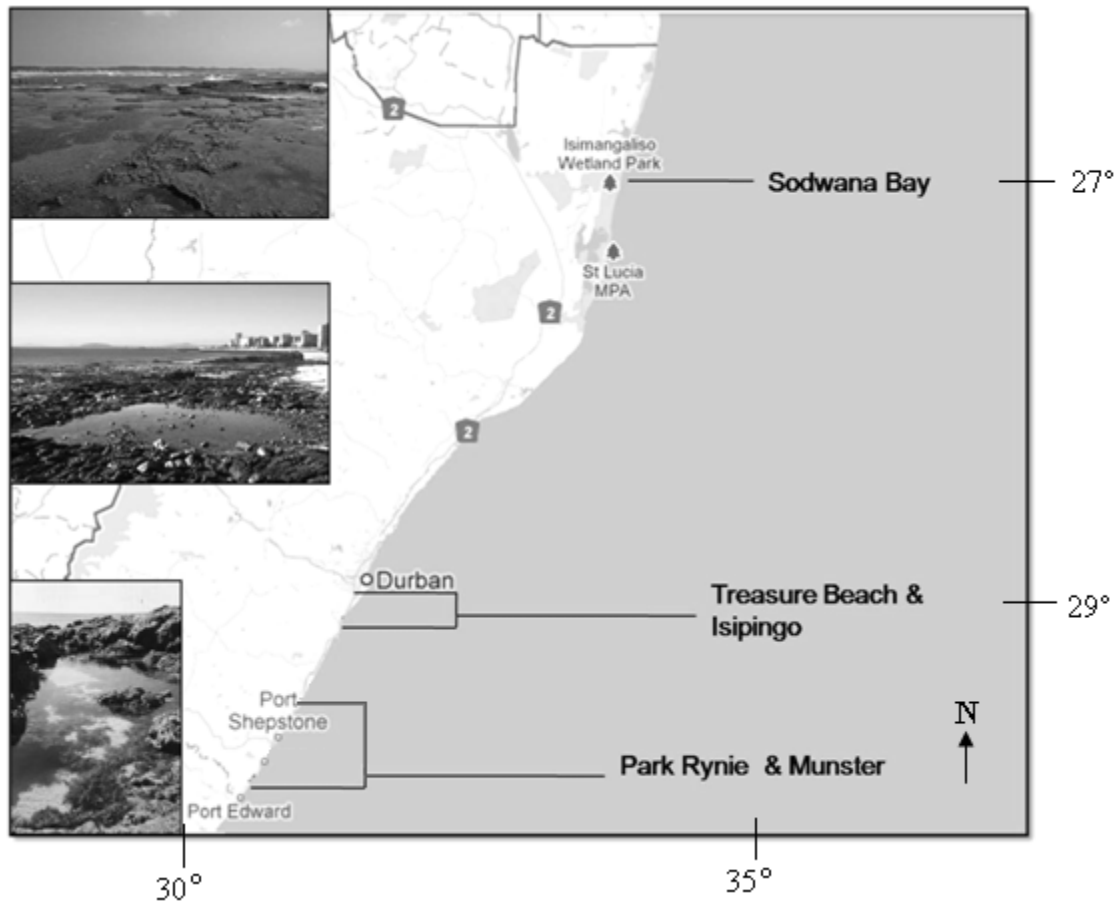


Fig. 2. The five sampling sites along the KwaZulu-Natal coastline.

2.4. Coral collection

Corals were collected from each of the five sites during spring (September-October 2012), summer (January-February 2013), autumn (April-May 2013) and winter (July-August 2013). Collection took place at spring low tide, usually 1-3 hours before and after peak low periods.

A baseline study was done to determine variation in zooxanthellae density and chlorophyll *a* between and within colonies of both species. From this it was established that three colonies of *A. irregularis* would be collected from each site. Colonies were removed from the substrate using a hammer and chisel. Depending on the size, each colony was further sub-sectioned into two equal pieces, each one constituting a replicate. Replicates ranged in size from 2-5cm in diameter. In order to avoid removing whole colonies of *P. verrucosa*, branches were sampled from individual colonies. Three branches (replicates) from three separate colonies were collected

from each site. Branches were removed using bone cutters, from the top or upper sides of the colony, and ranged in size from 5-30cm². All corals were collected and placed into individual pre-labeled plastic bags. Bags contained seawater from the collection site and were transported as soon as possible to the laboratory where they were frozen at -40°C.

2.5. Water temperature

Temperatures of individual rock pools were collected using small data loggers (ibutton from Maxim[®]). Two ibuttons were used at each site (Fig. 3). Park Rynie was excluded as it did not have isolated rock pools, and temperatures were therefore assumed to be similar to that of the surrounding sea surface temperature. Two rock pools of different size were chosen in order to reflect temperature differences due to size and depth of each pool. Individual ibuttons were sealed in a waterproof silicon casing and attached to the rocky substrate, out of sight of casual visitors, using waterproof epoxy putty, Aquamend[™]. The ibutton and casing were covered in the putty and set onto the rock surface. Attachment and hardening of the putty took approximately 5-10 minutes. Ibuttons were set to record temperatures every 30 minutes, and were replaced every 4-6 weeks. Once retrieved, data were captured via an adapter and daily temperature ranges were plotted for each season. Some ibuttons were lost in the field, and data were not retrieved for these periods. Not all sites are thus represented during each season.

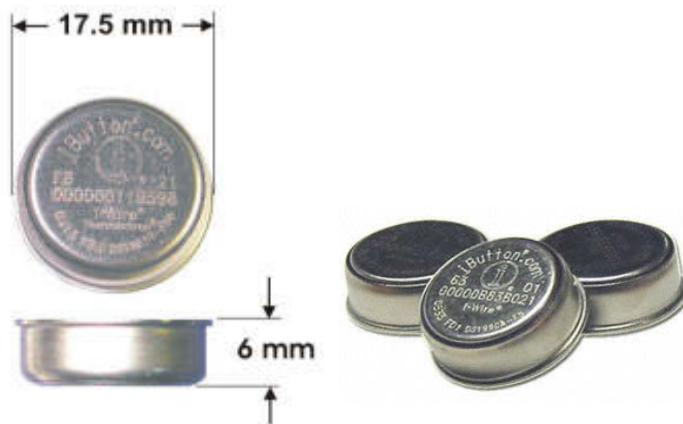


Fig 3. Dimensions and shape of the Maxim iButton used in this study, attached to the rocky substrate of the intertidal rock pools

2.6. Coral diversity survey

Little research has been conducted on the intertidal corals of KwaZulu-Natal. Some initial studies of genetic structure and diversity of *Acropora* spp. were conducted on the south coast of KwaZulu-Natal (Chiazzari *et al.*, 2013). The sexual reproduction of *Pocillopora damicornis* was also observed from two intertidal sites in KZN (Masse *et al.*, 2012). Despite this, very little is known regarding the diversity of corals that occur in these rock pools and their geographic distribution, let alone their tolerance to local environmental conditions. I therefore undertook a baseline survey of the coral taxa that occur along the KwaZulu-Natal coastline. At each site at least one colony of every coral species present was photographed using a Nikon underwater camera or a GoPro Hero3[®]. Corals were, where possible, identified to species level. Where this was not possible, due to the difficulties experienced during photograph capture and quality, they were identified to the highest resolution possible. Coral taxa were compared between sites to determine the distribution of intertidal corals.

2.7. Population size distribution

Coral size frequency distributions aim to represent the dynamic life history process of growth, recruitment, mortality and survivorship (Bak and Meesters, 1998). For this study, size frequency distributions of *P. verrucosa* and *A. irregularis* were constructed. A standard sampling time of 90 minutes around the spring low tide was set, ensuring a consistent sampling effort at each site. Sampling was done walking along the intertidal zone parallel to the shore, in order to avoid measuring the same coral twice. The height, length and width of all colonies of the two species were measured using calipers and an underwater slate. Only healthy corals were sampled, excluding those that had more than 50% bleaching or mortality, as partial mortality was not included in the analysis.

The geometric shape of the colony was determined to estimate the total surface area using the relevant geometric formula Bak and Meesters (1998). *P. verrucosa* was classified as a spheroid, and the surface area (cm²) was calculated using the following equation: $2(\pi \times r \times h)$, where r = radius and h = height. *A. irregularis* was classified as spherical segment using the following

equation: $2\pi r^2$, where r = radius. Total surface area was calculated and all colonies were grouped into 10 size classes. Colony size data were log transformed to become more normal and tested with a 1-sample Kolmogorov-Smirnov (KS) test. Bak and Meesters (1998) suggest that coral colonies increase in size as a power function, and size frequency distributions are therefore better modeled using log transformed size data (Bak and Meesters, 1998). Descriptive statistical parameters were applied to coral size data, including minimum, maximum and mean colony size, geometric mean and the upper 95% confidence interval (CI) of the mean. Coefficient of variation, skewness and kurtosis were applied to logged size distributions. Size frequency distributions were compared between sites and species.

2.8. Coral physiology

Tissue from the frozen corals was removed using an air-pik into 100ml filtered seawater (FSW). The tissue and FSW slurry was sieved through an 180 μ m nylon mesh and homogenised for 20s using an electrical Ultra-Turrax tissue homogeniser. The slurry was then sub-sampled for chlorophyll a analysis (15ml), total lipid analysis (50ml), and zooxanthellae density (10ml).

Sub-samples for zooxanthellae counts were fixed in 4% formalin and eight replicate counts were made using a haemocytometer and a light microscope at a 100 times magnification. Volumes of 1ml were extrapolated to 100ml (total replicate sample).

Sub-samples for chlorophyll a analysis were centrifuged at 4400 rpm for 5 minutes to pellet the algae. The supernatant was discarded and the algal pellet was resuspended in 10ml 99% acetone. Chlorophyll a was extracted in darkness at -20°C for 48 hours to break open the cells. Chlorophyll a and pheophytin absorbances were measured at 436nm and 405nm respectively using Turner Designs 10AU fluorometry and the standard equation (Jeffrey and Humphrey, 1975).

Lipids were extracted using a 2:1 (v/v) methanol: chloroform solution, following the procedure of Bligh and Dyer (1959). Subsamples were centrifuged at 4400rpm for 5 minutes. The supernatant was discarded. The pellet was resuspended in 6ml 1:2 (v/v) chloroform: methanol solution, and homogenised. 2ml of chloroform was added to the mixture and mixed well. Finally,

2ml of distilled water was added and mixed. The sample was then centrifuged at 1000 rpm for 10 minutes in order to separate the layers. The top layer was discarded leaving the organic bottom layer containing the extracted lipids. The lipid layer was collected using a pipette and collected in a pre-weighed tin foil weighing boat. Lipids were dried overnight, and weighed on a 4-digit mass balance. Lipids were represented in mg.

2.9. Coral surface area

Zooxanthellae density, chlorophyll a concentration and total lipid content were standardised to coral surface area (cm²). Surface area of *A. irregularis* was calculated using a geometric formula (see section “2.7. Population size distribution”). Coral surface area of *P. verrucosa* branches were measured using the paraffin-wax method (Stimson and Kinzie, 1991). Tissue-free branches were dipped in paraffin wax melted at 80°C in a water bath. The first wax coat eliminated the effect of porosity of the skeleton. Branches were dried for a constant time period and weighed. Corals were dipped for a second time and weighed again. Weight differences were used to estimate coral surface area using a wax weight to surface area calibration curve (Kisten 2013). The calibration curve was determined by comparing objects of known surface area to their respective wax weights (Kisten, 2013): coral surface area = (0.007- wax weight)/0.0158, $r^2 = 0.99$).

2.10. Stable Isotopes

Coral replicates from the summer and winter collections were used for isotope analysis. Frozen coral samples were air blasted to remove the tissue and collected in 100ml distilled water. The slurry was homogenised for 20s using a tissue homogeniser. The 100ml sample was subdivided into two equal parts. 50ml was used for the holobiont fraction (air blasted tissue) comprising the coral host cells and zooxanthellae combined. The remainder of the slurry was used for the host (coral tissue cells) and zooxanthellae fraction. This 50ml sub-sample was centrifuged three times at 3000 rpm for 10 minutes to separate the host component and zooxanthellae. The host fraction was checked under a microscope to ensure little or no contamination by zooxanthellae.

The zooxanthellae pellet was resuspended in distilled water. All three components were filtered through a vacuum pump on to a pre-combusted 0.45µm Whatmann GFF filter. Isotope analysis was performed on each of these components. Summer coral isotope analysis comprised only the holobiont fraction.

Samples were analysed for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ using an isotope ratio mass spectrometer, at the IsoEnvironmental laboratory at Rhodes University. Data were represented as a ratio according to the following equation: $\delta X = (R_{\text{sample}} : R_{\text{reference}} - 1) * 1000$, where R represents $\text{C}_{13}:\text{C}_{12}$ for carbon and $\text{N}_{15}:\text{N}_{14}$ for nitrogen (Peterson and Fry, 1987). Isotope ratios are expressed relative to Vienna PeeDee Belamnite (VPDB) and air for carbon and nitrogen respectively (Peterson and Fry, 1987).

2.11. Statistical analysis

The statistical packages IBM SPSS vol. 21 and Graphpad Prism 5 were used to analyse the data. A one-way Analysis of Variance (ANOVA) was used to compare significant differences in temperature. Data were not normally distributed despite log and square root transformations. A non-parametric Kruskal-Wallis test used to determine significant differences between site in autumn and winter. Where significant differences were found, Dunn's *post hoc* tests were carried out. A Mann-Whitney U test was used to compare summer temperature data between Munster and Isipingo.

Coral population size distributions were compared between sites and species using a 2-sample-KS Test. Similarity between size frequency distributions was calculated using a Spearman-rank correlation, and group means were compared with the Kruskal Wallis test as the data were not significantly normal. Descriptive statistical parameters were calculated in order to compare between site and season. This included mean, geometric mean, standard deviation, coefficient of variation, skewness and kurtosis.

In order to compare physiological parameters (zooxanthellae density, chlorophyll a and total lipid content) between sites and seasons, a two-way ANOVA was conducted. Site and season were factors in the model, with an interaction effect between site and season. Separate analyses were conducted for each coral species.

Isotope signatures were also compared using a two-way ANOVA, where site, season and an interaction effect were factors in the model. Standard plots were drawn for visual comparisons. P-values less than 0.05 were used for statistical comparisons of the null hypothesis.

Chapter 3: Results

3.1. Water temperature

Temperatures show large fluctuations over a short period of time with summer ranges much larger than that of winter (Figs. 4 & 5). Maximum temperature fluctuations reflect spring tides when exposure is longest. Highest temperatures occur during the day, especially at low tide when rock pools are isolated and exposed to the sun. Temperatures at low and high tide are cooler at night. During summer, temperatures at Munster and Isipingo occasionally experience a 10°C change over one tidal cycle throughout the day (Fig. 4). The lowest and highest recorded temperatures were 20°C and 32.5°C respectively. This is likely to occur at other sites too. In autumn, temperature fluctuations are still high (Figs. 4 & 5). Conversely, winter temperatures change by only 2-4.5°C throughout one tidal cycle (Fig. 4).

Munster and Sodwana Bay experience larger temperature fluctuations than Isipingo and Treasure Beach ($H = 402$ (autumn); 614.4 (winter); $p < 0.05$). Munster experiences the largest change in temperature in April, with a minimum and maximum of 17°C and 30°C respectively (Fig. 4). In winter, temperatures range from 17°C to 24.5°C across all sites (Fig. 5). Maximum temperatures at Munster are also higher than all other sites in autumn and winter, possibly throughout all seasons.

Mean and median temperature differences between sites are statistically significant (summer: $U = 270100$, $p < 0.0001$; autumn: $H = 402$, $p < 0.0001$; winter: $H = 614.4$, $p < 0.0001$), yet it is unlikely that these are biologically significant as differences are often less than 1°C. There are however significant differences overall between seasons ($H = 2993$; $p < 0.05$).

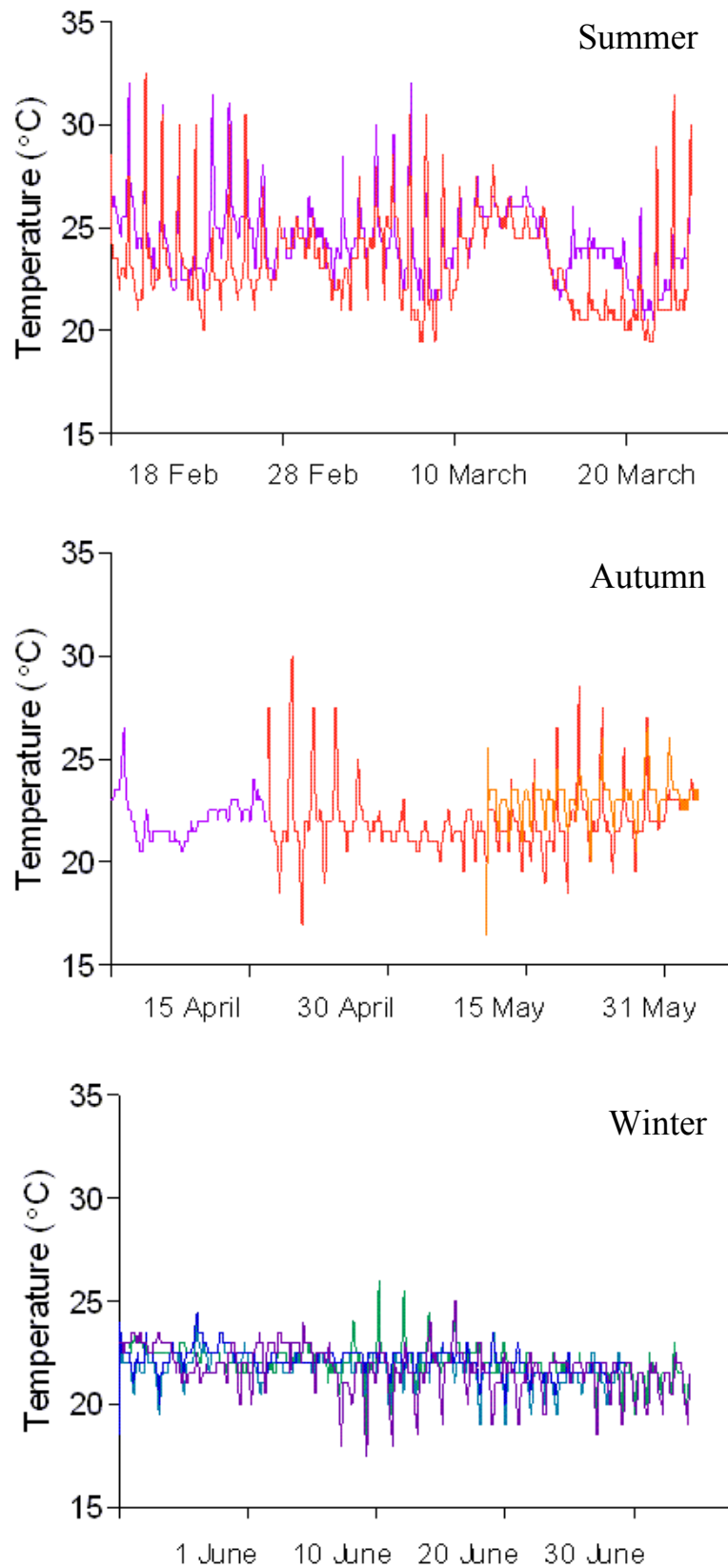


Fig. 4. Daily temperature range in the intertidal rock pools of KwaZulu-Natal, during summer [A; Munster (red), Isipingo (purple)], autumn [B; Munster (red), Isipingo (purple), Sodwana Bay (orange)] and winter [C; Munster (green), Isipingo (teal), Treasure Beach (blue), Sodwana Bay (purple)]. Temperatures were logged every 30minutes. Not all sites are represented for summer and autumn.

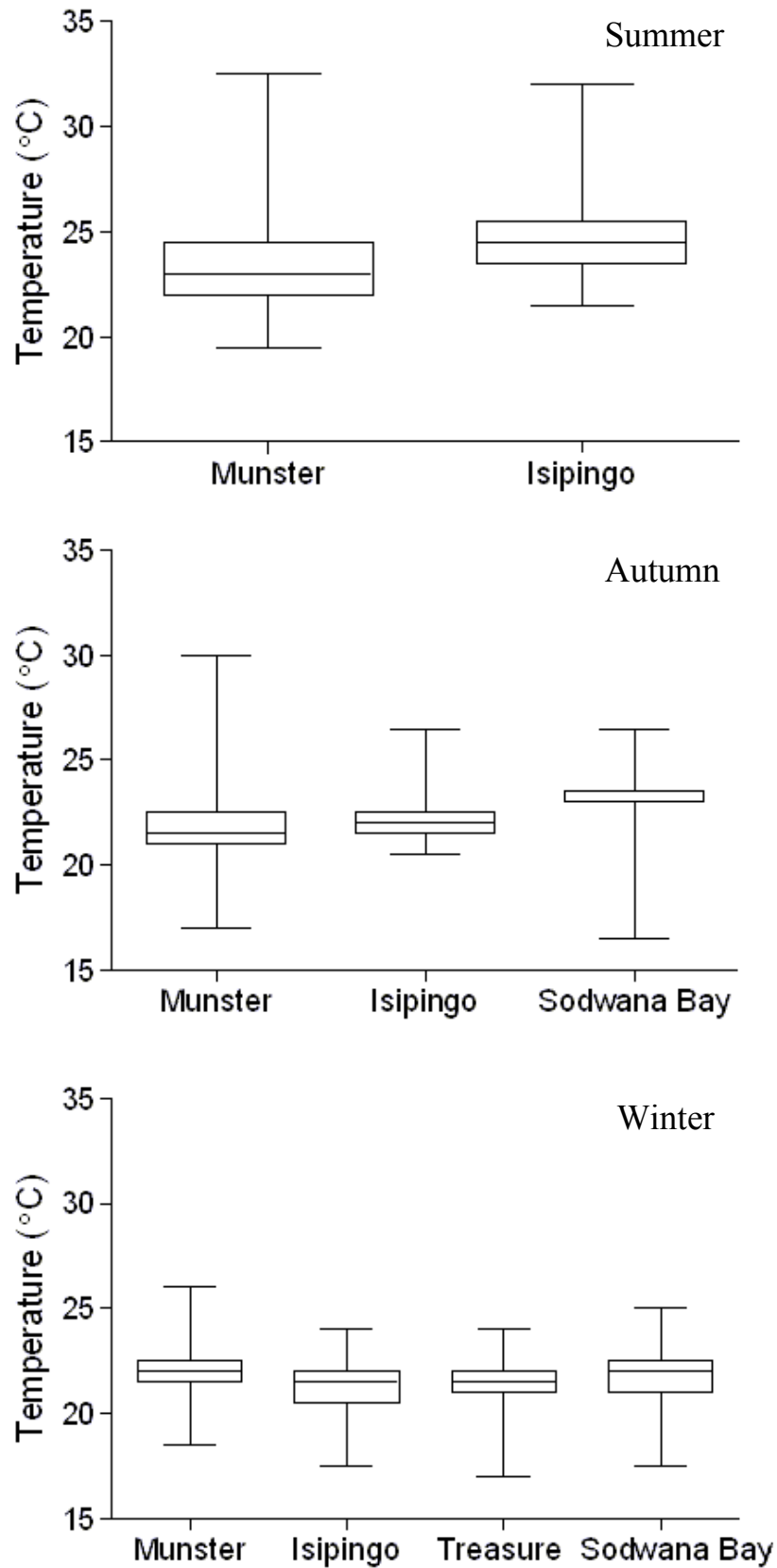


Fig. 5. Seasonal temperatures (median \pm min. & max.) of the intertidal rock pools at different sites along the KwaZulu-Natal coast.

3.2. Intertidal coral diversity

Eight scleractinian coral families are represented in the intertidal zone along the KwaZulu-Natal coast (Table 1). The highest diversity of coral taxa is found in the northern and central parts of the province, with Isipingo and Treasure Beach hosting an equal number of families and genera to the northern-most site, Sodwana Bay (Table 1). A sudden decline in coral diversity is observed at Munster, the southern-most site at latitude 31°S. Faviidae have the highest representation of coral genera and species, with Pocilloporidae and Mussidae showing the next highest diversity. Faviidae, Pocilloporidae, Mussidae and Siderastreidae exist at the southern range of the intertidal corals with all four families represented at Munster.

Table 1. Biodiversity of scleractinian corals in the intertidal rock pools of KwaZulu-Natal, at five sites. Species is unknown for those marked (a-h). (*) represents at least one observation of that group.

Family	Genus	Species	Sodwana Bay	Treasure Beach	Isipingo	Munster
Pocilloporidae	<i>Pocillopora</i>	<i>verrucosa</i>	*	*	*	*
		<i>damicornis</i>	*	*	*	
	<i>Stylophora</i>	<i>pistillata</i>		*		*
Acroporidae	<i>Acropora</i>	(b)	*	*	*	
		(c)		*	*	
Siderastreidae	<i>Anomastrea</i>	<i>Irregularis</i>	*	*	*	*
Agariciidae	<i>Pavona</i>	<i>venosa</i>	*	*	*	
Merulinidae	<i>Hydnophora</i>	(d)	*	*	*	
Mussidae	<i>Acanthastrea</i>	<i>echinata</i>	*	*	*	*
	<i>Blastomussa</i>	<i>merleti</i>			*	
Faviidae	<i>Favia</i>	<i>malthaii/pallida</i>			*	
		<i>speciosa</i>	*			*
	<i>Favites</i>	<i>pentagona</i>	*	*	*	*
	<i>Goniastrea</i>	(f)	*			
Poritidae	<i>Porites</i>	(g)	*	*	*	
Unidentified						
Mussidae			*	*		

3.3. Size frequency distributions

Size frequency distributions of non-transformed data are highly skewed to the right with a mean skewness of 2.045 and 2.286 for *P. verrucosa* and *A. irregularis* respectively (Table 2 & 3). Logarithmically transformed data showed distributions similar to a bell shape and improved normality, however *A. irregularis* at Isipingo and Sodwana Bay were the only sites that were statistically not significantly different from a normal distribution ($p = 0.1207$; $p = 0.3072$ respectively). *P. verrucosa* at Treasure Beach and Sodwana Bay showed a statistically significant normal distribution ($p = 0.0801$; $p = 0.2302$ respectively). All other sites were positively skewed (Table 2 & 3).

Population size distributions (log. transformed data) of *Pocillopora verrucosa* at Sodwana Bay had a significant correlation with those at Treasure Beach ($r_s = 0.704$, $p = 0.002$) and Isipingo ($r_s = 0.534$, $p = 0.033$). All other sites were not significantly similar. Size distributions of *Anomastrea irregularis* (log transformed data) at Munster were significantly correlated with Isipingo ($r_s = 0.476$, $p = 0.025$) and Sodwana Bay ($r_s = 0.539$, $p = 0.010$). All other sites were statistically not similar. Between species, there were no significant correlations in size frequency distributions at each site ($p > 0.05$).

The mean skewness of log transformed size frequency distributions of *P. verrucosa* and *A. irregularis* is 1.167 (± 0.401) and 1.154 (± 0.185) respectively. This suggests a larger representation of coral colonies in the smaller size classes. There was no significant relationship between skewness and geometric mean for *P. verrucosa* or *A. irregularis* (Fig. 10; $p = 0.4779$ & $p = 0.3298$, respectively).

Kurtosis of *P. verrucosa* is highly peaked compared to a normal distribution at Munster (Table 2), with Treasure Beach and Sodwana Bay showing more flattened distributions (Table 2). *A. irregularis* at Sodwana Bay also showed a more flattened distribution compared to the other sites (Table 3), with Isipingo also showing a negative kurtosis value (Table 3). Size distributions at all other sites showed positive kurtosis. The relationship between kurtosis and geometric mean was not statistically significant (Fig. 11; $p > 0.05$).

There appears to be a negative relationship between the coefficient of variation and geometric mean of *A. irregularis*, however again this was not statistically significant (Fig. 12; $p > 0.05$).

Sodwana Bay had the lowest coefficient of variation, a measure of variation of colony size, in both species (Table 2 & 3). Munster and Treasure beach had the highest coefficient of variation for *P. verrucosa* and *A. irregularis* respectively (Table 2 & 3).

Mean colony size of *P. verrucosa* was larger at Munster and Treasure Beach than at Isipingo ($F = 11.30$; $p < 0.0001$). The mean colony size of *P. verrucosa* at Isipingo was 66.72 ± 5.568 , which is a lot smaller than other sites (Table 2). This pattern is reflected in the geometric mean size of *P. verrucosa* (Fig. 8). There were also significant differences in the mean colony size of *A. irregularis* between sites ($F = 11.21$, $p < 0.0001$). Sodwana Bay had the largest colonies, followed by Munster and the Treasure Beach (Table 2). Similar to that of *P. verrucosa*, Isipingo had the smallest mean colony size of *A. irregularis*.

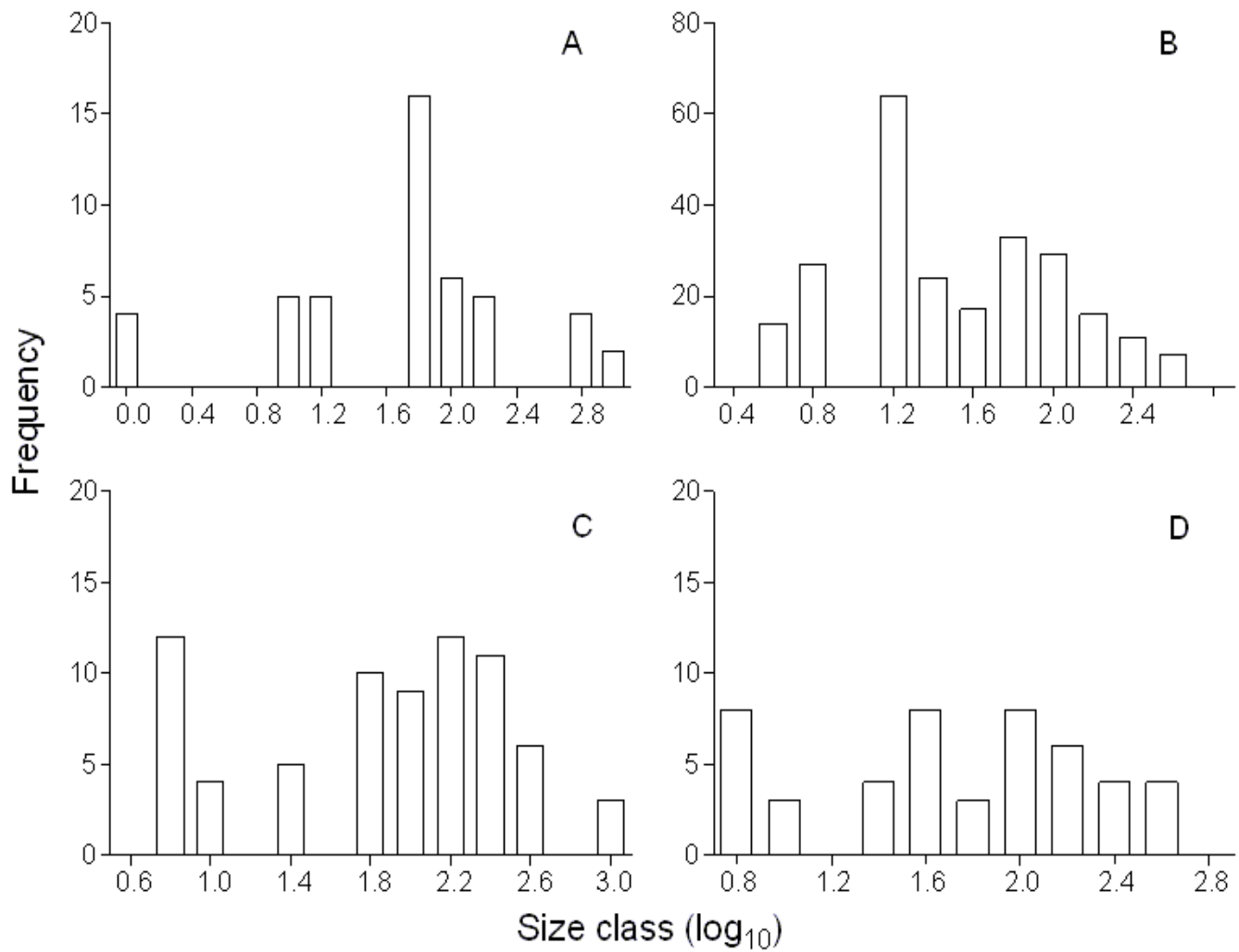


Fig. 6. Size frequency distributions (logarithmic scale) of *Pocillopora verrucosa* at four sites, Munster (A), Isipingo (B), Treasure Beach (C) and Sodwana Bay (D). Note different scales on the vertical (B) and horizontal axes (A-D). Values on the x-axis represent the median of the size class range.

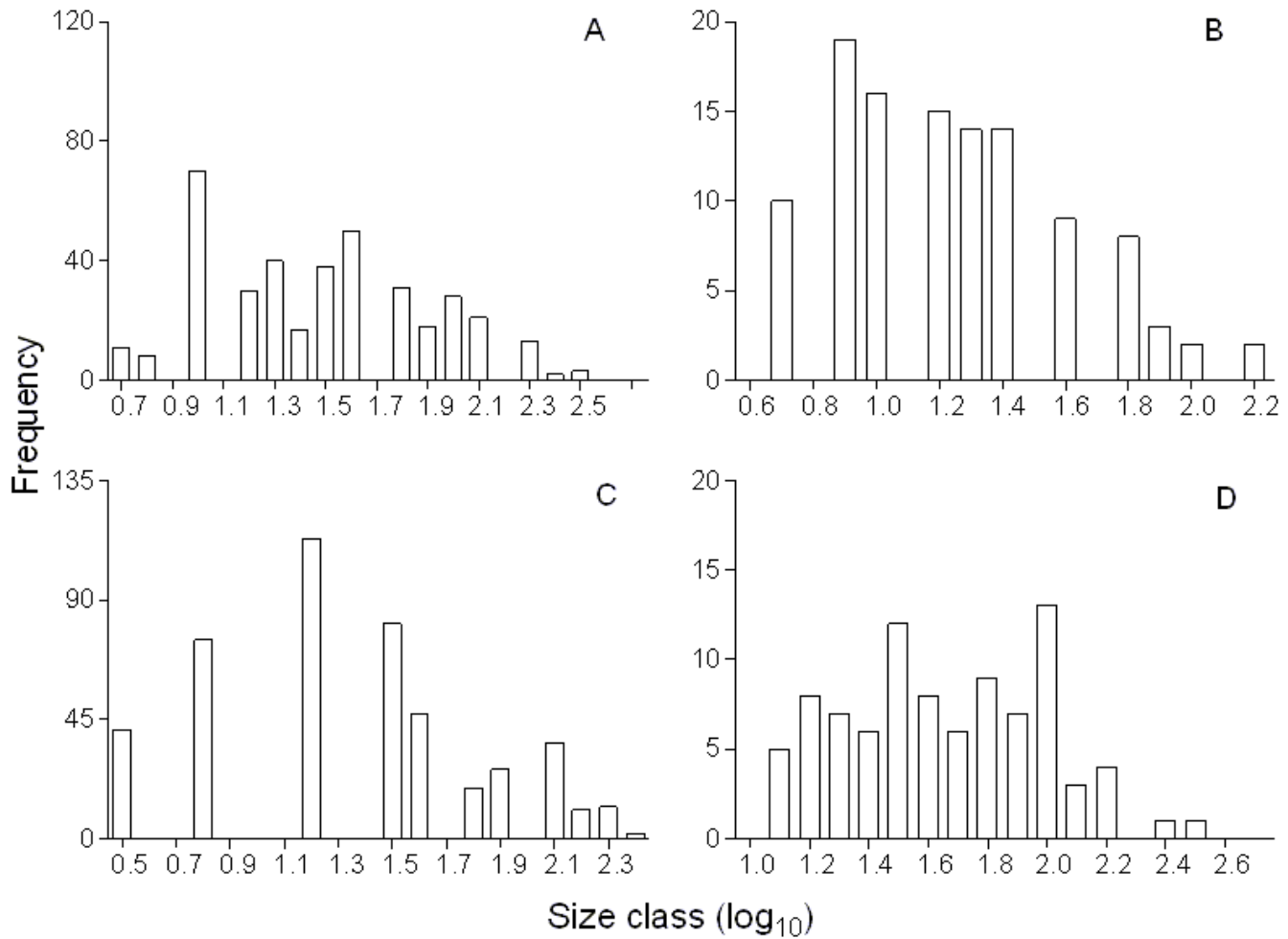


Fig. 7. Size frequency distributions (logarithmic scale) of *Anomastrea irregularis* at four sites, Munster (A), Isipingo (B), Treasure Beach (C) and Sodwana Bay (D). Note different scales on the vertical (A, C) and horizontal axes (A-D). Values on the x-axis represent the median of the size class range.

Table 2. Distribution parameters of linear (top) and logarithmically transformed (bottom) size data of *Pocillopora verrucosa* at each sampling site.

	Munster	Isipingo	Treasure Beach	Sodwana Bay
Linear scale				
N	47	242	72	48
Min	1.26	3.27	5.09	7.85
Max	942.5	395.8	848.2	417.8
Mean \pm SE	158 \pm 38.01	66.72 \pm 5.568	157.9 \pm 21.91	101 \pm 15.75
Geometric Mean	51.93	32.47	72.03	51.97
Upper 95% CI of mean	234.5	77.68	201.6	132.7
Skewness	1.939	2.718	1.339	1.78
Kurtosis	2.596	6.985	0.5441	2.182
Coefficient of variation (%)	185.88	231.44	150.37	177.50
log scale				
Min	0.09921	0.5142	0.7067	0.8951
Max	2.974	2.598	2.929	2.621
Skewness	2.138	1.515	0.4946	0.5204
Kurtosis	5.826	2.902	-1.48	-1.192
Coefficient of variation (%)	143.07	115.55	107.65	105.41

Table 3. Distribution parameters of linear (top) and logarithmically transformed (bottom) size data of *Anomastrea irregularis* at each sample site.

	Munster	Park Rynie	Isipingo	Treasure Beach	Sodwana Bay
Linear Scale					
N	380	174	112	463	90
Min	5.089	5.089	4.54	3.534	12.32
Max	353.4	127.2	157.1	226.2	344.1
Mean \pm SE	48.09 \pm 2.751	32.73 \pm 2.17	24.51 \pm 2.53	41.9 \pm 2.213	61.27 \pm 5.649
Geometric Mean	29.9	22.79	16.78	23.54	45.43
Upper 95% CI of mean	53.5	37.01	29.53	46.25	72.49
Skewness	1.648	2.405	2.619	1.836	1.89
Kurtosis	1.357	5.846	5.803	1.918	3.031
Coefficient of variation (%)	159.54	197.90	232.32	178.16	168.43
Log scale					
Min	0.7067	0.7067	0.657	0.5483	1.09
Max	2.548	2.105	2.196	2.354	2.537
Skewness	1.171	1.39	0.9054	1.684	0.6196
Kurtosis	1.005	0.8748	-0.7964	2.21	-0.7384
Coefficient of variation (%)	112.62	144.00	130.42	152.75	103.41

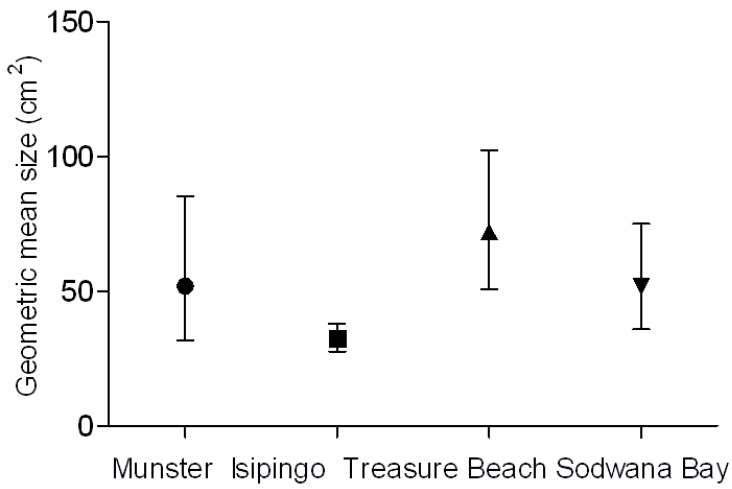


Fig. 8. Geometric mean size (cm²) of *Pocillopora verrucosa* at different sites.

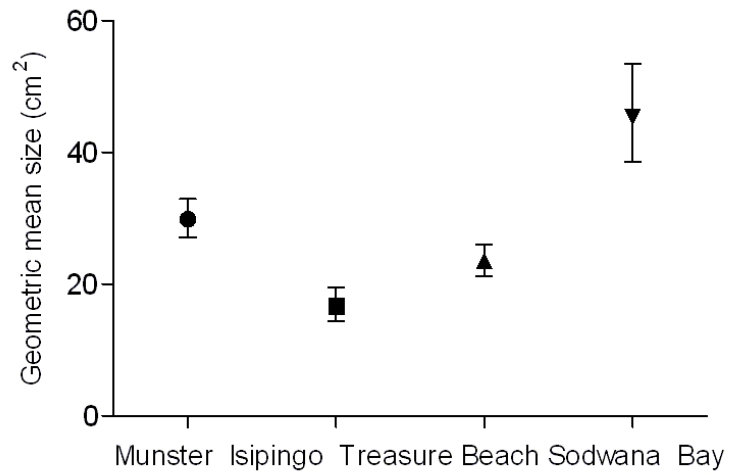


Fig. 9. Geometric mean size (cm²) of *Anomastrea irregularis* at different sites.

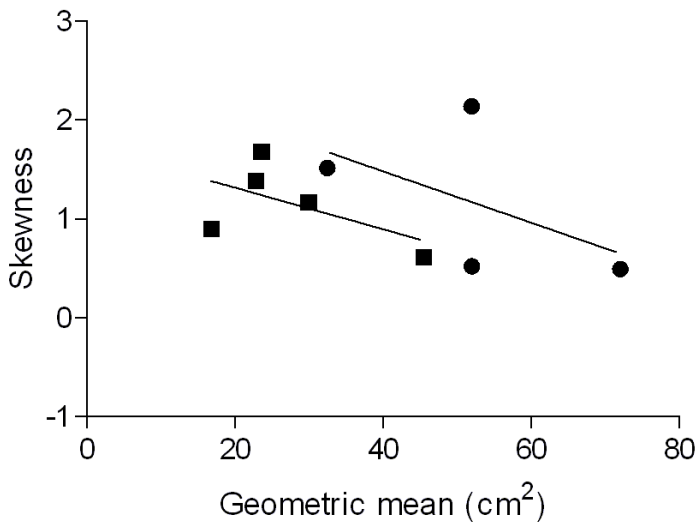


Fig. 10. Relationship between mean skewness (logarithmic scale) and Geometric mean (linear scale) of *Anomastrea irregularis* (squares) and *Pocillopora verrucosa* (circles).

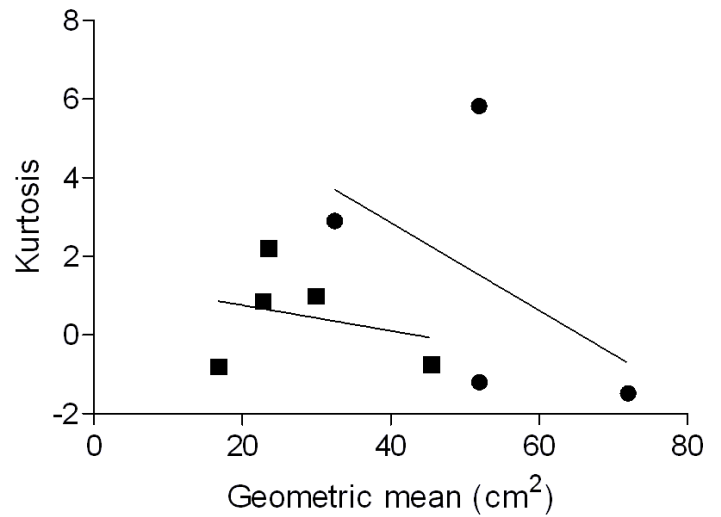


Fig. 11. Relationship between mean kurtosis (logarithmic scale) and Geometric mean (linear scale) of *Anomastrea irregularis* (squares) and *Pocillopora verrucosa* (circles).

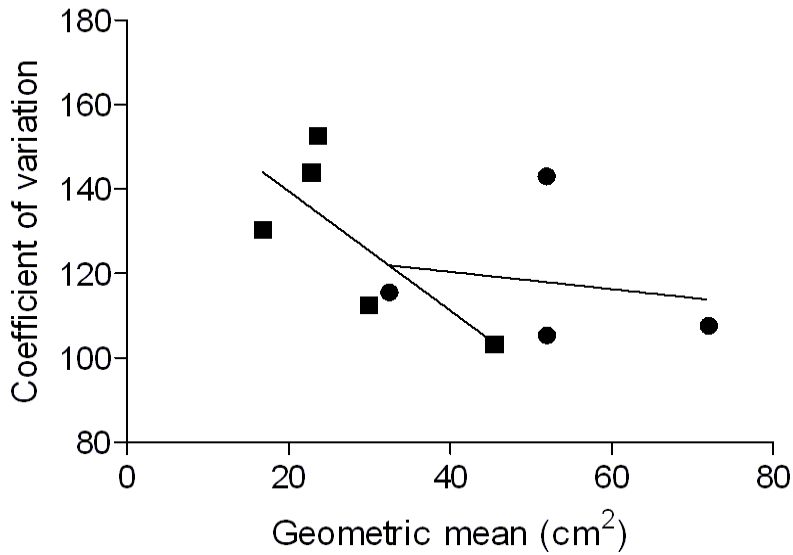


Fig. 12. Relationship between coefficient of variation (logarithmic scale) and Geometric mean (linear scale) of *Anomastrea irregularis* (squares) and *Pocillopora verrucosa* (circles).

3.4. Physiology: Effect of site, season and species

Colonies of *P. verrucosa* showed significant differences in all parameters between season, site and season x site, except between season x site of chlorophyll a (Table 4). *Post hoc* tests showed that zooxanthellae densities are significantly higher in summer than all other seasons. Significant differences in zooxanthellae density at Munster and Isipingo accounted for this (Fig. 13B). Zooxanthellae density was lowest during at all sites.

Site and season were significant factors for chlorophyll a in *P. verrucosa* (Table 4). We suspect that chlorophyll a levels are exaggerated in winter and spring due to technical difficulties with the fluorometer; however trends among season and species remain valid.

There is a significant decrease in chlorophyll a from summer to autumn. *Post hoc* tests showed that Munster and Isipingo mainly contribute to this. There is a significant increase in chlorophyll a from autumn to winter (Fig. 14), and *post hoc* tests showed that this was consistent at all sites.

Similar trends are observed for chlorophyll a per zooxanthella however differences between sites are not as strong (Fig. 15B). Site, season and season x site were significant. *Post hoc* tests showed that only Treasure Beach and Sodwana Bay slightly contributed to the change in chlorophyll a per zooxanthella from summer to autumn. All sites showed a significant increase from autumn to winter, with Isipingo and Treasure Beach decreasing their pigments per zooxanthellae from winter to spring (Fig. 15B).

Total lipid content of *Pocillopora verrucosa* showed similar patterns to zooxanthellae density, with a significant difference between sites and season (Table 4). Summer values are significantly higher than that of autumn, winter and spring, with *post hoc* tests showing that Munster and Treasure Beach account for these differences (Fig. 16 B). Munster showed a significantly higher total lipid content compared to both Isipingo and Sodwana Bay ($F = 7.373$, $p < 0.0001$). Lipid content is lowest during spring at all sites (Fig. 16B).

Table 4. Summary statistics of the two-way ANOVA comparing the mean \pm SD between site (Munster, Isipingo, Treasure Beach & Sodwana Bay) and season (summer & winter) of zooxanthellae density, chl. a, chl. a/zooxanthella & lipids of *P. verrucosa* and *A. irregularis*. p-values less than 0.05 show significant differences.

Parameter	<i>Pocillopora verrucosa</i>			<i>Anomastrea irregularis</i>		
	df	F	P	df	F	P
Zooxanthellae density						
Season	3	12.15	<0.0001	3	3.235	0.0256
Site	3	20.33	<0.0001	4	0.5437	0.7040
Season x Site	9	3.362	0.001	12	3.163	0.0008
Chl a						
Season	3	35.85	<0.0001	3	146.2	<0.0001
Site	3	8.936	<0.0001	3	6.655	0.0005
Season x Site	9	1.194	0.3048	9	3.348	0.0016
Chla/zooxanthellae						
Season	3	77.06	<0.0001	3	96.06	<0.0001
Site	3	2.718	0.0474	3	4.176	0.0084
Season x Site	9	3.673	0.0004	9	1.908	0.0624
Lipids						
Season	3	28.93	<0.0001	3	6.489	0.0006
Site	3	4.752	0.0036	3	6.909	0.0004
Season x Site	9	4.006	0.0002	9	2.915	0.0051

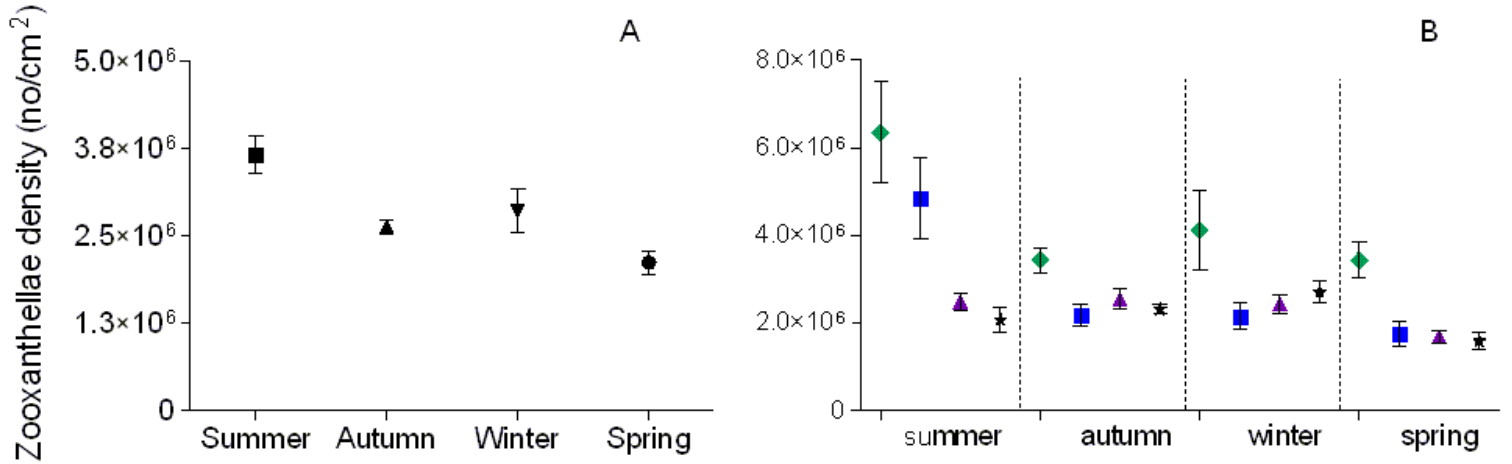


Fig. 13. (A) Zooxanthellae density (mean of all sites ± SD) of *Pocillopora verrucosa* from summer to spring 2013. (B) Zooxanthellae density at each site during each season; Munster (green diamond), Isipingo (blue square), Treasure Beach (purple triangle) and Sodwana Bay (black star).

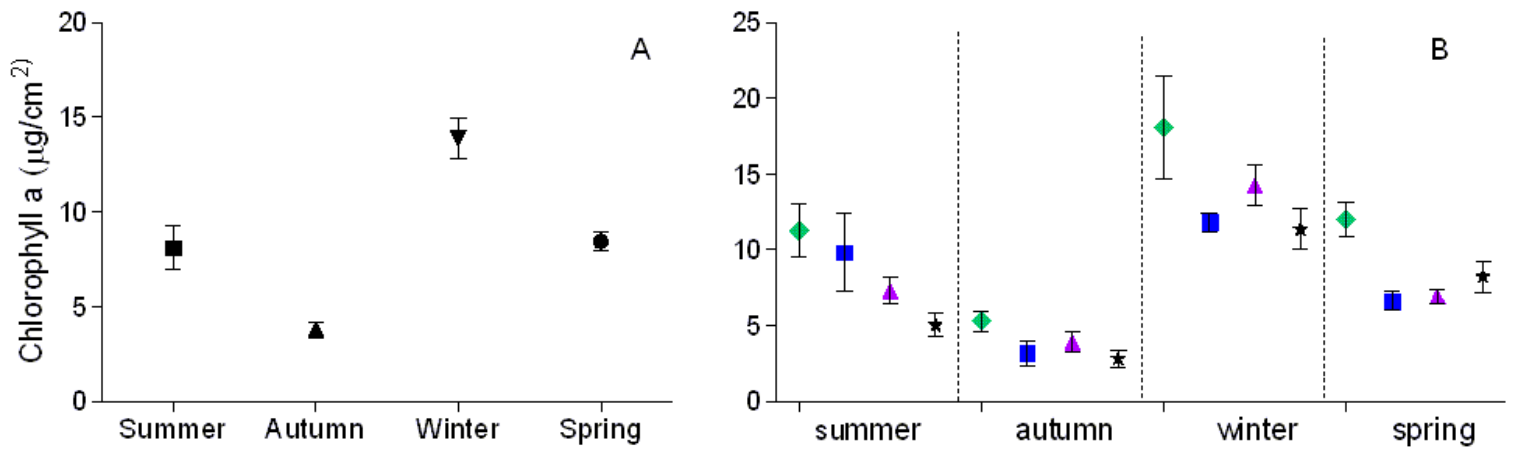


Fig. 14. (A) Chlorophyll a (Mean of all sites ± SD) of *Pocillopora verrucosa* from summer to spring 2013. (B) Chlorophyll a of each site during each season; Munster (green diamond), Isipingo (blue square), Treasure Beach (purple triangle) and Sodwana Bay (black star).

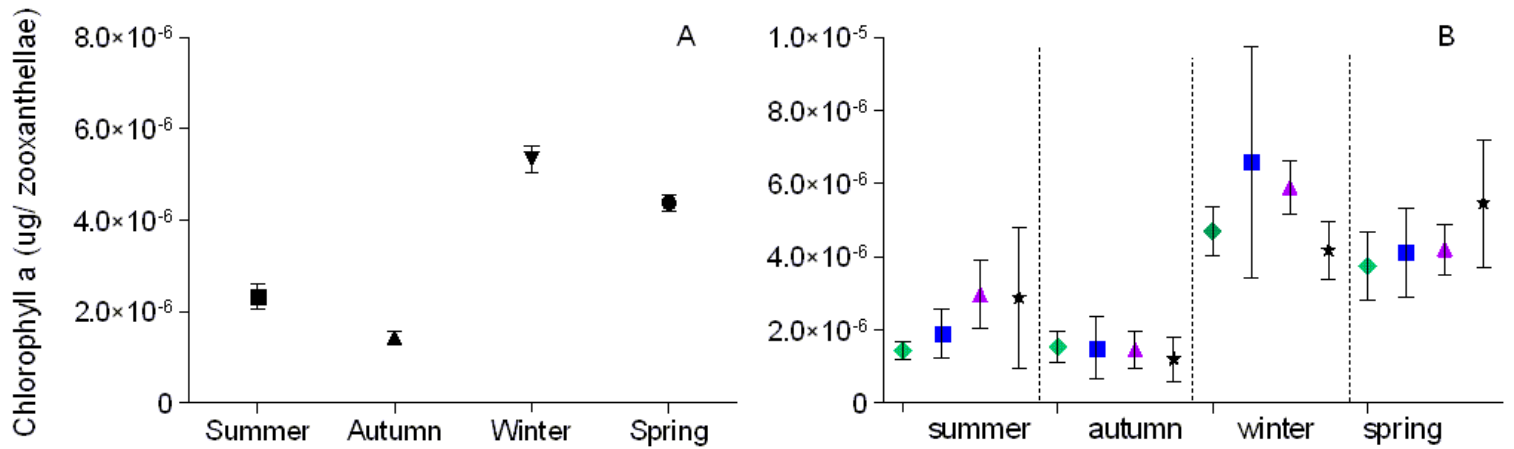


Fig. 15. (A) Chlorophyll a per zooxanthella (Mean of all sites \pm SD) of *Pocillopora verrucosa* from summer to spring 2013. (B) Chlorophyll a per zooxanthella of each site during each season; Munster (green diamond), Isipingo (blue square), Treasure Beach (purple triangle) and Sodwana Bay (black star).

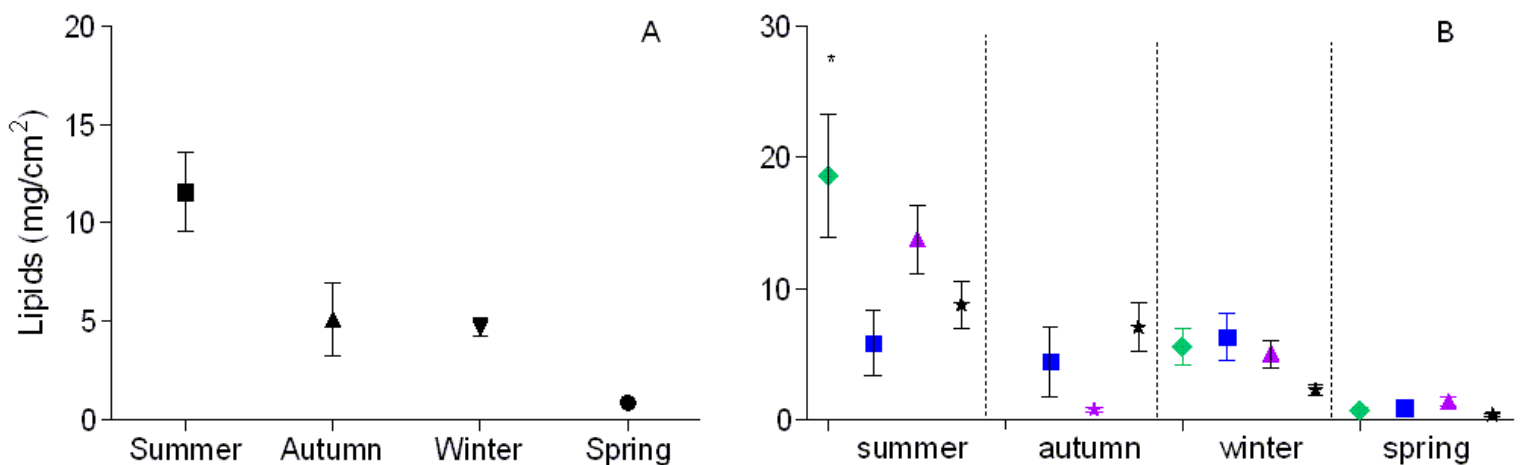


Fig. 16. (A) Total lipid content (mean of all sites \pm SD) of *Pocillopora verrucosa* from summer to spring 2013. (B) Total lipid content of each site during each season; Munster (green diamond), Isipingo (blue square), Treasure Beach (purple triangle) and Sodwana Bay (black star).

Zooxanthellae density of *Anomastrea irregularis* shows significant differences between seasons, but not sites (Table 4). Season x site is also significant (Table 4). There are however no clear patterns in zooxanthellae density among sites and seasons (Fig. 17B).

Significant differences are observed between site, season and season x site for chlorophyll a in *A. irregularis* (Table 4). There were no significant changes in chlorophyll a from summer to autumn. There is a significant increase in chlorophyll a from autumn to winter (Fig. 18). This increase is substantially larger than that of *P. verrucosa* (Figs. 14 & 18). *Post hoc* tests then showed that all sites except Munster had less chlorophyll a in spring than in winter (Fig. 18B).

There were no significant differences in chlorophyll a per zooxanthella among sites from summer to autumn. Significant increases were observed from autumn to winter at all sites (Fig. 19A). *Post hoc* tests showed that corals only at Treasure Beach and Sodwana Bay had less chlorophyll a per zooxanthella in spring than in winter (Fig. 19B).

The main trends in chlorophyll a and chlorophyll a/ zooxanthellae were an increase from autumn to winter.

Lipids show a significant difference between site, season and interaction effect (Table 4). Total lipid content in *A. irregularis* is significantly higher in summer than spring (Fig. 20 A; Table 4). *Post hoc* tests showed that seasonal differences in total lipid content are explained by corals at Isipingo and Sodwana Bay. Corals at Sodwana Bay have significantly higher lipid content in summer than winter and spring. Lipid content of corals at Isipingo is significantly higher in winter than all other seasons (Fig. 20 B). It is also noted that seasonal changes in total lipid content are much more pronounced in *Pocillopora verrucosa* compared to *A. irregularis* (Figs. 16 & 20).

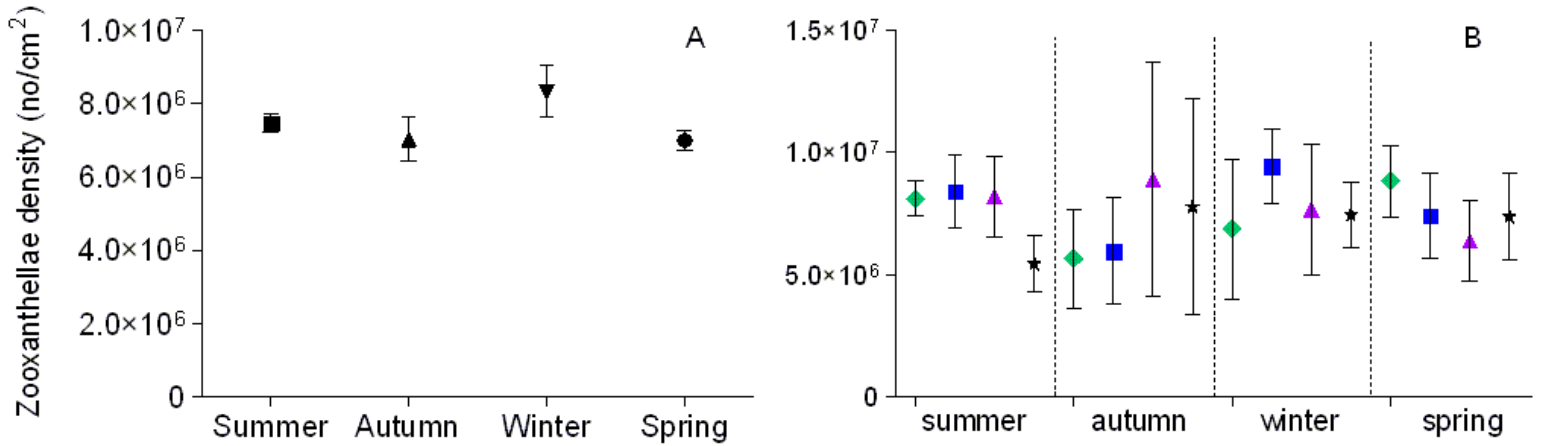


Fig. 17. (A) Zooxanthellae density (mean of all sites \pm SD) of *Anomastrea irregularis* from summer to spring 2013. (B) Zooxanthellae density at each site during each season; Munster (green diamond), Isipingo (blue square), Treasure Beach (purple triangle) and Sodwana Bay (black star).

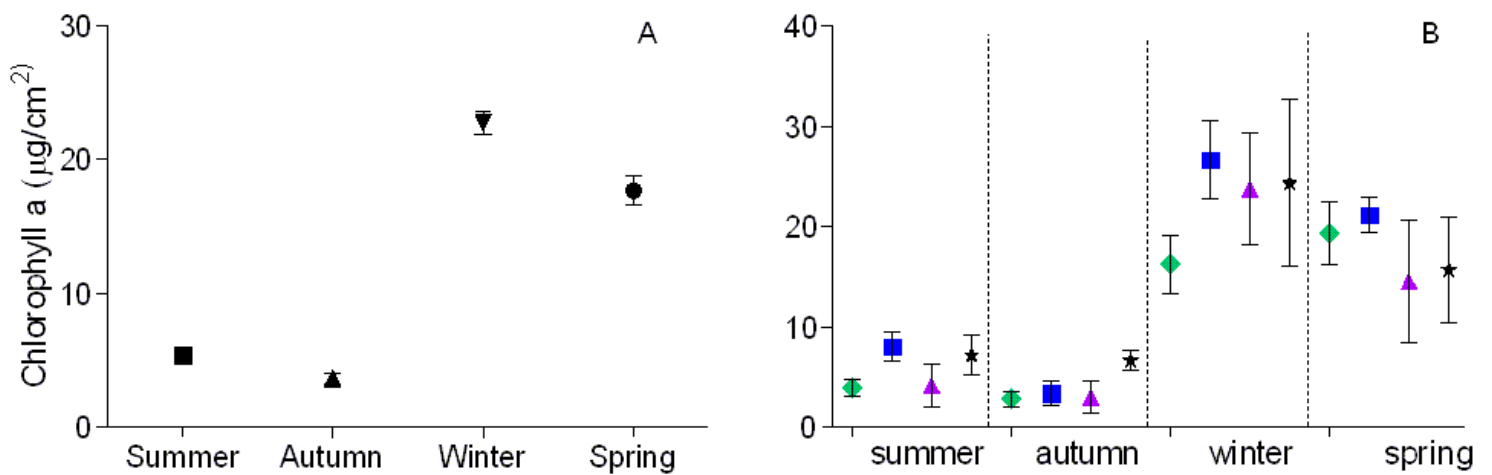


Fig. 18. (A) Chlorophyll a (Mean of all sites \pm SD) of *Anomastrea irregularis* from summer to spring 2013. (B) Chlorophyll a of each site during each season; Munster (green diamond), Isipingo (blue square), Treasure Beach (purple triangle) and Sodwana Bay (black star).

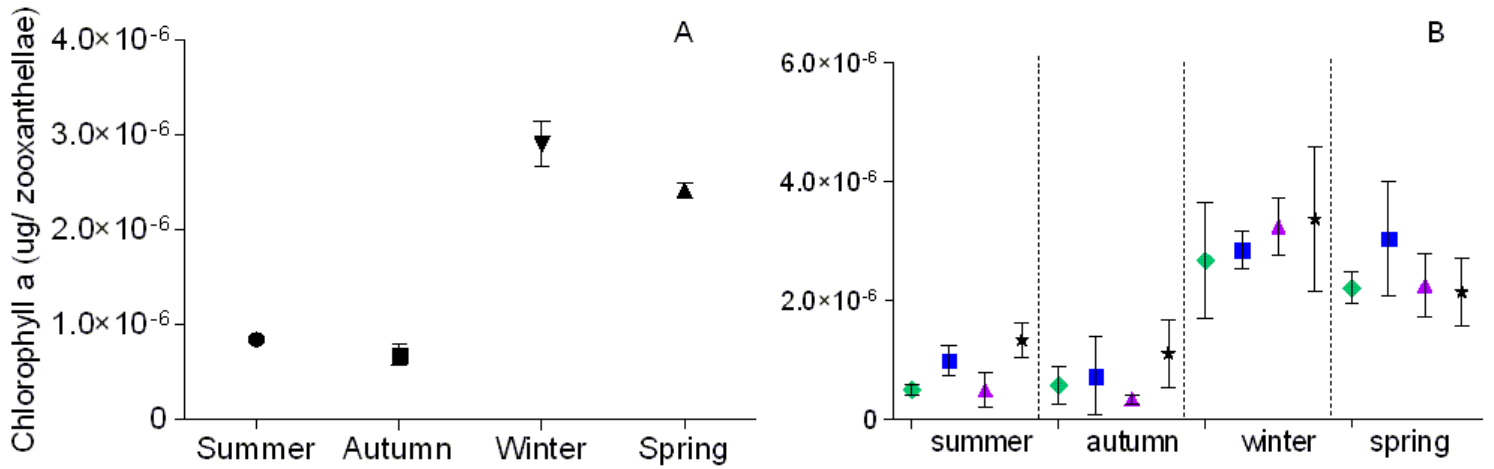


Fig. 19. (A) Chlorophyll a per zooxanthella (Mean of all sites \pm SD) of *Anomastrea irregularis* from summer to spring 2013. (B) Chlorophyll a per zooxanthella of each site during each season; Munster (green diamond), Isipingo (blue square), Treasure Beach (purple triangle) and Sodwana Bay (black star).

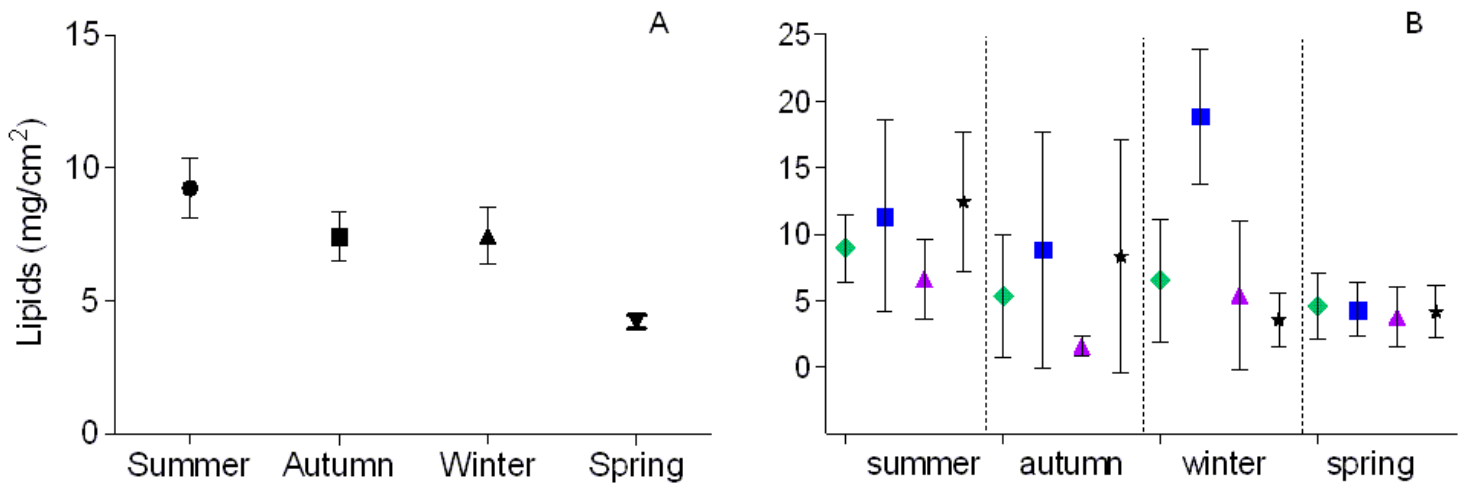


Fig. 20. (A) Total lipid content (mean of all sites \pm SD) of *Anomastrea irregularis* from summer to spring 2013. (B) Total lipid content of each site during each season; Munster (green diamond), Isipingo (blue square), Treasure Beach (purple triangle) and Sodwana Bay (black star).

3.5. Stable Isotopes

Some significant differences in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ between summer and winter occur in *P. verrucosa* and *A. irregularis* (Table 5). A significant depletion of $\delta^{13}\text{C}$ in winter was observed in *Pocillopora verrucosa* at Sodwana Bay (Fig. 21). Tukey *post hoc* tests showed that $\delta^{13}\text{C}$ of corals at Munster are significantly depleted in comparison to all other sites, and winter $\delta^{13}\text{C}$ of corals at Sodwana Bay are significantly depleted in comparison to those at Isipingo and Treasure Beach.

No significant within site differences of $\delta^{13}\text{C}$ were observed between seasons in *Anomastrea irregularis* (Table 5). *Post hoc* tests showed that Sodwana Bay was significantly depleted in comparison to all other sites (Fig. 21B).

Similar trends were observed in $\delta^{15}\text{N}$ signatures with both coral species at Sodwana Bay depleted compared to all other sites (Fig. 22). *Post hoc* tests showed *P. verrucosa* at Munster and Sodwana Bay depleted in $\delta^{15}\text{N}$ compared to Isipingo and Treasure Beach (Fig. 22A). Corals at Sodwana Bay are however significantly more depleted than those at Munster (Fig. 22A).

Differences in site, season and site x season were all statistically significant for *A. irregularis* (Table 5). A significant depletion of $\delta^{15}\text{N}$ in summer was observed at Munster and Treasure Beach (Fig. 22B). In winter, *post hoc* tests showed Treasure Beach corals to have the highest enrichment in $\delta^{15}\text{N}$, and *A. irregularis* at Sodwana Bay to be the most depleted (Fig. 22B).

Table 5. Comparisons of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures between site and season of *P. verrucosa* and *A. irregularis*. P-values less than 0.05 show significant differences.

Parameter	Carbon			Nitrogen		
	df	F	P	df	F	P
<i>Pocillopora verrucosa</i>						
Site	3	42.90	<0.0001	3	131.8	<0.0001
Season	1	7.832	0.0129	1	0.6126	0.4452
Site x Season	3	6.320	0.0049	3	1.520	0.2477
<i>Anomastrea irregularis</i>						
Site	3	47.82	<0.0001	3	95.76	<0.0001
Season	1	1.536	0.2342	1	14.00	0.0018
Site x Season	3	5.948	0.0070	3	13.24	0.0001



Fig. 21. $\delta^{13}\text{C}$ (mean \pm SD) signatures of the coral holobiont in summer (striped) and winter (white) of *Pocillopora verrucosa* (A) and *Anomastrea irregularis* (B). Letters above the bars show statistical groupings.

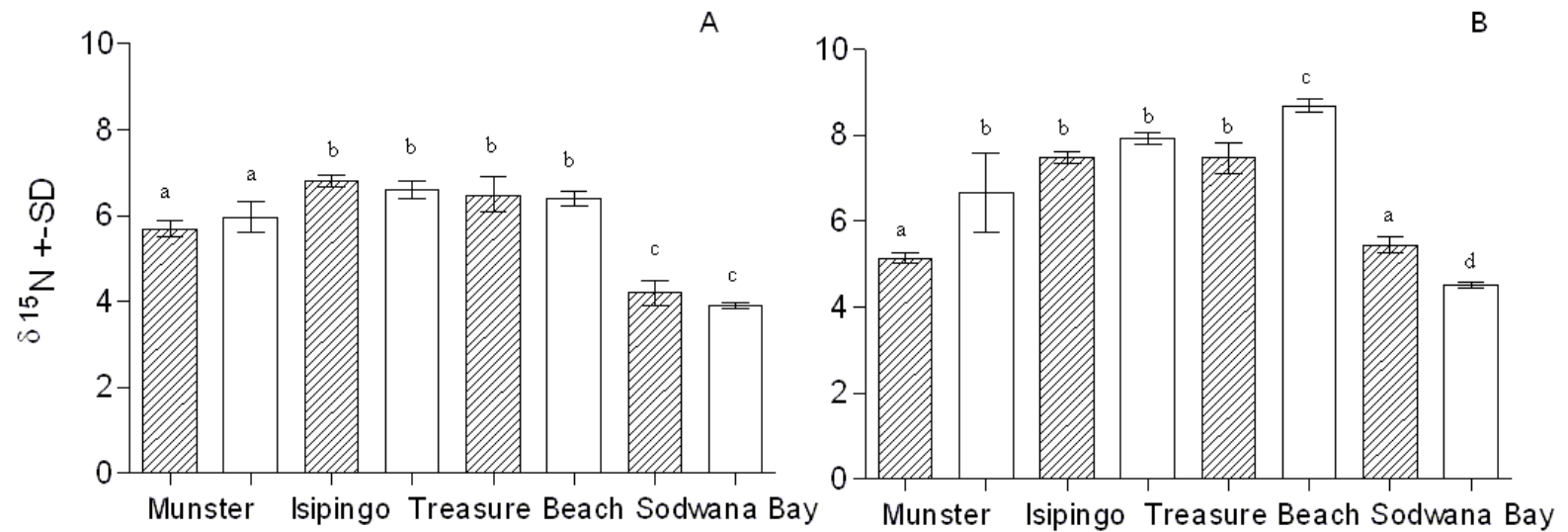


Fig. 22. $\delta^{15}\text{N}$ (mean \pm SD) signatures of the coral holobiont in summer (striped) and winter (white) of *Pocillopora verrucosa* (A) and *Anomastrea irregularis* (B). Letters above the bars show statistical groupings.

Significant differences in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ occur in *P. verrucosa* and *A. irregularis* between site and parameter (Table 6). Site x parameter is not significant for $\delta^{13}\text{C}$ in both coral species (Table 6). Site is a significant factor in both species for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (Table 6).

Post hoc tests showed that *P. verrucosa* (holobiont, host cells and zooxanthellae) is significantly depleted in $\delta^{13}\text{C}$ at Munster and Sodwana Bay to those at Isipingo and Treasure Beach. Host cells were significantly depleted in $\delta^{13}\text{C}$ compared to zooxanthellae in *P. verrucosa* at Isipingo and Sodwana Bay (Fig. 23).

Post hoc tests showed a similar pattern in *A. irregularis* (holobiont, host cells and zooxanthellae), where Sodwana Bay is significantly depleted in $\delta^{13}\text{C}$ compared to other sites (Fig. 24). Significant depletion of host cell $\delta^{13}\text{C}$ was observed in *A. irregularis* only at Treasure Beach (Fig. 24).

P. verrucosa is also more depleted in $\delta^{15}\text{N}$ at Sodwana Bay compared to the other sites (Fig. 23). *Post hoc* tests showed that zooxanthellae of *P. verrucosa* were significantly depleted in $\delta^{15}\text{N}$ compared to host cells at Munster and Isipingo.

Corals of *A. irregularis* (holobiont, host cells and zooxanthellae) were slightly depleted in $\delta^{15}\text{N}$ at Sodwana Bay and slightly at Munster, than those at Isipingo and Treasure Beach. $\delta^{15}\text{N}$ depletion of zooxanthellae to host cells was statistically significant at all sites in *A. irregularis* (Fig. 24).

Table 6. Comparisons of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures between site (Munster, Isipingo, Treasure Beach & Sodwana Bay) and parameter (holobiont, host cells, zooxanthellae) of *P. verrucosa* and *A. irregularis* in winter. P-values less than 0.05 show significant differences.

Parameter	Carbon			Nitrogen		
	df	F	P	df	F	P
<i>Pocillopora verrucosa</i>						
Site	3	143.9	< 0.0001	3	59.27	< 0.0001
Parameter	2	10.75	0.0005	2	17.85	< 0.0001
Site x Parameter	6	0.3855	0.8810	6	3.502	0.0125
<i>Anomastrea irregularis</i>						
Site	3	1666	< 0.0001	3	390.3	< 0.0001
Parameter	2	17.40	< 0.0001	2	102.9	< 0.0001
Site x Parameter	6	1.988	0.1071	6	4.226	0.0048

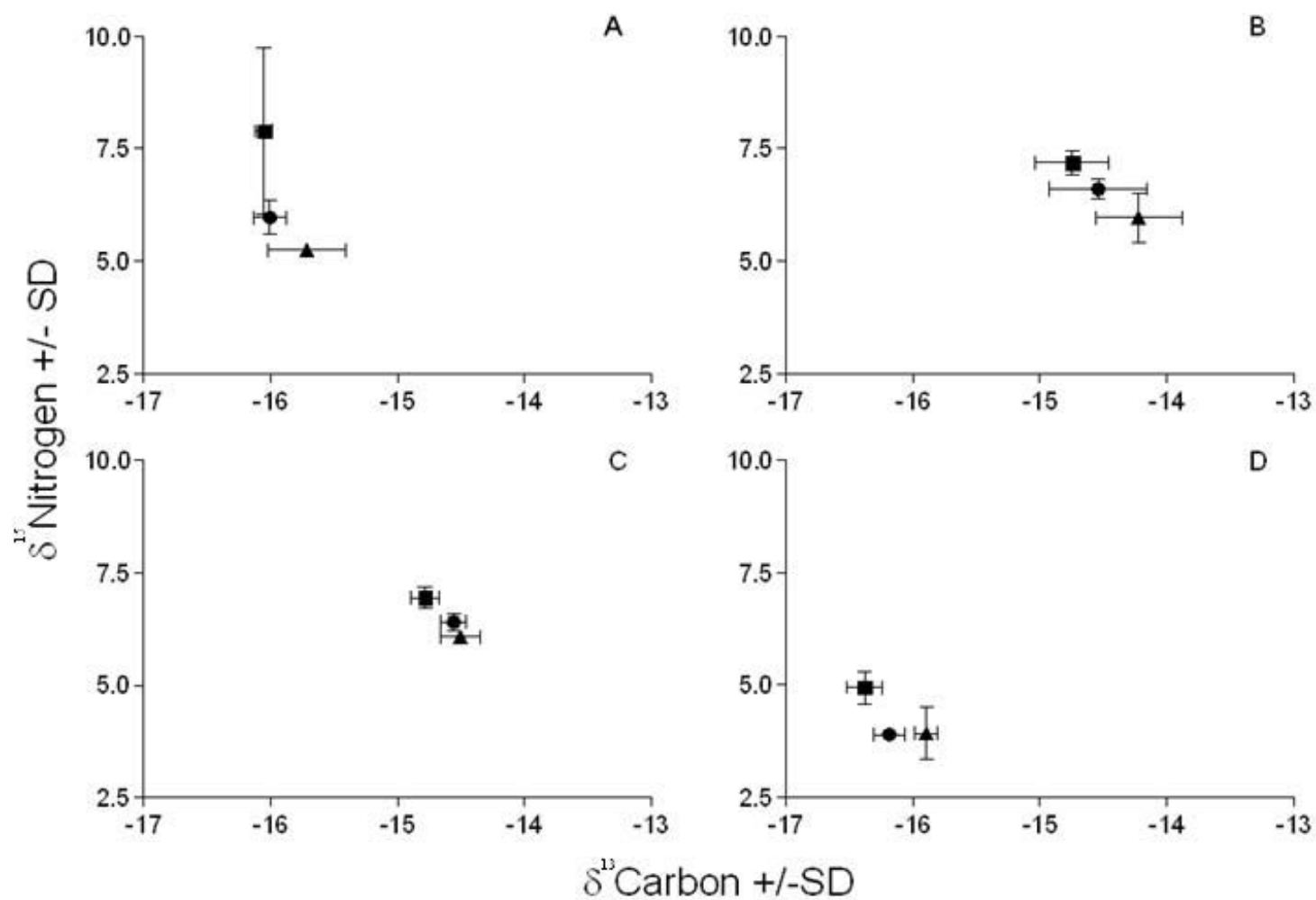


Fig. 23. Winter $\delta^{13}\text{C}$ vs. $\delta^{15}\text{N}$ (mean \pm SD) of the coral holobiont (circle), coral host cells (square) and zooxanthellae (triangle) of *Pocillopora verrucosa*, at each site Munster (A), Isipingo (B), Treasure Beach (C) and Sodwana Bay (D).

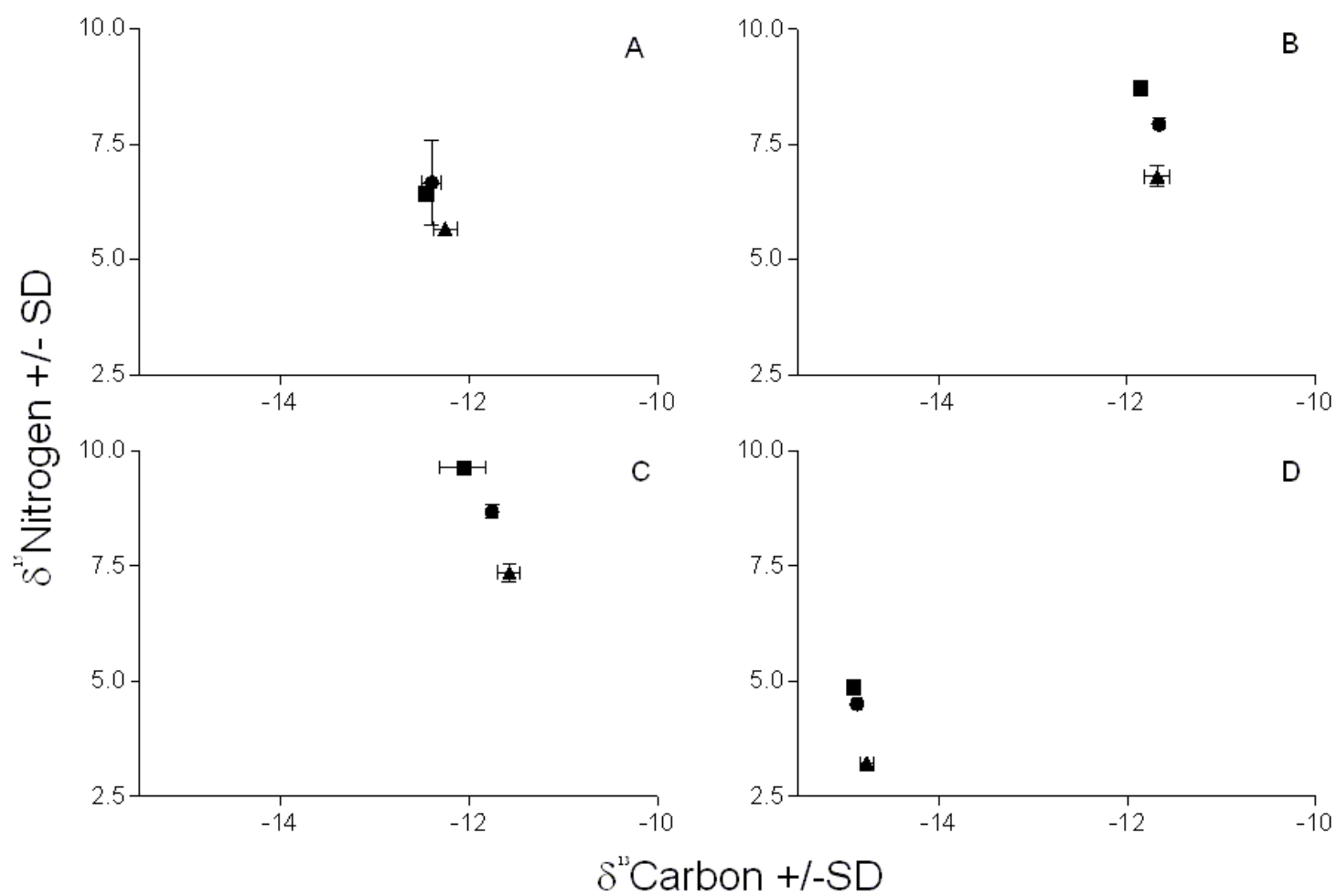


Fig. 24. Winter $\delta^{13}\text{C}$ vs. $\delta^{15}\text{N}$ (mean \pm SD) of the coral holobiont (circle), coral host cells (square) and zooxanthellae (triangle) of *Anomastrea irregularis*, at each site Munster (A), Isipingo (B), Treasure Beach (C) and Sodwana Bay (D).

Chapter 4: Discussion

4.1. Water temperature

Temperature is an important factor in structuring communities and species distributions, and thermal tolerance of an organism will influence the ability to live in a certain environment. Global satellite data for sea surface temperatures have been recorded over the last three decades and are becoming widely accessible for a variety of applications, in particular biogeography (Tyberghein *et al.*, 2012; Smit *et al.*, 2013). Some studies have quantified temperatures on reef flats and shallow coral reefs (Brown, 1997; 1999; Sheppard and Loughland, 2002; Edwards *et al.*, 1998; Winter *et al.*, 1998) however no *in situ* data is available for intertidal rock pools.

Mean temperatures of rock pools in this study differ significantly between seasons, however differences are minimal compared to other high latitude shallow water habitats, particularly the Arabian Gulf (Sheppard and Loughland, 2002; Riegl, 2003; Hume *et al.*, 2013). Summer and winter temperatures of 32-33°C and 19-20°C respectively have been recorded in the southern Arabian Gulf (Sheppard and Loughland, 2002; Hume *et al.*, 2013). Coles (2003) suggests maximum temperatures at Abu Dhabi have reached 36°C. Coastal summer temperatures in northern KZN, on 9-mile reef at Sodwana Bay, ranged from 27-29°C between 1993 and 2006 (Schleyer and Celliers, 2008), while mean summer temperatures on the south coast ranged from 20.5-22.4°C (Smit *et al.*, 2013). Coastal winter temperatures vary from 19.4°C on the south coast to 22.2°C on the north coast (Smit *et al.*, 2013). Seasonal temperature changes of coastal waters along KZN are larger than those in rock pools, where mean summer and winter temperatures of this study were 24.0°C and 21.46°C respectively. Small seasonal temperature differences of rock pools are likely caused by of large daily temperature fluctuations, in comparison to coastal sea surface temperatures (Figs. 4 & 5).

Daily and monthly temperature fluctuations in several shallow-reef habitats have not exceeded 3°C (Winter *et al.*, 1998; Brown *et al.*, 1999; Edwards *et al.*, 2001; Celliers and Schleyer, 2002; Schleyer and Celliers, 2008). This study reveals that in contrast to coastal waters, extreme temperature changes occur in intertidal rock pools (Figs. 4 & 5). Rock pools are heated during the day, but temperatures decrease rapidly when the tide comes in, and when rock pools are

cooled at night. Maximum summer temperatures at Munster and Isipingo often exceed 30°C, with the highest recorded temperature of 32.5°C (Fig. 4). Minimum summer temperatures range from 20-24°C. At spring tide, where the temperature range is highest, rock pool temperatures can change by more than 10°C throughout a tidal cycle (Fig. 4). Temperatures during neap tides are not as extreme however, with a change of 3-4°C. Temperature fluctuations in winter are significantly smaller than those in autumn and summer (Fig. 5). Corals in rock pools therefore endure acute thermal stress, which is very different to the more stable subtidal environment.

A latitudinal gradient in SST of coastal waters along the east coast (Smit *et al.*, 2013), is not however reflected in rock pools as there were no consistent trends among sites at different latitudes. Mean temperatures between sites were often less than 1°C and are likely not biologically significant. Rather, intertidal temperatures seem to be a function of rock pool size and type of habitat, in addition to local environmental and climate conditions. This affects the degree of heating and cooling. Rock pools at Munster and Sodwana Bay were smaller and more isolated than pools at Isipingo and Treasure Beach. Treasure Beach rock pools were larger and deeper, while Isipingo had mostly shallow gullies. During summer, Munster has a significantly higher temperature range than Isipingo (Fig. 5). Munster and Sodwana Bay have a significantly higher temperature range than Isipingo and Treasure Beach during autumn and winter (Fig. 5). Differences in rock pool type and habitat structure are thus likely the cause of different temperature patterns.

The ability of the rock pools to cool down rapidly within a tidal cycle inevitably lowers the mean temperatures experienced. Acute thermal stress is expected due to large temperature fluctuations, however maximum and minimum temperatures are not sustained for long periods of time. Coral health is threatened when temperatures exceed mean monthly ranges, especially for a prolonged period (Winter *et al.*, 1998; Brown *et al.*, 1999; Celliers and Schleyer, 2000; Schleyer and Celliers, 2003). Periodic heating, followed by cooling may thus allow corals to acclimatise to rock pool temperatures. This could further allow local adaption to thermal stress. Rock pool temperature patterns are similar throughout all sites, and high temperatures are maintained on the south coast, especially in winter compared to surrounding coastal sea surface temperatures. This

potentially explains how corals are able to survive and grow as far south as Munster at, allowing for the extension of their natural distribution.

4.2. Coral diversity

The majority of research along the South African coast focuses on subtidal reefs that predominantly occur in the northern reaches of KwaZulu-Natal (KZN). However, the genetic connectivity of *Acropora tenuis* along KZN (Chiazzari *et al.*, 2013), and the sexual reproduction of *Pocillopora damicornis* in rock pools (Masse *et al.*, 2012) comprise some of the only recent research on intertidal corals along our coastline. Physiological responses of intertidal corals to temperature and solar radiation have been measured in Thailand (Brown *et al.*, 1994; 1999; 2002; Le Tissier and Brown, 1996; Brown and Dunne, 2008). Type and dominance of zooxanthellae clade were determined in intertidal corals of Hengam Island in the northern Persian Gulf (Shahhosseiny *et al.*, 2011). Survey studies have also documented corals in the intertidal zone around the world (Ditlev, 1978; Brown and Holley, 1984; Ngoile, 1990; Bowman Bishaw Gorham, 1995 Obura *et al.*, 2011; Obura, 2012), but not many at high latitudes such as those in this study. There is thus a large gap in coral literature with little focus on the intertidal environment.

Crossland (1948) surveyed corals on the South African coastline, including intertidal rock pools, and found similar species to those that occur in these habitats today. *Pocillopora* was one of the most common corals along the east coast, which is reiterated in this study. In addition to *Pocillopora* there was a reasonably high diversity of corals observed in rock pools in this study. Isipingo and Treasure Beach have the same species diversity as Sodwana Bay (Table 2) despite the lower latitude and more tropical climate at Sodwana Bay. Temperatures in rock pools do not however differ significantly among sites at different latitudes, which could explain the lack of a latitudinal gradient in coral diversity. A sudden decline in coral diversity is however observed at Munster, yet there are still four families represented in these rock pools (Table 2). Mussidae and Faviidae occur at very low abundances though, with some species represented by only one colony. A minimum of 4-5 colonies of each taxon were observed at all other sites.

It is known that the tropics host more species than the cooler temperate environments, which could explain the decline in coral species at the southern reaches of KZN (Fisher, 1960; Macarthur, 1965; Pianka, 1966). The sudden drop in diversity could however be explained by localised factors that may be less conducive to coral survival and growth. Algal cover and substrate type may not be suitable for coral larval settlement. Recruitment may be limiting in this area, or post settlement survival may be limited by the competitive ability of coral recruits as conditions become more marginal in the south.

The most common and abundant corals in rock pools of this study include *Pocillopora verrucosa*, *P. damicornis* and *Anomastrea irregularis*, which were present at all sites (Table 1). *Pocillopora* spp. are also well documented on our subtidal reefs (Benayahu, 1993; Riegl, 1993; Schleyer and Celliers, 2003; 2008). *Pocillopora* has a wide distribution, occurring in most habitats suitable for coral growth (Veron, 2000), including other high latitude reefs in Australia (Crossland, 1981; Harriott *et al.*, 1995; Miller and Ayre, 2004), Japan (Tioho *et al.*, 2001), and eastern Pacific (LaJeunesse *et al.*, 2008). It is a hardy genus which explains the abundance in rock pools along the coastline. Despite the wide distribution of *Pocillopora* along our coast, *Anomastrea irregularis* was the most abundant species in all rock pools of this study. *A. irregularis* is classified as a “vulnerable” on the IUCN red list due to the lack of knowledge and species-specific conservation action (Sheppard *et al.*, 2008). *A. irregularis* is also classified as evolutionary distinct and endemic to the Western Indian Ocean (Obura *et al.*, 2011). Its high abundance and distribution in the subtidal and intertidal habitats of KZN provide an opportunity for the study and conservation of this species.

Conditions in rock pools thus seem tolerable for a variety of branching and massive species. Temperature patterns occurring in these pools are not harmful to corals, and can allow for the survival and growth of multiple species in these habitats. This may allow for the extended high-latitude distribution of those species that can cope in intertidal rock pools.

4.3. Size frequency distribution

Abundance of both species in this study varied among sites, with no discernable north-south trend, however the lowest abundance of both coral species was observed at Sodwana Bay. Isipingo had the highest abundance of *Pocillopora verrucosa* (Table 2), while Treasure Beach had the highest abundance of *Anomastrea irregularis* (Table 3). High abundances could reflect large recruitment, either through settlement of larvae or asexual budding (Miller *et al.*, 2000; Glassom and Chadwick, 2006). Corals at Isipingo and Treasure Beach potentially have a higher recruitment rate, or reflect higher post-settlement survival and growth rates than other sites.

The mean coral size was lowest at Isipingo for both species (Figs 8 & 9; Table 2 & 3). An abundance of small size classes can reflect a higher recruitment rate or lower survival and growth rates (Vermeij and Bak, 2000; Lins de Barros and Pires, 2006). High recruitment may be structuring the coral populations at Isipingo, in addition to the possible effect of low survival rates. Small juvenile corals and newly settled recruits are however difficult to detect, especially in the intertidal zone where there is high algal cover. It is thus possible that some corals in the small size classes may have gone undetected at any of the sites. Nevertheless, comparing corals in similar classes among sites, it is clear that there is an abundance of *P. verrucosa* at Isipingo, especially in the smaller size classes. High successful recruitment of *P. verrucosa* is therefore likely at Isipingo, in addition to a high survival rate. In *A. irregularis* however, coral abundance at Isipingo is much lower than at Munster and Treasure Beach, therefore the small mean size of corals at Isipingo is likely due to a lower survival rate rather than high recruitment. The effect of substratum and settlement success rate also contributes to differences between sites (Glassom and Chadwick, 2006). These were however not tested in this study, and should constitute future intertidal coral research.

Larger mean size variation among sites of *A. irregularis* could reflect differential growth rates (Meesters *et al.*, 2001). They potentially respond quicker than *P. verrucosa* to local environmental pressures as a result of faster growth and turnover rates or higher reproductive output. This could improve the ability of *A. irregularis* to adapt and create localised populations that have acclimatised to specific environmental conditions.

Bak and Meesters (1999) and Meesters *et al.* (2001) suggest that size distributions at degraded or more marginal sites will be negatively skewed, whereas Lins de Barros and Pires (2006) found sites affected by sedimentation to have positively skewed coral size distributions. Different disturbances are therefore likely to affect coral populations in a different ways. Positively skewed coral populations in this study could thus reflect sedimentation effects, especially on the south coast where water is characteristically more turbid than at the northern site of Sodwana Bay. Corals in this study, particularly *P. verrucosa*, were not of maximum attainable colony size, and corals mostly occurred in smaller size classes. Size frequency distributions are thus shifted to the left, and may create a biased representation of distribution factors such as skewness and kurtosis. Size frequency distributions of intertidal coral populations may thus be naturally less skewed than larger, subtidal populations. This does not however imply that intertidal coral colonies do not reach maturity, but rather that the size ranges of these corals are likely limited by marginal habitat conditions.

Size frequency distributions can provide insight into the reproductive strategies of corals. Vermeij and Bak (2000) suggest that spawning species will have no juvenile input for most of the year, resulting in a depletion of the small colony size classes. *P. verrucosa* is a spawning species, yet its population size structure does not reflect this pattern. Perhaps very small corals or newly settled recruits were not detected in the survey. It is therefore possible that population structures do not accurately depict the reproductive strategy of all species. Brooders have a high representation of small colonies (Vermeij and Bak, 2000). This was observed more in *A. irregularis* than *P. verrucosa* (Figs. 6 & 7). Vermeij *et al.* (2007) also suggest that brooders are more successful in variable and unstable conditions. Small massive species, including *Siderastrea* were shown to be brooding compared to larger massive species that were spawning (Soong, 1993). The reproductive mode of *A. irregularis* is unknown; however the observed size distribution patterns, and the observed reproductive mode of other small species in the same family could potentially imply that it is a brooding species (Vermeij and Bak, 2000; Vermeij *et al.*, 2007).

There were no significant trends in skewness, kurtosis and coefficient of variation against geometric mean, suggesting that disturbances have the same effect on all size classes, or possibly those disturbances are not having any effect on the coral populations. There are no consistent patterns in any of the size distribution parameters among sites or between species. This makes it difficult to determine those sites or latitudes that are more conducive to coral survival and growth. Similarly to the findings of Lins de Barros and Pires (2006), localised disturbances and environmental conditions, rather than large scale factors such as latitude, are therefore likely to structure these coral populations. In addition to this, the structure of the rocky intertidal zone and individual rock pools will influence the degree of disturbance experienced by the corals. Factors such as shading and light intensity, wave action, sedimentation and substrate quality can vary between rock pools, which will inevitably influence the local coral populations.

Populations that have a normal or close to normal distribution are stable, likely due to favorable environmental conditions (Lins de Barros and Pires, 2006; Goffredo *et al.*, 2008). Population structure of both species was significantly normal at Sodwana Bay (Table 2 & 3). The significantly higher geometric mean size of *A. irregularis* at Sodwana Bay in addition to both species showing normal population distributions, suggests conditions at Sodwana Bay are more favourable than at other sites, especially for *A. irregularis*. This is expected, at lower latitude representing tropical conditions conducive to coral survival and growth.

Normally distributed populations of *P. verrucosa* and *A. irregularis* and the structure of these populations suggests there is an adequate representation of large colonies at these sites, bearing in mind that these are not considered maximum colony sizes. Large colonies are nonetheless more fertile (Lins de Barros and Pires, 2006) and should be able to contribute to the stability of these populations. Colonies of *Pocillopora* do not reach maximum size in these rock pools; however populations along our coast are reproductively viable (Sere, 2010; Masse *et al.*, 2012). Populations, especially at Sodwana Bay, but also at other sites are therefore likely to persist, and potentially contribute recruits to neighboring reefs and intertidal habitats.

4.4. Physiology: Effect of site, season and species

4.4.1. *Zooxanthellae* density

The loss of symbionts, associated with stress can be detrimental to coral health through the lack of nutrition required for metabolic processes (Brown, 1997; Jokiel, 2004). In this study, different zooxanthellae densities were observed among species, seasons and sites. Combining all sites, *P. verrucosa* shows a decline in zooxanthellae density from summer to spring (Fig. 13A). High summer symbiont density was a result of significantly higher densities at Munster and Isipingo than other sites (Fig. 13B). Zooxanthellae density at Treasure Beach and Sodwana Bay was stable from summer to winter, with densities only significantly lower in spring (Fig. 13). Zooxanthellae density changes thus vary among sites, however overall, densities are lower in spring than summer.

Zooxanthellae densities of *P. verrucosa* in this study contrast with the majority of other studies that found zooxanthellae densities to be highest in winter and lowest during summer (Stimson, 1997; Brown *et al.*, 1999; Fagoonee *et al.*, 1999; Fitt *et al.*, 2000; Pillay *et al.*, 2005). In tropical corals in particular, corals become stressed at elevated temperatures and UV radiation. The literature however shows varied responses of zooxanthellae to environmental pressures. No change in symbiont density was observed during experimentally elevated temperatures (Dove *et al.*, 2006) and high UV radiation (Falkowski and Dubinsky, 1981). In temperate habitats though, corals cope better in summer when temperatures and solar radiation are highest (Porter *et al.*, 1984; Fabricius, 2006; Stambler *et al.*, 2008). In these studies increased zooxanthellae densities were proposed as a strategy to cope with the low light levels of high latitude habitats, in order to maximise efficiency and production. Vareschi and Fricke (1986) found lower zooxanthellae densities in low light levels, which could be a strategy to reduce the effect of self-shading, and cope with limiting light (Pillay *et al.*, 2005). This coincides with the seasonal patterns of zooxanthellae density of *P. verrucosa* in this study.

Corals have also bleached in response to cold sea surface temperatures (Hoegh-Guldberg and Fine, 2004; Hoegh-Guldberg *et al.*, 2005; Paz-Garcia *et al.*, 2012). In the Gulf of California, bleaching of *Pocillopora* spp. occurred at temperatures below 19°C (Paz-Garcia *et al.*, 2012).

This emphasises that corals can become stressed at low SST's too. Sampling during September coincides with the end of the winter season, characterised by the lowest water temperatures and light levels. Minimum winter temperatures in this study were often recorded below 19°C. Observations of bleaching were made during winter and spring, suggesting that some colonies were stressed during this time. Low zooxanthellae densities of *P. verrucosa* in spring could thus also be a result of lower SST's and stress during this season.

Zooxanthellae densities are also related to changes in nutrient concentrations, in particular dissolved nitrates. High nutrient concentrations can increase zooxanthellae densities (Stimson, 1997; Fagoonee *et al.*, 1999; Godinot *et al.*, 2001). Effluent canals near sampling sites at Isipingo and Treasure Beach could have resulted in elevated nutrients in the surrounding water column. Riverine input at Sodwana Bay could also influence local nutrient dynamics. Summer has the highest rainfall along the east coast of South Africa, potentially increasing the amount and duration of nutrient outflows at these sites. This could also explain high zooxanthellae densities in summer. An effluent canal at Isipingo is less than 100m from the collection site, which could explain the high zooxanthellae densities of *P. verrucosa* here (Fig. 13B). This however does not explain the high densities at Munster as there are no outflows or major river inputs in this area.

There are no apparent trends among sites despite elevated zooxanthellae densities in *P. verrucosa* at Munster (Fig. 13B). Munster is the southern-most site, and receives lower solar radiation than other sites, especially Sodwana Bay (SolarGIS, 2012), yet it has the highest density of symbionts throughout all seasons. Corals at Munster may potentially have higher zooxanthellae densities in order to compensate for low light conditions.

A. irregularis showed no significant changes in zooxanthellae density among seasons (Fig. 17). Symbiont densities of *A. irregularis* therefore do not seem to be affected by seasonal changes, latitude or local environmental conditions at each site. Costa *et al.* (2005) found high variability in zooxanthellae densities in three hard coral species, also with a lack of conclusive seasonal patterns. Since both species are exposed to the same environmental conditions at each site, *A. irregularis* seems to be less affected by local and seasonal stress and can cope better than *P. verrucosa*, possibly using reserve energy stores or heterotrophic feeding.

The lack of consistent patterns among sites again suggests that latitude is not a major influence in zooxanthellae densities in *P. verrucosa* and *A. irregularis*. The seasonal trend in *P. verrucosa* is likely linked to seasonal changes in temperature and more so light, in addition to other localised environmental conditions that may vary between sites. Nevertheless, changes in zooxanthellae density can affect the nutritional component of the holobiont, thus the physiological response of different species will inevitably influence coral influence. Findings from this study showed that species react differently to local and seasonal environmental conditions, with evidence of *P. verrucosa*, a branching species, more susceptible to changes in environmental or physical condition.

4.4.2. Chlorophyll a content

Chlorophyll a, measured by fluorescence, is used as a proxy for coral production, specifically how well photosystem II is functioning (Lesser and Gorbunov, 2001). In this study *P. verrucosa* displays more pronounced seasonal trends than *A. irregularis* (Figs. 14 & 18), where chlorophyll a decreases throughout the year from a peak in winter (Fig. 14). Changes in chlorophyll a reflect changes in zooxanthellae density in addition to chlorophyll a per symbiont (Figs 13-15). This is conspicuous at Munster and Isipingo where large differences in chlorophyll a between summer and autumn were a result of large changes in zooxanthellae density between those months. There seems to be a lag effect between seasonal changes in zooxanthellae density and chlorophyll a in *P. verrucosa*. In *A. irregularis*, the only significant change in chlorophyll a is an increase from autumn to winter which is a result of increased chlorophyll a concentration per zooxanthella.

Chlorophyll a concentrations can be regulated independently of symbiont density, and are important in coping with thermal stress and light regulation (Le Tissier and Brown, 1996; Jones, 1997; Anthony and Hoegh-Guldberg, 2003; Dove *et al.*, 2006). Reductions in chlorophyll a are associated with coral bleaching (Coles and Jokiel, 1977; Salih *et al.*, 1998; Jokiel, 2004; Lesser and Farrell, 2004). Total chlorophyll a in this study however increased from summer and autumn to winter in both species, with a larger increase in *A. irregularis* than *P. verrucosa* (Figs. 14 &

18). Increases are a response of zooxanthellae efficiency, reflected in increases of chlorophyll a per symbiont between these seasons (Figs. 15 & 19).

Corals that bleached due to temperature and light stress had a higher chlorophyll a per zooxanthella than non-bleached colonies (Le Tissier and Brown, 1996; Jones, 1997). *P. damicornis* also showed an increase of chlorophyll a per zooxanthella at sustained elevated temperatures (Mayfield *et al.*, 2013). Regulation of chlorophyll a in these conditions is likely a means of coping with zooxanthellae loss. Algae become more efficient in their production by increasing the amount of chlorophyll per cell, which maintains the amount of energy available to the coral host (Le Tissier and Brown, 1996; Jones, 1997). Alternatively, chlorophyll a can be regulated under low light and temperature conditions. Corals in low light microhabitats, or shade adapted colonies had higher chlorophyll a per zooxanthella than corals in exposed habitats (Porter *et al.*, 1984; Anthony and Hoegh-Guldberg, 2003). Chlorophyll a concentrations were at a peak during winter compared to summer (Brown *et al.*, 1999; Fitt *et al.*, 2000). Peirano (2007) also found an increase in efficiency of zooxanthellae from summer to winter. These findings are concurrent with the seasonal pattern observed in this study, where chlorophyll a was highest in winter in both species. Increasing chlorophyll a may thus be an effective way of coping with low light and temperatures during the winter months, which is pertinent at high latitudes.

There is a decline of chlorophyll a in *P. verrucosa* from south to north (Munster to Sodwana Bay) (Fig. 14). Changes at Isipingo and Treasure Beach are not consistent, yet *P. verrucosa* at Munster has significantly higher concentrations of chlorophyll a than Sodwana Bay (Fig. 14 B). These trends clearly mimic zooxanthellae densities during these seasons (Fig. 13 B & 14 B). There is however no consistent change in total chlorophyll a in *A. irregularis* between sites. The main trend for this species is thus a seasonal shift, with elevated total chlorophyll a and chlorophyll a per zooxanthella in winter and spring.

It seems to be more efficient for *A. irregularis* to improve symbiont production and efficiency rather than regulating zooxanthellae densities (Le Tissier and Brown, 1996; Jones, 1997). *A. irregularis* undergoes smaller changes in chlorophyll a per symbiont than *P. verrucosa*, yet the changes in total chlorophyll a are substantially higher. This is a result of stable zooxanthellae densities during these seasons, whereas *P. verrucosa* showed a loss of symbionts resulting in a

loss of chlorophyll a, resulting in the need to increase zooxanthellae efficiency more than *A. irregularis*. *A. irregularis* therefore invests less energy in regulating zooxanthellae efficiency, resulting in a higher total productivity than *P. verrucosa* (Le Tissier and Brown, 1996; Anthony and Hoegh-Guldberg, 2003).

Both species showed increases in zooxanthellae efficiency, reflecting higher chlorophyll a concentrations in winter than summer, coinciding with findings from other studies. *P. verrucosa* however displays an opposite seasonal pattern in zooxanthellae density whereby summer densities were higher than winter. This contradicts the findings on corals in the tropics. As discussed earlier however, the seasonal change of zooxanthellae density in this study could be a response to conditions at high latitudes. Low zooxanthellae densities in winter could be a response to low temperatures and light during these months. In order to compensate for the loss of zooxanthellae density, in addition to the low water temperatures and UV radiation in winter, chlorophyll a per zooxanthella increases, resulting in higher total chlorophyll a. This may function as an effective means of coping with marginal conditions during this time.

4.4.3. Total lipid content

Lipids constitute at least 40% dry weight of coral polyps, and serve as an energy reserve for coral metabolism (Stimson, 1987). Lipids occur within coral tissue, endosymbiotic algae and also in gametes during reproductive processes (Stimson, 1987). Lipid depletion represents a use of important energy reserves, as a function of coping with environmental stress (Anthony and Fabricius, 2000; Grottoli *et al.*, 2004; Swart *et al.*, 2005; Rodrigues and Grottoli, 2007; Borell *et al.*, 2008). This can affect coral fitness, in particular resistance and resilience to thermal stress and bleaching. The coral species of this study have different patterns of lipid use. *P. verrucosa* depletes its lipid reserves, with lipid content significantly lower in spring than summer (Fig. 16). It is important to note that some corals can display natural cycles in lipid content. Stimson *et al.* (1987) found a monthly cycle of lipids in *P. damicornis*, which seemed to coincide with planulation, thus linking the lipid production and use to reproductive cycles. Gametogenesis in *P. verrucosa* could thus affect lipid stores throughout the year.

A depletion of total lipid content in *P. verrucosa* from summer to spring is consistent among all sites except Isipingo where lipid concentrations were stable throughout summer, autumn and winter (Fig. 16B). Corals at Munster have significantly more lipids than those at Sodwana Bay (Fig. 16B). Differences between sites are not consistent among seasons which suggest site-specific conditions that could affect coral stress and lipid utilisation throughout the year.

A. irregularis showed no significant depletion of lipids throughout the year, except a slight decline in lipid concentration in spring. There are also no consistent trends in lipid content of *A. irregularis* among sites. The absence of lipid depletion in this massive intertidal coral species regardless of local or seasonal environmental conditions demonstrates that, in contrast to the branching *P. verrucosa*, it does not rely on lipids as an alternative energy source.

Comparing bleached versus non-bleached colonies of *Porites compressa* and *Montipora verrucosa*, only *P. compressa* showed a reduction in total lipid content, with a local depletion observed at bleached areas of the colony, while *M. verrucosa* showed no depletion of lipid reserves in bleached colonies (Grottoli *et al.*, 2004). Contrasting species responses are thus concomitant with the findings of this study where *P. verrucosa* depleted lipid reserves from summer to winter, whereas no significant changes in total lipid content were observed in *A. irregularis* (Fig. 20B). Grottoli *et al.* (2004) propose that *M. verrucosa* either reallocates lipids to bleached (or stressed) areas of the colony, or it is able to conserve lipid reserves by having a lower metabolic rate than *P. compressa*. The ratio of photosynthesis to respiration (P: R) of *M. verrucosa* was 25-30% higher than *P. compressa* (Grottoli *et al.*, 2004), as a result of lower respiration rates (Coles and Jokiel, 1977). In another study, a lower oxygen consumption rate of *Galaxea fascicularis* than *Stylophora pistillata*, also allowed for a lower metabolic rate to conserve lipid stores (Borell *et al.*, 2008). Higher P: R ratios increase resilience to bleaching and ratios were shown to decrease with increasing temperatures, emphasising that as corals become thermally stressed, respiration rates are increased in relation to photosynthesis (Coles and Jokiel, 1977). The lower depletion of lipids in *A. irregularis* in this study could be a result of lower respiration and metabolic rates.

Lipid conservation by *A. irregularis* in rock pools could be a result of lower respiration rates and therefore metabolic rates. Lipid conservation may also be enhanced by the availability of other

energy sources. Grottoli *et al.* (2004) suggest that *M. verrucosa* was potentially using carbohydrate and protein reserves rather than lipids as source of energy for metabolic process. Differential sources of energy could also explain differences observed between species in this study. Despite species-specific differences, lipid content was lowest when chlorophyll a content was highest in both species but more so in *P. verrucosa*. This suggests that energy available from stored lipid reserves may allow for the ability to increase zooxanthellae efficiency and enhance chlorophyll a production.

4.5. Heterotrophy

One alternative source of energy is to feed heterotrophically, which can influence the tolerance of corals to local environmental stress (Anthony and Fabricius, 2000; Reynaud *et al.*, 2002; Ferrier-Pages *et al.*, 2003; 2011; Grottoli *et al.*, 2006; Rodrigues and Grottoli, 2006; 2007; Borell *et al.*, 2008; Hoogenboom *et al.*, 2010). Feeding experiments have repeatedly shown that increased heterotrophy leads to improved coral health and functioning. Corals that were fed had significantly higher concentrations of Chlorophyll a, and proteins than starved corals (Ferrier-Pages *et al.*, 2003; Kisten, 2013), and improved tissue and skeletal growth rates (Reynaud *et al.*, 2002). Higher feeding rates of *Montipora capitata* than *Porites lobata* and *P. compressa* resulted in an increased resilience to bleaching, which should improve the survival of those that can sustain metabolic demands through heterotrophy. Feeding and lipid utilisation will both play an important role in improving coral fitness and coping with environmental stress. While bleached and during recovery, *M. capitata* depleted its lipid reserves only when the ability to feed heterotrophically was eliminated from the experiment (Rodrigues and Grottoli, 2006). Feeding allowed *M. capitata* to conserve lipids and maintain a faster recovery rate from bleaching (Rodrigues and Grottoli, 2006). This was consistent with the findings of Hoogenboom *et al.* (2010).

Stable $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotope signatures reflect a variety of metabolic and physiological states in corals. This includes zooxanthellae densities, photosynthesis and respiration, growth rates and feeding (Reynaud *et al.*, 2002; Swart *et al.*, 2005; Rodrigues and Grottoli, 2006). Holobiont

isotopic signatures of this study did not show large differences between summer and winter among sites in either species (Figs. 21 & 22). Enriched $\delta^{13}\text{C}$ signatures have been shown to reflect high levels of photosynthesis and zooxanthellae productivity (Rodolfo-Metalpa *et al.*, 2008). *P. verrucosa* at Sodwana Bay showed a significant depletion of $\delta^{13}\text{C}$ from summer to winter, yet there was a significant increase in chlorophyll *a* in winter. The isotope signatures of corals at Sodwana Bay are therefore not consistent with the findings of Rodolfo-Metalpa *et al.* (2008). In *A. irregularis*, no statistically significant depletion occurred (Fig. 21).

If corals are feeding heterotrophically, $\delta^{13}\text{C}$ signatures reflect the food source as it gets incorporated into the coral tissue (Reynaud *et al.*, 2002; Ferrier-Pages *et al.*, 2011). Differences in isotopic signatures could be a result of different community composition of food sources and allochthonous carbon in the water column. Without $\delta^{13}\text{C}$ of potential food sources, it is difficult to make conclusions about the degree of feeding. The lack of seasonal differences could infer similar food sources throughout the year, except at Sodwana Bay where a significant difference was found between summer and winter, implying a potential change in diet composition, or amount of feeding.

$\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in coral tissue and zooxanthellae are also used to determine the amount of feeding by corals. There was a significant difference in $\delta^{13}\text{C}$ between host tissue and zooxanthellae only in *A. irregularis* at Treasure Beach (Fig. 24C). These signatures will again rely on the isotopic signature of the food source. Ferrier-Pages *et al.* (2011) showed that when corals were not feeding, $\delta^{13}\text{C}$ of zooxanthellae and coral host cells were similar (-17‰), whereas the host cells were more depleted and similar to the food source (-24 to -25‰) when corals were feeding. Reynaud *et al.* (2002) also showed that *Artemia* carbon was incorporated into the coral tissue, reflecting signatures of -10.1 to -11.7‰. The lack of significant differences in $\delta^{13}\text{C}$ in this study may be a result of the food source having a similar $\delta^{13}\text{C}$ to the zooxanthellae.

Overall, $\delta^{13}\text{C}$ of *P. verrucosa* is depleted compared to *A. irregularis*. Swart *et al.* (2005) suggest that $\delta^{13}\text{C}$ will change due to the amount and type of organic material that is utilised during respiration. Lipids have a more negative isotope composition than other biochemicals (Galimov,

1974), and are the primary organic compound that is respired in corals (Crossland *et al.*, 1980). Therefore as lipids are respired, this depletes the $\delta^{13}\text{C}$ of respired CO_2 , resulting in a more depleted signature of the holobiont (Swart *et al.*, 2005). Depleted $\delta^{13}\text{C}$ of *P. verrucosa* could reflect the higher utilisation of lipids than *A. irregularis*.

Changes in $\delta^{15}\text{N}$ can reflect variable food sources and changes in P: R (Swart *et al.*, 2005b). Enriched $\delta^{15}\text{N}$ signatures would also reflect feeding at a higher trophic level; therefore it can be used to determine the degree of heterotrophic feeding (Peterson and Fry, 1987; Reynaud *et al.*, 1999; Ferrier-Pages *et al.*, 2011). In *P. verrucosa*, there were no significant differences in $\delta^{15}\text{N}$ of the holobiont between summer and winter (Fig. 22A). Corals at Sodwana Bay however were significantly depleted compared to other sites (Fig. 22A), implying that they are potentially feeding at a lower trophic level and corals at other sites are feeding more than those at Sodwana Bay. The same trend is observed in *A. irregularis* (Fig. 22B). *A. irregularis* at all sites except Sodwana Bay, showed a higher enrichment in $\delta^{15}\text{N}$ in winter than summer (Fig. 22B). Significant differences were only observed at Munster and Treasure Beach however. This suggests a potential increase in the contribution of heterotrophy in winter than summer at these sites (Reynaud *et al.*, 2009; Ferrier-Pages *et al.*, 2011).

Comparisons of $\delta^{15}\text{N}$, show that there are significant differences between coral tissue and zooxanthellae at all sites except Treasure Beach in *P. verrucosa*, and Munster in *A. irregularis* (Figs. 23 & 24). A feeding experiment using *Stylophora pistillata* found a significant enrichment in the host tissue compared to zooxanthellae whether the corals were fed or not (Reynaud *et al.*, 2009). This is because a natural enrichment occurs from the autotrophic contribution of zooxanthellae to host tissue (Swart *et al.*, 2005a). As feeding increases, the isotopic difference between host cells and zooxanthellae should also increase (Swart *et al.*, 2005a). Swart *et al.* (2005a) suggest a natural enrichment in $\delta^{15}\text{N}$ of approximately 1.5‰ from zooxanthellae to host. The difference in $\delta^{15}\text{N}$ of host tissue and zooxanthellae in *P. verrucosa* is less than 1.5‰ at all sites, except Munster which had a difference of 2.5‰ (Fig. 23). Contrary to this, *A. irregularis* had a difference higher than 1.5‰ between host cells and zooxanthellae at all sites except Munster, where there was no significant difference (Fig. 24). These results suggest that with the

exception of corals at Munster, *A. irregularis* could be relying more on the contribution of heterotrophic feeding than *P. verrucosa*. If the interpretation of these results is correct, then the opposite seems to be happening at Munster. Colonies of *A. irregularis* are potentially not feeding while *P. verrucosa* is feeding the most at this site, which is not expected.

Feeding is also an energy-requiring process, and it is not always beneficial to the coral host. Heterotrophy was shown to have a negative effect on the reproduction of *P. verrucosa*, suggesting an energetic trade-off between feeding and other metabolic or physiological process (Sere *et al.*, 2010). From this study it is not possible to make any conclusions about the reproductive outputs or strategies of *P. verrucosa* and *A. irregularis*. Yet, this could be a possible explanation for the isotopic signatures of colonies at Munster.

The isotopic signatures of this study are somewhat different to others in the literature, particularly with corals in temperate habitats (Ferrier-Pages *et al.*, 2011). Differences observed between host, zooxanthellae and holobiont are much larger than this study, with a clearer distinction between summer and winter. The lack of food source isotopes limits the ability to make sound conclusions from this study. Inconsistency and variability in the literature (Muscattine *et al.*, 1989; Reynaud *et al.*, 2002; 2009; Swart *et al.*, 2005; Ferrier-Pages *et al.*, 2011) and the wide scope of interpretation of both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ also makes it very difficult to determine the precise causes and physiological or metabolic processes responsible for the observed isotopic signatures. For this reason results from this study will provide a good foundation for further isotopic research within these two species. Differences between *P. verrucosa* and *A. irregularis* suggest variable responses to local environmental conditions. Further analysis will be able to distinguish specific metabolic or physiological mechanisms that are utilised by each species.

Additional mechanisms that corals use to cope with marginal conditions include changes in tissue thickness, metabolic states and other cellular responses. A reduction in coral thickness was shown in *Montipora monasteriata* as a means of photoadaptation and acclimation to low light in caves/overhangs (Anthony and Hoegh-Guldberg, 2003). Corals in caves also had lower rates of dark respiration than those in exposed habitats (Anthony and Hoegh-Guldeberg, 2003), which can reflect lower basal metabolic rates (Gates and Edmunds, 1999; Anthony and Heogh-

Guldborg, 2003). A decrease in tissue thickness can also be a negative response to bleaching or environmental stress (Ainsworth *et al.*, 2008). Protein turnover in connection with growth and metabolic rates can be used to understand response of corals to the environment (Gates and Edmunds, 1999; Mayfield *et al.*, 2003). The expression of heat-stress protein (HSP70) is important in tolerating high SST's and aids in the resistance and recovery from thermal stress (Sharp *et al.*, 1997; Fitt *et al.*, 2009; Mayfield *et al.*, 2003; Texeira *et al.*, 2013). HSP 70 was expressed in the *P. damicornis* and in *Symbiodinium* at elevated temperatures (Mayfield *et al.*, 2013). Coral mucus, a predominantly lipid-based product, is used for waste removal, defense against microbes/pathogens and coral health (Wild *et al.*, 2004). Mucus release from coral tissue can also be used as a functional response to stress, which increases the energetic demand of corals (Crossland *et al.*, 1987; Ainsworth *et al.*, 2008). Further investigation into these metabolic, physiological and cellular responses will contribute to understanding coral resistance and resilience to environmental stress

4.6. Overall discussion & summary

Intertidal corals provide wide scope for understanding adaptation and acclimatisation to stress. Rock pools on the east coast of South Africa maintain a high diversity despite the harsh environmental conditions of the intertidal zone. The scope for coral survival and growth could therefore extend beyond the current limits of coral distribution. Intertidal rock pools may constitute an important habitat, especially at high latitudes, and when subtidal conditions are not conducive to coral survival.

A latitudinal gradient in temperature is not observed in rock pools in KZN. Small temperature differences among sites suggest that latitude is not a structuring influence in terms of thermal stress in intertidal corals. Microhabitats in rock pools and large-scale habitat structure within each site influence the degree of temperature and light stress. This includes caves, overhangs, gullies and rock formations which will determine light availability and degree of heating and cooling in the rock pool (Brown *et al.*, 2002; Anthony and Hoegh-Guldberg, 2003). Habitat structure will also influence the degree of wave activity and water motion. Wave action can have a detrimental effect on corals, causing increased physical stress; however it can also promote resistance to other environmental stressors, including temperature (Patterson *et al.*, 1991; Smith, 2004; Finelli *et al.*, 2006).

Temperature fluctuations of up to 10°C can be experienced in rock pools during spring tides. This range is extremely high compared to subtidal reefs where temperatures fluctuate between only 2 and 4°C. Corals that are able to tolerate these conditions are fundamental to the understanding of adaptation and acclimatisation to thermal stress. Thermal histories can be very important in tolerance and resistance to thermal stress (Brown *et al.*, 2002; Dunne and Brown, 2008; Thompson and Woesik, 2009; Guest *et al.*, 2012). For example, susceptibility to bleaching differed on east- vs. west-facing sides of the colony as a response to variations in temperature and UV radiation (Brown *et al.*, 2002; Dunne and Brown, 2008). Corals that bleached in the 1998 and that had experienced greater historical temperature variability did not bleach in a recurring temperature-induced bleaching event in 2010 (Guest *et al.*, 2012). They were able to adapt and/or acclimatise to thermal stress, resulting in greater resistance to bleaching (Guest at

al., 2012). Their thermal histories thus allow them to acclimatise and potentially adapt to local conditions, making them less susceptible to thermal stress. Corals in rock pools that are able to tolerate acute temperature changes may constitute an important group of species that could be more resistant to thermal pressures.

The temperature data and findings from this study may also relate to micro-habitats that experience similar temperature patterns. A subtidal reef in Nanwan Bay, Taiwan, experiences periodic upwelling that results in temperature fluctuations of up to 10°C within a 24 hour period (Lee *et al.*, 1999). An experiment conducted by Putnam *et al.* (2010) suggests that extreme temperature fluctuations can benefit larvae of *Pocillopora damicornis*. Thus, temperatures in rock pools may be perceived as marginal and stressful to corals, yet it is possible that they can be beneficial to some species living in those conditions.

In this study *A. irregularis* seems to cope best in intertidal conditions. *P. verrucosa* is also highly abundant in rock pools, thus massive and branching species seem to thrive in these conditions. The lack of any consistent patterns in size distributions of either species among sites suggests that local conditions outweigh the effects of general, large-scale gradients. Descriptive statistics and population structures between sites have provided some insight into differential recruitment and mortality, yet it is difficult to make any sound conclusions without measuring these factors. The occurrence of reproductively mature colonies of both species, and the overall structure of populations at most sites suggest that these species are able to persist in intertidal habitats, with a continual recruitment input. Differential mortality rates in response to localised disturbances are then likely to structure the local coral population. Nevertheless, findings from this study show that *P. verrucosa* and *A. irregularis* populations are able to persist at very high latitudes, in highly marginal conditions.

Different physiological responses and mechanisms of recovery from stress will affect coral fitness and overall resilience to environmental perturbation. The lack of zooxanthellae density change and the conservation of lipids in *A. irregularis* may allow this massive species to invest excess energy in other physiological processes, and cope with the stressful conditions rock pools. Some of these may include improving reproductive output, investing energy into tissue and skeletal growth, feeding, and response to harsh physical conditions of the intertidal zone. The

depletion of lipids in *P. verrucosa* from summer to spring may constitute an important means of acquiring energy in times of increased pressure and stress. Increasing chlorophyll a content in winter in both species suggests a coping mechanism for low light and temperatures during these months, which becomes significant in temperate high-latitude environments. Lipid use and increasing zooxanthellae efficiency may thus constitute a means of coping with these stressful conditions.

Heterotrophy in both species, but more so in *A. irregularis*, appears to be a potential means of acquiring energy for metabolic and physiological processes. The potential ability of *A. irregularis* to feed more than *P. verrucosa* could be an adaptive mechanism of tolerating stress in intertidal rock pools. Food availability and identification of exogenous carbon and nitrogen in corals would improve the understanding of the degree of heterotrophy in *P. verrucosa* and *A. irregularis* in rock pools. Nevertheless, stable isotope signatures of this study showed that *P. verrucosa* and *A. irregularis* are indeed acquiring additional energy through feeding, which could be vital in tolerating such marginal conditions. Differences between sites suggest that Isipingo and Treasure Beach (which showed similar $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures) could reflect inputs from local effluent canals. Sodwana Bay was depleted in both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures of both species, suggesting that feeding strategies are different here or possibly reflect different sources of exogenous carbon and nitrogen. The Ngobozeleni estuary mouth at Sodwana Bay may be the source of allochthonous inputs to intertidal coral populations. Further isotope analysis for heterotrophy, in conjunction with feeding experiments will improve the understanding of coping mechanisms in corals, especially in high latitude marginal habitats.

Functional responses to environmental stress including cellular, physiological and metabolic processes will combine with morphological characteristics and life history traits to promote the survival, growth and reproduction of a species in a variety of habitats. Studies suggest that massive coral species should be “winners” in community composition in response to local, regional and global environmental change (Gates and Edmunds, 1999; Loya *et al.*, 2001; Brown *et al.*, 2002). *A. irregularis* was most abundant in KZN rock pools, however, other massive species that were found occurred at lower abundances than *P. verrucosa* and *A. irregularis*. Results of this study however showed that *P. verrucosa*, a branching species, has a wide

distribution and high abundance in rock pools along KZN. Despite the community composition consisting predominantly of massive species, the presence of other branching species including *Stylophora* and *Acropora* and the predominant *Pocillopora*, shows that “susceptible” species are still able to persist in these environments. Guest *et al.* (2012) suggest that these taxa have life history traits that favor rapid adaptation. Hardy massive species already seem to be “winners” in these intertidal rock pools, yet there is possible scope for future acclimatisation and increased tolerance of branching species too.

Chapter 5: Conclusion

The size structure of intertidal populations of *P. verrucosa* and *A. irregularis* shows they are mostly stable and likely to persist in rock pools of KwaZulu-Natal. They can tolerate acute temperature stress, enduring temperature fluctuations of more than 10°C throughout a tidal cycle. To my knowledge, temperature ranges of this magnitude have not been recorded in coral habitats, and are extremely different to what has been considered optimal for coral survival and growth on subtidal reefs. High temperatures are maintained in rock pools at high latitudes but occur for short periods of time, thus do not seem harmful to corals in these environments. This may allow for the southward extension and distribution of tropical coral species that can survive in rock pools. Similar environments, especially at high latitudes may thus constitute an important habitat for corals, especially for range expansion.

Utilising lipids and increasing zooxanthellae efficiency, thus increasing chlorophyll a production, are possible ways of coping in marginal conditions of intertidal rock pools, especially during low temperature and light conditions in winter. This is conspicuous in *P. verrucosa*, whereas *A. irregularis* conserved most of its lipids throughout the year, possibly obtaining additional energy through other means. These physiological responses may play a role in coping with stressful conditions in other high latitude habitats, and those characterised by low light, in micro-habitats through shading or in turbid waters.

Stable isotope analysis revealed that external nutrient inputs may help the holobiont in coping with the stressful conditions of intertidal rock pools. Heterotrophic feeding is a likely contribution to this, probably more so in *A. irregularis* than *P. verrucosa*. In areas where allocthonous nutrient inputs and sufficient food sources are available, corals are likely to persist in conditions and habitats that are stressful and marginal for survival and growth. This will be imperative in similar high latitudes habitats.

Rock pools thus contribute an important habitat for corals, especially in the poleward extension of their range through global climate change, with those species that can survive, grow and reproduce in intertidal rock pools likely to be more tolerant and resilient to environmental disturbances.

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