# THE FERTILISATION AND RECRUITMENT DYNAMICS OF SCLERACTINIAN CORALS ON SOUTH AFRICA'S HIGH-LATITUDE REEFS

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As the candidate's supervisor I have/have not approved this thesis/dissertation for submission

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## Preface

The work described in this thesis was carried out at the Oceanographic Research Institute (ORI), which is an affiliated institute of the School of Biological and Conservation Sciences at the University of KwaZulu-Natal, Westville. Field work was conducted at Sodwana Bay, South Africa from November 2012 - April 2015, under the supervision of Professor Michael Schleyer. This thesis represents original work by the author and has not otherwise been submitted in any form for any degree or diploma to any tertiary institute. Where use has been made of the work of others, it is duly acknowledged in the text.

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Detail of contribution to publications that form part and/or include research presented in this thesis.

**Publication 1 (Published):**
JR Hart, MH Schleyer (2016). A novel settlement tile design to facilitate the *in situ* detection of coral recruits. Reef Encounter (31) 2: 43-45.
*Author contributions:* JH and MS conceived the paper. MS procured financial support for the study, JH wrote the article and MS contributed comments on the manuscript.

**Publication 2 (in prep):**
JR Hart, MH Schleyer. Fertilisation ecology of *Hydnophora exesa* and *Acropora austera.*
*Author contributions:* JH and MS conceived the paper. JH collected and analysed the data, MS procured financial support for the study and contributed comments on the manuscript.

**Publication 3 (Under review with PLOS ONE):**
JR Hart, MH Schleyer. Larval settlement and post-settlement success in *Acropora austera* and *Hydnophora exesa.*
*Author contributions:* JH and MS conceived the paper. JH collected and analysed the data, MS procured financial support for the study and contributed comments on the manuscript.

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JR Hart, MH Schleyer. Recruitment of scleractinian corals on a high-latitude reef in South Africa: Micro-spatial patterns and the effect of caging.
*Author contributions:* JH and MS conceived the paper. JH collected and analysed the data, MS procured financial support for the study and contributed comments on the manuscript.

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# Abstract

The production of coral offspring and their survival through early ontogeny to sexual maturity are both vitally important for the persistence of coral-dominated reefs. Understanding factors which affect these processes is important where limited connectivity occurs. This is the case on the high-latitude Two-mile Reef (TMR) at Sodwana Bay in South Africa. A combination of *in situ* and *ex situ* experimental work was conducted, investigating factors which affect the pre- and post-settlement stages of corals. *In vitro* experiments conducted on two representative scleractinian broadcast spawning corals, *Acropora austera* and *Hydnophora exesa*, revealed that fertilisation success in both species diminishes significantly with a reduction in sperm concentration and water salinity. Fertilisation success was highest for *A. austera* at $10^6$ sperm ml$^{-1}$ (56.46% ± 0.83, mean ± SE), and at $10^5$ sperm ml$^{-1}$ (38.76% ± 1.29) for *H. exesa*. At $10^4$ sperm ml$^{-1}$ there was a significant reduction in fertilisation of 80% and 58% for the respective species. Additionally, fertilisation success of *A. austera* and *H. exesa* decreased significantly by 56% and 79% respectively, when salinity was reduced by 7.06 psu. *Ex situ* settlement experiments were then conducted to assess the settlement of their larvae in response to the presence of two crustose coralline algae (CCA) a *Hydrolithon* sp. and *Mesophyllum* sp. and filtered sea water (FSW) control. Settlement in the presence of *Mesophyllum* was not significantly different from FSW, but a significant trend was observed in the presence of *Hydrolithon*, where settlement of both corals peaked. While *H. exesa* post-settlement success was also greatest in the *Hydrolithon* treatment (55.00 ± 10.47%), this was not the case for *A. austera,* which obtained highest post-settlement success in the *Mesophyllum* treatment (21.67 ± 7.23%). However, these trends were not significant. *Acropora austera* and *H. exesa* were still capable of settlement 69 and 75 days after fertilisation respectively in FSW. In general, more settlement occurred on container surfaces than on CCA fragments. Results from this study suggest that the inducing effect of CCA is coral and CCA taxon-specific, and that *A. austera* planulae are more stringent in their settlement requirements.

*In situ* experiments were conducted by attaching settlement tiles to concrete Y-frames on TMR for six months to assess how coral recruitment differs according to method of settlement tile attachment onto concrete y-frames and how the exclusion of herbivores and predators affects coral recruitment onto tiles. A new, grooved settlement tile was designed to provide refuge microhabitats on the top surface of the tiles. In total, 579 recruits were detected on the settlement tiles, with pocilloporids dominating the recruit composition (64%).

Grooved tiles were also used to assess whether coral recruit density varied between different microhabitats adjacent to the tile edge (a narrow, 5 mm gap; a wide, 15 mm gap; and tiles raised above the gap). Most recruitment occurred on the vertical edges and towards the edge perimeter of grooved tiles regardless of treatment. The majority of recruitment on the top surface of tiles occurred in the grooves (74.17%). Coral recruit densities differed significantly between the three edge microhabitats, with recruit density significantly less on tiles adjacent to narrow gaps. Raised tiles and tiles with a wide gap had two- and three-fold more recruits (644.33 ± 149.43 and 979.29 ± 170.88 recruits m$^{-2}$) than tiles with a narrow gap (311.05 ± 80.82 recruits m$^{-2}$). This suggests that the microhabitat associated with the method of tile attachment can have a significant effect on recruitment. Finally, the effect of large herbivores and predators on coral recruitment and the benthic communities was assessed by placing exclusion cages over tiles. Recruit densities had a two-fold reduction when herbivores and predators were excluded. Additionally, CCA cover was also significantly reduced on caged tiles, and the percentage of erect foliose algae, encrusting macroalgae, and turf algae was significantly greater compared to uncaged tiles. This indicates that grazers may assist coral recruitment on TMR.

This study provided the first assessment of fertilisation success in corals at high-latitude in South Africa and the results are related to information on gene flow and reef resilience. The importance of suitable settlement microhabitats and grazers are also highlighted and stress the need for a multi-faceted management approach to coral conservation. Furthermore, from an experimental point of view, the methodological techniques used to quantify *in situ* recruitment, such as settlement surface design and attachment technique, may have important implications in quantifying recruit densities and settlement preferences. Such differences must be considered when comparing the results of recruit densities in studies using dissimilar techniques.

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# Chapter 1:

# General introduction

## 1.1. Persistence of coral reefs in a changing world

Coral reef ecosystems are the most biodiverse ecosystem in the ocean (Connell, 1978; Veron, 1995) which provide an array of ecological goods and services (Cinner, 2014; Moberg and Folke, 1999). Consequently, these ecosystems are of considerable economic value (Costanza et al., 2014) and support the livelihoods of millions of people (Cinner, 2014). The survival of many coral reefs is threatened by the inability of reef-building scleractinian corals to tolerate and recover from local anthropogenic stressors and stressors associated with global climate change (Carpenter et al., 2008; Hoegh-Guldberg, 1999; Hoegh-Guldberg et al., 2007; van Hooidonk et al., 2016; Veron et al., 2009; Wilkinson, 1999). Consequently, a decline in coral abundance (Bruno and Selig, 2007; Gardner et al., 2003), a change in coral community structure (Darling et al., 2013), and a phase-shift in benthic community structure from coral dominance to algal dominance (Roff et al., 2015) has occurred on certain reefs due to the fragility of ecosystem processes which are required for them to survive in a changing world (Mora et al., 2016; Mumby, 2009). However this is not always the case, and coral reefs can recover quite well after disturbance provided key processes, such as recruitment and herbivory remain intact (Gilmour et al., 2013).

The environmental requirements of coral reefs (e.g. shallow enough for sufficient light), render these ecosystems vulnerable to both local anthropogenic and global climate change stressors which can be additive. The effect of local anthropogenic stressors, which include exploitation, sedimentation and pollution, pre-date the effect of climate change stressors created since the industrial revolution (Pandolfi et al., 2003), and can potentially be controlled with effective local management. Climate change potentially poses the greatest threat to coral reefs and a drastic reduction in global carbon emissions is required to mitigate the effect of stressors, such as ocean warming and acidification, to prevent widespread mortality of corals (Hughes et al., 2017). Since stress levels may differ significantly between coral communities, not all reefs will suffer the same fate (Aronson et al., 2005; van Hooidonk et al., 2016) and it is believed that deeper reefs could be potential refuge areas. However, although less susceptible than shallow environments, these too can be compromised by climate change (Frade et al., 2018) and the protection of both deep and shallow reefs is advised (Bridge et al., 2013).

The ability of coral-dominated ecosystems to persist through disturbance events is dependent on their resilience, which is defined by Hughes et al. (2010) as their "capacity to absorb recurrent disturbances or shocks and adapt to change without fundamentally switching to an alternative stable state". Two key components of resilience are resistance (the ability of an ecological community to resist or survive a disturbance) and recovery (the rate a community takes to return to its original condition) (Côté and Darling, 2010; West and Salm, 2003). Key components of resistance include the presence of stress-resistant corals and symbionts, and the occurrence of high annual temperature variability on a given reef, which can promote coral tolerance to irregular temperatures (McClanahan et al., 2012). An understanding of local environmental conditions and the early life stages of corals is imperative for effective reef management (Ritson-Williams et al., 2009) as high-latitude coral communities are commonly isolated (Montoya-Maya et al., 2016; Noreen et al., 2009), which could result in them being slower to recover from disturbance (Fellegara et al., 2013). Furthermore early life stages of corals are more sensitive to environmental stressors in comparison to other life stages (Hedouin et al., 2015).

Coral recruitment (defined here as the introduction of new corals into the population) has been identified as a vital factor in coral recovery (Colgan, 1987; Edmunds and Carpenter, 2001; McClanahan et al., 2012; Mumby and Harborne, 2010) and a key structuring process in coral communities (Connell et al., 1997; Harrison and Wallace, 1990; Hughes and Jackson, 1985; Richmond, 1997). Consequently, an understanding of factors which affect coral recruitment is essential for their effective management and to envisage how they may respond to future environmental changes (Guest et al., 2008; Hughes et al., 1999; Hughes et al., 2003), particularly in terms of coral reef resilience (e.g. Adjeroud et al., 2009; Hughes and Tanner, 2000). However, studies pertaining to the ecological processes involved in coral recruitment have at large been restricted to tropical locations near research stations (see review by Baird et al., 2009) with comparatively fewer studies originating from high-latitude reefs.

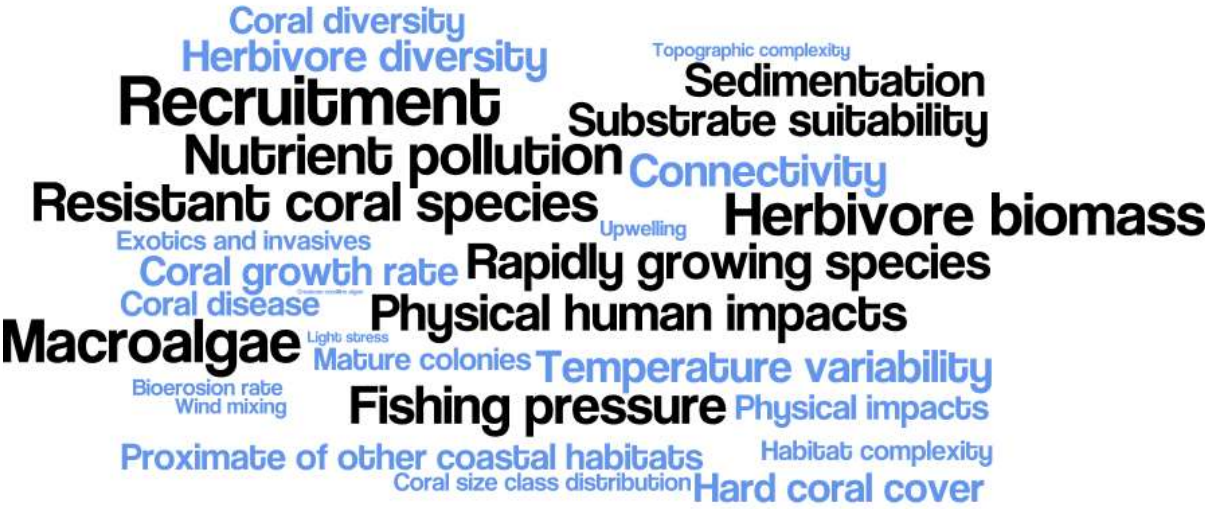

**Fig. 1.1.** Infographic of the top 31 factors reported in the scientific literature to affect the recovery of corals. Font size illustrates the order of importance from large font to small font, and the top ten factors are listed in black (adapted from McClanahan et al., 2012).

## 1.2. Coral recruitment

Coral recruitment occurs by either asexual or sexual reproduction (Harrison and Wallace, 1990; Richmond, 1997). Asexual reproduction of corals may occur by means of polyp bail-out (Sammarco, 1982), colony fragmentation (Foster et al., 2013; Highsmith, 1982) and parthenogenesis (Ayre and Resing, 1986; Stoddart, 1983). All of these facilitate reproduction without the involvement of another colony, but do not add genetic variability to the population as offspring contain the same genetic makeup as their parent colony (Harrison, 2011). Consequently asexual reproduction only prolongs the continued existence of a parental genotype. In contrast, sexual reproduction promotes genetic diversity which is essential for adaptation to a changing environment (van Woesik, 2010) and plays a central role in the speciation of corals (Veron, 1995). Despite these differences, both modes of reproduction can be used in coral restoration techniques to assist coral recovery (Boch and Morse, 2012; Chamberland et al., 2017; Guest et al., 2013; Rinkevich, 1995; Rinkevich, 2014).

Recruitment of corals by means of sexual reproduction is dependent on the production and release of gametes, egg fertilisation, embryonic and larval development, and larval settlement followed by post-settlement survival (Ritson-Williams et al., 2009). Sexual maturity of broadcast spawners is reached after 3-5 years (Babcock, 1991; Baria et al., 2012; Chamberland et al., 2016). The early life stages of corals are particularly vulnerable to high levels of mortality and propagules need to proceed through a 'gauntlet' of barriers which might be encountered during each life stage in order to become successful recruits (Arnold et al., 2010; Chong-Seng et al., 2014).

Corals employ a remarkable diversity of sexual reproductive strategies which can be differentiated into two sexual systems (hermaphroditism and gonochorism) and reproductive modes (spawning and brooding). The result is four patterns of sexual reproduction into which the majority of scleractinian corals can be categorized: hermaphroditic spawners, hermaphroditic brooders, gonochoric spawners and gonochoric brooders (Harrison, 2011). However, although not common, protandry (Loya and Sakai, 2008), bi-directional sex changes (Loya and Sakai, 2008) and even pseudo-gynodioecy have been recorded in corals (Harrison, 1988; Keshavmurthy et al., 2012). Taxonomic patterns of corals have shown that sexual systems are fairly fixed, while reproductive modes are somewhat plastic (Baird et al., 2009). For example, *Pocillopora verrucosa* is a brooder in the Philippines (Villanueva et al., 2008), but a broadcast spawner in Japan (Kinzie III, 1993), South Africa (Kruger and Schleyer, 1998; Massé et al., 2012; Séré et al., 2010) and in the Red Sea (Bouwmeester et al., 2011). In more unique cases, corals can brood and broadcast spawn at one particular location (Ward, 1992).

The manner in which corals sexually reproduce can play a role in the spatio-temporal distribution, composition and abundance of their recruits (Harrison and Wallace, 1990). Simultaneous hermaphroditic broadcast spawning (hereafter referred to as broadcast spawning) is the dominant reproductive pattern among scleractinian corals (87.6% of 404 scleractinians reported in Harrison, 2011). For the purposes of this study, aspects involved in broadcast spawning will be the focus of further discussion, as this is the reproductive strategy used by the majority of scleractinian corals studied to date (Baird et al., 2009; Harrison, 2011), including all scleractinians studied on the high-latitude reefs of South Africa (Kruger and Schleyer, 1998; Massé, 2014; Massé et al., 2013), and the two focal taxa used in this study (Chapter 3 and Chapter 4). For details pertaining to brooding in corals see Harrison and Wallace (1990).

### *1.2.1. Gamete production and spawning*

Broadcast spawners typically have a single annual reproductive season, which involves a six- to fourteen-month oogenic cycle that occurs in temporary gonads located in mesenteries (Baird et al., 2009; Harrison and Wallace, 1990; Veron, 1995). However, some corals may exhibit bi-annual spawning (e.g. Gilmour et al., 2009; Guest et al., 2004; Mangubhai and Harrison, 2008). The investment in the production of coral gametes is dependent on the availability of stem cells, which are traded away from growth and tissue repair to produce gametes (Rinkevich, 1996). The fecundity of coral colonies is dependent on the reproductive output per polyp and the number of reproductively active polyps (Hall and Hughes, 1996). Gamete production can vary spatially within colonies, usually being greater in central polyps compared to the colony edges (Chornesky and Peters, 1987; Wallace, 1985), but there are exceptions to the rule (Nozawa and Lin, 2014). Additionally, not all colonies necessarily partake in a reproductive season (Babcock et al., 1994), consequently fecundity can differ significantly between conspecifics (Sier and Olive, 1994). Corals in areas with greater coral cover have been shown to produce more larvae per square centimeter than corals occupying less dense populations (Hartmann et al., 2018). Environmental conditions have a significant effect on coral fecundity. Stressors such as salinity (Jokiel, 1985), nutrients (Cox and Ward, 2002; Ward and Harrison, 2000), sedimentation, water turbidity (Jones et al., 2015; Kojis and Quinn, 1984; Tomascik and Sander, 1987), coral bleaching (Baird and Marshall, 2002), and colony fragmentation (Zakai et al., 2000) have all been shown to significantly reduce fecundity. Reabsorption of eggs may occur if a coral becomes stressed during gametogenesis (Okubo et al., 2005; Okubo et al., 2009; St Gelais et al., 2016a), or if they are not released during spawning (Sier and Olive, 1994).

Simultaneous hermaphroditic broadcast spawners typically package eggs and sperm from a reproductively active polyp together into positively buoyant egg-sperm bundles, which are synchronously released by polyps and conspecifics annually on a select few nights at a particular location, thereby enabling cross-fertilisation (Harrison, 2011). The reproductive effort of coral polyps (size or biomass of gametes produced) can differ significantly between coral taxa (Harriott, 1983), with as many as 180 eggs found in a single egg-sperm bundle (Richmond, 1997). A significant portion of eggs are comprised of lipids, which provide buoyancy to egg-sperm bundles and energy for embryonic and larval development (Arai et al., 1993; Harii et al., 2007).

Multi-species synchronised spawning is characteristic of most species-rich coral assemblages (e.g. Babcock et al., 1986; Bouwmeester et al., 2014; Guest et al., 2005; Penland et al., 2004; Sola et al., 2016) and results in the formation of spawn slicks comprising gametes from all corals which spawned synchronously. In spite of 30 years of research, the identification of broad-scale cues that initiate spawning events remains contentious (see Keith et al., 2016), but the resulting spawning time is believed to coincide with optimal environmental conditions (Foster et al., 2018; Richmond, 1997). Annual spawning events of different coral taxa are predictable at specific sites, but can differ significantly between locations (Keith et al., 2016; Sorek and Levy, 2014), presumably due to adaptations to particular cues and local environmental conditions (Richmond and Hunter, 1990). Environmental cues are believed to work at progressively finer scales, with water temperature (Keith et al., 2016), lunar cycle (Sweeney et al., 2011), and solar light cycles (Brady et al., 2009) believed to be key parameters which enable conspecifics at a particular location to synchronise gamete release during the same month, day and hour. Aside from water temperature, other environmental parameters such as rainfall (Mendes and Woodley, 2002), wind (van Woesik, 2010), and solar insolation (van Woesik et al., 2006) have been investigated as broad-scale spawning cues and correlated to the month in which corals spawn. However, these parameters are often only assessed in isolation, at a limited geographic scale and replicate years, thereby making it difficult to determine their relative importance. In contrast, the effect that lunar and solar cycles have in determining the day and time of spawning after sunset, respectively, is less contentious due to definitive experimental studies (Jokiel et al., 1985). Cryptochromes enable corals to detect changes in light that occurs during lunar cycles, resulting in the majority of corals spawning between dusk and midnight on a specific day following the full moon, and in some instances, the new moon. Only a few coral taxa have been documented spawning during the day (e.g. Bouwmeester et al., 2011; Bronstein and Loya, 2011; Harii et al., 2001; Muller and Vermeij, 2011). Experimental work has shown that increased hormone levels occur in the surrounding water during spawning, providing a possible chemical cue for conspecifics to spawn (Atkinson and Atkinson, 1992; Twan et al., 2006).

Records from the south western Indian Ocean report coral spawning at Vamizi Island, northern Mozambique, between September and December (Sola et al., 2016). Additionally, inferred spawning has been recorded during March in the Maldives (Sier and Olive, 1994) and *Acropora* species were observed spawning in October at Zanzibar (Franklin et al., 1998), and November in Mauritius (Munbodh et al., 1999). *Fungia danai* corals have been observed spawning during February in the Chagos Archipelago (Mangubhai et al., 2007a). *Acropora* spawning was observed during September in Madagascar (Gress et al., 2014) and during November at Reunion (Massé, 2014). In the north western Indian Ocean, spawning occurs progressively later in the year as reef latitudes increase, with low latitudes experiencing spawning from January to March, mid-latitudes from March to May, and high latitudes from June to September (Howells et al., 2014). However, a latitudinal trend is not evident in the south western Indian Ocean based on present records. For details pertaining to coral reproduction in South Africa see Appendix 1.

### *1.2.2. Planktonic life stages – fertilisation, embryogenesis and larval development*

Following release, egg-sperm bundles float to the water surface where they dissociate and eggs emit attractants which stimulate sperm motility, and fertilisation occurs (Morita et al., 2006). The positive buoyancy of eggs and an abundance of sperm at the water surface enhances the likelihood of fertilisation as gamete concentration from synchronously spawned conspecifics is maximized at the two-dimensional water surface (Moláček et al., 2012). The temporal overlap between viable gametes released from multi-specific spawning events can result in hybridization between certain corals (Fogarty, 2012; Fogarty et al., 2012; Willis et al., 1997). Fertilisation success can differ significantly between genotypic crosses (Baums et al., 2013), and typically peaks within the first three hours of spawning (Babcock and Heyward, 1986; Chui et al., 2014), after which gamete dilution can result in a significant reduction in fertilisation (Chui et al., 2014; Oliver and Babcock, 1992).

Coral fertilisation success can be affected by a parent colony’s pre-spawning condition (e.g. bleaching of parent colonies prior to spawning can compromise sperm motility (Omori et al., 2001). Furthermore the quality of gametes may differ significantly between the nights of spawning (Chui et al., 2014; Hedouin and Gates, 2013). Environmental and biological conditions experienced during coral spawning and embryogenesis are pivotal to reproductive success as positively buoyant eggs and fertilised embryos are ‘naked’, passive particles at the mercy of conditions at the water surface prior to developing into actively swimming larvae (Heyward and Negri, 2012). Success of the pelagic life stages of corals can be compromised by increased water temperature (Albright and Mason, 2013; Bassim and Sammarco, 2003; Chua et al., 2013b; Edmunds et al., 2001; Negri et al., 2007; Randall and Szmant, 2009), pH, (Albright and Mason, 2013; Chua et al., 2013a; Iguchi et al., 2015), salinity (Hedouin et al., 2015; Scott et al., 2013; Vermeij et al., 2006), irradiance (Gleason et al., 2006), turbulence (Heyward and Negri, 2012; Jiang et al., 2015) and pollutants such as oils (Mercurio et al., 2004), eutrophication (Lam et al., 2015) and herbicides (Negri et al., 2005). For a review of the effect of seawater properties on coral fertilisation and the early larval stages see Woods et al. (2014).

The high-latitude reefs of South Africa are typically deeper than tropical reefs and experience greater turbulence at the surface (Schleyer and Tomalin, 2000). This could result in more rapid gamete dilution. Additionally, previous studies have shown that spawning on Maputaland reefs occur during the summer months when peak rainfall is experienced (Kruger and Schleyer, 1998; Massé, 2014). It is predicted that the increased frequency and intensity of rainfall events associated with climate change, could negatively influence fertilisation success through gamete dilution (Hedouin et al., 2015; Oliver and Babcock, 1992) and the creation of hyposaline conditions on the water surface (Scott et al., 2013).

Fertilisation between conspecific genotypes introduces genetic recombination (which is beneficial in changing environments). However, some coral communities cope with low concentrations of conspecific sperm for by self-fertilisation which has ramifications on the genetic structure of coral communities (Shearer et al., 2009).Fertilisation. Barriers do exist to prevent self-fertilisation. For example eggs are only capable of being fertilised after a certain time period (Heyward and Babcock, 1986; Oliver and Babcock, 1992), resulting in low or non-existent levels of self-fertilisation success (Fogarty et al., 2012; Heyward and Babcock, 1986; Knowlton et al., 1997). However, these barriers may break down over time (Heyward and Babcock, 1986). Some corals are capable of self-fertilisation (Bassim et al., 2002; Heyward and Babcock, 1986) and while it is not generally desirable, it can be important for some species, particularly brooders (Brazeau et al., 1998; Gleason et al., 2001). Additionally it has been hypothesized that it is beneficial on geographically isolated reefs where the availability of conspecific gametes is low (Bachtiar, 2001; Bassim et al., 2002). However, where fewer colonies are present, more rapid gamete dilution may occur, limiting fertilisation success in general (Levitan et al., 2004; Oliver and Babcock, 1992).

The free gametes and early embryonic stage of corals are susceptible to high mortality as they constitute a nutritious food source for planktivorous fish (McCormick, 2003; Pratchett et al., 2001; Westneat and Resing, 1988) and are even preyed upon by other mature corals (Fabricius and Metzner, 2004). Fish predation can lead to a 20-36% reduction in the supply of coral propagules (Pratchett et al., 2001). Indeed, whale shark aggregations have been associated with spawning events (Taylor, 1996). However, predation levels vary between coral species as their propagules' palatability differs (Pratchett et al., 2000). In addition, microbial infections can cause planular mortality, which can be indirectly enhanced by macroalgae that increase microbial loads or enhance coral susceptibility to infection (Vermeij et al., 2009). Eggs which are successfully fertilised and have survived this gauntlet mature into embryos which proceed through morula, blastula, and gastrula stages, with completion of embryogenesis marked by the formation of a ciliated, actively swimming planula (Ball et al., 2002).

The period during which larvae are able to settle and metamorphose (i.e. competency period) differs according to reproductive mode employed and coral taxa (Babcock and Heyward, 1986; Szmant and Meadows, 2006; Tay et al., 2011). Brooded larvae are competent to settle immediately after release and are capable of an extended larval duration as they obtain zooxanthellae from parents (Harrison and Wallace, 1990). Broadcast spawners have a pre-competency period, generally do not receive zooxanthellae from their parent colony and typically survive for a shorter duration when compared with brooders (Harrison and Wallace, 1990). These planulae are thus aposymbiotic (Strader et al., 2015) and only appear to acquire zooxanthellae once they settle and metamorphose (Yamashita et al., 2014). Brooded planulae are able to settle after release within centimetres of parent colonies, whereas planulae from broadcast spawners require a developmental period within the water column to reach settlement competency (Richmond, 1997). This developmental period can vary between taxa and can occur as soon as 1-2 days after spawning (Nozawa and Harrison, 2005). Although coral planulae from broadcast spawners have the potential for large-scale dispersal, they tend to settle a lot closer to their natal colony than was originally thought (Miller and Mundy, 2003).

### *1.2.3. Settlement and post-settlement survival*

Coral larvae need to attach to an appropriate substratum, metamorphose into a primary polyp, grow by asexual budding, and survive to sexual maturity to become a successful colony which contributes to future generations. Settlement involves the physical adhesion of planulae by mucus threads (Abelson et al., 1994), flattening of the posterior half of the larva, and deposition of a calcium carbonate exoskeleton during metamorphosis, thereby forming a coral spat. The skeleton deposited after metamorphosis provides a record that settlement occurred and can be used to identify a spat (Babcock et al., 2003; Grasso et al., 2011). The settlement of coral larvae is dependent on both environmental conditions and the response of coral larvae to cues that are effective over short or long distances and vary in magnitude and importance (Gleason and Hofmann, 2011; Jackson, 1991; Maida et al., 1994). Selectivity can differ significantly between coral taxa, which in turn influences a species' role in early successional settlement (Baird and Morse, 2004). Larvae with different fluorescent colours have been found to respond differently to settlement cues (Kenkel et al., 2011). The buoyancy of coral larvae changes from positive to negative as they develop (Szmant and Meadows, 2006; Tay et al., 2011). Combined with local hydrodynamics, this plays an important role in the direction and distance of coral larvae dispersal, and the supply of larvae to a particular site (Gleason and Hofmann, 2011). Coral larvae are weak swimmers (Chia et al., 1984) and their swimming ability is usually not sufficient to overcome local flow so that, although settlement-inducing cues may be present, larvae may not necessarily be able to respond to them due to hydrodynamics that prevent this (Hata et al., 2017). Hydrodynamics also have a significant effect on the ability of coral planulae to adhere to the substratum (Abelson et al., 1994).

Settlement of coral larvae can be a highly selective process and can influence their depth distribution (Baird et al., 2003), but microhabitat selectivity is not always evident (Baird and Morse, 2004; Erwin and Szmant, 2010). For example, it has been suggested that more common coral species show less preference for settlement surface textures (Carleton and Sammarco, 1987). Coral larvae are capable of detecting and responding to reef sound (Vermeij et al., 2010), barometric pressure (Stake and Sammarco, 2003), light (Levy et al., 2007; Mundy and Babcock, 1998a), substratum colour (Mason et al., 2011), chemical cues (Heyward and Negri, 1999), substratum orientation (vertical vs horizontal), and surface micro-structure (Carleton and Sammarco, 1987), which can influence settlement and post-settlement survival of corals. Higher levels of settlement occur in cracks and crevices (Brandl and Bellwood, 2016; Doropoulos et al., 2016; Nozawa, 2008; Whalan et al., 2015). As a result, surface microstructure has been considered in the design of settlement surfaces to assess the settlement of coral larvae in laboratory (Petersen et al., 2004; Tebben et al., 2014; Whalan et al., 2015) and field studies (Hart and Schleyer, 2016; Nozawa et al., 2011; Roeroe et al., 2013).

The importance of waterborne chemical cues has been highlighted in a study which shows varying settlement in response to water chemistry from one meter above degraded, algae-dominated, and pristine reefs (Gleason et al., 2009). A chemical's solubility in seawater and dilution within prevailing currents will determine the distance over which it can act (Gleason and Hofmann, 2011). Long distance cues become increasingly important when attracting coral settlement to degraded reefs in particular (Gleason and Hofmann, 2011). Insoluble chemicals trigger settlement choices at the point of surface contact or within a few centimetres above it, and are important triggers for permanent attachment and larval metamorphosis (Gleason and Hofmann, 2011). Indeed, the power of this relationship has been demonstrated in crustose coralline algae (CCA) which have strong settlement-inducing effects on coral larvae (Heyward and Negri, 1999; Morse et al., 1996; Morse et al., 1988). Yet, the exact chemical cues which trigger these responses remain undetermined and are probably a combination of various triggers acting together (Gleason and Hofmann, 2011). The importance of CCA as a settlement-inducing cue is species-specific and depends on both the coral and CCA species (Harrington, 2004). Indeed, some corals do not require settlement-inducing cues from CCA or microbes and settle readily on inert surfaces (Baird and Morse, 2004; Erwin and Szmant, 2010). In addition to CCA chemical cues, bacterial biofilms on their surfaces and the surrounding substrata may also induce coral settlement (Erwin et al., 2008; Negri et al., 2001). The importance of these biofilms is now well established (Patterson et al., 2016; Webster et al., 2004) and they may either act alone or in conjunction with chemical cues (Negri et al., 2001; Webster et al., 2004). Biofilm composition fluctuates with substratum orientation, time and water depth (Erwin et al., 2008; Golbuu and Richmond, 2007; Webster et al., 2004). In contrast, some biota release chemicals which have an allelopathic effect, thereby inhibiting settlement, e.g. some soft corals (Maida et al., 1995), macroalgae (Baird and Morse, 2004; Birrell et al., 2008b; Diaz-Pulido et al., 2010; Kuffner et al., 2006) and the cyanobacteria *Lyngbya majuscula* (Kuffner and Paul, 2004; Kuffner et al., 2006).

Surfaces suitable for coral settlement and post-settlement survival are often limiting on reefs. The substrata on coral reefs are usually occupied by biota which can out-compete recruits or comprise ephemeral surfaces which can result in dislodgement of the recruits (Nugues and

Szmant, 2006). The benthic cover can differ according to the successional stage on the reef (Smith et al., 2010) and the herbivores present, as grazing regulates macroalgal growth (Burkepile and Hay, 2010; Edmunds and Carpenter, 2001; Hughes et al., 2007). This reduces the risk of overgrowing and smothering of new recruits, which is particularly important in nutrient-rich environments where contending biota often flourish (Birkeland, 1977). Macroalgae further inhibit coral recruitment by releasing chemicals which interrupt or inhibit settlement or increase coral larvae mortality (Birrell et al., 2005). Additionally, macroalgae indirectly affect settlement by housing microbes that can infect coral larvae (Vermeij et al., 2009). Indeed, the majority of studies report negative effects of macroalgae on coral settlement, (Baird and Morse, 2004; Birrell et al., 2008a; Diaz-Pulido et al., 2010; Kuffner et al., 2006), yet chemicals released by the macroalga *Lobophora variegata* have been shown to positively influence *Acropora millepora* settlement, despite its general negative effect on other coral species (Birrell et al., 2008b). Although coral larvae may successfully settle on ephemeral surfaces such as macro- and turf algae (Birrell et al., 2005; Kuffner et al., 2006; Nugues and Szmant, 2006), some species of CCA exhibit epithelial sloughing (Harrington et al., 2004) which inevitably results in recruit dislodgment and mortality. Turf algae also indirectly decrease settlement by trapping sediment which is unfavourable for settlement (Babcock and Davies, 1991; Babcock and Mundy, 1996; Hunte and Wittenberg, 1992).

Although understudied, there is evidence of plasticity whereby recently settled *Pocillopora damicornis* (Richmond, 1985) and *Acropora tenuis* (Kariyazono and Hatta, 2015) propagules are capable of ejecting from their skeletons (polyp bail-out), thereby reverting back to a planktonic phase. *Pocillopora damicornis* is capable of resettling elsewhere (Richmond, 1985), but resettling was not observed in the study on *A. tenuis* (Kariyazono and Hatta, 2015). Post-settlement mortality of coral juveniles is usually extremely high (Babcock, 1985; Fairfull and Harriott, 1999; Rylaarsdam, 1983; Smith, 1992; Szmant and Miller, 2006; Vermeij and Sandin, 2008), within both short (the first 24 hours (Martinez and Abelson, 2013) and long periods (weeks) following settlement (Penin et al., 2010). As recruit size increases, post-settlement mortality declines (Doropoulos et al., 2015; Raymundo and Maypa, 2004) and this is independent of the species of coral which may exhibit dissimilar post-settlement growth rates (Babcock, 1985; Doropoulos et al., 2015; Rylaarsdam, 1983). Aggregated settlement of coral planulae may be a strategy which results in recruits reaching their size-escape threshold faster. Factors which limit post-settlement growth rates such as ocean acidification can further exacerbate post-settlement bottlenecks (Doropoulos et al., 2012a). New coral recruits are generally weaker competitors compared to more mature individuals (Vermeij and Sandin, 2008) and may incur predation from a variety of sources, including fireworms (Wolf and Nugues, 2012), and face competitive challenges from macroalgae (McCook et al., 2001) and some species of CCA (Dunstan and Johnson, 1998; Maida et al., 1994), to name a few. Settlement within grooves, such as those caused by grazing echinoderms (Birkeland and Randall, 1981; Sammarco, 1980), can facilitate post-settlement survival by offering protection from predation (Brandl and Bellwood, 2016; Brock, 1979; Doropoulos et al., 2016). This facilitating role may differ between herbivore guilds, whereby both herbivorous fish and urchins create free space, but urchins may also cause significantly higher levels of post-settlement mortality when their densities are high due to ‘accidental’ recruit mortality during grazing (O’Leary et al., 2013). Intermediate levels of grazing may thus be preferred for optimal settlement (Sammarco and Carleton, 1981) as algal cover is reduced and refuges for settlement are formed (Birkeland and Randall, 1981; Mumby et al., 2007).

## 1.3. Motivation for this study

While assessments associated with the early life stages of corals date back to the early 1900s (see references in Fadlallah, 1983), published studies investigating the reproduction and recruitment of corals within the south western Indian Ocean (SWIO), remain scant compared to other locations. Marginal, high-latitude reefs, such as those situated along the Maputaland coastline of South Africa, constitute unique ‘model’ systems as they occur in sub-optimal environmental conditions compared to those typically associated with tropical coral reefs (Kleypas et al., 1999; Perry, 2003). Nonetheless, they are considered to be potentially important refuges for climate-sensitive reef species (Beger et al., 2014; Greenstein and Pandolfi, 2008; Perry, 2003). South African coral communities, which are of great economic (Laing, 2013) and biological importance (Floros and Schleyer, 2017; Schleyer and Celliers, 2003), are less likely to experience coral bleaching caused by elevated sea surface temperature due to their depth and supply of cool upwelling water (Riegl, 2003). All reefs are dependent on coral reproduction and recruitment, amongst other factors to ensure their perpetuation. However, coral reproduction and recruitment have been shown to diminish at some high-latitude reef (Hughes et al., 2002), thereby highlighting the importance of investigating the dynamics at such locations.

A summary of peer-reviewed articles which have considered coral reproduction and recruitment in the SWIO is provided in Appendices 1 and 2. Reproductive studies have predominantly been confined to assessments of reproductive seasonality, fecundity and documentation of the coral spawning period (Appendix 1). Aspects associated with the early life stages of corals (fertilisation until settlement) are yet to be investigated in the SWIO. Furthermore little effort has been made to assess how ecological processes, such as herbivory, affect the benthic community, settlement and early life stages of corals on marginal, high-latitude reefs. This thesis thus addresses these parameters and aims to advance the limited knowledge of how they affect the early life stages of scleractinian corals at their southern distributional limit on the East African coast by assessing the following:

1. Do sperm concentration and salinity affect the fertilisation success of representative the corals, *A. austera* and *H. exesa*?
2. Does the presence of *Hydrolithon* sp. and *Mesophyllum* cf *funafutiense* crustose coralline algae affect the settlement and post-settlement survival of *A. austera* and *H. exesa* planulae?
3. Do coral recruitment and benthic community differ on the substratum according to surface microhabitat?
4. Does the exclusion of herbivores and predators have an effect on coral recruitment and benthic community structure?

### 1.4. Study species

Assessments of reproductive or early ontogeny dynamics of Scleractinia on the high-latitude reefs in South Africa are currently limited. *Hydnophora exesa* and *Acropora austera* were selected for this study, being considered representative species that are relatively abundant on the high-latitude reefs in South Africa. They have differing life history strategies which may endow them with different adaptive capacity (Obura, 2001) and there is a current lack of knowledge globally regarding the reproduction and early life stages of these two coral taxa. Furthermore, the identification of the annual timing of spawning of *H. exesa*, along with spot assessments of *A. austera*, enabled the early ontogeny of these two species to be investigated (Chapters 3 and 4).

### *1.4.1. Hydnophora exesa* (Pallas, 1766)

*Hydnophora exesa* is a common scleractinian coral which occurs on protected slopes and in lagoons in the Indian, Pacific and Atlantic Oceans (Sheppard et al., 2014; Veron, 2000). While colonies may be submassive, encrusting, laminar or sub-arborescent depending on location, they are only encrusting on the high-latitude reefs of South Africa (Hart pers. obs.). It is the third highest in relative abundance (14.6%) on the upper fore-reef of Two-mile Reef, but becomes less common on the fore-reef, reef flat, and pinnacles respectively (Celliers, 2001). There is scant information on the reproductive dynamics of the genus *Hydnophora*. *Hydnophora exesa* has been observed to be a hermaphroditic broadcast spawner on the Great Barrier Reef, where it has been observed to spawn 1:55 hr after sunset on the 6th, 7th, and 8th night after full moon (NAFM) at Magnetic Island (Babcock et al., 1986) and 1:44 hr after sunset on the 5th NAFM, on reefs surrounding Orpheus and Pelorus Islands (Baird, 2001). In addition, *Hydnophora rigida* has been observed to spawn 3-6 NAFM at Lizard Island (Babcock et al., 1986). Elsewhere, Bachtiar (2001) showed that *Hydnophora rigida* is a simultaneous hermaphroditic broadcast spawner in Indonesia, with spawning predicted to occur after the November full moon based on the disappearance of mature eggs in December. Tagged colonies which spawned in November were found to contain gametes again two months later, indicating that this species may undergo more than one gametogenic cycle in a year (Bachtiar, 2001), or that their gametogenic cycle may last 10 months.

### *1.4.2. Acropora austera* (Dana, 1846)

*Acropora austera* is found in the Indian and Pacific Oceans, ranging from the Red Sea, Gulf of Aden and southwest Indian Ocean, across the northern Indian Ocean to Southeast Asia, Japan and the East China Sea, and the West and Central Pacific Ocean (Aeby et al., 2008). Despite occurring in a wide range of reef environments, *Acropora austera* is typically uncommon except on upper reef slopes where it is exposed to water turbulence and it has an arborescent growth form (Veron, 2000). As a result, this species is predominantly found between depths of 0.5 and 20 m (Aeby et al., 2008). This species forms significant patches on reef crests and flats in South Africa and, on TMR, reaches a peak abundance of 7% on the reef flat, but diminishes in abundance on pinnacles and the upper fore-reef (Celliers, 2001). An overall mean density of 0.08 colonies $m^{-2}$ has been found on Maputaland reefs, with colonies ranging in size from 3.5-130 cm and the smallest size of a sexually mature colony found at 9.5 cm (Montoya-Maya et al., 2014). However larger stands in excess of 8 m diameter have been observed (Hart pers. obs.). This species seems to be dynamic, and was once dominant on Five-mile Reef (Celliers and Schleyer, 2008), where it constituted 43.9% of the cover of hard corals on the reef crest. The majority of this has subsequently vanished (Schleyer pers. comm.). *Acropora austera*, is one of the few corals that may be responsible for reef framework production on South African reefs. It forms large, monospecific stands, which increase in size with an increase in depth (Riegl and Riegl, 1996) Although *Acropora austera* has a fast linear extension growth rate of 2.45 cm $y^{-1}$, the skeletal structure is fragile and susceptible to storm and diver damage (Grimmer, 2011; Riegl and Cook, 1995; Riegl and Riegl, 1996). This species broadcast spawns locally (Massé, 2014), further north at Vamizi Island in northern Mozambique (Sola et al., 2016) and at Moorea in French Polynesia (Carroll et al., 2005). Acroporids, in particular *A. austera*, have been shown to constitute nursery habitats for fish on local reefs (Floros and Schleyer, 2017).

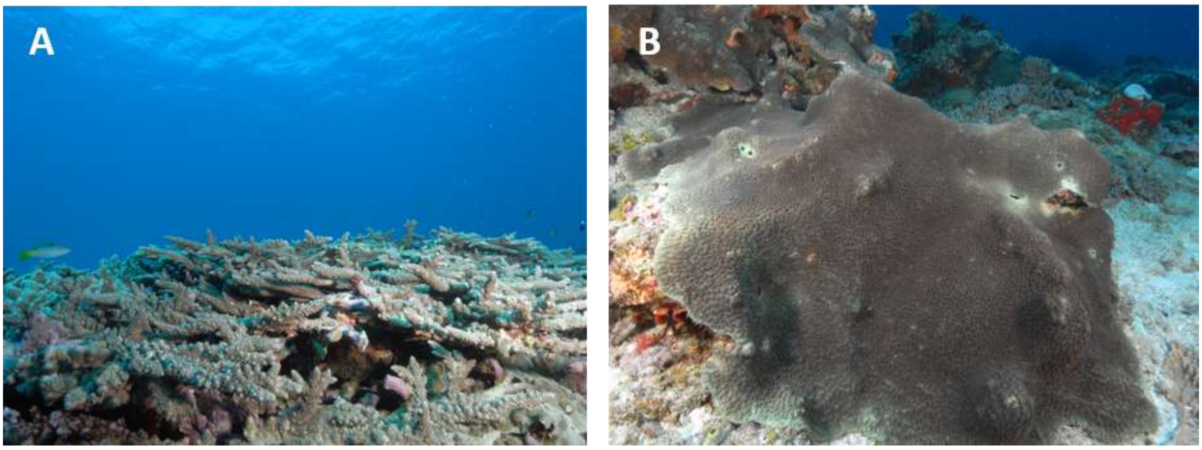

**Fig. 1.2.** *Acropora austera* (A) and *Hydnophora exesa* (B) colonies on Two-mile reef, Sodwana Bay.

## 1.5. Chapter overviews

This thesis consists of six chapters which cover a combination of field and laboratory work. A literature review and background to the rationale with research question and study aims are provided in Chapter 1. An overview of the study location and the global materials and methods used in this thesis are provided in Chapter 2. The fertilisation ecology of two representative scleractinians is investigated in Chapter 3. This is followed by an *ex situ* assessment of whether two crustose coralline algae taxa induce the settlement of coral larvae of the two focal coral taxa in Chapter 4. An *in situ* assessment of the spatial dynamics of coral recruitment and the effect of herbivore and predator exclusion on a focal high-latitude reef in South Africa is provided in Chapter 5. Finally a conclusion is provided in Chapter 6. As chapters were prepared for publication in peer-reviewed journals, some repetition was unavoidable.

# Chapter 2:

# Global materials and methods

## 2.1. Maputaland marginal high-latitude reefs and coastline

Coral-dominated reefs extend down the east coast of Africa and reach their southern distributional limit along the Maputaland coastline in northern KwaZulu-Natal, South Africa (Riegl et al., 1995). Consequently, the high-latitude coral communities on Maputaland reefs are among the southernmost coral-dominated reefs in the world (Fig. 2.1). These dispersed reefs are situated ~700 m offshore on the narrow (~3 km wide) continental shelf, parallel to the Maputaland coastline, which is straight and comprised of sandy beaches backed by elevated dunes (Mitchell et al., 2005) with intermittent aeolianite or rocky points (Anderson and Bolton, 2005). Smaller rivers drain into an inland lake system behind the dune-line, which resulted from sea level changes over a number of ice ages (Mitchell et al., 2005). No large rivers flow into the sea in the vicinity of the Maputaland reefs (Schleyer, 2000) and horizontal water clarity is seldom less than 15 m (Ramsay, 1991). However, tropical cyclones can occasionally reach these Maputaland reefs between September and February, resulting in swells of 10 m and flood damage from heavy rainfall of as much as 700 mm over a three day period (see Hunter, 1988; Maud, 1980). Distinct bands in sediment cores collected on a Maputaland reef provide evidence of flooding events which could have resulted in the transport of sediment from St. Lucia Estuary northwards to Sodwana Bay (Hayman, 2015).

Maputaland reefs are comprised of eroded Pleistocene dune and beach rock sequences (Ramsay, 1996; Ramsay and Mason, 1990). The substratum is predominantly flat with low pinnacles and shallow drop-offs and gullies. Few pinnacles approach the surface, with the majority of the reef structure lying between 9-34 m (Ramsay and Mason, 1990); the distinct zonation of true coral reefs is absent (Ramsay and Mason, 1990; Riegl et al., 1995). They are not true accretive reefs (Riegl et al., 1995) and are marginal reefs with a thin veneer of coral growth (Ramsay and Mason, 1990; Schleyer and Celliers, 2003).

Decreased water temperature, light and carbon saturation state are believed to be key factors which limit coral growth and reef accretion at high-latitudes (Kleypas et al., 1999). However, coral growth rates on Maputaland reefs do not seem to be restricted as the growth rates of *Porites lutea* (Ramsay and Cohen, 1997) and *Acropora austera* (Grimmer, 2011), are comparable to more tropical regions. Instead, large swells regularly damage both living and dead corals (Grimmer, 2011; Riegl, 2001) and the high turbulence experienced on the reefs results in bio-erosion and sediment resuspension rather than accretion and cementation (Grimmer, 2011). Three submarine canyons breach the shelf in the Sodwana Bay region; Jesser, Wright and White Sands Canyons (Ramsay, 1994) which feed cooler, upwelled water that potentially limits coral bleaching (Riegl, 2003). Unlike elsewhere in East Africa, the 1998 bleaching event affected <1% of the hard corals on the South African reefs, and relatively minor bleaching was recorded in 2000, 2002, 2010 and 2016 (Celliers and Schleyer, 2002; Floros et al., 2004; Porter, 2018)

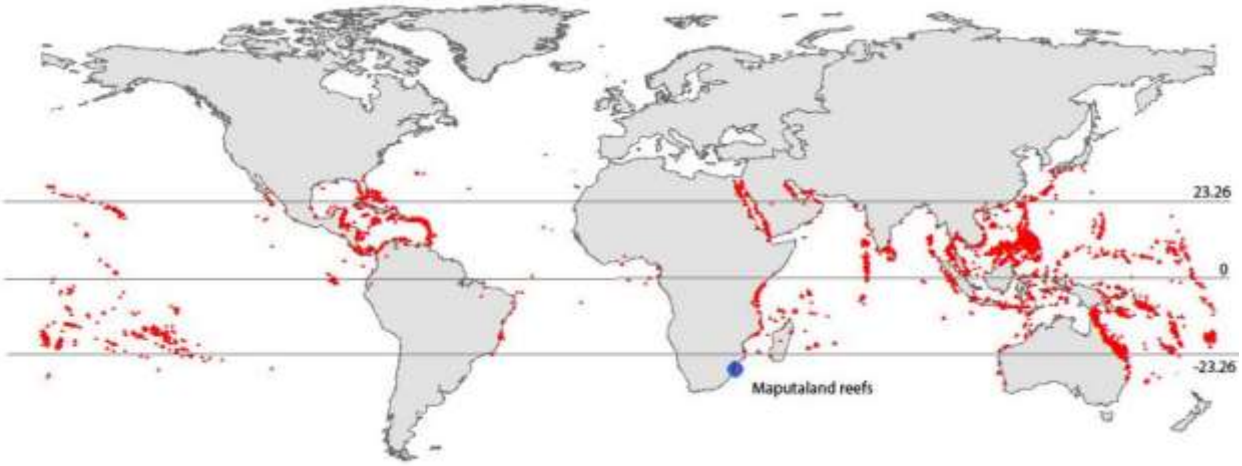

**Fig. 2.1.** Global distribution of coral reefs, including marginal reefs. Map comprised of data from ReefBase (http://www.reefbase.org/gis_maps/datasets.aspx).

## 2.2. Spatial structure and management of reefs

Maputaland reefs are located within two adjoining Marine Protected Areas (MPAs) that constitute the greater marine component of the iSimangaliso Wetland Park (iSWP), a United Nations Educational, Scientific and Cultural Organisation (UNESCO) World Heritage Site, which spans 155 km and extends 3 nautical miles offshore. The Maputaland MPA (proclaimed in 1986), and the St Lucia MPA (proclaimed in 1979) extend from Kosi Bay down to White Sands Canyon, and from White Sands Canyon down to Cape St. Lucia respectively. Spatially, Maputaland reefs have been partitioned into three geographical complexes (northern, central, and southern) and comprise restricted-use and sanctuary zones which fall under the Marine Living Resource Act. Human activities are prohibited in sanctuary zones. In contrast, restricted zones occur in the central complex, where recreational fishing (boat- and shore-based), spearfishing and SCUBA diving are permitted. An exception is Two-mile Reef where fishing may occur at depths >30 m, and SCUBA diving is permitted. Boat-based fishing is restricted to gamefish species, while shore-based fishers are allowed to catch both game and reef fish. The majority of the subtidal reefs are only accessible by vessel and no anchoring is allowed. The central complex at Sodwana Bay is a focal point for boat-based fishing and recreational SCUBA diving which generates revenue in excess of R33 261 836 and R8260224 respectively (Laing, 2013). An increase in diving pressure on these reefs during the 1980s and 1990s resulted in measurable damage and subsequent recommendations on sustainable diving limits (Schleyer and Tomalin, 2000). The mean yearly number of dives conducted on reefs in the central complex from 2012-2015 was 63174 (Olbers pers. comm.).

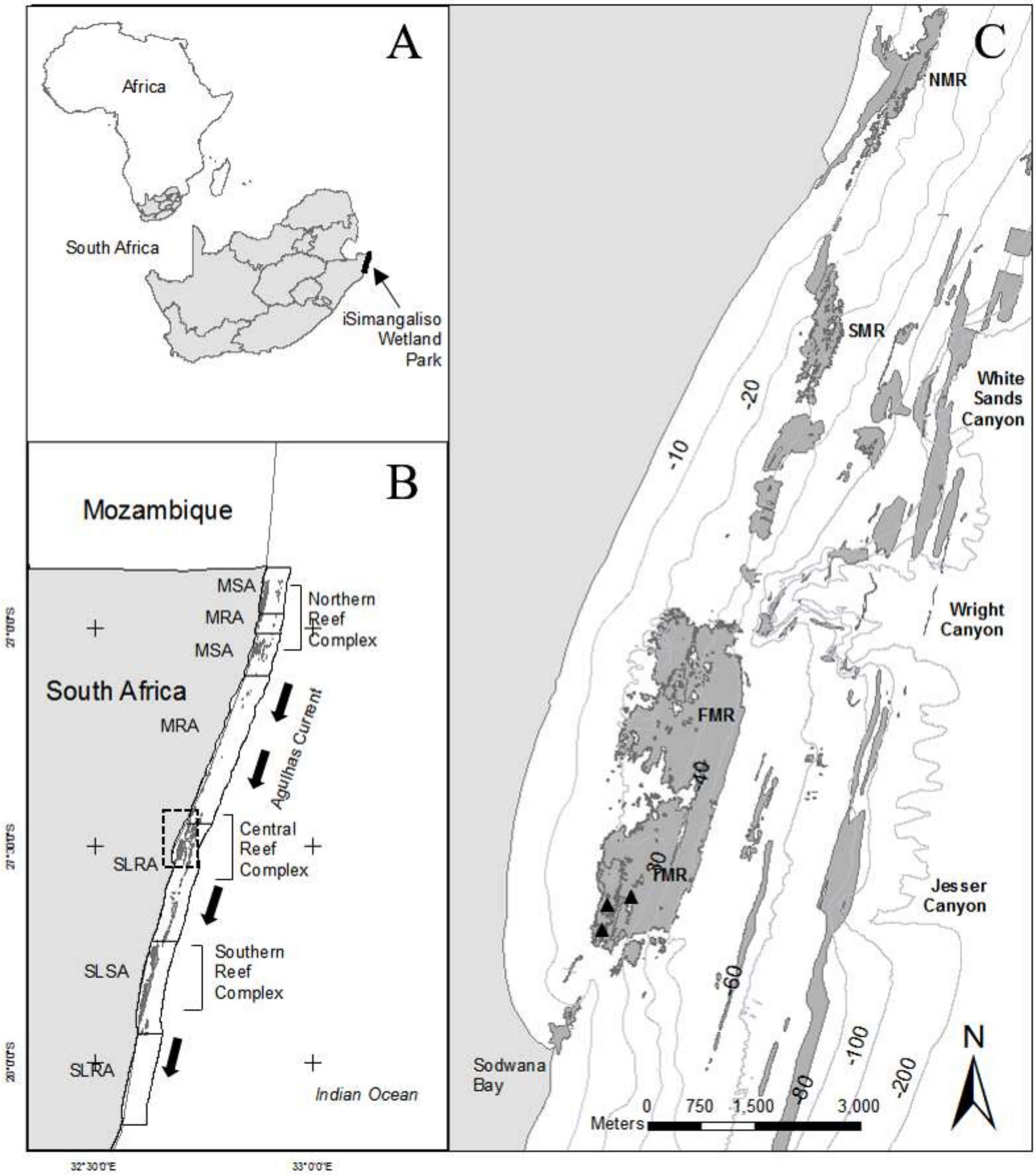

**Fig. 2.2.** Location of the iSimangaliso Wetland Park on the Maputaland coastline of South Africa (A), with (B) the spatial separation of the northern, central and southern reef complexes within the protected area (SLRA = St. Lucia Restricted Area, SLSA = St. Lucia Sanctuary Area, MRA = Maputaland Restricted Area, MSA = Maputaland Sanctuary Area); and (C) the location of the prominent reefs within the central complex (TMR = Two-mile Reef, FMR = Four-mile Reef and NMR = Nine-mile Reef). The three monitoring sites used in this study on TMR are indicated with solid triangles.

### 2.3. Currents, upwelling, swells and tides

The Agulhas Current, a typical western boundary current, flows southward along the shelf edge of the east coast of South Africa with a mean velocity of 1.4 m/s, conveying warm tropical and subtropical water southwards (Hutchings et al., 2002; Lutjeharms, 2006, Fig. 2.3B). The current flow on the reefs is predominantly north-south, with occasional reversal currents due to southerly winds (Morris, 2009). A northern counter-current exists inshore which is generated by winds and wave refraction (Morris, 2009). This feeds sediment to the beaches and large coastal dunes on the shores of this coastline (Mitchell et al., 2005). Upwelling of cooler water occurs along the narrow continental shelf and may be transported to inshore reefs on the shelf (Morris, 2009). The high energy Maputaland coastline (Mitchell et al., 2005; Riegl et al., 1995) receives substantial swells which are predominantly >1 m (Celliers, 2001; Schleyer, 1999). Additionally, large storm swells originate in the Mozambique Channel and can result in or breaking water on the shallower reef areas (Riegl, 2001). Current flow and surge generated by swells results in considerable water movement on the reefs, but only weak tidal currents occur on the reefs due to their depth. The reefs are exposed to a semi-diurnal tidal regime, with an average tidal range of ~0.5 m to 2 m during spring and neap tides respectively.

### 2.4. Precipitation and seawater physico-chemical parameters

Of the total rainfall, 61% falls during the austral summer from December to March (Fig. 2.3.A), which coincides with the reproductive period of corals in the region (Chapter 1.4). A Star-Oddi Starmon underwater temperature recorder was installed at a depth of 18 m on Nine-mile Reef in 1993 to record long-term changes in water temperature. Hourly average readings taken from minute recordings between 1993 and 2000 showed an increase of  0.15°C p.a., after which the temperature decreased by 0.07°C p.a. up until 2008 (Schleyer et al., 2008). A recent update of this ongoing dataset has indicated that water temperature at the study site has been decreasing by 0.03 °C p.a. between 2000 and 2016 (Porter and Schleyer, 2017). Over the past five years (Dec 2012-Dec 2017), the overall mean temperature has been 24.25 ± 1.82°C (SE). A consistent seasonal temperature pattern is evident, ranging from the lowest monthly average of 21.34°C in August to the highest monthly average of 26.27°C recorded in February (Fig. 2.3.B). Salinity values for Maputaland reefs have been reported to range from 34.33-35.92 and as predicted for their high-latitude location these reefs experience extremely low ΩAr concentrations in winter (mean: 3.00±0.37 SD), slightly higher in summer (mean: 3.54±0.36 SD), which is anticipated to limit their accretion (Hayman, 2015; Kleypas et al., 1999).

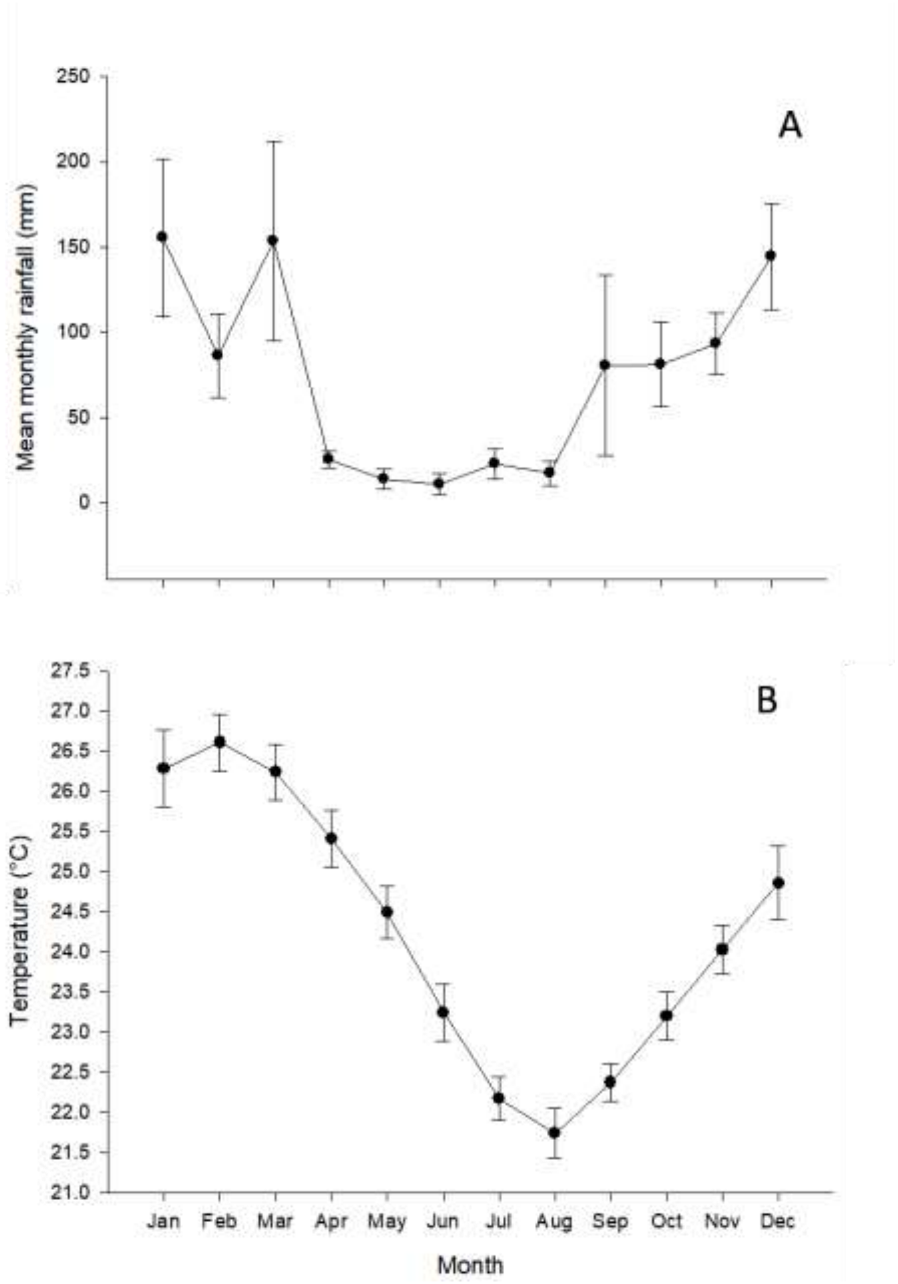

**Fig. 2.3.** Monthly mean ± SE (A) rainfall recorded at Mbazwana Airfield ~3 km from Two-mile Reef (2012-2015) and (B) water temperature recorded at 18m depth on Nine-mile Reef within the central reef complex at Sodwana Bay during the study period (2011-2016). Rainfall and seawater temperature data were provided by the South African Weather Service and from the Oceanographic Research Institute respectively.

## 2.5. Biodiversity

Maputaland reefs comprise a blend of both tropical and temperate marine organisms (Schleyer and Celliers, 2003). Coral communities on Maputaland reefs attain a high level of biodiversity of Indo-Pacific corals, with soft coral cover comprising relatively few species (39 species) exceeding that of the more diverse scleractinian cover (93 species) over most of the reef area (see Schleyer and Celliers, 2003). Collectively, hard and soft corals constitute the majority of the living epibenthic cover (26.9±15.0 % and 32.0±11.9 % respectively) (Celliers and Schleyer, 2008).The diversity and percentage cover of corals reduces drastically further south of Leven Point (Schleyer, 1999; Schleyer et al., 2006). Long-term monitoring of the benthic community cover on NMR has revealed a reduction of 0.95% pa in soft coral cover in an ongoing decline (Porter and Schleyer, 2017). In contrast, an increase in hard coral cover of 0.26% pa has occurred, which is largely attributable to their increase in cover between 1993 and 2005, as the overall hard coral cover has remained constant at around 18% for the last nine years (Porter and Schleyer, 2017). Seaweed communities on the Maputaland reefs are structurally and floristically similar to other tropical coral reefs and mainly consist of compact turfs. A total of 104 non-coralline macroscopic algal taxa have been recorded on shallow subtidal reefs at Sodwana Bay, comprising 82 Rhodophyta, 14 Chlorophyta and eight Phaeophyta (Anderson et al., 2005). *Lobophora variagata* and non-geniculate corallines are dominant in the seaweed assemblage on TMR (Gersun et al., 2016).

The overall fish species richness on South African coral reefs is comparable to that of other reefs in the Western Indian Ocean, with six families found to contribute more than 50% towards the fish community composition; namely Labridae, Acanthuridae, Chaetodontidae, Lutjanidae, Pomacentridae and Serranidae (Floros et al., 2013). The fish community structure on Maputaland reefs has been found to differ significantly according to reef protection status, with greater abundance on sanctuary reefs compared to open reefs (Floros et al., 2013).

## 2.6. Study reef

The collection of gravid corals for experimental work conducted in Chapters 3 and 4, and the attachment of settlement tiles used in Chapter 5, was conducted on TMR, the largest reef within the central complex. This reef covers approximately 1.9 km$^2$, with a maximum length and width of 2.1 km and 0.9 km respectively (see Ramsay and Mason, 1990). This reef is the closest to the boat launch site at Jesser Point and, as a result receives the greatest diving pressure (Riegl and Riegl, 1996; Schleyer and Tomalin, 2000). Consequently TMR is anticipated to have the highest chance of becoming degraded within this reef complex (Celliers, 2001). The reef structure of TMR is typical of other Maputaland reefs, ranging in depth from 6–10 m on its shallowest pinnacles, to 14–19 m on extensive reef flats, and 24–27 m at the outer edge of the fore-reef (Celliers and Schleyer, 2008).The majority of TMR is populated by the dominant benthic community found on the high-latitude reefs in South Africa (Celliers and Schleyer, 2008), with scleractinians constituting 29±7.8% cover (Celliers, 2001).

### 2.7. Collection and husbandry of gravid *Acropora austera* and *Hydnophora exesa* colonies for gamete harvesting and *ex situ* experimental work

Spot assessments of the reproductive status of six *A. austera* and *H. exesa* colonies were conducted five nights prior to the full moon in December 2014, January 2015, February 2015, and March 2015 to enable the collection of gravid colonies for *ex situ* experimental spawning work (Chapters 3 and 4). The timing of reproductive sample collection was based on previous work which had established that gamete release of broadcast spawning corals occurred in January, February or March (Kruger and Schleyer, 1998; Massé, 2014; Massé et al., 2013). Stainless steel corers with an inner diameter of 18 mm and sharpened at one end were used to collect core samples from *H. exesa* colonies by driving corers 2 cm into colonies with a hammer. This enabled sufficient material to be collected to obtain an accurate assessment of the reproductive status of colonies, but minimized the amount of damage to colonies during sample collection (Fig. 2.4). Reproductive samples were taken from *A. austera* branches with side-cutters. Samples were only collected from colonies greater than 40 cm minimum diameter to ensure their maturity. Reproductive samples from both species of corals were collected from the central area of colonies, as fecundity can be significantly reduced towards the edge (Chornesky and Peters, 1987). In addition, *A. austera* branches were cut at least 5 cm away from the branch tip to ensure reproductively active material was collected. The colour of oocytes was used to predict the month in which colonies were anticipated to spawn (Guest pers. comm.). Both *A. austera* and *H. exesa* colonies contained pigmented oocytes when they were assessed two days prior to the full moon in March 2015 (Fig. 2.5).

Hand-sized fragments (~20 cm width) from six *A. austera* and *H. exesa* colonies were collected from TMR at a depth of between 11-12 m a day before the full moon in March, as this immediately preceded the predicted spawning period of these species. Fragments were packaged individually into plastic bags filled with 2/3 water and 1/3 oxygen and transported to the ORI research aquarium in fibreglass coolers. Fragments were acclimated and added to two indoor 1400 L (200 cm x 100 cm x 70 cm) temperature controlled (26±0.5°C), flow through tanks (0.024 l/hr) illuminated with Odyssea T5-120 lighting (150 $\mu Em^{-2}s^{-1}$) on a 10 hr light cycle from 8:00-16:00. Fragments were housed on Eggcrate sheeting, positioned ~40 cm below the water surface. A weighted cylinder (inverted 20 L bucket with the base removed) was placed around each colony just before the lights turned off (Fig. 2.6). These allowed water exchange from below but captured spawned gametes at the surface once they were released. Details regarding the processing of gametes for fertilisation experiments and larval rearing are provided in Chapter 3 and 4.

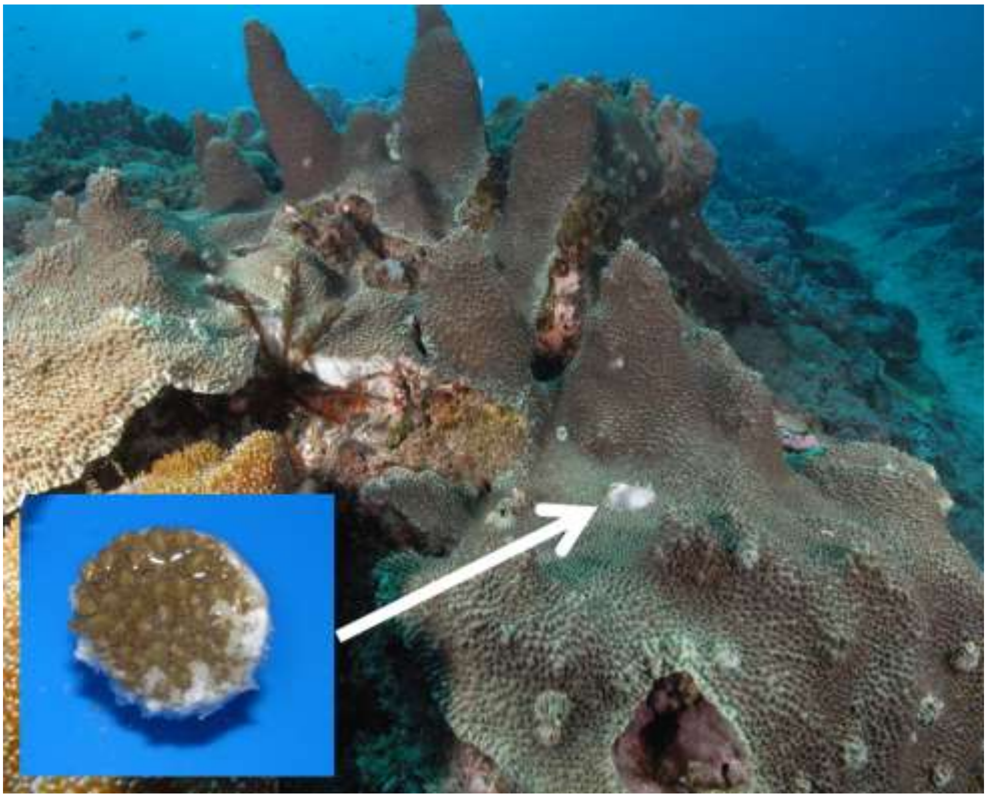

**Fig. 2.4.** *Hydnophora exesa* sample collected with a corer to determine reproductive status.

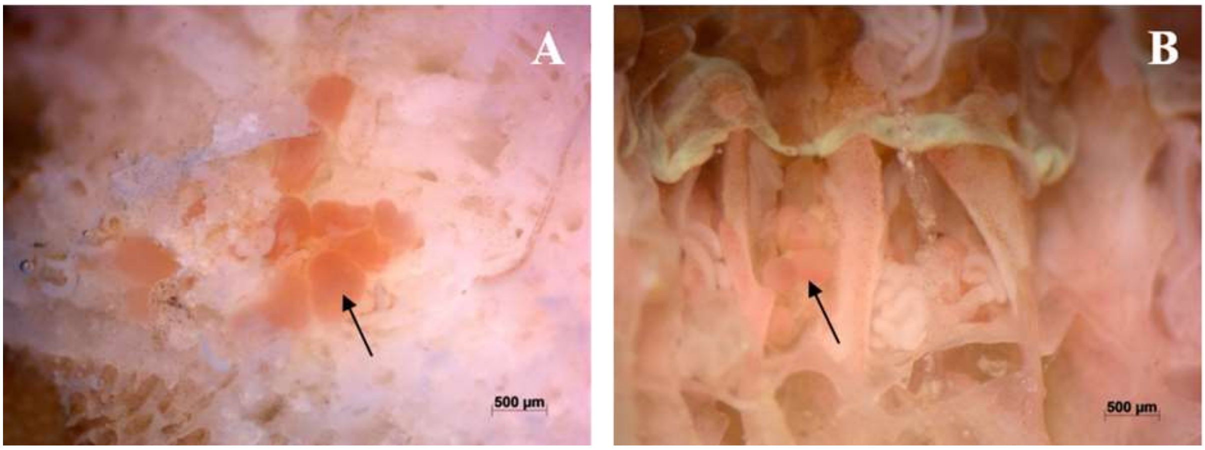

**Fig. 2.5.** Pigmented *Acropora austera* (A) and *Hydnophora exesa* eggs (B) which indicate that colonies were gravid and anticipated to spawn after the next full moon.

**Fig. 2.6.***Acropora austera* (A) and *Hydnophora exesa* (B) moments prior to spawning and the collection of gametes from the water surface (C)

# Chapter 3:

# Fertilisation ecology of *Hydnophora exesa* and *Acropora austera*

## 3.1. Abstract

The successful fertilisation of coral gametes is the first step in a new colony's life but the dynamics of this process is dependent on the coral's reproductive strategy and the environmental setting at the time of spawning. Broadcast spawning corals typically synchronously release gametes as positively buoyant egg-sperm bundles which float to the surface and dissociate. This provides a narrow time-frame for fertilisation to occur before sperm become too diluted or die. Here, *in vitro* fertilisation experiments were conducted on two scleractinian broadcast spawning corals, *Acropora austera* and *Hydnophora exesa,* situated at their distributional limit in South Africa. Their dependence on sperm concentration ($10^6$-$10^2$sperm ml$^{-1}$) and salinity (17.65 psu to 35.29 psu) for successful fertilisation were assessed. An equal contribution of gametes from four colonies were combined for each species, following rinsing, and left for 3 hrs under sperm concentration and salinity treatment levels. Fertilisation success was then quantified by calculating the proportion of cleaved embryos. Fertilisation success of both *A. austera* and *H. exesa* diminished with a reduction in sperm concentration. Fertilisation success of *A. austera* and *H. exesa* was highest at $10^6$ and $10^5$ sperm ml$^{-1}$ respectively (56.46% ± 0.83 and 38.76% ± 1.29, mean ± SE), with a significant 80% and 58% reduction for the respective species occurring at $10^4$ sperm ml$^{-1}$. A reduction in surface salinity by 7.06 psu from ambient levels on the night of spawning significantly reduced the fertilisation success of *A. austera* and *H. exesa* by 56% and 79% respectively. This study provides the first assessment of fertilisation success of corals on a high-latitude reef in South Africa with implications for reef resilience and elucidates differences among these two representative coral species from reefs which are typically turbulent, deeper and contain less coral cover than tropical counterparts.

## 3.2. Introduction

Fertilisation of coral gametes following sexual reproduction enables corals to adapt to changing environments. Simultaneous hermaphroditic broadcast spawning is the dominant reproductive pattern among scleractinian corals (87.6% of 404 scleractinians reported in Harrison, 2011) whereby polyps release their gametes on a select few nights each year for external fertilisation (see Baird et al., 2009; Guest et al., 2008; Harrison, 2011; Richmond and Hunter, 1990). Gametes are typically packaged together as egg-sperm bundles, bound together by mucous from eggs. Bundles float to the water surface after release, due to the lipid content of eggs, where dissociation occurs and cross-fertilisation of gametes to occur. Egg-sperm bundles are therefore an efficient strategy that maximises the chance of gamete encounters (Padilla-Gamiño et al., 2011) as the time in which fertilisation can occur  is limited by the aging of gametes and sperm dilution (Oliver and Babcock, 1992). Eggs play a role in sperm attraction, activation, chemotaxis and suppression (Morita et al., 2006). Fertilisation of gametes is dependent on both the status of parent stock (for example proximity of mates (Levitan and Petersen, 1995), fecundity (Chui et al., 2014), and synchrony in the release of gametes from parent corals (Carlon, 1999)) and the environmental conditions, such as wind and water turbulence during spawning (Padilla-Gamiño et al., 2011). Bundles are broken up quicker in rough surface conditions, thereby shortening the pre-competency period before fertilisation can occur. Investigations into the stressors which disrupt reproductive success of corals are needed as these may not necessarily affect mature coral colonies, but can compromise reproduction and the subsequent recruitment of new genetically diverse individuals. Therefore this study considered two factors which could potentially affect fertilisation success of corals, namely reduced sperm concentration and hyposalinity.

### *3.2.2. Effect of sperm concentration on fertilisation success*

The majority of reef-building corals mass spawn in synchrony, driven by the lunar cycle, which probably results in increased fertilisation success (Babcock et al., 1986; Hayashibara et al., 1993). Sperm have a relatively limited life span after egg-sperm bundles have dissociated (Knowlton and Jackson, 1993) and rapidly become diluted, thereby decreasing the occurrence of sperm-egg collisions (Levitan and Petersen, 1995). Although *in vitro* studies have shown that coral gametes can successfully fertilise as much as six hours after spawning (Omori et al., 2001), they did not take into account the progressive dilution of gametes over time which can result in a reduction of the fertilisation window to less than an hour. Many broadcast spawning corals' sperm concentrations range between $10^5$ and $10^6$ sperm $ml^{-1}$ after release (Nozawa et al., 2015; Oliver and Babcock, 1992), with a reduction in fertilisation success below $10^5$ due to sperm limitation, or above $10^7$ due to polyspermy (Marshall, 2006). Of concern are the results of a study which has indicated that a 50 fold increase in sperm concentration is required to achieve comparable fertilisation success when temperature and $pCO_2$ are increased to levels predicted to be reached by the end of this century (Albright and Mason, 2013).

### *3.2.3. Effect of salinity on fertilisation success*

A consequence of the release of positively buoyant egg-sperm bundles by broadcast spawners is that conditions on the sea surface have a significant effect on the fertilisation success of gametes and their subsequent embryonic development (Heyward and Negri, 2012; Ricardo et al., 2015). One such factor is the periodic reduction in salinity of ocean surface water due to riverine input and rainfall, which are predicted to become more prevalent due to increases in the frequency and severity of storms associated with climate change (Du Plessis and Burger, 2015; Trenberth, 1999). Indeed, coral spawning has been observed during rainfall (Harrison et al., 1984; Nozawa, 2012b, Hart pers observation), which has resulted in hyposalinity of the surface layers (Hedouin et al., 2015; Vermeij et al., 2006). Changes in surface salinity due to rainfall are dependent on the amount of rain, wind speed (Drushka et al., 2016) and the size of raindrops, whereby smaller drops cause a large change in surface salinity, but a much less pronounced change at depth due to less mixing (Katsaros and Buettner, 1969). As a result of its density, low salinity water generally remains at the surface. Although understudied, osmotic stress has been shown to result in a reduction in the fertilisation success of corals, with indications that their tolerance is taxon specific (Hedouin et al., 2015; Scott et al., 2013; True, 2012; Vermeij et al., 2006). Few studies have investigated this aspect, with a limited number of coral taxa considered (Hedouin et al., 2015; Humphrey et al., 2008; Scott et al., 2013). The fertilisation of gametes is more affected by hyposalinity than the subsequent embryonic development, highlighting the need for investigations during this vital reproductive process (Hedouin et al., 2015).

### *Study aims*

While the production of coral gametes (Kruger and Schleyer, 1998) and larval settlement (Glassom et al., 2006) have been described on the high-latitude reefs of South Africa, there has been no investigation of their fertilisation success. In this study we assessed how a reduction in sperm concentration and water salinity affect the fertilisation success of *Acropora austera* and *Hydnophora exesa*, from a marginal reef in South Africa.

## 3.3. Materials and methods

### *3.3.1. Study site and coral gamete collection*

Fragments from six gravid colonies of *A. austera* and *H. exesa* were randomly collected from Two-mile Reef (TMR) at Sodwana Bay, South Africa (27°33’28”S; 32°41’10”E) a week before the full moon of their predicted month of spawning. Fragments were transported in fibreglass coolers to the Oceanographic Research Institute at uShaka Sea World (29°52’06”S; 31°02’39”E), where they were collectively maintained on a rack (~ 40 cm bellow the water surface) in two 1400 l flow through aquariums with T5 lighting (150 $\mu Em^{-2}s^{-1}$) on a 10 hr light cycle from 8:00-16:00. Submersible pumps provided water movement in the aquarium (See Chapter 2.7 for further details).

Weighted cylinders were placed around each colony before dusk to contain the spawn released from each colony (Fig. 2.6), thereby enabling selective cross-fertilisation experiments (described below) to be conducted. Corals were inspected briefly every 15 minutes after the ‘gamete collectors’ had been installed to determine coral setting and spawning times. Gamete collectors were briefly raised from the underlying rack during each inspection before spawning occurred to enhance water exchange to the corals and submersible pumps were turned off at the first sign of corals setting. Gametes from both species of coral were collected over two consecutive nights that they spawned (two and three nights after full moon for *H. exesa* and six and seven nights after full moon in March 2015 for *A. austera*). For both species, a minor spawn occurred on the first night, with fewer corals participating and each releasing less gametes than the second night of spawning. The sperm concentration experiments for both coral species were conducted on the first night of spawning, and the salinity and self-fertilisation experiments were conducted on the second night of spawning (See sections 3.3.2, 3.3.3 and 3.3.4 below). For all experiments, spawned colonies were each left to spawn for ~20 min once spawning had commenced, after which egg-sperm bundles from each colony were harvested off the water surface within gamete collectors with plastic cups, minimizing the amount of water collected in the process (Fig. 2.6). This was done to enable the collection of egg-sperm bundles before they naturally separated, and to ensure that fertilisation experiments commenced within three hours of spawning after which fertilisation can be compromised (Chui et al., 2014).

The cups were gently swirled to break up the egg-sperm bundles and the liquid was poured through a 100 μm sieve to separate the eggs from the sperm. Separate sieves were used for each coral to avoid cross-fertilisation during the cleaning of eggs. The resulting sperm from each colony was stored in 50 ml falcon centrifuge tubes. The sperm concentration was calculated from eight replicate counts using a haemocytometer and adjusted to a density of $10^6$ sperm $ml^{-1}$ by the addition of UV-sterilized 0.2 μm filtered seawater if required. Eggs were rinsed nine times with UV-sterilized 0.2 μm filtered seawater and then placed into graduated sterile 15 ml falcon centrifuge tubes. 'Master' egg and sperm stock solutions were created for the sperm concentration and salinity experiments and comprised the same volume of eggs (10 ml) and sperm (60 ml) in seawater from each of the four most fecund colonies that spawned on the particular night that the experiment was done. The master stocks were repeatedly inverted to ensure mixing and equal representation of gametes from the four individuals. The density of the master sperm stock was calculated from eight replicate readings taken with a hemocytometer (Levitan et al., 2004).

All the experiments described below were conducted on the laboratory counter in ambient light at a temperature of ~26°C. The addition of eggs to sperm in all experiments was accomplished 2:15 hrs after spawning and the experiments were terminated three hours after adding the eggs to the sperm vials by adding formaldehyde to fix samples at a final stock of 4% formal saline. Final assessments were done 5:15 hrs after spawning. This was within the time frame for which the majority of coral fertilisation occurs following spawning (Oliver and Babcock, 1992; Willis et al., 1997). Vials were stored in a dark cupboard until processing. During processing, the proportion of eggs which had been fertilised was calculated, with all eggs that were at or beyond the two-cell stage considered to have been fertilised.

### *3.3.2. Effect of sperm concentration on fertilisation success*

The sperm master stock ($10^6$ sperm $ml^{-1}$) from both coral species was serially diluted to $10^5$, $10^4$, $10^3$, and $10^2$ sperm $ml^{-1}$, thereby creating 5 working stock solutions which included the undiluted $10^6$ sperm $ml^{-1}$ stock. A 1 ml sample of each of the sperm stocks was fixed in 4% formalin for later confirmation of the sperm count. Seven milliliters of each sperm stock was added to 5 replicate glass vials with 20 μl of eggs from the egg master stock. In addition, five control vials were created which comprised 7 ml of sperm-free UV-sterilized 0.2 μm filtered seawater and 20 μl of eggs.

### *3.3.3. Effect of salinity on fertilisation success*

Five salinity levels of natural seawater (35.29 psu), viz. 35.29, 31.76, 28.23 24.70, 21.17, and 17.65 psu (i.e. a natural control, 90, 80, 70, 60 and 50%) were prepared in five replicate vials for each salinity treatment. To each vial was added 1 ml of master sperm stock ($10^6$ sperm ml$^{-1}$), 9 ml of UV-sterilized FSW at the desired psu, and 20 µl of eggs. This resulted in a reduction in the sperm concentration in vials to $10^6$ sperm ml$^{-1}$. Salinities were confirmed from three replicate readings of a 20 ml sample from each treatment with a 856 Metrohm conductivity module and a five ring conductivity measuring cell at 25°C against a 12.87 mS/cm Metrohm conductivity standard.

### *3.3.4. Data analysis*

Kruskal-Wallis ANOVAs were used to assess whether fertilisation success of *A. austera* and *H. exesa* differed among water salinities and sperm concentrations since the distribution of residuals resulting from ANOVA tests were non-normal, even following standard transformations. Bonferroni-adjusted pairwise comparisons were made following the finding of a significant treatment effect ($P < 0.05$). All statistical tests were conducted using IBM SPSS v23.

## **3.4. Results**

### *3.4.1. Effect of sperm concentration on fertilisation success*

Fertilisation success in the five sperm concentration treatments differed significantly in both *A. austera* and *H. exesa* (Kruskal-Wallis ANOVA: $H_{5,27} = 21.79$, $P < 0.001$ and $H_{5,27} = 21.60$, $P < 0.001$ respectively). The mean fertilisation success of no self-sperm controls was 5.62 ± 0.45 and 9.09 ± 3.33% for *A. austera* and *H. exesa* respectively. As sperm concentration decreased from $10^4$ sperm ml$^{-1}$and lower, fertilisation success for *A. austera* was significantly reduced (Fig. 3.1A). The highest fertilisation success of more than 50% was observed when sperm concentration was at a maximum ($10^6$ sperm ml$^{-1}$; Fig. 3.1A). In contrast, highest fertilisation success of nearly 40% was obtained when sperm concentration was $10^5$ sperm ml$^{-1}$ for *H. exesa* (Fig. 3.1B).

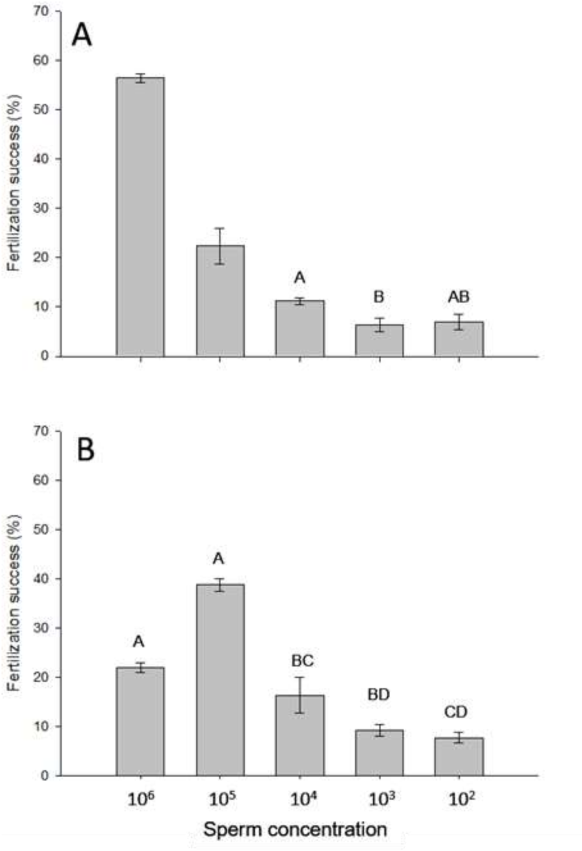

**Fig. 3.1.** Mean ± SE fertilisation success of *Acropora austera* (A) and *Hydnophora exesa* (B) at varying sperm concentrations. The same letter above bars indicates no significant difference at $P < 0.01$ with a Bonferroni adjustment.

### *3.4.2. Effect of salinity on fertilisation success*

Fertilisation success in the six salinity treatments differed significantly for both *A. austera* and *H. exesa* (Kruskal-Wallis ANOVA: $H_{5,30} = 28.34$, $P < 0.001$ and $H_{5,29} = 21.99$, $P < 0.001$ respectively, Fig. 3.2). The fertilisation success was greatest in the control treatment (35.29 psu) for both *A. austera* (53.92 ± 1.86; mean ± SE) and *H. exesa* (69.43 ± 1.86) and decreased with a reduction in salinity (Fig. 3.2). The mean fertilisation success of both *A. austera* and *H. exesa* was reduced by 17% and 19% respectively with a 3.5 psu reduction from current conditions (35.29 psu). However, the mean fertilisation success between these two treatments was not significantly different in either *A. austera* or *H. exesa* ($P = 0.02$ and $P = 0.32$ respectively). A significant reduction in mean fertilisation success occurred in treatments with a reduction of 7.06 psu or more from current conditions in both coral species. This reduced fertilisation success by 56% and 79% in *A. austera* and *H. exesa* respectively. No fertilisation of gametes occurred in treatments at or lower than 21.07 psu for *A. austera* and 17.65 psu for *H. exesa* (Fig. 3.2).

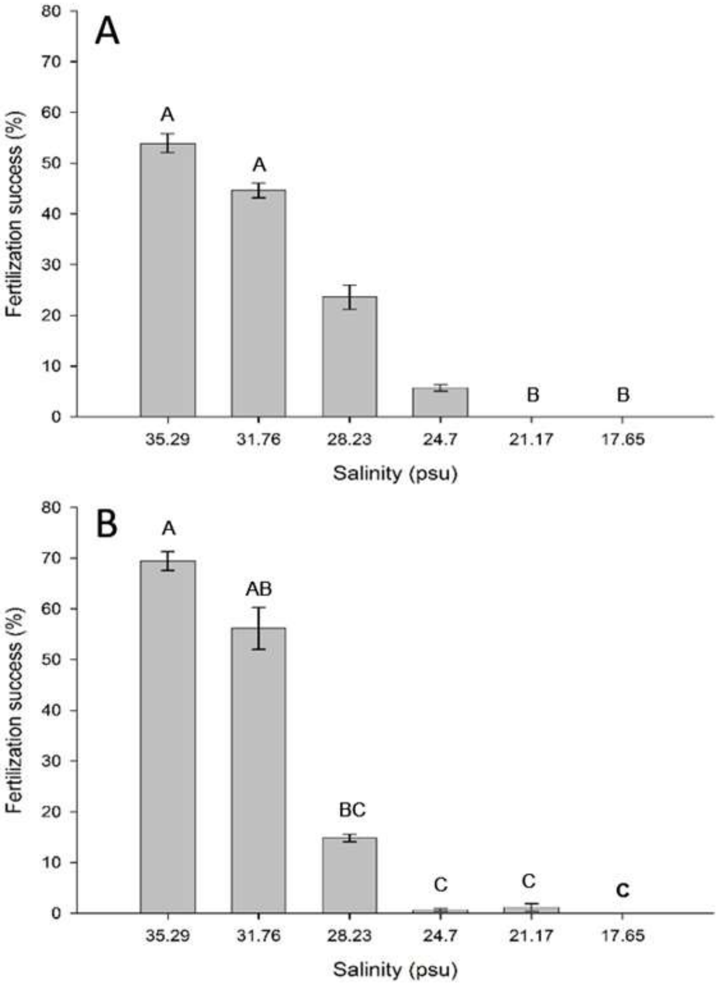

**Fig. 3.2.** Mean ± SE fertilisation success of *Acropora austera* (A) and *Hydnophora exesa* (B) in response to a reduction in water salinity. The same letter above bars indicates no significant difference at $P < 0.01$ with a Bonferroni adjustment.

## 3.5. Discussion

### *3.5.1. Effect of sperm concentration on fertilisation success*

As in other investigations, this study confirms that a sperm concentration of $10^5$-$10^6$ sperm ml$^{-1}$ results in optimum fertilisation success of coral eggs (Oliver and Babcock, 1992; Willis et al., 1997), and that a reduction in sperm concentration from $10^5$-$10^4$ can significantly reduce fertilisation success (Nozawa et al., 2015). Broadcasts spawners typically have bell-shaped fertilisation curves, where low sperm density limits fertilisation success and polyspermy prevents fertilisation when sperm densities are high (Marshall, 2006). Additionally, increased $CO_2$, reduced $pO^2$ levels and low pH at high sperm concentrations can further limit fertilisation (Oliver and Babcock, 1992). Consequently, although not statistically different from $10^5$ sperm $ml^{-1}$, the lower fertilisation success of *H. exesa* eggs at a sperm concentration of $10^6$ sperm $ml^{-1}$ may have resulted from polyspermy (Levitan et al., 2004). In contrast, fertilisation success in *A. austera* was the highest in the most concentrated sperm treatment ($10^6$ sperm $ml^{-1}$). Cross-fertilisation success from this study was however lower than other *in vitro* experiments, which are frequently above 80% success (Erftemeijer et al., 2012; Heyward and Babcock, 1986; Nozawa et al., 2015; Willis et al., 1997). However, other Acroporids (*A. millipora* and *A. pulchra*) have also had low (49%) cross-fertilisation success (Willis et al., 1997). Low fertilisation rates could be the result of unhealthy gametes (Chui et al., 2014) and compatibility of the individuals crossed (Baums et al., 2013; Iguchi et al., 2009; Willis et al., 1997). Iwao et al. (2014) also report that the highest fertilisation success is achieved with crosses from six or more colonies, which was not possible in the current study as not all of the fragments collected spawned.

Field observations for surface slicks could not be conducted at night due to unsafe conditions at Sodwana Bay for night launches. However, water surface conditions on the exposed, high-energy Maputaland reefs in South Africa are generally turbulent, particularly during the spawning season. This has the potential for increasing sperm dilution, thereby reducing the window for successful fertilisation. Although gamete viability in *in vitro* experiments do not drop significantly until 6-8 hours after spawning in the field (Willis et al., 1997), sperm dilution could reduce the fertilisation period to less than an hour (Omori et al., 2001). Consequently, i*n vitro* studies are possibly overestimates of *in situ* fertilisation success, where sperm dilution occurs (Iguchi et al., 2009).

### *3.5.2. Effect of salinity on fertilisation success*

While the tolerance of coral fragments to hyposaline conditions has been extensively studied (Downs et al., 2009; van der Merwe et al., 2014), the impact that hyposalinity has on the fertilisation of coral gametes remains understudied. Hyposalinity can play a role in the fertilisation of eggs and the embryonic development of coral larvae since the majority of corals release positively buoyant eggs, which float to the water surface where they remain during embryogenesis (approximately 2 days depending on species e.g. Tay et al., 2011). Studies which have investigated the effect of hyposalinity on the fertilisation and early life stages of corals corroborate the results obtained in this study whereby coral fertilisation success can be significantly reduced with a reduction in salinity (Hedouin et al., 2015; Palaki, 1998; Scott et al., 2013; True, 2012; Vermeij et al., 2006). Furthermore, a study which assessed embryonic development in addition to fertilisation success indicated that the fertilisation process is more vulnerable to hyposaline conditions than subsequent life stages (Hedouin et al., 2015).

Similarly Scott et al. (2013) found a significant reduction in the fertilisation success of *A. millipora* and *Platygyra daedalea* below 29.4 psu in Australia and *A. cytherea* and *A. pulchra* incurred significant reductions in fertilisation success at 29 psu and 30 psu respectively in French Polynesia (Hedouin et al., 2015). Hyposaline conditions due to rainfall have been shown to result in a drop in salinity to 28 psu in the Florida Keys (Vermeij et al., 2006) and to 20 psu in French Polynesia (Hedouin et al., 2015). However, detailed assessments of changes in the seawater surface salinity at Sodwana Bay in South Africa have not been conducted. As no major rivers drain into Sodwana Bay, water salinity will probably only be affected by rainfall.

### *3.5.3. Conclusion*

Reduced salinity or low sperm concentrations resulted in reduced fertilisation success for both coral species in this study. Of concern is the lack in current knowledge of surface water conditions (such as salinity and turbidity) experienced during spawning events in South Africa. Thus documenting *in situ* spawning events and associated water conditions at this time is needed. There is a greater potential of gametes encountering reduced surface salinity and increased turbidity due to increases in storm intensity and frequency associated with current climate change predictions. This is particularly relevant on marginal, exposed reefs such as Sodwana Bay, where bundle dissociation and subsequent sperm dilution could occur more rapidly than observed elsewhere.

### 3.6. Acknowledgements

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# Chapter 4:

# Larval settlement and post-settlement success in *Acropora austera* and *Hydnophora exesa*

## 4.1. Abstract

Larval settlement and post-settlement success of coral recruits are fundamental processes for the maintenance of coral populations and the persistence of coral reefs, making identification of factors which influence these critical. We assessed larval settlement and post-settlement success of two common South African corals, *Acropora austera* and *Hydnophora exesa,* in response to the presence of two crustose coralline algae species: *Mesophyllum sp.* and *Hydrolithon sp.* with filtered seawater (FSW) controls. Both sampling time and treatment had a significant effect on settlement of *A. austera* and *H. exesa* larvae, but no significant interaction effects were found. Settlement of both coral species in the presence of *Hydrolithon* was significantly greater than FSW; this was not the case in the presence of *Mesophyllum*. Peak settlement of *A. austera* and *H. exesa* occurred in the presence of *Hydrolithon* (48% compared to 10% in FSW for *A. austera* and 65% compared to 45% in FSW for *H. exesa*). Physical contact with CCA chips at the moment of settlement was not a requirement for larval settlement. More settlement of both coral species generally occurred on the well surfaces in the CCA treatments apart from *H. exesa* for which settlement was greater on *Hydrolithon* fragments. At termination *A. austera* obtained the greatest post-settlement success in the *Mesophyllum* treatment (21.67 ± 7.23%) whereas *H. exesa* post-settlement success was greatest in the *Hydrolithon* treatment (55.00 ± 10.47%). However, these differences in post-settlement success were not significant. *Acropora austera* and *H. exesa* were still capable of settlement 69 and 75 DAF respectively in FSW. These results show the contribution of chemosensory communication during the settlement process of coral larvae and how these differ between taxa. Trends suggest that settlement requirements are more stringent for *A. austera* planulae than *H. exesa* and that *Mesophyllum* collected from the exhibit at uShaka Sea World was not an efficient settlement inducer for larvae of the corals investigated in this study.

## 4.2. Introduction

Successful settlement and metamorphosis of free swimming coral planulae and post-settlement success is essential for completion of their dispersal and progress towards becoming recruits (Babcock and Mundy, 1996; Harrington et al., 2004). Once coral embryos have developed into planulae, they develop cilia and receptors which enable them to sense and respond to environmental stimuli (Grasso et al., 2011; Morse and Morse, 1996). As with other benthic marine invertebrates, coral larval settlement is widely considered to rely on receptor-mediated processes (Hadfield, 2011). Site selectivity in coral larvae plays a role in their colonizing ability during settlement (Doropoulos et al., 2016), as taxa with less stringent requirements have a greater area to choose from. While some corals may settle without any apparent cue (Baird and Morse, 2004), others may delay or cease settlement altogether in the absence of appropriate settlement cues (Graham et al., 2008; Qian et al., 2007). Coral planulae attach to the substratum after detecting suitable settlement cues and begin to secrete their calcium carbonate skeleton, forming juvenile polyps (Harrison and Wallace, 1990). Detecting an appropriate substratum is crucial as, once planulae attach, they have a limited capacity to detach and re-enter the pelagic phase (Richmond, 1985) and need to be able to deal with post-settlement conditions (e.g. competition with other biota, evading predation).

Physical and environmental cues such as colour (Mason et al., 2011), sound (Vermeij et al., 2010), light (Levy et al., 2007; Lewis, 1974; Maida et al., 1994; Mundy and Babcock, 1998b), temperature (Winkler et al., 2015), depth (Babcock and Mundy, 1996; Baird et al., 2003; Suzuki et al., 2008), changes in pressure (Stake and Sammarco, 2003), physical substratum texture or topography (Davies et al., 2013; Doropoulos et al., 2016; Nozawa, 2012a; Petersen et al., 2004; Whalan et al., 2015), substratum orientation (Mundy and Babcock, 1998a), water chemistry (Dixson et al., 2014) and the presence of crustose coralline algae with their associated bacteria (Harrington et al., 2004; Heyward and Negri, 1999; Morse and Morse, 1991; Quéré and Nugues, 2015; Tebben et al., 2015) affect the suitability for coral larval settlement.

Crustose coralline algae are a key functional group, which facilitate coral recruitment by providing consolidated surfaces, suppressing antagonistic macro-algae, and by inducing coral settlement. They directly deter macroalgal establishment on their surfaces (Figueiredo et al., 1997; Johnson and Mann, 1986) and indirectly control algal growth by harbouring microherbivores (Steneck, 1982). It has long been recognized that conditioning of settlement surfaces with crustose coralline algae (CCA) or microbes results in enhanced settlement by coral larvae (Morse et al., 1988; Raimondi and Morse, 2000; Ritson-Williams et al., 2009). Extracts from CCA are potent settlement and metamorphosis cues for hard corals (Harrington et al., 2004; Heyward and Negri, 1999; Morse and Morse, 1991; Tebben et al., 2015) and bacterial isolates from reef biofilms associated with CCA have also been shown to modify larval behaviour and enhance settlement (Negri et al., 2001; Sneed, 2014; Tebben et al., 2011; Tran, 2011). The settlement-inducing ability of CCA has proven to be species-specific (Doropoulos et al., 2016; Harrington et al., 2004; Ritson-Williams et al., 2014), with only a few CCA taxa shown to facilitate coral settlement (Harrington et al., 2004). Furthermore the inducing effect has been shown to be dependent on the health status of the CCA as CCA disease can significantly affect settlement and post-settlement success of coral larvae (Quéré and Nugues, 2015). Acroporids have been shown to exhibit significant selective responses to certain substrata during settlement (Baird and Morse, 2004; Doropoulos et al., 2016; Golbuu and Richmond, 2007; Harrington et al., 2004; Morse et al., 1996; Morse and Morse, 1991; Negri et al., 2001; Raimondi and Morse, 2000; Ritson-Williams et al., 2010; Ritson-Williams et al., 2014). Both *A. tenuis* and *A. millepora* have been found to preferentially settle on *Titanoderma prototypum* over other CCA species, including *Hydrolithon onkodes* (Harrington et al., 2004). The effect of CCA on the settlement of *Hydnophora* species has not yet been investigated.

Both *Hydrolithon* (Harrington et al., 2004) and *Mesophyllum* CCA (Heyward and Negri, 1999) have been reported to induce settlement of coral larvae. More recently, *Mesophyllum* has been shown to encourage early substrate testing and settlement of *A. muricata* larvae, but ultimately results in a lower settlement rate than seawater controls (Denis et al., 2014). Knowledge remains limited on the diversity and ecology of CCA on the high-latitude reefs of southern Africa and the effect of CCA and their associated microbes on coral settlement. Four species of *Hydrolithon* have been identified on the high-latitude reefs in South Africa, viz. *Hydrolithon farinosum* (Penrose and Chamberlain, 1993), *H. onkodes*, *H. samoënse* and *H. superficial* (Keats and Chamberlain, 1994a). A *Hydrolithon* sp. (hereafter referred to as *Hydrolithon*) has been readily observed growing on *A. austera* rubble on high-latitude reefs in South Africa (Hart pers. obs.). *Mesophyllum* cf *funafutiense* (hereafter referred to as *Mesophyllum*) also occurs on the high-latitude reefs in South Africa (Keats and Chamberlain, 1994b). It also grows prolifically in uShaka Sea World aquaria, and may thus constitute a convenient settlement inducer.

The settlement response and post-settlement success of *A. austera* and *H. exesa* to *Hydrolithon* and *Mesophyllum* was assessed in this study. We hypothesised that CCA would enhance larval settlement in both coral species, and that these responses would be species-specific. We predicted that settlement would occur more rapidly and be more successful in CCA treatments than filtered seawater controls.

## 4.3. Materials and methods

### *4.3.1. CCA collection and rearing of coral larvae*

*Acropora austera* and *Hydnophora exesa* are well represented on Two-mile Reef (TMR) at Sodwana Bay, South Africa (27°33'28"S; 32°41'10"E), have different life-history strategies, and appear to have different tolerances to thermal stress. A large fragment of *Hydrolithon*-encrusted *A. austera* rubble was collected from TMR with a hammer and chisel to obtain this CCA. Fragments of *Mesophyllum* were collected from the rockwork in a coral exhibit at uShaka Sea World, South Africa (29°52'06"S; 31°02'39"E). These CCA were identified according to Keats and Chamberlain (1994a; 1994b).

Fragments of both CCA taxa were maintained in a flow-through aquarium system at the Oceanographic Research Institute (ORI) at an irradiance of 150 $\mu Em^{-2}s^{-1}$for a week until the start of the settlement experiments. Six gravid colonies of both *A. austera* and *H. exesa* were collected from TMR prior to their predicted annual spawning and maintained in a flow-through system at the ORI research aquarium. *Hydnophora exesa* spawned on 7 March 2015 and *A. austera* spawned six nights later on 13 March 2015. Following spawning, gametes released by the four most fecund colonies were combined in separate 20 l buckets for fertilisation, rinsed to avoid polyspermy after 30 mins, and embryos were reared in 100 l tubs according to the protocol of Guest (2010). The tubs received daily water changes of 0.2 μm filtered seawater (FSW) and were placed in a 26°C water bath to maintain a constant temperature until the larvae displayed benthic searching behaviour. The project was registered with the iSimangaliso Wetland Park authority who granted permission for this research. Samples were collected from

TMR under permit RES2015/36 issued by the South African Department of Environmental Affairs and Department of Agriculture, Forestry and Fisheries. Permission for the collection of *Mesophyllum* fragments was granted by uShaka Sea World management and no permit was required.

### *4.3.2. Settlement assays*

Settlement experiments were started on 19 March 2015, seven days after fertilisation (DAF) of *A. austera* and 13 DAF of *H. exesa;* at which time the planulae were elongated, active and exhibiting demersal swimming and benthic searching behaviour. Settlement was tested on a chip of *Mesophyllum* or *Hydrolithon* on *A. austera* skeletal fragment, or in 0.2 μm FSW without CCA. Each treatment was randomly allocated to six replicate wells on three six-well culture plates (Greiner bio-one CELLSTAR). Untreated wells contained 15 ml of 0.2 μm FSW. The chips of CCA (approximately 5 x 5 mm) were cut from larger fragments with sidecutters, and were rinsed repeatedly with UV sterilized 0.2 μm FSW before being added to the wells. The survival of CCA chips was not compromised during the duration of the study as fragments of both *Hydrolithon* and *Mesophyllum* grew during the experiment (Fig S4.1). Ten healthy larvae of either *A. austera* or *H. exesa* were randomly selected from the grow-out tubs and added to each well. Culture plates were placed out of direct sunlight in the laboratory at a temperature of 24-26°C. Every 2-3 days, 10 ml of the water in each well was replaced with 0.2 μm UV sterilized FSW from the inlet pipes supplying water to uShaka Sea World with a pipette under a Zeiss Stemi 2000-C microscope. Experimental water conditions could differ from that of the sea due to biofouling in inlet pipes (Alexander et al., 2015). Larvae were counted in each well before and directly after water changes to ensure no healthy larvae had accidently been removed. Detritus was removed during water changes (including partially decomposed larvae which had died) to maintain water quality and separate pipette tips were used for each well to prevent contamination.

The outcome of the 10 larvae added to each well at the start of the experiment was assessed 15 times over a 92-day period. During each assessment, the number of settled larvae, unattached larvae, and dead larvae in each well was counted with the aid of a Zeiss Stemi 2000-C microscope and these were recorded as cumulative values. Settled larvae comprised larvae which physically attached to a substrate and deposited skeletal material. The location of settled larvae on either the plastic well surfaces or CCA fragments was noted during each assessment (Fig. 4.1). Unattached larvae comprised swimming larvae, attached but not metamorphosed, or metamorphosed but not yet attached. The latter comprised either unattached polyps with a floating buoyant skeleton (only observed in *H. exesa*) or fleshy metamorphosed polyps that lay on the bottom of the wells. Unattached larvae which had metamorphosed were not removed as polyps with a floating buoyant skeleton can potentially settle at a later stage (Vermeij, 2009) and it was unknown whether metamorphosed polyps that lay on the bottom were capable of successfully settling. Larval mortality was calculated by subtracting the count of living, unattached and settled larvae from the initial number of larvae. Consequently, larval mortality comprised the number of dead, partially decomposed larvae and those which had died and decomposed. Post-settlement success was quantified as the number of settled recruits in each well which possessed living tissue at the end of the experiment (98 DAF and 104 DAF for *A. austera* and *H. exesa* respectively). No overgrowth of coral recruits by CCA or dislodged recruit skeletons were observed in the study.

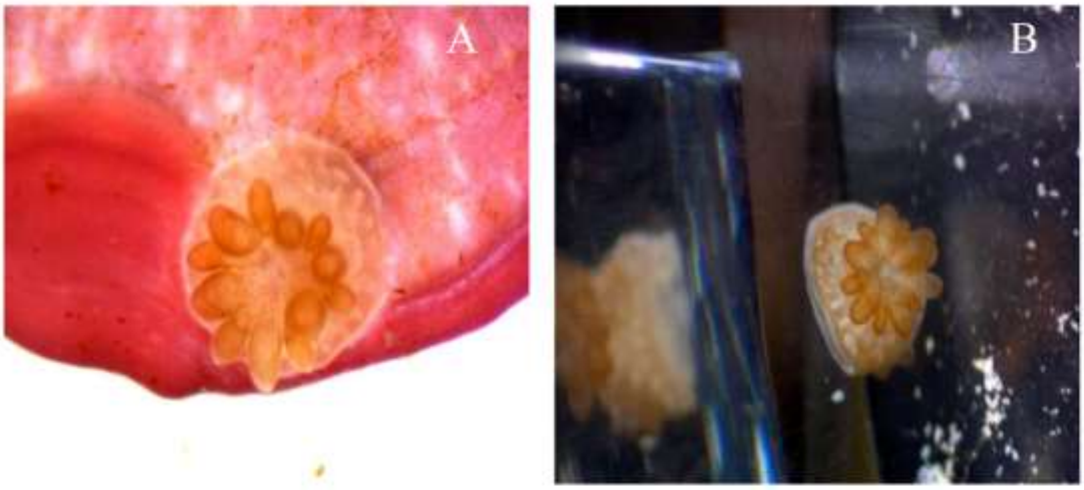

**Fig. 4.1.** Representative images of *Acropora austera* recruits at termination of the experiment. (A) *Acropora austera* recruit on CCA and (B) on the side of a plastic well.

### *4.3.3. Data analysis*

Cumulative settlement (i.e. the number of larvae which had settled at a particular time-point, regardless of whether they were alive or not) is reported in this study and values are reported as percentages (mean ± SE) of the original ten larvae added to each well. Repeated measures analysis of variance (RM ANOVA) tests, with *post hoc* Tukey tests, were used to assess the treatment effect (*Hydrolithon*, *Mesophyllum* and FSW) on larval settlement over time. Since assumptions could not be met despite data transformations, Kruskal-Wallis ANOVAs were used to assess whether post-settlement success (the amount of larvae which successfully settled and were alive at the end of the experiment) differed among treatments (*Hydrolithon*, *Mesophyllum* and FSW) for the two coral species. Bonferroni-adjusted pairwise comparisons were made following the finding of a significant treatment effect. All statistical tests were conducted using IBM SPSS v23.

## **4.4. Results**

Both time and treatment had a significant effect on the settlement of *A. austera* and *H. exesa* larvae but the interaction between time and treatment was not significant in either coral species (Table 4.1). Settlement in wells with *Hydrolithon* and *Mesophyllum* fragments commenced within the first two days of the experiment in both coral species but only occurred in FSW 27 and 25 DAF for *A. austera* and *H. exesa* respectively (Fig. 4.2). The settlement in wells with *Hydrolithon* was rapid during the first 25 DAF for *A. austera* and *H. exesa*, and yielded the highest settlement (48.33 ± 6.42% and 65.00 ± 5.65% respectively, mean ± SE, Fig. 4.2, Table 4.2). This was 2.1 and 3.2 times greater than peaks in the *Mesophyllum* and FSW treatments respectively for *A. austera*, and 1.5 and 1.4 times higher for *H. exesa* (Table 4.2). Overall settlement of *A. austera* and *H. exesa* larvae in FSW was significantly lower than that in *Hydrolithon* (Tukey's HSD, $P = 0.002$ and $P < 0.05$ respectively), but not *Mesophylum* treatments (Tukey's HSD, $P = 0.159$ and $P = 0.480$ respectively). Settlement of *H. exesa* larvae in the *Hydrolithon* treatment was significantly greater than that in the *Mesophyllum* treatment (Tukey's HSD, $P = 0.001$), but this was not the case for *A. austera* larvae (Tukey's HSD, $P = 0.105$). Settlement success did not differ significantly between treatments for both *A. austera* and *H. exesa* at the end of the experiment (Kruskal-Wallis ANOVA, $H_{2,18} = 1.51$, $P < 0.05$ and $H_{2,18} = 1.52$, $P > 0.05$ respectively).

**Table 4.1.** Summary of Repeated Measures ANOVA statistics for *Acropora austera* and *Hydnophora exesa* planulae settlement in *Hydrolithon*, *Mesophyllum* and filtered seawater controls over 92 days (*n* = 6 wells for each treatment).

| **Species** | **Variability** | **Source** | **Df** | **MS** | ***F*** | ***P*** |
|---|---|---|---|---|---|---|
| *Acropora austera* | Within subjects | Time | 2.085 | 41.425 | 9.040 | 0.001 |
| | | Time x Treatment | 4.169 | 9.423 | 2.056 | 0.108 |
| | | Residual | 31.269 | 4.582 | | |
| | Between subjects | Treatment | 2.000 | 267.244 | 8.574 | 0.003 |
| | | Residual | 15.000 | 31.170 | | |
| *Hydnophora exesa* | Within subjects | Time | 2.812 | 69.937 | 8.823 | <0.001 |
| | | Time x Treatment | 5.625 | 9.407 | 1.187 | 0.332 |
| | | Residual | 42.185 | 7.927 | | |
| | Between subjects | Treatment | 2.000 | 321.433 | 20.436 | 0.000 |
| | | Residual | 15.000 | 15.729 | | |

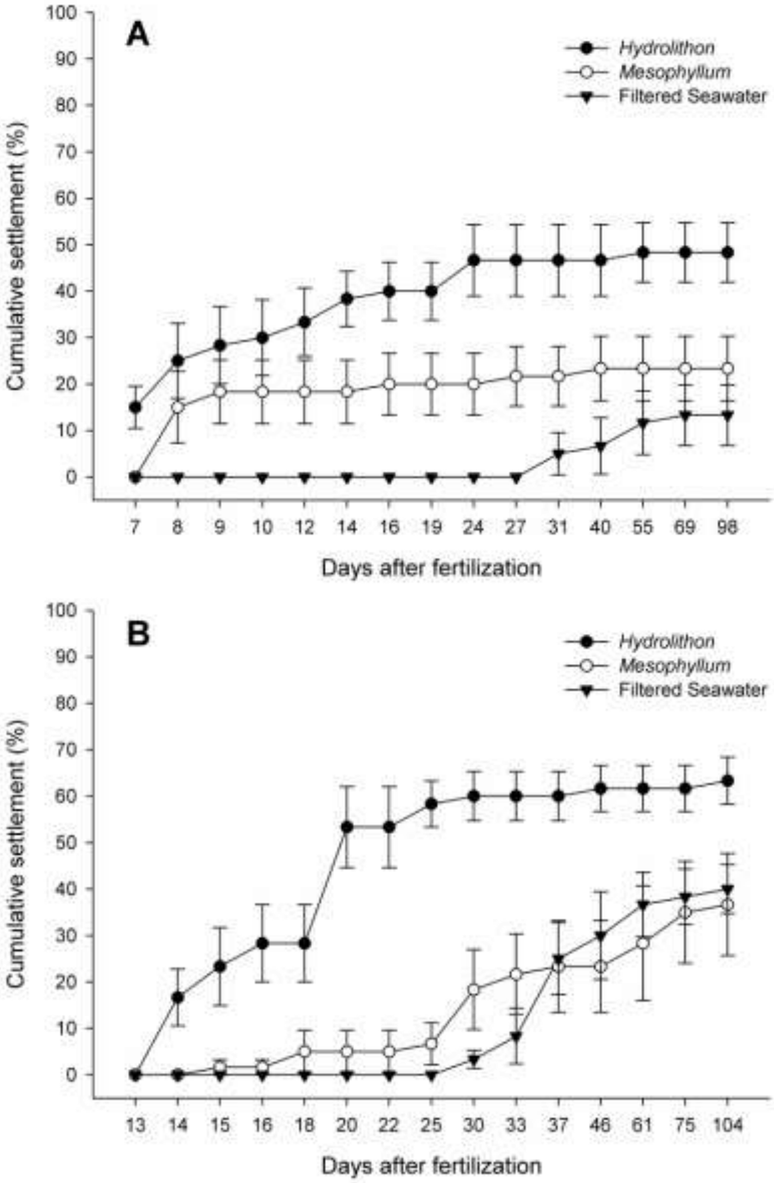

**Fig. 4.2.** Cumulative settlement of coral larvae over time. Mean ± SE cumulative settlement of *Acropora austera* and *Hydnophora exesa* larvae in response to *Hydrolithon*, *Mesophyllum* and filtered seawater treatments ($n$ = 6 wells per treatment).

In general, larval mortality of both coral species was initially rapid in the CCA treatments compared to the FSW controls (Fig.4.3), while after ~20 days, very little additional mortality occurred. In contrast, mortality of *A. austera* and *H. exesa* planulae in FSW treatments remained more consistent throughout the experiment (Fig.4.3). The final mortality was lower in *Hydrolithon* treatments for both corals compared to *Mesophyllum* and FSW (Fig. 4.2). A considerable number of *A. austera* larval mortality (58.33 ± 10.91%) occurred in the *Mesophyllum* treatments between the first two sampling periods, thereby drastically reducing the number of larvae available for settlement (Fig.4.3). The majority of larvae in all treatments had either settled or died at the end of the experiment (Fig. 4.3).

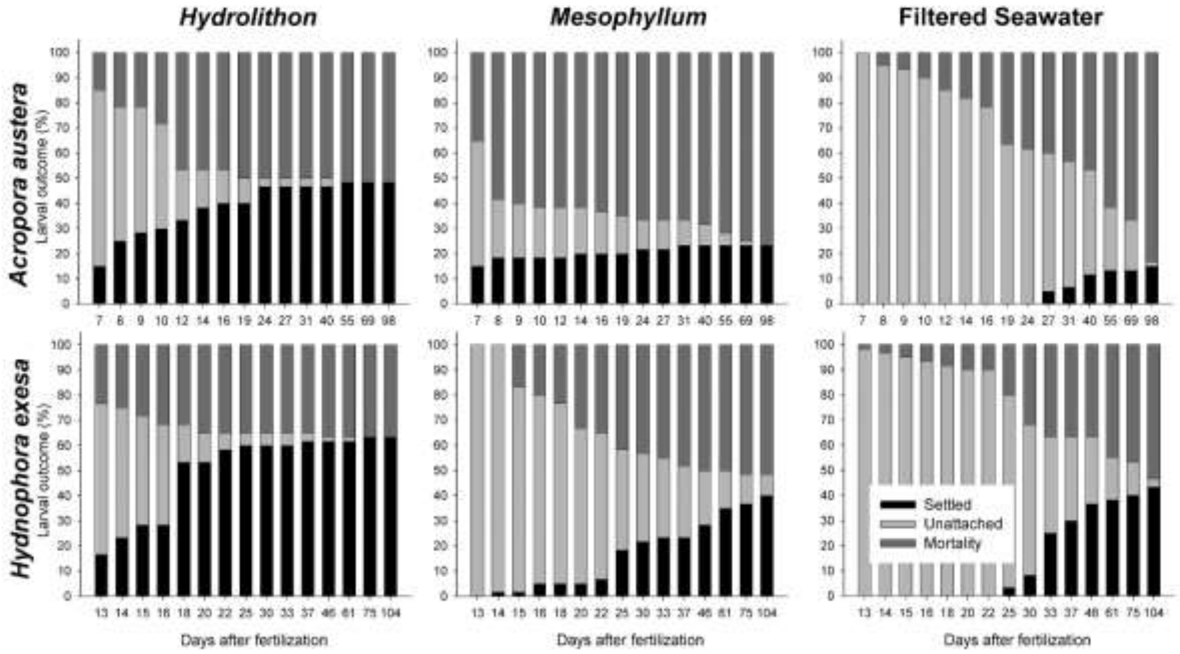

**Fig. 4.3.** Larval outcome throughout the experiment. Mean cumulative contribution of settled larvae (black bars), unattached larvae (light grey bars), and larval mortality (dark grey bars) for both coral species in the three treatments (*n* = 6 wells per treatment).

In *A. austera*, settlement occurred predominantly on the well surfaces regardless of CCA treatment (Fig. 4.4). In contrast, settlement of *H. exesa* on CCA fragments was dependent on the CCA taxon (Fig. 4.4). More settlement of *H. exesa* larvae occurred on *Hydrolithon* than well surfaces (40.00 ± 10.95% and 25 ± 8.06% respectively), but not on *Mesophyllum* (11.67 ± 4.01% and 31.67 ± 10.33% respectively, Fig. 4.4). Larval settlement of both coral species on the well surfaces in CCA treatments predominantly occurred on the vertical edges and bottom edges and not necessarily under the CCA fragments. The majority of *H. exesa* settlement which occurred in the *Mesophyllum* treatment 22 DAF occurred on the well surface (Fig. 4.4).

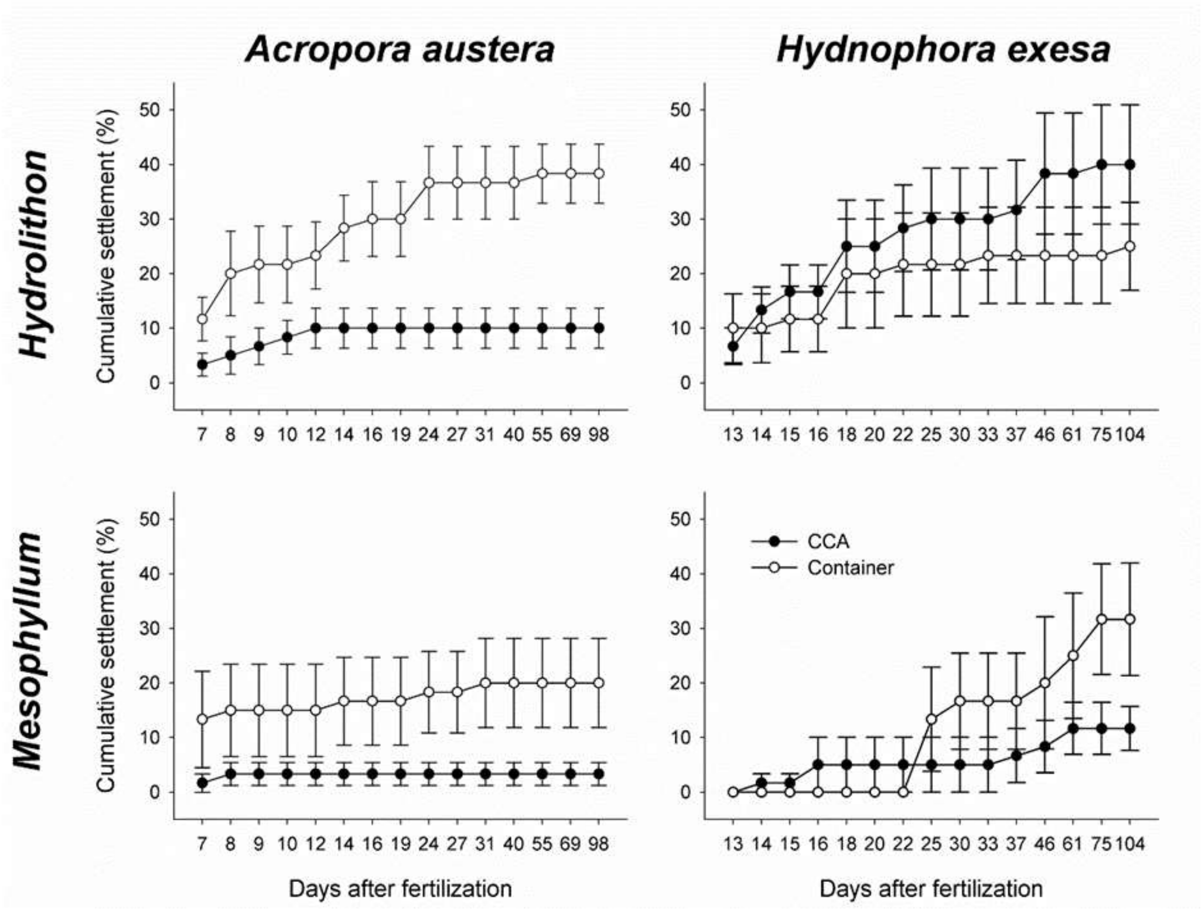

**Fig. 4.4.** Surface settlement preference of coral larvae in response to CCA treatments. Mean ± SE cumulative settlement of the original ten *Acropora austera* and *Hydnophora exesa* larvae added to each well which settled on the container and CCA surfaces in *Hydrolithon* and *Mesophyllum* treatments (*n* = 6 wells per treatment).

A significant difference was found in the number of live compared to dead recruits in the three *A. austera* treatments; this was not so for *H. exesa* (Table 4.2). More recruits were alive than dead at the end of the experiment in all treatments, except for *A. austera* recruits in the *Hydrolithon* treatments, which exhibited higher mortality (Table 4.2).

**Table 4.2.** Overall settlement and post-settlement success in each treatment at the end of the experiment for *Acropora austera* and *Hydnophora exesa* (98 and 104 DAF respectively).

| **Coral species** | **Treatment** | **Overall settlement (%)** | **Post-settlement success (%)** |
|---|---|---|---|
| *Acropora austera* | *Hydrolithon* | 48.33 ± 6.42 | 20.00 ± 8.50 |
| | *Mesophyllum* | 23.33 ± 6.94 | 21.67 ± 7.23 |
| | FSW | 15.00 ± 7.30 | 11.66 ± 6.83 |
| *Hydnophora exesa* | *Hydrolithon* | 65.00 ± 5.65 | 55.00 ± 10.47 |
| | *Mesophyllum* | 43.33 ± 9.91 | 38.33 ± 10.12 |
| | FSW | 45.00 ± 3.91 | 45.00 ± 3.91 |

## 4.5. Discussion

In accordance with other studies, this investigation has shown that coral settlement can be induced by CCA fragments and that the response is coral- and CCA-specific (e.g. Davies SW, 2014; Denis et al., 2014; Golbuu and Richmond, 2007; Harrington, 2004). Settlement of *A. austera* and *H. exesa* larvae was significantly enhanced by inclusion of *Hydrolithon* fragments in wells, but not *Mesophyllum*. The rate of settlement over time and between treatments was variable. The slower settlement rate and moderate settlement success evident in this study compared to others (Baird and Morse, 2004; Harrington et al., 2004; Heyward and Negri, 1999) may indicate that the larvae were not at peak settlement competency at the start of the experiment, experienced greater mortality rates than in other studies, or that the CCA fragments were relatively weak inducers.

Both *A. austera* and *H. exesa* can be added to the list of corals in which larval settlement is enhanced by *Hydrolithon* or its associated bacteria (Negri et al., 2001). These include *Acropora palmata*, *A. cervicornis* (Ritson-Williams et al., 2010), *A. willisae*, *A. millepora* (Negri et al., 2001), *A. palifera* (Baird and Morse, 2004), *Agaricia humulis* (Raimondi and Morse, 2000), *Goniastrea retiformis* and *Stylaraea punctata* (Golbuu and Richmond, 2007). The encrusting *Hydrolithon* CCA and associated bacteria (or possibly the coral base on which it was growing, or both, appeared to provide a positive settlement cue for the *A. austera* and *H. exesa* larvae. Cumulative settlement of both *A. austera* and *H. exesa* peaked ~25 DAF in the presence of *Hydrolithon*, after which the availability of larvae limited further settlement as the larvae had either died or already settled. The insignificant difference between settlement of larvae of both coral species in FSW and *Mesophyllum* indicates that *Mesophyllum* collected from the exhibit at uShaka Sea World was not an efficient settlement inducer for larvae of the corals investigated in this study.

Regardless of CCA treatment, more settlement of both coral species occurred on well surfaces compared to on CCA fragments, indicating that a chemical cue from the CCA or the associated microbes is probably responsible for the inducing effect and that attachment to CCA is not required. The effect of CCA surfaces on coral larval settlement and post-settlement success has been shown to be hindered by anti-settlement strategies exhibited by CCA (Harrington et al., 2004) and could have contributed to the preferential settlement on well surfaces. Numerous studies have shown that enhanced settlement can occur with the addition of CCA chemical extracts, for example from *Hydrolithon reinboldii* (Dixson et al., 2014). Similarly, water chemically seeded with macroalgal derivatives has been shown to induce acroporid settlement (Birrell et al., 2008b; Denis et al., 2014; Dixson et al., 2014; Morse et al., 1996). Heyward and Negri (1999) found that, although the addition of a variety of CCA taxa (including a *Mesophyllum* sp.) significantly enhanced settlement of *A. millepora* larvae, all of the settlement occurred on the well surface, with no settlement occurring on the living surface of the CCA. The interaction between where larvae settle and the CCA pieces provides insight into potential competitive interactions that larvae may have to encounter.

Settlement of both *A. austera* and *H. exesa* planulae in FSW treatments indicates that the presence of a CCA settlement cue is not a strict requirement for this to occur in these two coral species. Although most settlement studies have revealed negligible settlement in seawater controls (Heyward and Negri, 1999; Tebben et al., 2015), other studies have reported settlement in seawater control treatments (e.g. Birrell et al., 2008b; Denis et al., 2014; Mason et al., 2011). It has been proposed that settlement in seawater controls without CCA occurs because of the presence of amino acids and other small water-borne molecules (Baird and Morse, 2004). Settlement in FSW controls only commenced 27 DAF in *A. austera* and 25 DAF in *H. exesa*, despite larvae of both species being competent to settle from the start of the experiment. Interestingly, this coincided with the time at which cumulative settlement of both corals peaked in the *Hydrolithon* treatment. In the absence of the required settlement cues, coral planulae can remain unattached for several weeks (Baird et al., 2009; Graham et al., 2008). Delayed settlement in this study suggests that the larvae may have reached a point where planulae either settled non-selectively or died due to a depletion of energy reserves (see Toonen and Pawlik, 2001). Alternatively, despite the fact that 67% of the water was changed every 2-3 days, a microbial build-up on the well surfaces over time could have provided a settlement-inducing cue (Vermeij et al., 2009). *Acropora austera* not only took longer to start settling in FSW treatments, but also only attained a mean settlement of 10% in this medium. In contrast, settlement of *H. exesa* planulae in FSW attained a mean of 40%. Elsewhere, 63% of *A. muricata* larvae (Denis et al., 2014) and 37% of *A. millepora* larvae (Birrell et al., 2008b) settled in seawater controls after 24 hours. The cumulative settlement of both *A. austera* and *H. exesa* in FSW in the terminal stages of this study shows that the maximum settlement competency of *A. austera* and *H. exesa* exceeds 69 and 75 DAF respectively. Elsewhere, the maximum settlement competency of *A. digitifera* and *A. tenuis* occurs at 54 and 69 DAF respectively (Nishikawa and Sakai, 2005), and 93-105 DAF in *Platygyra daedalea* (Nozawa and Harrison, 2000). Therefore, both *A. austera* and *H. exesa* have potential for long distance dispersal. However, recent genetic work has revealed that *A. austera* incur high levels of self-seeding on Maputaland reefs (Montoya-Maya et al., 2016). Collectively this supports the premise that although coral larvae possess the potential for long distance dispersal, rapid settlement occurs resulting in high levels of local retention (Miller and Mundy, 2003). Determining the minimum time to competency of the two coral species in future studies is required. Furthermore, the assessment of microbial build-up on the well surfaces, and coral larvae energetics over time warrants investigation to provide explanations for trends obtained in this study.

As in this study, high levels of coral larval mortality have been found to occur during the early larval phases (Nozawa and Okubo, 2011) with a steady increase in mortality from 3-12 days (Denis et al., 2014). Higher mortality of larvae was observed in CCA treatments compared to FSW during the first month of this experiment. This could potentially be due to defence mechanisms of CCA due to handling prior to the start of the experiment. Although chemical cues associated with CCA are known to induce the settlement of coral larvae, CCA use chemical defences to prevent fouling and their potential allelopathic effect on coral larvae has received little attention (Kim et al., 2004; Suzuki et al., 1998). A bacterial load resulting from dying larvae could also have affected the water quality within the wells (Denis et al., 2014).

Although settlement of *A. austera* was greatest in *Hydrolithon*, more than half of the *A. austera* planulae which settled in this treatment were dead at the end of the experiment. In contrast, the majority of the *A. austera* recruits in the *Mesophyllum* and FSW treatments were still alive. Therefore settlement does not necessarily translate into post-settlement success. *Hydrolithon* has been shown to outcompete coral juveniles elsewhere (Golbuu and Richmond, 2007), however competitive overgrowth was not observed during this study and therefore did not contribute to the high *A. austera* post-settlement mortality. The majority of the settlement (79%) occurred on the well surfaces, out of contact with the CCA. In contrast, 51% of *H. exesa* settlement occurred on well surfaces and the majority of *H. exesa* recruits in all three treatments remained alive at the end of the experiment. Collectively, this indicates that the post-settlement success of planulae differs between the two coral species in the presence of *Hydrolithon* fragments. However, caution must be applied to the interpretation of post-settlement success results in this study, as recruits were ‘of different ages’ (settlement records were cumulative) when the experiment was terminated and the probability of recruit survival can change with age (Raymundo and Maypa, 2004). Post-settlement success of settled recruits in this laboratory study probably constituted over-estimates as many natural pressures (e.g. predation and competition with other biota) were absent (Arnold et al., 2010; Doropoulos et al., 2016; Penin et al., 2011; Tebben et al., 2014), which can result in as much as 55% of settled larvae dying within the first 24 hours on a reef (Martinez and Abelson, 2013).

The assessment of larval outcomes over a prolonged duration in this study provided valuable insight into the effect that treatments can have on the survival of larvae, their settlement, and post-settlement success. The maladaptive tendency of *A. austera* in the *Hydrolithon* treatment (i.e. enhanced settlement but reduced post-settlement success) indicates that, as found elsewhere (e.g. Nugues and Szmant, 2006), enhanced settlement does not necessarily translate into high recruitment success. While the identification of larval settlement inducers provides an important contribution to the recruitment puzzle in corals, experimental work which incorporates both settlement and post-settlement success are recommended in further studies to investigate potential bottleneck affects. The use of individual, isolated larvae is recommended in future studies to eliminate the possible confounding effect that the status of other larvae can have on larval settlement (e.g. fouling of the water by dead larvae). The isolation of more CCAs and their assessment on the high-latitude reefs of South Africa are required to establish whether there are other CCA taxa that may also influence coral settlement.

## 4.6. Acknowledgements

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## 4.7. Supplementary data

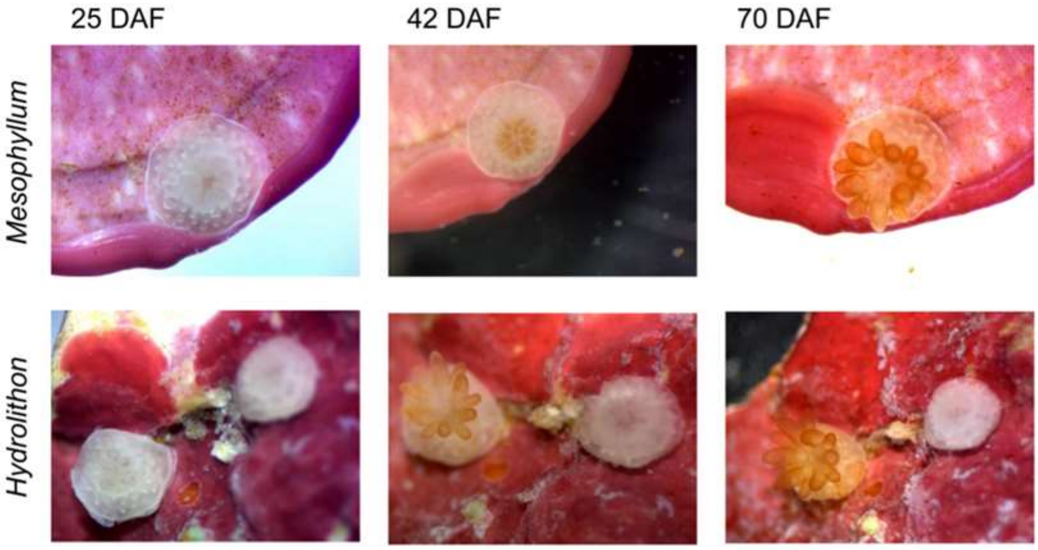

**Fig. S4.1.** *Acropora austera* recruit survival on *Mesophyllum* and *Hydrolithon* fragments

# Chapter 5:

# Recruitment of scleractinian corals on a high-latitude reef in South Africa: Micro-spatial patterns and the effect of caging

## 5.1. Abstract

The location where coral larvae settle has a profound influence on the fate of coral propagules. Once settled, resulting coral recruits are required to withstand conditions experienced at their attachment site. As a result, settlement of coral planulae is a selective process and spatial patterns of recruitment are governed by pre- and post-settlement processes. Here we assessed how coral recruitment (density and spatial settlement patterns) varied on settlement tiles, according to different attachment orientations (wide gap, narrow gap, and raised tiles) on concrete structures. Tiles were attached for six months onto a marginal, high-latitude reef in South Africa. The effect that herbivores and predators had on coral recruitment and the associated benthic community was also assessed with the use of exclusion cages. Recruitment was dominated by pocilloporids, regardless of study site and experimental treatment. The majority of settlement occurred on the vertical edges of tiles, regardless of treatment with a greater propensity to settle closer to the edges on the top surface of tiles than towards the centre. The majority (74.17%) of recruitment on the top surface of tiles occurred in the grooves, regardless of study site and tile treatment. Mean recruit densities differed significantly between tile treatments. Raised tiles and tiles with a wide gap between their edge and the concrete Y-frame received two- and three- fold more recruits than that of tiles with a narrow gap (644.33 ± 149.43 and 979.29 ± 170.88 recruits $m^{-2}$ respectively vs 311.05 ± 80.82 recruits $m^{-2}$). Additionally, when herbivores and predators were excluded, a two-fold reduction in recruitment occurred. The results confirm that the surface texture on settlement tiles plays an important role in the micro-spatial settlement pattern of corals, while orientation and caging settlement tiles do not. Both coral recruitment density and the benthic community on settlement tiles differed between tile treatments, but recruit density and the benthic community were not correlated. Comparably more macroalgae and crustose coralline algae cover occurred on uncaged tiles. This suggests that factors other than benthic community structure and herbivore pressure are drivers of coral recruitment on these reefs. Coral recruitment was highest at the northern (deepest) study site, regardless of settlement surface used. Together, the results

indicate that coral recruitment on a high-latitude reef in South Africa is heterogeneous at both the broad (study site) and narrow (settlement surface) spatial scale.

## 5.2. Introduction

The spatial dynamics of coral communities are largely determined by factors influencing larval dispersal, settlement and post-settlement survival (Brazeau et al., 2011). For corals to successfully recruit, larvae need to find a suitable surface on which they can settle, outcompete surrounding biota, and avoid being predated upon during post-settlement growth. Coral recruitment involves both allelopathic and physical competitive dynamics in which corals are typically weak competitors. This results in demographic bottlenecks due to significantly high levels of post-settlement mortality (Vermeij and Sandin, 2008), which is particularly prevalent within the first 24 hours of settlement  (Martinez and Abelson, 2013). The probability of survival increases as recruits grow bigger (Doropoulos et al., 2015; Raymundo and Maypa, 2004).

### *5.2.1. Spatial pattern of recruitment on settlement tiles*

Space is a limited resource in coral reef benthic communities (Eynaud et al., 2016). Microhabitats which facilitate coral settlement and post-settlement survival are thus vital as they enable the maintenance of coral-dominated communities (Harrison and Wallace, 1990; Hughes et al., 1999) and affect mature population abundance and distribution (Vermeij and Sandin, 2008). Coral larvae respond to a variety of abiotic and biotic stimuli to select their settlement location (Arnold et al., 2010; Baird et al., 2003; Gleason et al., 2009; Golbuu and Richmond, 2007; Harrington et al., 2004; Heyward and Negri, 1999; Morse et al., 1996; Mundy and Babcock, 1998a; Richmond, 1997; Vermeij et al., 2010). Influential abiotic parameters include light availability (Maida et al., 1994), sound (Vermeij et al., 2010), hydrodynamics (Abelson et al., 1994), surface composition (Benayahu and Loya, 1984; Burt et al., 2009; Field et al., 2007; Green et al., 2010; Harriott and Fisk, 1987; Lee et al., 2009), colour (Mason et al., 2011), and surface micro-topography (Brandl and Bellwood, 2016; Carleton and Sammarco, 1987; Whalan et al., 2015). While some conditions (e.g. light and nutrients) may be more favourable for coral growth, these also favour species such as algae which have a competitive edge through rapid growth (Birkeland, 1977). Thus, recruit survival increases where these conditions are less favourable for competitive species and enable them to reach size-escape threshold before being overgrown (Birkeland, 1977).

Previously, the spatial pattern of coral recruitment on horizontally attached settlement tiles on a high-latitude reef in South Africa yielded negligible recruitment on the vertical edges (Glassom et al., 2006). In contrast, Hart (2012) found that recruitment occurred predominantly on the vertical edges of tiles horizontally attached within recessed grooves on concrete anchoring structures on the same reef. It was hypothesized that the contrasting spatial pattern resulted from the edge microhabitat provided by the recess created by a 5 mm gap between the vertical edges of tiles and the juxtaposed concrete frame (Hart, 2012). Consequently, a new, grooved settlement tile was designed and manufactured from resin (Appendix 3) with the aim of increasing coral recruitment on a grooved top surface of tiles. Settlement surfaces are made more appealing by creating micro-crevices on the tile surface (Brandl and Bellwood, 2016; Nozawa, 2008; Nozawa, 2012a; Nozawa et al., 2011; Petersen et al., 2004; Tebben et al., 2014; Whalan et al., 2015), or in the way that the tiles are attached, e.g. inclining them to avoid sediment entrapment (English et al., 1997), or by raising them off the substratum to create a gap below their under-surface (Maida et al., 1994).

### *5.2.2. Effect of herbivore and predator exclusion*

Cracks and grooves provide refuge for recruits and support more diverse algal communities (Arnold and Steneck, 2011; Brandl and Bellwood, 2016), as predation and competition are lower in these microhabitats than on exposed surfaces (Bak and Engel, 1979; Carleton and Sammarco, 1987). Animals which may predate on coral recruits include, but are not limited to, fireworms (Wolf and Nugues, 2012), urchins (O’Leary et al., 2013), and various fish (Penin et al., 2011). Herbivores play an instrumental role in maintaining coral dominance and reef resilience by restricting algal growth and by providing clean substrata suitable for coral settlement and crustose coralline algae (CCA) colonization (Arnold et al., 2010; Belliveau and Paul, 2002). Certain species of CCA induce coral settlement (Harrington et al., 2004; Morse et al., 1996; Webster et al., 2004), consolidate reefs and create favourable settlement habitats which can promote post-settlement success (Harrington et al., 2004; Vermeij et al., 2006). CCA also suppresses macroalgae (Vermeij et al., 2011), which may inhibit and outcompete coral recruits (Arnold et al., 2010; Birrell et al., 2008b; McCook et al., 2001). Controlling competing biota on settlement tiles can also have a significant effect on the micro-spatial settlement and post-settlement survival of recruits (Tebben et al., 2014). However, herbivory can also result in the mortality of recruits through accidental removal (Penin et al., 2011; Penin et al., 2010). High coral recruit mortality has also been observed in exclusion treatments, but was attributed to sedimentation and algal competition in the absences of herbivores and predators (Penin et al., 2011). This highlights the dynamic interactions at play in terms of coral recruit settlement survival and the surrounding biota.

While coral reproduction (Kruger and Schleyer, 1998) and spatial-temporal recruitment dynamics (Glassom et al., 2006; Hart, 2012; Massé, 2014)have been assessed previously on the high-latitude reefs in South Africa, indicating that coral communities are reproductively active and attain comparable recruitment rates to their tropical counterparts, the effect that predators and herbivores have on the early ontogeny of corals on these reefs remains to be explored. Furthermore, the colonization of benthic organisms on settlement tiles, which coral recruits must inevitably compete with, remains to be investigated. The aims of this study were thus to: 1. Assess the spatial distribution of scleractinian coral recruitment on settlement tiles according to their orientation on concrete structures; 2. determine whether the density of coral recruitment and the benthic community structure differed on settlement tiles according to their orientation on concrete structures; and 3. to assess whether the exclusion of herbivores and predators from settlement tiles had a significant effect on the density of coral recruitment and benthic community structure on settlement tiles. Coral recruits were defined in this study as a ‘detectable corals’ on settlement surfaces.

## 5.3. Materials and methods

### *5.3.1. Study location and design*

This study was conducted at three study sites (Table S5.1) located at 11 m, 12 m, and 17 m (southern, central and northern respectively) on Two-mile Reef (TMR: 27°33’28”S; 32°41’10”E), a high-latitude reef within the iSimangaliso Wetland Park, South Africa. The high-latitude reefs within the Park constitute the southernmost coral-dominated reefs along the African coastline, yet provide habitat for a diverse assemblage of hard and soft corals on ancient fossilized sandstone (see Chapter 2 for further details).

Logistical and environmental considerations played a role in selecting the method of attachment of settlement surfaces in this study. While the direct attachment of individual settlement tiles to the reef substratum is desirable (as per Mundy 2000), this was not feasible as previous attempts to drill into the reef, which consists of aeolianite base rock, proved futile (Schleyer pers. comm.). Concrete Y-frames were thus designed to maximize stability and to withstand the high energy environment (Figure 5.1B). The edges of the concrete structures were chamfered at 60 degrees and the top was recessed so that the upper surface of settlement tiles was flush with the top of the concrete structure. Three replicate concrete Y-frames were installed at each study site in 2012 and were situated 5-10 m apart of each other at each study site.

Custom-designed resin settlement tiles made from polyurethane resin (AXSON Fastcast F16) with calcareous sand filler were used in this study (Appendix 3). The tiles had inclined grooves 5 mm wide and 3 mm deep, spaced 7 mm apart on their top surface and were of two sizes; 10 x 10 x 1 cm and 8 x 8 x 1 cm (Fig. 5.1A). The tiles had a rough surface and were centre-drilled, with horizontal attachment to concrete Y-frames (Fig. 5.1B).

Forty-five settlement tiles were attached parallel to the substratum to three of the aforementioned concrete Y-frames (Fig 5.1B). Each Y-frame arm contained a randomly attached tile for each of the five treatments (see section 5.3.2 - 5.3.4 below), resulting in three tiles per treatment on a Y-frame (Fig. 5.1.B). Results from the nine tiles of each treatment were pooled for each study site. Each treatment thus had a total sample size of 27 settlement tiles. Settlement tiles were ‘soaked’ for six months (Oct 2014-Apr 2015), encompassing the peak recruitment period on this reef (Glassom et al., 2006; Hart, 2012). The three aims of the study were investigated concurrently. The investigations and their associated tile treatments are detailed below.

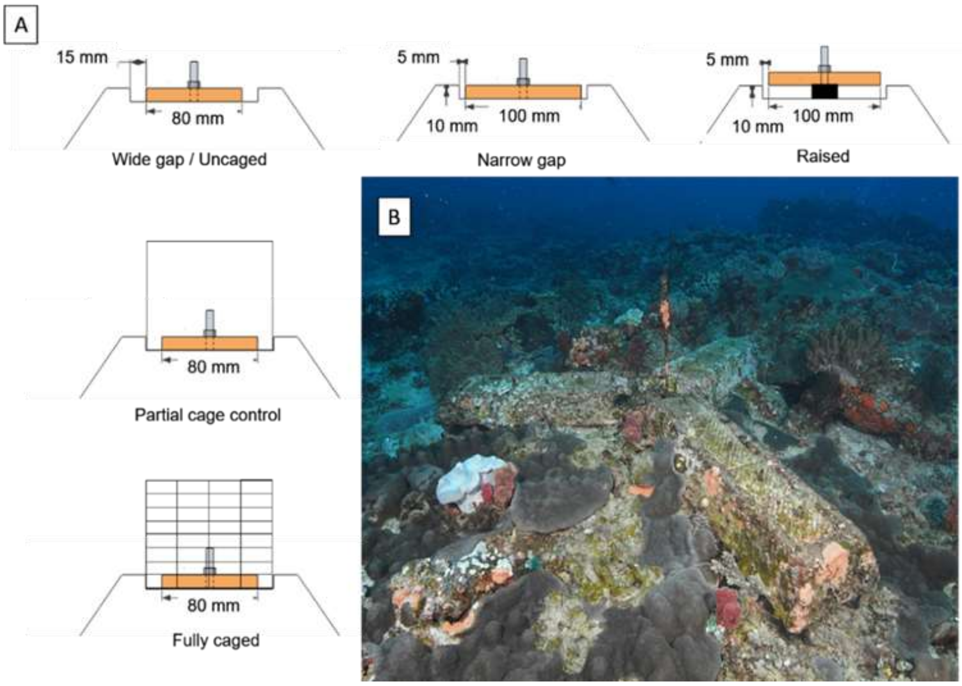

**Fig. 5.1.** Tile treatments applied in this study (A), and illustration of a concrete Y-frame used for settlement tile attachment (B). A 10 mm PVC spacer was used to raise settlement tiles out of the recessed groove on the top surface of Y-frames.

On recovery, settlement tiles were gently removed from the Y-frames and carefully transported to the Oceanographic Research Institute (ORI) research aquarium (29°52’06”S; 31°02’39”E) in a transport container filled with aerated seawater. The tiles were placed on skewers, with spacers in between to prevent them from touching. The skewers were placed in perforated cylinders in the transport container, thereby limiting tile corner damage during transit. Settlement tiles were then maintained in a flow-through aquarium system at ORI (Fig. S.5.1). Tiles were photographed with a Sea and Sea DX-1G camera and CPCe 4.1 software (Kohler and Gill, 2006), which employs point intercept technology, to quantify the percentage cover of crustose coralline algae (CCA); encrusting macroalgae (EMA); erect foliose algae (EFA); turf algae and sediment (TS); encrusting bryozoans (EB); bare substratum (B); and other (OT). Sediment was frequently trapped between turf algae filaments; therefore these two categories were combined. A standardized number of points per unit area (two points per cm$^2$) were overlaid on each edge surface, ensuring equal sampling effort on the surfaces of the two tile sizes.

After the settlement tiles were photographed, the four vertical edges, top surface, and underside of raised tiles were examined under a Zeiss Stemi DV4 stereo-microscope with the aid of a NightSea Blue Star fluorescent torch and barrier filter in a dark laboratory (Fig. S.5.2). The use of fluorescence assists with the detection of fluorescent recruits which may have settled in a cryptic location (e.g. Baird et al., 2006; Hsu et al., 2014; Piniak et al., 2005). Since not all living recruits exhibit fluorescence (Martinez and Abelson, 2013), or may be obscured by algae or sediment, tiles were re-analysed under the microscope with white light by gently brushing the tiles with a fine paint brush to detect additional non-fluorescing recruits. This was also done to confirm fluorescent detections were indeed scleractinian corals. Tiles where then placed in household bleach for 72 hours, rinsed, dried and re-analysed. Recruits detected using the three methods were tallied. The identity of recruits was determined based on their bleached skeletal structure according to Babcock et al. (2003) and allocated to either the Pocilloporidae, Acroporidae, Poritidae or an ‘Other’ category (see Appendix 4). Three recruits had severely damaged skeletons and were included in the ‘Other’ category. Any new recruits which were only detected during post-bleaching analysis were assumed to have been dead at the time of bleaching. Thus, recruitment success reported here could be underestimates of absolute survival. Each recruit’s spatial position on a tile was referenced with a Vernier calliper. Settlement on the under surface of raised tiles was negligible and was excluded from subsequent analyses.

### *5.3.2. Spatial pattern of recruitment on settlement tiles*

A digitized, two-dimensional tile screen was created using ArcMap (v9.2, ESRI) and the surface of 10 x 10 x 1 and 8 x 8 x 1 cm tiles were divided into six and five, one centimetre wide concentric grids respectively (from the vertical edge to the centre of the top surface of tiles). The proportion of recruits in each grid was calculated by counting recruits with Hawth's Tools (H. Beyer, Hawth's Analysis Tools for ArcGIS, available at http://www.spatialecology.com/htools) and divided by the total count of recruits on each tile. Results from the smaller 8 x 8 x 1 cm tiles were excluded from the statistical analyses to enable direct comparisons between tile types of the two sizes. The settlement location of recruits on the horizontal top surface of grooved tiles was assessed to determine what features of the grooved surface attracted the most recruitment (Fig. 5.2).

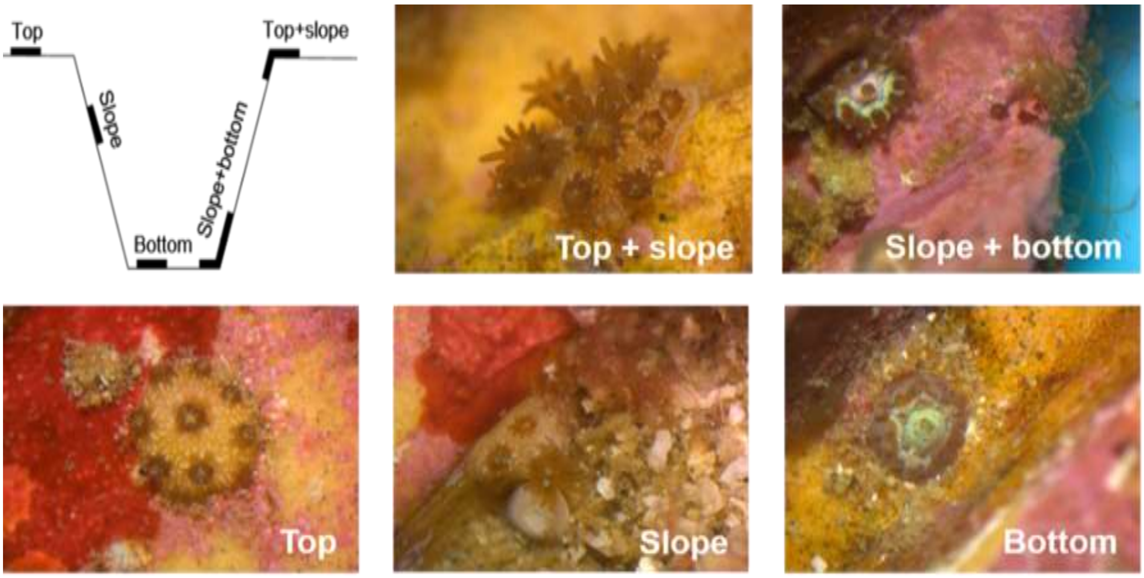

**Fig. 5.2.** Settlement location categories on the grooved top surface of tiles with representative images of a coral recruit in each category.

Three of the five tile treatments listed in section 5.3.1 above were assessed for the effect of edge microhabitat (Fig. 5.1A). Tile treatments included: recessed tiles (10 x 10 cm) with a narrow 5 mm gap between their edge and the concrete Y-frame (NG); tiles (8 x 8 cm) similarly recessed but with a wider, 15 mm gap (WG); and 10 x 10 cm tiles raised 1 cm above the Y-frame with a spacer (RA). This resulted in three replicates of each treatment per Y-frame, nine per study site and a total of 27 from the three study sites. Only recruitment, and benthic community structure on the left and right vertical edges of tiles were considered in this experiment as they were the only edges that were juxtaposed to the concrete edge on the Y-frames which formed the edge microhabitat under investigation. One tile from each treatment was excluded from analysis as these had no recruits.

### *5.3.3. Effect of herbivore and predator exclusion*

Results from fully-caged (FC), partially-caged controls (PC) and uncaged (UC) grooved, 8 x 8 x 1 cm tiles were employed to investigate the effect of predation on scleractinian recruitment and benthic cover (Fig. 5.1A). A 2 mm thick galvanized mesh with apertures of 23 mm x 10 mm was used to construct full and partial cages (10 x 10 x 8 cm, L x W x H), which were dip-coated in plasti-dip (Plasti-Dip International, Blaine, MN, USA) to prevent corrosion. Partial cages consisted of two sides connected across the top by a 50 mm wide strip for attachment onto the tile securing studs. A pilot study was conducted in which five replicate pairs of clod cards (Jokiel and Morrissey, 1993) were fully caged or uncaged for 24 hours at the shallowest study site (subjected to the most water movement) (Fig 5.3). The dissolution rates of the clod cards inside cages did not differ significantly from uncaged cards (Paired T-test: $P > 0.05$) and the cages were thus assumed to have a negligible effect on water flow, permitting comparisons between the FC and UC data. The benthic community structure on the four edges and top surface of the FC, PC and UC tiles was quantified from images taken of each tile.

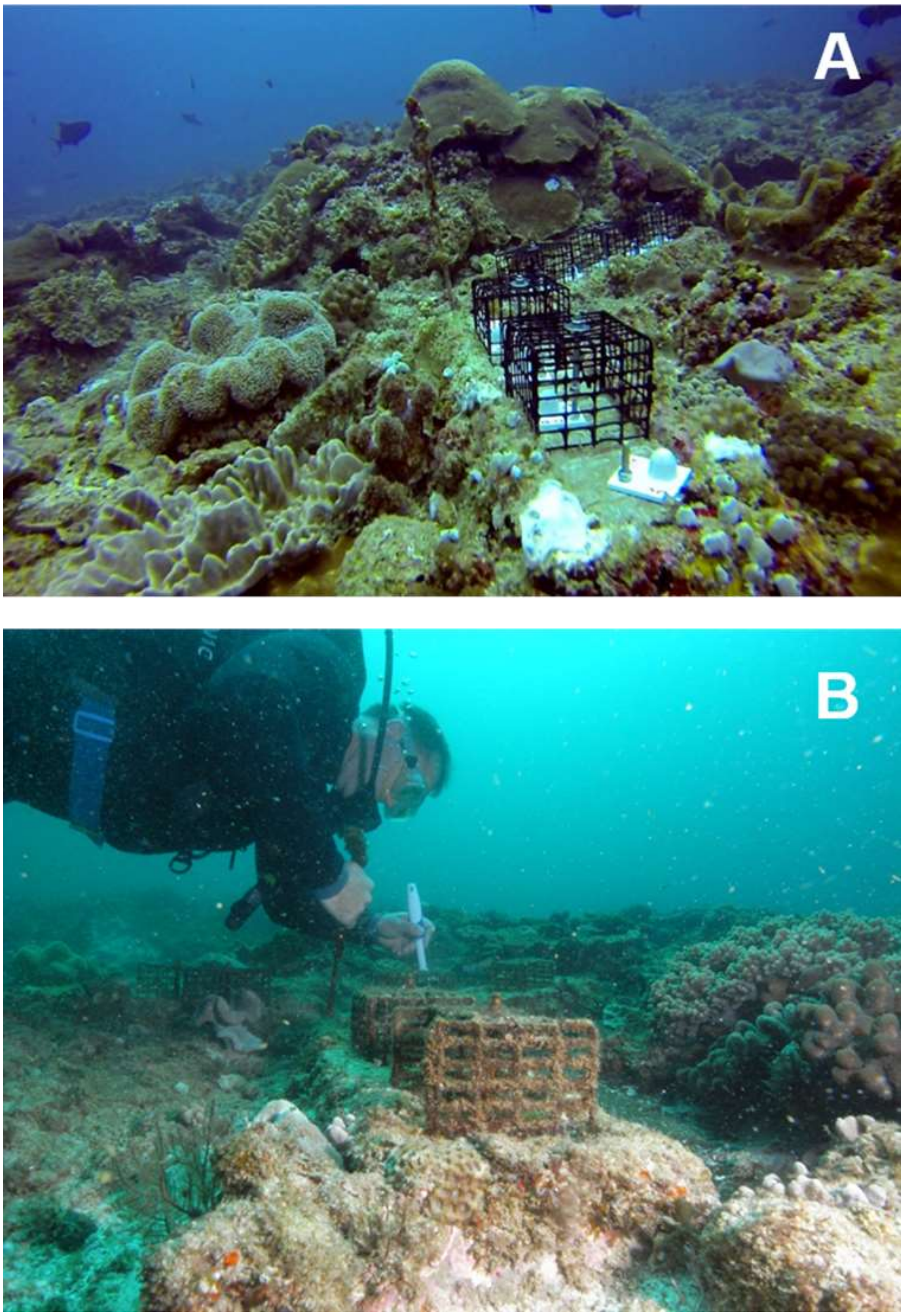

**Fig. 5.3.** Pilot experiment with replicate clod cards attached within and outside full exclusion cages (A) and monthly cleaning of cages during the six-month experiment (B).

### *5.3.4. Data analysis*

Statistical tests were undertaken using PRIMER v6 with the PERMANOVA extension (Anderson et al., 2008). Tile treatments and study sites were considered fixed factors in all analyses. PERMANOVA tests with 9,999 permutations based on Euclidean distance (Anderson, 2001) were used to 1) assess the spatial pattern of recruitment in the five settlement tile treatments and 2) assess if coral recruit density (number of corals per $m^2$ surface area) differed between the edges of NG, WG and RA tiles, and between FC and UC tiles. PERMANOVA tests based on the Bray-Curtis similarity matrix were also used to assess whether the benthic community structure on tiles differed significantly in the latter tests. The assumption of homogeneity of dispersion in all PERMANOVA analyses was tested with the PERMDISP function and, if this could not be satisfied with transformation, the raw data were used with a conservative cut-off value of 0.01 (Underwood, 1997). Due to low sample size, there was a risk of type II error. Pairwise Mann-Whitney U tests were performed to identify different groups when significant differences were found. Coral recruit density and benthic community structure were correlated on tiles considering the effect of edge microhabitat and herbivore and predator exclusion using Spearman's Rank Correlations with the RELATE function in PRIMER.

## **5.4. Results**

### *5.4.1 Spatial pattern of recruitment on settlement tiles*

Overall, the distribution in settlement differed significantly on the tiles (PERMANOVA, *df* = 4, *P* = 0.001), with significant grid x tile treatment and grid x study site interactions (PERMANOVA, *df* = 20, *P* = 0.001 and *df* = 8, *P* = 0.001 respectively). The majority of settlement occurred on the vertical edges of tiles, regardless of treatment and study site with a greater propensity to settle closer to the edges on the top surface of tiles than towards the centre (Fig 5.4). WG tiles had significantly less recruits 0-1cm from the edge on the top surface of tiles compared to NG tiles (t = 2.887, *P* = 0.013), but did not differ significantly between any of the other zones. RA tiles had similar proportions of recruits in each of the grids. FC tiles had a significantly lower proportion of recruits on the edge of tiles (t = 2.586, *P* = 0.009) but significantly more recruits 0-1 cm from the edge on the top surface compared to UC tiles (t = 2.133, *P* = 0.034). The proportion of recruits in grids on FC and UC tiles did not differ significantly. The greater proportion of recruitment on the vertical edges of tiles did not differ significantly between study sites (Fig. 5.5), regardless of tile treatment (Fig. 5.4).

On average, the majority (74.17%) of recruitment on the top surface of grooved tiles occurred on the inclined slopes within grooves, with recruitment on the remaining surfaces contributing <10% to the total recruitment (Table 5.1). Most recruitment occurred in the grooves, regardless of study site and tile treatment (Table 5.1). Although the majority of acroporids settled on the slope in the grooves on the top surface of tiles, a large proportion (22.2%) was found on the combined slope/bottom edge.

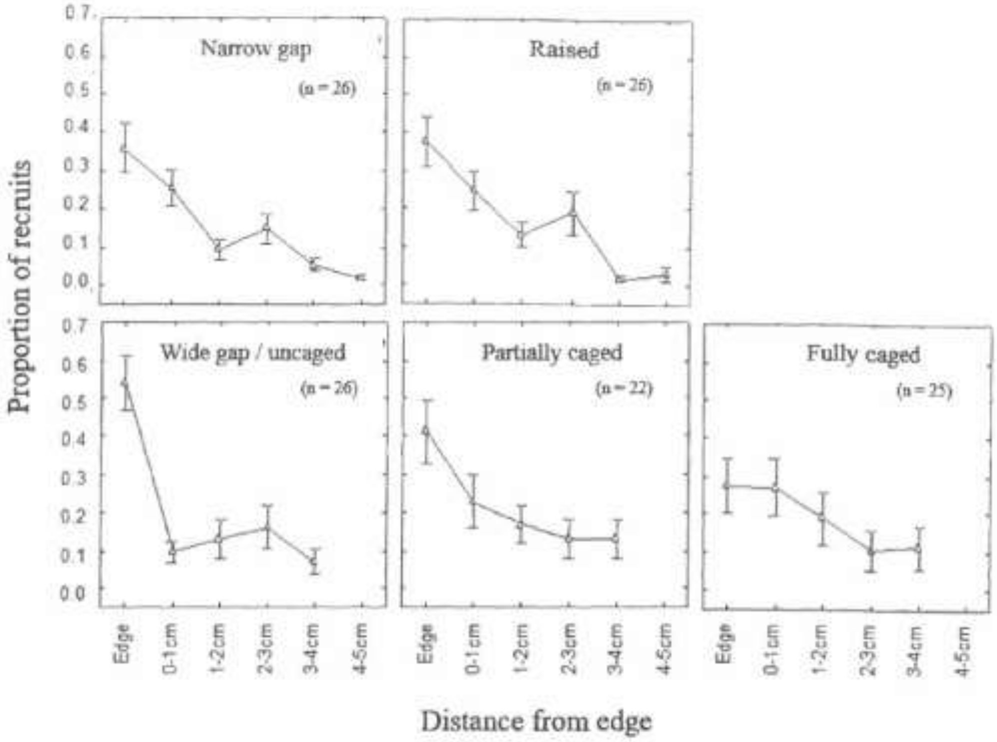

**Fig. 5.4.** Mean ± SE proportion of coral recruitment in the six tile zones. (*n* = number of tiles included in the analyses, i.e. those with at least one recruit).

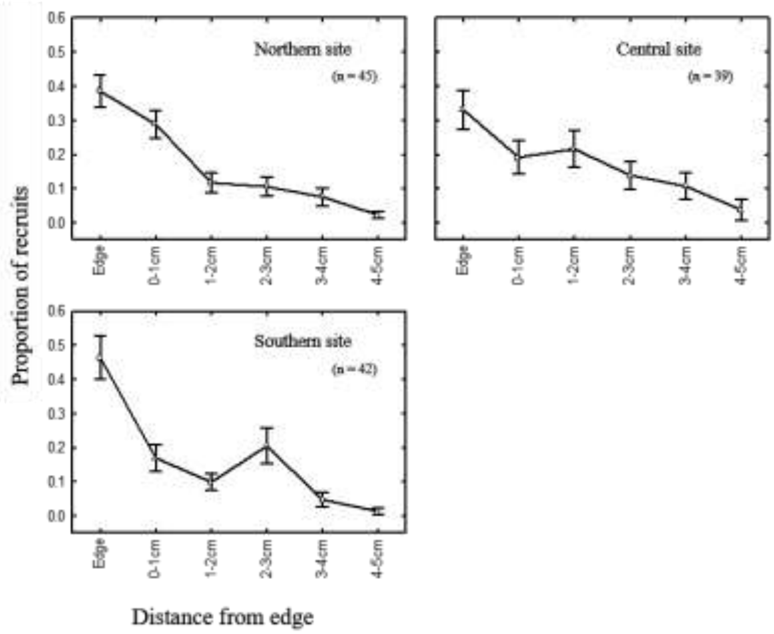

**Fig. 5.5.** Mean ± SE proportion of coral recruitment in the six tile zones (all treatments combined) at the different study sites on Two-mile Reef (*n* = number of tiles with recruits).

**Table 5.1.** Proportional coral recruit distribution (%) on the top surface of grooved tiles. The overall mean is the average percentage of each surface category, regardless of study site, tile treatment or coral taxa (See Fig. S5.2 for illustrations of each category).

| | | **Bottom** | **Slope** | **Slope+bottom** | **Top** | **Top+slope** | ***n*** |
|---|---|---|---|---|---|---|---|
| **Study Sites** | Northern | 6.87 | 79.39 | 0.76 | 7.63 | 5.34 | 131 |
| | Central | 7.41 | 79.63 | 5.56 | 5.56 | 1.85 | 54 |
| | Southern | 2.50 | 78.75 | 8.75 | 10.00 | 0.00 | 80 |
| **Tile Treatment** | Narrow gap | 7.55 | 78.30 | 2.83 | 8.49 | 2.83 | 106 |
| | Raised | 4.85 | 80.58 | 1.94 | 8.74 | 3.88 | 103 |
| | Wide gap/uncaged | 3.57 | 78.57 | 10.71 | 5.36 | 1.79 | 56 |
| | Fully caged | 5.71 | 74.29 | 5.71 | 8.57 | 5.71 | 35 |
| **Coral Taxa** | Pocilloporidae | 2.63 | 77.89 | 5.79 | 8.95 | 4.74 | 190 |
| | Other | 6.80 | 74.81 | 8.40 | 9.16 | 0.83 | 131 |
| | Acroporidae | 5.56 | 61.11 | 22.22 | 5.56 | 5.56 | 18 |
| | Poritidae | 0.00 | 100.00 | 0.00 | 0.00 | 0.00 | 5 |
| | **Overall mean** | 4.79 | 74.17 | 9.24 | 8.96 | 2.84 | |

Coral recruit density was greatest on WG tiles followed by RA tiles and NG tiles (979.29 ± 170.88, 644.33 ± 149.43, and 311.05 ± 80.82 recruits m$^{-2}$ respectively, Fig. 5.6). Mean recruit densities differed significantly between tile treatments, but not study sites nor the interaction between factors (PERMANOVA, *df* = 2, *P* = 0.003; *df* = 2, *P* = 0.066 and *df* = 4, *P* = 0.202 respectively). The mean density on NG tiles was significantly lower than that on RA and WE tiles (t = 2.023, *P* = 0.044 and t = 3.648, *P* = 0.001 respectively). RA and WG tiles were not significantly different (t = 1.535, *P* = 0.131). A significant difference was found in the benthic community composition between the three treatments, study sites and the interaction of treatment x study site (PERMANOVA, *df* = 2, *P* = 0.008; *df* = 2, *P* = 0.001 and *df* = 4, *P* = 0.018). Pairwise comparisons indicated that benthic community composition on NG tiles was significantly different from both RA tiles and WE tiles (t = 2.751, *P* = 0.025 and t = 2.451, *P* = 0.032) and was significantly different between all three study sites (northern vs central: *P* = 0.015, northern vs southern: *P* = 0.002 and central vs southern: *P* = 0.003). However, the patterns of recruit density on tiles was not significantly correlated to benthic community structure (Spearman Rank Correlation: r = 0.037, *P* = 0.221).

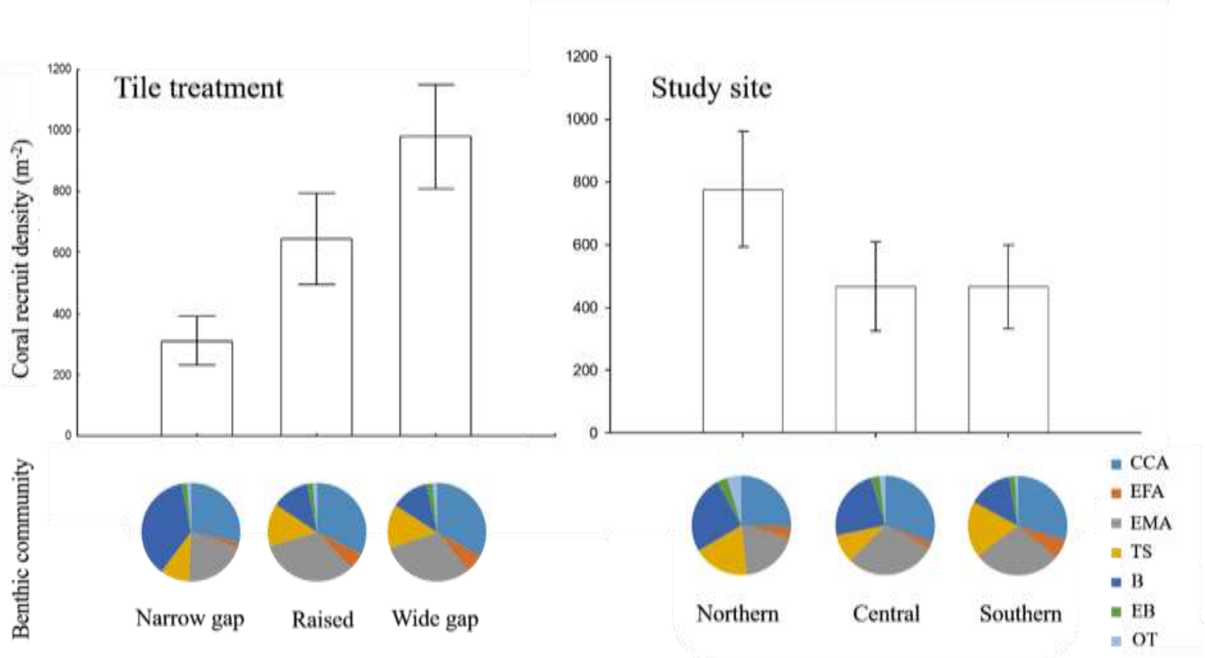

**Fig. 5.6.** Mean ± SE recruit density and benthic cover on settlement surfaces used to assess the effect of edge microhabitat. CCA = crustose coralline algae; EFA = erect foliose algae; EMA = encrusting macroalgae; TS = turf and sediment; B = bare substrata; EB = encrusting bryozoans; OT = other (*n* = 27 tiles per treatment and per study site).

### *5.4.2. Effect of herbivore and predator exclusion*

In total 60 recruits were found on FC tiles, 73 on PC tiles and 123 recruits on UC tiles (Table 5.2). Five PC and two FC tiles had no recruits on them. A significant difference was found between the overall density of recruits on FC and UC tiles (PERMANOVA, *df* = 1, *P* = 0.002; Fig. 5.7) and between study sites (PERMANOVA, *df* = 2, *P* = 0.004; Fig. 5.7), but not the interaction between treatment and study site (PERMANOVA, *df* = 2, *P* = 0.069). Benthic community differed between FC and UC treatments (t = 0.036, *P* < 0.001). The benthic community at the northern study site was significantly different from that at the central and southern study sites (t = 2.278, *P* = 0.001 and t = 2.014, *P* = 0.005), but the density of recruits at the central and southern sites were not significantly different from each other (t = 1.199, *P* = 0.218; Fig. 5.7). Coral recruit density was not significantly correlated to benthic community structure (Spearman Rank Correlation: r = 0.067 *P* = 0.147).

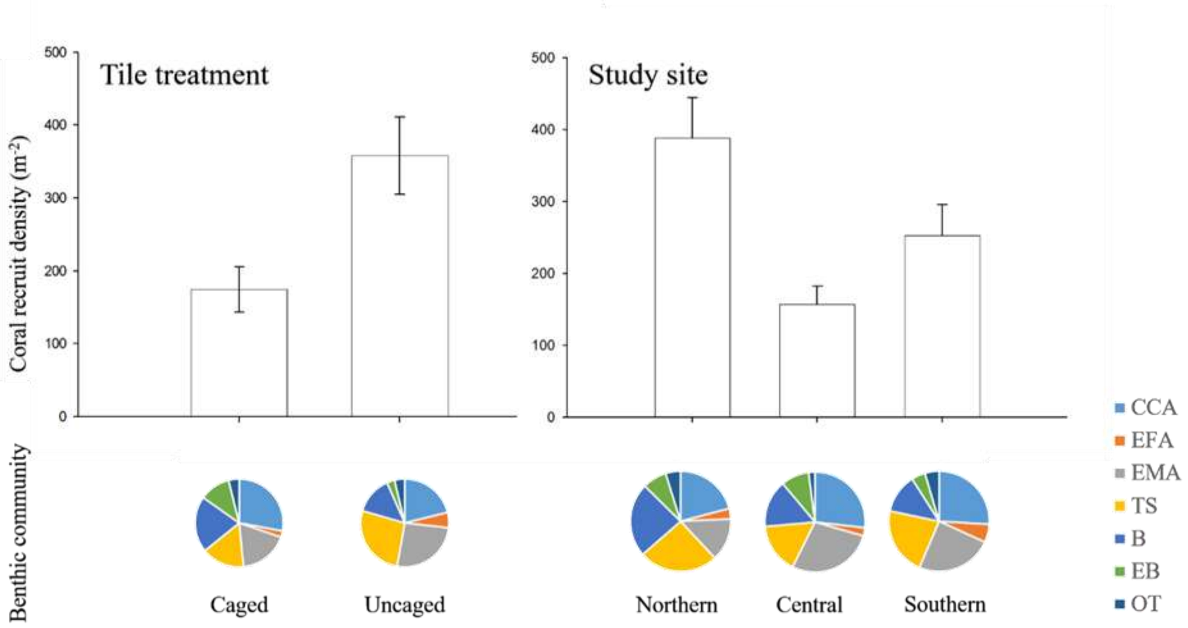

**Fig. 5.7.** Mean ± SE recruit density and benthic cover on settlement surfaces used to assess the effect of herbivore and predator exclusion. CCA = crustose coralline algae; EFA = erect foliose algae; EMA = Encrusting macroalgae; TS = turf and sediment; B = bare substrata; EB = encrusting bryozoans; OT = other (*n* = 27 tiles per treatment and per study site).

## 5.5. Discussion

### *5.5.1. Spatial pattern of recruitment on settlement tiles*

The dominant coral genera (Acroporidae and Pocilloporidae) which settled in this study are branching corals, which generally have lower survival than massive species (Tamelander, 2002). Acroporids constituted a small proportion of recruits (34 of 579 recruits in total). Post-settlement mortality of coral recruits is traditionally high (Martinez and Abelson, 2013) and can differ markedly between coral taxa (Doropoulos et al., 2015). In addition to its effects on recruitment rates, surface texture has been shown to influence the survival of coral recruits (Doropoulos et al., 2016; Nozawa, 2010), the most effective size of refugia for coral survival being ca. ≤ 10 mm wide and ≥ 2 mm deep (Nozawa, 2012a). Recruit survival has been found to be significantly greater on gridded surfaces of 2.5 cm (which experience lower grazing intensity) compared to larger grid sizes of 4 and 8 cm (Suzuki et al., 2011). Both the grooves on the tiles surfaces, and the gap-edge habitats of NG and WG tiles used in this study, fall within the size range of refuges effective for coral recruitment.

Heterogeneous patterns of coral recruitment may be due to differential supply and selection of coral larvae during settlement, or post-settlement mortality processes which vary between different locations on settlement tiles (Doropoulos et al., 2016). The overall heterogeneous pattern of recruitment between study sites and across settlement tiles found here corroborates results in other studies (Brandl and Bellwood, 2016; Maida et al., 1994; Petersen et al., 2004; Tebben et al., 2014). As per Glassom (2006), significantly greater recruitment was observed at ~18 m, compared to the shallower 12 m study site on TMR. Shallower sites can experience greater turbulence, while light becomes limiting as depth increases. Coral recruits grow faster on upper surfaces of settlement tiles and on shallower reefs where there is increased competition from fouling biota, while survival of recruits is greater on shaded vertical and under sides of tiles and increases with reef depth up to 20 m (Birkeland, 1977). At Sodwana Bay, coral cover reduces from depths beyond 18 m (Hart pers. obs.), with colonies being sparse at 27 m (Schleyer, 1999). Intermediate depths could therefore favour higher recruitment rates on these reefs (Roth and Knowlton, 2009).Negligible recruitment was observed on the underside of RA tiles in this study. Recruitment predominantly occurs on the under surface of raised settlement tiles in the tropics and at shallow study sites (Adjeroud et al., 2007; Arnold et al., 2010; Maida et al., 1994; Nzali et al., 1998; Vermeij, 2006). This is due to a trade-off between the need for light as well as sufficient water movement and refuge from predators and benthic competitors (see Baird and Hughes, 1996; Bak and Engel, 1979; Carleton and Sammarco, 1987; Mundy, 2000). A reduction in light from the edge of tiles towards the centre on their under surface results in a tendency for coral recruitment to be greatest towards the periphery (Maida et al., 1994). In contrast, recruitment is generally greater on the top surface of tiles where light becomes limiting e.g. at greater depths (Bak and Engel, 1979) and at high latitudes (Glassom et al., 2006). We found no significant difference in the proportion of recruits on the vertical edges of tiles between study sites which differed in depth (11 - 17m). Thus the reduction in light at the deepest study site was not sufficient to limit recruitment on the edges of tiles. This is corroborated by Birkeland (1977) who only found a significant shift in the proportion of recruits on the vertical edges versus the horizontal top surface at depths greater than 20 m.

Settlement on the top surface of tiles attached horizontally to the substratum may also be compromised by high sediment loads which inhibit coral settlement (Birrell et al., 2005) and are detrimental to the their post-settlement survival (Jones et al., 2015). This results in higher levels of recruitment on vertical edges than the horizontal top surface (dela Cruz and Harrison, 2017; Goh and Lee, 2008; Rogers et al., 1984; Tomascik, 1991). Results in this study corroborate this, as recruitment was greatest on the vertical edges and inclined edges within grooves on the top surface of the settlement tiles (which in themselves constitute a narrow edge). Micro-crevices and larger gap microhabitats have been proven to be preferential for coral recruitment on reefs elsewhere (Brandl and Bellwood, 2016; Doropoulos et al., 2016; O'Leary and Potts, 2011). This could be due to reduced water flow (Abelson and Denny, 1997; Boxshall, 2000) and entrainment of larvae (Abelson and Denny, 1997). The grooved tile design used in this study provided a structurally complex surface. The lower abundance of recruits at the bottom of grooves is probably due to high sediment loads, which are partially re-suspended during strong surges (Hart pers. obs.). Although no riverine sediment input occurs on Sodwana Bay reefs, considerable sediment deposition (1721 g m$^{-2}$ day$^{-1}$) has been recorded due to bioclastic sediment re-suspension associated with turbulence at the study sites (Grimmer, 2011). There are only a few studies which have described the distribution of recruitment on the top surface of tiles. In general, more recruits settled closer to the perimeter on the top surface of tiles in this study. Similarly, Glassom et al. (2006) found that the majority of settlement on the top surface of flat, 12 x 12 x 1 cm ceramic tiles occurred within 20 mm of the perimeter. If there is a preference for corals to settle on tile edges, increasing the ratio of the perimeter of settlement tiles to their area would influence the number of recruits (Field et al., 2007). In contrast, recruitment would increase uniformly as the area of the tiles increased if homogenous recruitment occurred (Field et al., 2007). Thus, care should be taken when comparing settlement rates between studies where recruitment is heterogeneous and different sized settlement tiles have been used.

WG tiles recruited the greatest density of coral larvae, followed by RA tiles and lastly NG tiles. It is predicted that sediment loads could also have contributed to the low levels of coral recruitment on edges of NG tiles, which is substantiated by the considerable bare surface on the edges of NG tiles that likely resulted from sediment loads precluding biota growth. Although WG tiles were attached in recessed grooves, less sedimentation was observed and this possibly resulted from flow dynamics differing at the edges of NG and WG tiles (Abelson and Denny, 1997; Hata et al., 2017). In addition, enhanced light at the edges of WG and RA tiles could have provided more preferential conditions for settlement compared to NG tiles (Mundy and Babcock, 1998a). Light intensity has been shown to significantly affect the spatial pattern of coral larvae elsewhere (Lewis, 1974; Maida et al., 1994; Mundy and Babcock, 1998a; Strader et al., 2015). This too could explain why RA tiles received greater recruitment than NG tiles, but less recruitment than WG tiles which probably experienced greater levels of larval retention within vortices in the gap depression.

Elsewhere, recruitment studies which have utilized different attachment methods within the same temporal and spatial scales have yielded results that conflict with those obtained in this study (Abelson et al., 2005; Glassom et al., 2004). Previously, Glassom et al. (2006) found that, at Sodwana Bay, recruitment on flat ceramic settlement tiles attached horizontally to the substrata on steel frames was greatest on the horizontal top surface (67.8%), with only 0.8% occurring on vertical edges. However, their devices were elevated some centimetres off the reef. Nevertheless, their results contrasts with those of Hart (2011) in which the majority of recruitment (82%) occurred on vertical edges of flat tiles attached to the recessed concrete structures used in this study. These differences are probably attributable to the different conditions (e.g. hydrodynamics) associated with the two attachment techniques. Other studies have yielded no significant difference in coral recruitment on settlement surfaces, whether attached directly to the substratum or on tile racks (Field et al., 2007; Mundy, 2000). However the racks used by Field et al. (2007) and Mundy (2000) had no gap habitats such as those on the concrete structures in this study.

### *5.5.2. Effect of herbivore and predator exclusion*

Caging of settlement tiles significantly reduced the density of recruitment. As the density of recruits on PC tiles did not differ significantly from UC tiles, it is unlikely that the cage design had a confounding effect on settlement. Greater spat densities have been found elsewhere in well-grazed areas compared to exclusion areas (Arnold et al., 2010). Herbivores have long been recognized to play a key role in the resilience of coral reef ecosystems (Hughes et al., 2007), as coral settlement has been shown to be inhibited by macroalgae (Kuffner et al., 2006), sediment, turf algae and other biota such as bivalves and sponges (Vermeij, 2006). The effect of herbivory is dependent on the functional group of herbivores present. Croppers regulate algal turfs in refuges by removing the upper sections of algae, while detritivores reduce both algae and particulate matter on flat surfaces through scraping (Brandl and Bellwood, 2016; Edmunds et al., 2014). These algae can smother coral recruits; however, intensive grazing can also result in significant recruit mortality due to ‘accidental’ predation (Baria et al., 2010; Penin et al., 2011). Thus, a balance must be reached whereby the benefits of grazing out-weigh the costs of coral mortality (Penin et al., 2011).

Recruitment success did not differ significantly between FC, PC and UC tiles. As found in previous recruitment studies on the high-latitude reefs of South Africa (Glassom et al., 2006; Hart, 2012; Massé, 2014), pocilloporids dominated recruit composition. However, in the tropics pocilloporid recruit mortality is greatest on exposed surfaces, compared to caged surfaces (Doropoulos et al., 2016). Their high numbers in this study may be attributable to the protection provided by the gaps and micro-crevices on the surface of the tiles. While small gaps of 2-3 mm (Harriott and Fisk, 1987; Petersen et al., 2004) have been found to favour coral settlement, larger gaps of 12-30 mm have also proven favourable as they deter large predators and grazers, but still allow a free flow of water and light penetration (Maida et al., 1994; O'Leary and Potts, 2011). Indeed, light has been proposed to be more influential for the settlement success of coral larvae than the avoidance of predation (Maida et al., 1994).

The benthic community assessment conducted in this study identified the key benthic categories found on recruitment tiles, which recruits will probably have to interact or compete with during their early ontogeny. A significant difference between benthic communities on different tile treatments and study sites was found in this study. As with coral recruitment, variations in light and hydro-dynamics could have influenced the resulting benthic community structure on different tile treatments. The lack of correlation between recruit density and benthic community structure obtained in this study may be due to the fact that pocilloporids tend to be non-selective of their settlement habitat (Baird and Hughes, 2000; Harrison and Wallace, 1990). Other studies have also shown that settlement of coral larvae in a reef environment is not significantly correlated with the benthic community structure on settlement tiles (Field et al., 2007; Glassom et al., 2004). This could be due to the scale at which the benthic community is assessed as fine scale assessments may highlight significant trends that could be masked at broader scales. Additionally, selective preferences may only be evident when settlement surfaces become limiting or larval densities are high. Although certain functional groups such as CCA facilitate coral settlement (Morse et al., 1988; Raimondi and Morse, 2000; Chapter 4), the inducing effect of CCA can differ between both coral and CCA species (Harrington et al., 2004; Chapter 4). High CCA cover could constitute ‘pre-empted space’ and not necessarily translate into areas available for coral settlement. However, increased levels of settlement may occur in the presence of CCA but not directly on its surface (Chapter 4). The interaction zones associated with CCA provide an environment that is not hypoxic and has non-pathogenic microbes, in contrast to other biota such as algae (Barott et al., 2012). CCA cover increases as the number of grazers increase as they remove competitive algae (O’Leary and McClanahan, 2010). Elevated grazing pressure on reefs results in benthic communities with high CCA cover and less heterotrophic invertebrates and fleshy algae, which in turn benefits coral recruitment (Hughes et al., 2007; Mumby et al., 2015; Smith et al., 2010). However, the greater algal cover and lower CCA on the uncaged settlement tiles suggests that grazing pressure occurs at reduced levels on TMR. While a fish community study conducted on the high-latitude reefs of South Africa has identified *Acanthurus nigrofuscus* as the most abundant grazer on TMR (Floros, 2010), the effect of herbivores on the benthic community needs investigation. Urchins also play a pivotal role as herbivores on reefs elsewhere (Davies et al., 2013; Korzen et al., 2011; O’Leary et al., 2013) and their dynamics on the high-latitude reefs of South Africa also needs to be assessed. However, their role in controlling benthic structure is anticipated to be less than fishes due to their low abundance (Hart pers. obs.).

*Lobophora variagata*, was found to be the dominant algal colonizer on artificial settlement surfaces in the present study. Corals compete with macroalgae for space on reefs and the growth and survival of their recruits. The outcome of these competitive interactions are species-specific and an increase in macroalgal biomass can occur in the event of herbivore exclusion (Lirman, 2001). In addition to pre-emption of space, macroalgae can reduce coral recruitment through allelopathy (Birrell et al., 2008b; Denis et al., 2014; Dixson et al., 2014; Doropoulos et al., 2014). Turf algae and sediment also contributed prominently to benthic cover in this study. As a functional group, turf algae are commonly considered inhibitors of coral settlement and their effect may differ according to turf algae assemblage and their sediment-trapping capacity (Birrell et al., 2005). Additionally, the bacterial community associated with turf algae can result in increased pathogenicity (Barott et al., 2012).

In conclusion, further experimental work on the competitive interactions between coral recruits, herbivores and benthic biota will provide valuable information on the bottlenecks in the early life history stages of corals on the high-latitude reefs of South Africa. There was an overall heterogeneous pattern of coral recruitment on the study reefs and it is recommended that future studies consider tile type, attachment technique, and tile size; particularly for comparisons between studies. For example, when vertical edges of tiles cannot be assessed *in situ*, the use of grooved tiles is recommended as these generally result in more recruitment occurring on their top surfaces. This will facilitate more efficient *in situ* assessment of coral recruitment (e.g. flourescent detection techniques, Baird et al., 2006; Mazel, 2005).

## 5.6. Acknowledgements

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## 5.7. Supplementary data

**Table S5.1.** Description of environmental conditions at the three study sites.

| **Factor** | **Northern site** | **Central site** | **Southern site** |
|---|---|---|---|
| Depth | 17m | 12m | 11m |
| Rugosity | Relatively flat with few gullies | Spur and groove formation around a stand of *A. austera*, more gullies than northern site | Variable topography with sharp drop offs into sand gullies |
| Water flow | Low – laminar | Medium-high surge | High surge |
| Representative image |  |  |  |

**Fig. S5.1.** Temporary housing of settlement tiles in a flow-through aquarium for three days during pre-bleaching microscopic analysis.

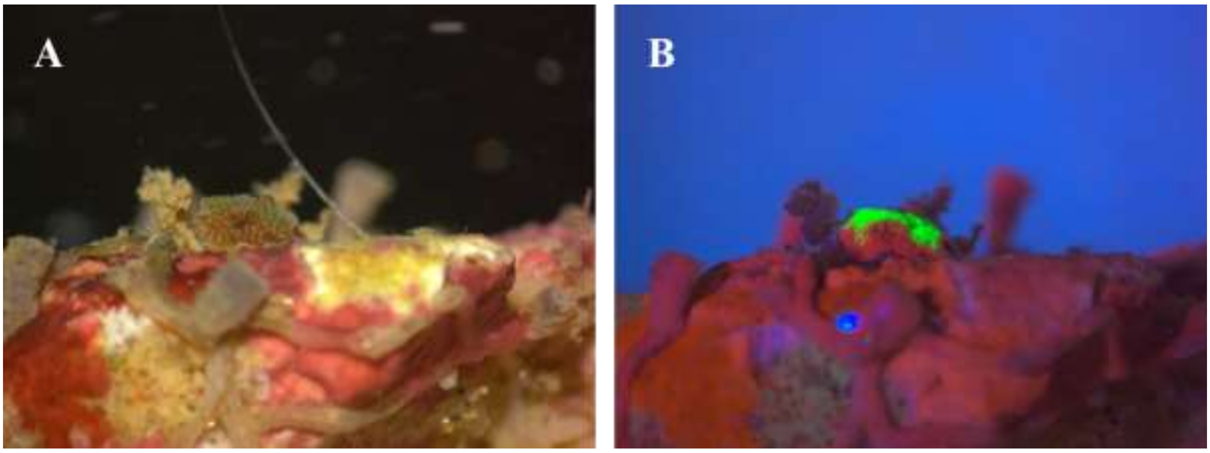

**Fig. S5.2.** Representation images of a scleractinian coral recruit that was detected during pre-bleaching with fluorescence (A) and a comparative image taken under white light (B) illustrating the benefit of using fluorescence during pre-bleaching.

# Chapter 6:

# Final discussion and conclusions

Our understanding of coral reproduction and recruitment has progressed in the past two decades, but detailed assessments on specific aspects of the early life stages of corals are limited to certain geographic locations and taxa. Consequently, extending our research efforts to incorporate less studied locations and taxa will add to our global understanding of these vital life stages. Furthermore, elucidation of bottlenecks which limit the quantity of gametes produced and their successful recruitment is needed for application in coral reef restoration work (Guest et al., 2013). This is becoming ever more urgent in light of the damage that has been incurred on many reefs around the world, with more than a third of hard coral species facing an elevated risk of extinction (Carpenter et al., 2008). Investigations of such ecological processes are essential, and can be used to predict the future responses of reefs to environmental change (Lam et al., 2017). Settlement studies further contribute to restoration and captive breeding projects as they enable genetically diverse individuals to be cultured and the vulnerable early life stages to be monitored to maximise survival. Thereafter recruits can be transplanted into protected microhabitats to increase survival rates in the field. However, limited resources and logistical challenges often impede multifaceted studies investigating different life history stages of corals. For example, night dives were not feasible in this study due to safety concerns. Consequently, it combined *in situ* and *ex situ* experimental research to asses aspects associated with the fertilisation, settlement and recruitment success of scleractinian corals on a high-latitude reef in South Africa.

This study contributes to the growing list of research which has reported sexual activity in corals at or near their latitudinal limit (see Baird et al., 2015; Harii et al., 2001; Harrison, 2008; Nozawa et al., 2006; St Gelais et al., 2016b; van Woesik, 1995; Wilson and Harrison, 1997; Wilson and Harrison, 2003). *Ex situ* spawning of *A. austera* and *H. exesa* colonies was observed after the March 2015 full moon in this study. This, in conjunction with other coral reproductive research (Kruger and Schleyer, 1998; Massé, 2014; Schleyer et al., 1997), illustrated that corals on South African high-latitude reefs spawn predominantly earlier in the year, over two to three months when water temperatures are close to their annual maxima. Spawning of corals frequently occurs over a 2-3 month period elsewhere (Baird et al., 2015), often during warmer months (Harrison and Wallace, 1990), including high-latitude locations such as Lord Howe island in Australia (Baird et al., 2015) and Kochi in Japan (Nozawa, 2012b).

*In situ* observations and reproductive assessments of other taxa will further elucidate spawning trends on South African reefs. Determining the precise date and time of gamete release can be extremely beneficial as it enables various aspects of the early life stages of corals to be assessed (e.g. fertilisation success, dispersal, effect of environmental conditions on the early life stages etc.). Knowing when gametes are released can be used in management to limit potential anthropogenic effects which may be detrimental to the survival of offspring e.g. boat traffic could result in oil pollution and thereby affect reproductive success (Loya and Rinkevich, 1980; Negri et al., 2016).

Synchrony in the reproductive seasonality of the broader coral community needs further assessment on the high-latitude reefs in South Africa. However, multi-specific broadcast spawning is anticipated to occur here, as found in most speciose coral communities (Baird et al., 2009). The identification of the timing of spawning of *A. austera* and *H. exesa* in this study not only enabled aspects associated with their fertilisation and larval settlement to be investigated, but will be of use in the event that their propagation is required for reef rehabilitation if this is ever needed. In such cases, this could be accomplished by active restoration with the seeding of new offspring. This may be done by sexual reproduction employing selective breeding for resilience (van Oppen et al., 2015) or asexual propagation (Page et al., 2018) which is becoming more common in an attempt to save coral reefs. Drastic approaches such as cryopreservation techniques are even being developed in an attempt to save genotypes of corals before they go extinct (Hagedorn and Carter, 2016)

Not all corals are anticipated to respond to environmental changes in the same way, as varying life history strategies affect their tolerance and recovery potential. Although *A. austera* and *H. exesa* both follow the same reproductive strategy of broadcast spawning, this study has shown that the fertilisation and early life stages of these corals can differ significantly. The Maputaland reefs comprise the southern distributional limit for *A. austera* along the African coast. A paucity of reefs and high turbidity south of Maputaland probably limits their distribution to higher latitudes, along with other coral taxa. Coral communities found further south consist mainly of pocilloporids and other hardy corals such as faviids, with only a few resilient *Acropora* species. The southernmost documented record of *H. exesa* is on Aliwal Shoal (Olbers et al., 2009), which is situated ~300 km south of Maputaland. The current distribution of the two coral taxa considered here provides an indication of their different 'tolerance' and ability to survive in a marginal environment. No records of *H. exesa* have been documented between these two locations and it is therefore plausible that the reefs along the Maputaland coastline could be the larval source for the southern location. The fast-flowing Agulhas Current would facilitate their transport, as well as the loss of coral larvae to reef-less areas further south after spawning (Morris, 2009).

Despite the fact that coral eggs and embryos are positively buoyant and have the capacity for large-scale dispersal, many manifest a trend of localised retention (Ayre and Hughes, 2000; Miller and Mundy, 2003; Montoya-Maya, 2014). Furthermore the dispersal of corals and the resulting connectivity of coral reefs is predicted to be influenced by climate change, as an increase in water temperature has been shown to significantly increase the development rate of coral larvae and reduce the time required before larvae can settle (Figueiredo et al., 2014).

## 6.1. Research Findings

Four key questions were targeted at the beginning of the study:

1. Do sperm concentration and salinity affect the fertilisation success of representative corals, *A. austera* and *H. exesa*?

The fertilisation success of coral gametes at the water surface following broadcast spawning is dependent on both pre- and post-release factors. Pre-release factors include the number of sexually active colonies, their geographic proximity, their fecundity and synchronization in the timing of gamete release. Post-release factors include environmental conditions such as currents and turbulence at the water surface and biological conditions such as gamete longevity. Although coral fecundity and recruitment may be lower at high-latitudes compared to the tropics (Hughes et al., 2002; St Gelais et al., 2016b) due to resource limitations, fecundity and recruitment in South Africa were shown to exceed that of tropical counterparts in Reunion (Massé, 2014). This and the fact that corals are genetically diverse on Sodwana Bay reefs (Montoya-Maya, 2014) suggests that fecundity is currently adequate.

There is little riverine input at Sodwana Bay and any noteworthy salinity changes are anticipated to result from heavy rainfall. Spawning during peak rainfall months is reported in Hong Kong (Chui and Ang Jr, 2017), Guam (Richmond, 1993), French Polynesia (Hedouin et al., 2015) and South Africa (Kruger and Schleyer, 1998; Massé, 2014; Schleyer et al., 1997), with spawning observed during rainfall in Japan (Nozawa, 2012b) and this study. Storms are predicted to increase in intensity and frequency with global climate change (Du Plessis and Burger, 2015; Trenberth, 1999), increasing hyposaline conditions in the surface microfilm of water. This has been shown to significantly reduce fertilisation (Hedouin et al., 2015; Scott et al., 2013; Vermeij et al., 2006). Rainfall is also predicted to increase surface water turbulence which is anticipated to result in the faster dilution of gametes. Therefore, under these conditions, coral gamete production would have to be adequate to ensure fertilisation success.

Egg-sperm bundles from a diverse range of coral taxa have been found to contain a mean of between $2.04 \times 10^6$ to $1.93 \times 10^7$ sperm per bundle, with high variability in the amount of gametes released within a population and even within a colony (Teo et al., 2016). A reduction in sperm concentration and water salinity reduced fertilisation success in both species (Chapter 3). In accordance with other studies (e.g. Nozawa et al., 2015; Oliver and Babcock, 1992), fertilisation success for both coral species was found to be greatest at a concentration between $10^5$ and $10^6$ sperm ml$^{-1}$. Fertilisation success reduced significantly once sperm concentration fell below $10^4$ sperm ml$^{-1}$ (Chapter 3). Although decreased salinity negatively affects fertilisation, a recent study on marginal reefs in Hong Kong has revealed that the interactive effect of increased temperature and decreased salinity may in fact benefit recruit settlement and post-settlement survival of a dominant coral species (Chui and Ang Jr, 2017). Thus investigating the interactive effects of predicted climatic conditions on the early life stages, particularly fertilisation, on marginal reefs will be of value.

2. Does the presence of *Hydrolithon* sp. and *Mesophyllum* cf *funafutiense* crustose coralline algae affect the settlement and post-settlement survival of *A. austera* and *H. exesa* planulae?

The majority of settlement of both *A. austera* and *H. exesa* larvae occurred soon after developing into planulae, but the longevity of some larvae of both species indicated the potential for long-distance dispersal along the east African coastline (Chapter 4). However, genetic assessments of *A. austera* stands on TMR indicate that there is localised retention of larvae (Montoya-Maya et al., 2016) which is a common trend found elsewhere (Ayre and Hughes, 2000; Miller and Mundy, 2003).

It is postulated that the complex and selective nature of pre- and post-settlement processes in corals evolved due to the need for specific conditions for settlement (Morse et al., 1988). The results of this study suggest that settlement conditions required by *A. austera* planulae are more specific than those for *H. exesa* (Chapter 4). Settlement of both *A. austera* and *H. exesa* larvae was significantly greater in the presence of *Hydrolithon*, but not *Mesophyllum* (Chapter 4). However, the presence of CCA is not a strict requirement for settlement as larvae from both species were capable of settling in filtered seawater alone (Chapter 4). While *H. exesa* settled predominantly on *Hydrolithon* fragments, most *A. austera* settlement occurred on container surfaces that held the CCA fragments (Chapter 4).

This contrasts with studies that have shown a preference for corals to settle on CCA surfaces, including *Hydrolithon* species (Harrington, 2004). This disparity supports the notion that both chemical (Negri et al., 2001) and physical cues (Whalan et al., 2015) can trigger settlement, and that these vary according to the coral and CCA taxa under consideration (Doropoulos et al., 2016; Harrington et al., 2004). However, settlement induction may not necessarily translate into post-settlement success. For example, settlement on the macroalgae *Halimeda opuntia,* an ephemeral surface, results in significant post-settlement mortality (Nugues and Szmant, 2006). Furthermore, some CCA species are known to slough their outer layers (Harrington et al., 2004), and could dislodge settled coral recruits in the process. Thus, post-settlement success can also depend on the species of CCA or coral (Chapter 4, Harrington et al., 2004). CCA taxa are frequently combined into a single functional group in benthic surveys as their identification is difficult. However, the species-specific nature of their effect on the early life stages of corals highlights the importance of identifying them and their environmental interactions (Harrington et al., 2004). For example, the growth of CCA is compromised by ocean acidification, which could in turn affect the settlement of corals (Doropoulos et al., 2012b).

Past studies of CCA on Maputaland reefs have been predominantly taxonomic (Keats and Chamberlain, 1994a; Maneveldt et al., 2008), with limited research on their ecology and distribution. On TMR, *Mesophyllum* CCA are most common at 18-25 m and grow under dim light (Keats and Chamberlain, 1994b). A study on TMR quantifying benthic cover on coral rubble and settlement tiles revealed that CCA were most prolific (Gersun et al., 2016). Furthermore, CCA were the dominant group surrounding coral recruits on settlement tiles on TMR (Hart, 2012). CCA have been commonly observed growing on branches of *Acropora* skeletons (Keats and Chamberlain, 1994b), with *Hydrolithon* spp. being the most prevalent on *A. austera* (Hart pers. obs.). It is not known whether this is a competitive outcome whereby the CCA gradually kills the coral, or whether colonization by *Hydrolithon* constitutes secondary growth on coral skeletons. Coral recruits have also shown a preference to settle on bare coral skeletons (Lee et al., 2009). Established *A. austera* stands with CCA (and associated dead skeletal material) could thus provide a cue to recruits that an area is suitable for settlement. Indeed, large *A. austera* patches are a feature of the Sodwana reefs (Floros and Schleyer, 2017). In addition to potentially attracting recruits, their growth will to some degree be attributable to vegetative regrowth from natural breakage.

3. Do coral recruitment and benthic community differ on the substratum according to surface microhabitat?

The results of this study highlighted the heterogeneous recruitment of corals on TMR at both narrow and broad spatial scales, with pocilloporid recruits constituting the most common taxa in all tile treatments and at all locations (Chapter 5). At high latitudes, pocilloporid recruits are more prevalent than acroporids which are more dominant at low latitudes (Hughes et al., 2002). Most recruitment occurred at the deepest (northern) site in this study, highlighting depth as a potentially important factor in coral recruitment in South Africa. This is corroborated by other studies which have likewise found greater recruitment at a depth of ≥17 m on South African reefs (see Glassom et al., 2006) and elsewhere (Rogers et al., 1984; Smith, 1997). Thus deeper sites constitute significant areas for coral recruitment and understanding the drivers for this warrants investigation. The micro-spatial patterns of recruitment assessed in this study highlight the importance of surface microstructure. The experimental design used in this study assessed spatial patterns of coral recruitment rather than settlement, as surfaces were analysed after a six month soak time and therefore include post-settlement processes. The chosen experimental design provided a valuable snapshot of what recruitment dynamics on settlement tiles are like during the peak reproductive season of corals. Further fine-scale temporal analysis of settlement dynamics (involving frequent repeat observations of settlement tiles during the first settlement stages, such as those conducted by Martinez and Aronson (2013) would be beneficial as they could provide insight into spatial patterns observed in this study.

Textured surfaces more resemble natural reef substratum than smooth surfaces. The majority of settlement on the top surface of tiles occurred in the grooves in this study. Consequently the grooved settlement tile design created in this study is considered an improvement on traditionally used flat ceramic surfaces. Concentrated settlement on tile edges has important implications for the use of settlement tiles with different dimensions, as greater edge to surface area ratios could result in elevated measures of recruit density. Therefore, standardisation of settlement surfaces is imperative for cross-study comparisons (Field et al., 2007). The orientation of settlement tiles in this study, in terms of elevation and spacing, affected both the benthic community and density of coral recruits, although the two were not correlated (Chapter 5). While substratum availability is probably not limiting coral recruitment on South African reefs, an understanding of settlement preferences and post-settlement dynamics on these marginal reefs will be important in their management and the monitoring of coral recruitment. Since the wide gap tile arrangement incurred the greatest amount of settlement, which was significantly greater than previously used narrow gap and raised treatments, the choice of this treatment (comprising a smaller 8 x 8 cm tiles) is recommended for future studies at this study site.

This aspect of the study has implications if the reefs ever suffer extensive damage. As has been elaborated, they occur in a high-energy environment and strong swell and surge action roll coral rubble repeatedly over the reefs during severe storms (J Hart & M. Schleyer, pers. obs). The reef surface is left scoured and smooth, yielding a surface less suitable for coral recruitment. Indeed, the absence or slow recovery of *A. austera* patches was noted by Floros & Schleyer (2017). While retexturing extensive areas of damaged reef would seem beyond the realms of possibility, a reef rehabilitation programme could incorporate reseeding damaged reef with fragments of live rock covered with CCA to promote their growth on the bare reef surface, thereby encouraging coral recruitment.

4. Does the exclusion of herbivores and predators have an effect on coral recruitment and benthic community structure?

Exclusion cages did not affect the spatial pattern of coral recruitment in this study but did have a significant effect on the amount of recruitment that occurred (Chapter 5). Recruitment was greatest on uncaged surfaces, which is a trend that has been observed in the Caribbean and Micronesia (Arnold et al., 2010; Doropoulos et al., 2016). As was documented by Gersun et al. (2016) on TMR, CCA and macroalgae constituted the dominant benthic cover categories, regardless of settlement surface (Chapter 5). More algae but less CCA were observed on uncaged tiles (Chapter 5). As discussed previously (Chapter 4), some CCA species can negatively influence recruitment, which could explain the reduced settlement observed on caged tiles. There was no correlation between recruit density and the benthic community. This is probably due to the majority of recruits being pocilloporids, which are considered generalist settlers.

The results of this study suggested that grazing pressures are not negatively influencing coral recruitment on TMR. The reduction in algae on the caged tiles could indicate that not all herbivores and predators were excluded, as small biota could fit through the cage bars. Fish communities play a vital role in the health of coral reef systems (Cinner et al., 2016; McClanahan et al., 2012), with herbivory known to play a significant part in reef resilience (McClanahan et al., 2012). While a detailed assessment of the fish community structure has been conducted on the high-latitude reefs of South Africa (Floros et al., 2013), limited research has been conducted on the ecology of fish on these reefs (but see Floros and Schleyer, 2017). Although the exploitation of non-game fish has long been prohibited on the reefs, the ecological role of herbivores warrants further investigation. In particular, studies should consider herbivorous taxa other than fish, as their functional roles may differ (Davies et al., 2013). Varying levels of grazing pressure on these reefs should also be considered as this would further facilitate reef management at the community level. This is especially needed in light of the important role that herbivores play in controlling macroalgal cover on reefs, which in turn can affect the suitability of surfaces for coral larval settlement (Doropoulos et al., 2014).

### 6.2. Concluding remarks

The life histories, habitats and abundances of *A. austera* and *H. exesa* differ markedly. *Acropora austera* form dense, branching stands (which may coincidentally be promoted by the high levels of CCA associated with them), encouraging selective larval settlement within such patches (Chapter 3). Observations have shown that these large stands successfully form, senesce and die (Schleyer pers. comm.). In contrast, *H. exesa* colonies grow as isolated persistent encrustations randomly scattered on the reefs and occur in slightly deeper water than *A. austera*. While *A. austera* stands thus have growth flushes and are not necessarily long-lived, *H. exesa* colonies are persistent competitors on the reefs. In addition, the two corals differ in their bleaching tolerance, with *A. austera* more sensitive than *H. exesa* (Hart pers. obs.). Indeed, an increase in 2°C has been shown to negatively affect *A. austera* larval development, while a more robust species, *P. daedalea*, was able to withstand a 4°C increase in temperature (Massé, 2014). Furthermore, the growth morphology of *A. austera* is more susceptible to storm and diver damage (Schleyer and Tomalin, 2000). Collectively, these differences between *A. austera* and *H. exesa* suggest that, proportionately, more corals similar in characteristics to *H. exesa* will occur on the high-latitude reefs of South Africa in the future.

Although *A. austera* colonies on TMR take longer to reach sexual maturity than other acroporids found in the tropics (Hall and Hughes, 1996; Kojis, 1986; Montoya-Maya et al., 2014), presumably in response to marginal conditions (Montoya-Maya et al., 2014), their fecundity is greater (Massé, 2014). Stands of *A. austera* form important nurseries for fish (Floros and Schleyer, 2017) and it is predicted that these stands may be reduced in the future and thereby affect not only coral community structure, but have a ripple effect on fish communities. This may collectively alter the benthic community structure, with, for example macroalgae proliferating on exposed reefs with reduced herbivore pressure. However, in comparison to tropical reefs, the negative effects of global warming have occurred to a lesser extent, or not at all, in recent years on the high-latitude reefs of South Africa (Porter and Schleyer, 2017). Thus these reefs could provide a refuge for corals.

Although many of the world's diverse coral reef ecosystems as we know them are possibly under threat of extinction within the next 30 years, this threat varies spatially. Environmental stress could result in reduced gamete production, which in turn has implications for coral recruitment and reef resilience. Broadcast spawning corals are not being replenished in some locations, which is concerning as they are major contributors to reef structure (Kinzie III, 1999). Tropical locations are at greater risk, while high-latitude locations, such as those along South Africa's north-east coast, constitute potential refugia (Beger et al., 2014; Riegl and Piller, 2003). Additionally, the high-latitude reefs along the Maputaland coastline of South Africa are well managed within protected areas and their value and importance should not be underestimated.

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## Appendix 1: Summary of peer-reviewed publications dealing with coral reproduction within the south western Indian Ocean.

| **Topic** | **Study location and site** | **Reference** |
|---|---|---|
| Reproductive seasonality of *Pocillopora verrucosa* | South Africa , Maputaland | Kruger, Schleyer (1998) |
| Gametogenesis and larval brooding in *Anthelia glauca* | South Africa , Maputaland | (Kruger et al., 1998) |
| Reproductive seasonality of *Sarcophytum glauca* | South Africa , Maputaland | (Schleyer et al., 2004) |
| Reproductive seasonality of *Platygyra daedalea* | Kenya, Mombasa | (Mangubhai and Harrison, 2008) |
| Reproductive seasonality of *Echinopora gemmacea* and *Leptoria Phrygia* | Kenya, Mombasa | (Mangubhai, 2009) |
| Effect of heterotrophic feeding on the reproduction of *Pocillopora verrucosa* | South Africa, Vetch's pier | (Séré et al., 2010) |
| Sexual reproduction of *Pocillopora damiconis* | South Africa, Vetch's pier | (Massé et al., 2012) |
| *Ex situ* observations of spawning behaviour of *Platygyra daedalea* | South Africa, Maputaland | (Massé et al., 2013) |
| *In situ* observation of *Acropora* assemblage spawning | Madagascar, Andavadoaka | (Gress et al., 2014) |
| Reproductive seasonality and synchrony in *Acropora* assemblage | Mozambique, Vamizi Island | (Sola et al., 2016) |
| Size at first maturity of *Acropora austera* and *Platygyra daedalea* | South Africa, Maputaland | (Montoya-Maya et al., 2014) |

## Appendix 2: Summary of peer-reviewed publications dealing with coral recruitment within the south western Indian Ocean.

| Topic | Study location and site | Reference |
|---|---|---|
| Temporal patterns of scleractinian recruitment | Tanzania, Zanzibar | (Franklin et al., 1998) |
| Effect of dynamite fishing on scleractinian recruitment | Tanzania, Taa Reef | (Nzali et al., 1998) |
| Scleractinian recruitment following 1998 bleaching | Kenya, Mombasa | (Tamelander, 2002) |
| Spatio-temporal dynamics of scleractinian recruitment | South Africa, Maputaland | (Glassom et al., 2006) |
| Spatio-temporal patterns of scleractinian recruitment | Kenya, Mombasa | (Mangubhai et al., 2007b) |
| Scleractinian and alcyonacea recruitment success | South Africa, Maputaland | (Schleyer et al., 2008) |
| Spatial variation in coral recruitment | Kenya, Mombasa | (O'Leary and Potts, 2011) |
| Indirect effect of fishing on coral recruitment | Kenya, multiple sites | (O’Leary et al., 2012) |
| Effect of fish and urchins on scleractinian coral recruitment | Kenya, multiple sites | (O’Leary et al., 2013) |
| Scleractinian recruitment on settlement tiles and the natural substratum | Seychelles, inner islands | (Chong-Seng et al., 2014) |
| Scleractinian recruitment on settlement tiles and the natural substratum at Vamizi Island | Mozambique, Vamizi Island | (Sola et al., 2015) |
| Effect of sediment on coral recruitment | Kenya, multiple sites | (Mwachireya et al., 2015) |
| Novel settlement tile design for *in situ* assessment of coral recruitment | South Africa, Maputaland | (Hart and Schleyer, 2016) |
| Update of scleractinian and alcyonacea recruitment success | South Africa, Maputaland | (Porter and Schleyer, 2017) |

# Appendix 3: A novel settlement tile design to facilitate the *in situ* detection of coral recruits.

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Short Communications: Spawning of outplanted nursery-grown *Acropora*

spawning was observed. Two additional *A. cervicornis* genets showed gamete formation 19 months aftert out-planting (Carne et al. 2016 in review). Spawning times for both years (2015-2016) were around 20:50-21:20 hrs (Belize time) and spawning dates and times coincided with the spawning of wild acroporids at Carrie Bow Caye, Belize (N. Fogerty pers. comm).

**Figure 2.** Spawning in nursery reared, outplanted *Acropora cervicornis*. Photo Annelise Hagan.

Documenting these spawning events is an essential monitoring tool to illustrate the success of the use of *in situ* cultivation and outplanting of genetically diverse acroporid populations. In future work, the proximity of outplanted corals should be manipulated to investigate optimal spacing for successful larval production. Cultivation followed by outplanting is an effective management strategy to enhance endangered acroporid populations.

***Acknowledgements***
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## A novel settlement tile design to facilitate the in situ detection of coral recruits

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Microhabitat of settlement surfaces is important for coral recruitment with surface structure and attachment technique shown to affect the suitability of surfaces for coral planulae settlement. Unglazed ceramic tiles have been widely used in coral recruitment studies (Doropoulos et al. 2014; Glassom et al. 2006; Harriott and Fisk, 1987). Surface irregularity influences the suitability of surfaces for settlement (Carleton & Sammarco 1987), with most recruitment occurring in micro-crevices on settlement tiles used in the field (Brandl & Bellwood 2016;

Nozawa et al. 2011; Roeroe et al. 2009) and laboratory (Doropoulos et al. 2016; Petersen et al. 2005; Tebben et al. 2014; Whalan et al. 2015). Planulae settlement at low latitudes occurs predominantly on the under surface of raised settlement tiles (Maida et al. 1994; Mundy 2000) or on the surfaces between stacked tiles (Mundy 2000; O'Leary and Potts, 2011). At high latitudes more settlement occurs on the upper, exposed surfaces of tiles, presumably because light is a limiting factor (Harriott and Banks 1995).

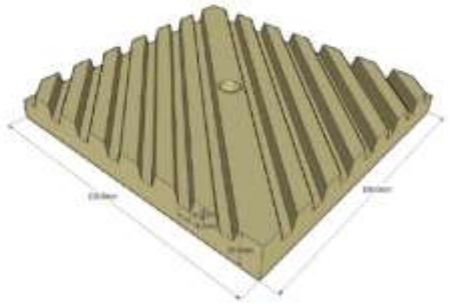

**Figure 1.** Oblique view of the grooved tile design.

**Figure 2.** Example of a coral recruit which has settled at the base of a tile groove.

Previously, coral settlement on a high-latitude reef in South Africa was found to occur predominantly on the vertical edges of horizontally attached ceramic tiles on which the horizontal top surface and vertical edges were exposed for coral settlement (Hart and Schleyer, submitted). This behaviour restricted the number of recruits which could be detected in situ with fluorescent photography. Here we describe a new customised tile design where the top surfaces have been structured to enhance the availability of microhabitats suitable for coral settlement.

A tile prototype was machined from HDPE plastic to create inclined grooves 4 mm deep and 4.2 mm wide at the base (Fig. 1). The prototype was sandblasted to create a textured surface and used to make replicate box moulds with Mold Max 10 (Smooth-On Inc.) silicone rubber. This enabled the production of multiple tiles which were cast from polyurethane resin (AXSON Fastcast F16) with a silica sand filler (25 g Part A, 25 g Part B, 65 g silica sand per tile). Tiles were numerically engraved, using a sharp implement, before they were fully set in order to facilitate identification. Multiple moulds were used as the production rate of tiles must be rapid due to the short pot life (~5 mins) of the resin. The tiles were cured in flow-through sea water before use. The use of this new tile design resulted in an increase in the proportion of settlement that occurred on the top surface of tiles compared to the edges. The majority of recruits settled in the grooves (Hart and Schleyer submitted) (Fig. 2), which potentially provide refuge and preferential light conditions for coral recruits. This in turn increased the number of recruits that could be detected and monitored in situ. The tile design may also be of benefit in settlement research on other benthic marine organisms.

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# A Coral Bleaching Event at Secas Islands, Chiriqui Bay, Pacific Coast, Panama

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Increasing sea surface temperatures have been established as the primary cause of coral bleaching (Brown 2009), with bleaching reported as occurring either when mean seasonal temperature increases by as little as 1°C above the normal seasonal average for a period of weeks, or is at 2°C above average summer peak temperature for one week, or at 1°C above normal for 2 weeks (Jokiel and Coles 1990; Sapp 1999; Rowher and Youle 2010), depending in part on previous exposure to increased temperatures. Increasing solar radiation also often exacerbates coral bleaching (Brown 2009). At a national meeting of US reef scientists in 1991 global warming was concluded not to be the main culprit causing coral bleaching (Sapp 1999); instead, with bleaching being observed mostly in El Niño years, changes in ocean temperature due to this phenomenon were then considered the more important. Subsequently, even with the significance of climate change becoming clear (Hoegh-Guldberg 1999; Veron et al. 2009), it is nevertheless in El Niño years that many regions are most prone to experience coral bleaching, among them the Pacific coast of Panama, where in the past elevated sea surface temperatures have generally occurred semi-regularly every 3-7 years.

**Figure 1.** Map of Panama to show the locations of the Seca Islands, Playa Pargo and Coiba Island.

With global annual mean temperatures continuing to rise, the El Niño beginning in 2015 has been one of the most intense on record (Eakin et al. 2016). In Panama warmer than usual water may have been present as early as April (2015), since the Smithsonian Tropical Research Institute in Panama City reported that corals on Coiba Island, on the Pacific coast, had started to fade at that time (Smithsonian Tropical Research Institute website). By August, in the same area, there

## Appendix 4: Representative pre-bleaching and post-bleaching images of coral recruits from the four taxonomic categories.