CORAL RECRUITMENT ON A HIGH-LATITUDE REEF AT SODWANA BAY, SOUTH AFRICA: RESEARCH METHODS AND DYNAMICS

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Abstract

Coral recruitment is a key process that contributes to the community structure and resilience of coral reefs. As such, quantification of this process is important to assist with the management of these threatened ecosystems. While coral recruitment has been the focus of numerous studies over the past 30 years, an understanding of this process on the high-latitude reefs of South Africa is limited. In addition, variations in methods used in recruitment studies make the results difficult to compare. A rapid in-situ method for universal application in the detection of early post-settled recruits would thus be useful.

In this study, scleractinian coral recruitment was investigated at three study sites on Two-mile Reef, over two six-month sampling periods, covering summer and winter. Two components were investigated by attaching settlement tiles consisting of ceramic and marble tiles, and ceramic tiles conditioned with crustose coralline algae (CCA) onto the reef in a spatially structured experimental design. Firstly, coral recruitment was compared on the three different tile surfaces and fluorescence photography was investigated as a rapid *in situ* technique to detect early post-settled recruits. Fluorescence photography was then used to compare recruitment on tiles with the surrounding natural substrata. Secondly, the spatial and temporal variation in the abundance, composition and size of recruits was investigated. Additionally, the percentage cover of biota surrounding each recruit within three millimeters of its corallum was visually estimated to quantify the microhabitat surroundings of coral recruits.

Overall recruitment on the three tile types differed, yet spatial variation in coral recruitment, regardless of tile surface, accounted for most of the variance in recruitment. While the highest recruitment occurred on CCA tiles, this was not significantly greater than ceramic tiles, indicating that the conditioning of ceramic tiles with *Mesophyllum funafutiense* CCA did not enhance coral settlement in this study. Although many recruits were not detected with fluorescent photography (73%), it proved useful to reveal recruits as small as 0.75 mm in corallum diameter, and indicated that recruitment on the tiles and natural substratum differ significantly. Spatially, the abundance and composition of coral recruits differed between study sites, within sites, and predominantly occurred on tile edges. Coral recruitment was lowest at shallower sites, and was dominated by pocilloporids regardless of study site. Additionally, the abundance and composition of recruits differed between the two sampling periods, with a 6.6-fold decrease in the mean abundance of recruits from summer

to winter, with only pocilloporid settlement occurring in the latter season. The majority of recruits were <3 mm, and their microhabitat was dominated by bare substrata and crustose coralline algae. The results suggest that, while the choice of artificial settlement surface used in such studies can have a profound influence on the results, spatial variation in recruitment can be greater. The recovery of scleractinian coral taxa on Two-mile Reef in the event of a severe disturbance is expected to differ, with greatest recovery in areas of high levels of recruitment. The microhabitat surrounding recruits is described here for the first time, suggesting that further research into coral-crustose coralline algae interactions is warranted. Finally, while fluorescence photography has its limitations, it shows promise as a useful tool for rapid qualitative, but not quantitative, assessment of recruitment.

Preface

The work described in this dissertation 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 Apr 2009 - April 2011, under the supervision of Professor Michael Schleyer. This dissertation represents original work by the author and has not otherwise been submitted in any form for any degree or diploma to any tertiary institute. Where use has been made of the work of others, it is duly acknowledged in the text.

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I, Justin R. Hart, declare that:

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Declaration 2 - Publications

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

Publication 1 (in prep):

JR Hart, MH Schleyer and D Glassom. Methods for studying coral recruitment: The influence of settlement surface and recruit detection techniques

Author contributions:

JH and MS conceived the paper. JH collected and analyzed the data, MS provided financial support for the study and both MS and DG contributed comments on the manuscript

Publication 2 (in prep):

JR Hart, MH Schleyer and D Glassom. Recruitment dynamics of scleractinian corals on a high-latitude reef at Sodwana Bay, South Africa

Author contributions:

JH and MS conceived the paper. JH collected and analyzed the data, MS provided financial support for the study and both MS and DG contributed comments on the manuscript

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Acknowledgements

"The sea, once it casts its spell, holds one in its net of wonder forever"

- Jacques Cousteau

Chapter 1:

General Introduction

1.1. Background to the process of coral recruitment and its importance

Coral reefs and their associated biota are truly one of nature's greatest beauties which have persisted over millennia (Veron 1995). These physical structures comprise the most diverse and complex ecosystem in the ocean (Connell 1978, Moberg & Folke 1999) and provide an array of essential ecological goods and services (see Moberg & Folke 1999). However, the long-term survival of these ecosystems is threatened by various anthropogenic stressors and global climate change (Hoegh-Guldberg 1999, Carpenter et al. 2008, Veron et al. 2009). Consequently, understandings of ecological processes which are influential in their resilience have become a high priority (e.g. Hughes & Tanner 2000, Adjeroud et al. 2009, Elmhirst et al. 2009). One such process is the attachment of coral planulae (settlement), and the subsequent introduction of new coral individuals (recruitment) (Harrison & Wallace 1990). Coral recruitment is well recognized for its role in coral reef resilience and structuring coral communities (Harrison & Wallace 1990, Caley et al. 1996, Connell et al. 1997). Consequently, it is important to quantify this demographic process and incorporate it into coral reef management strategies (Hughes et al. 1999, Hughes et al. 2003).

Corals rely on the passive dispersal of offspring which may be produced either sexually or asexually (Harrison & Wallace 1990, Richmond 1997). Although asexual recruits can play a significant role in the composition of corals on various reefs (Stoddart 1983, Miller & Ayre 2004), the production of ciliated planulae from sexual reproduction enables corals to maintain genetic diversity and cope with changes in the system (Richmond 1997). After dispersing, planulae need to settle on appropriate substrata, metamorphose and survive to maturity (Harrison & Wallace 1990, Richmond 1997, Veron 2000). High mortality of planulae, and a lack of suitable settlement surfaces commonly results in a reduction in the number of planulae which settle (Birrell et al. 2008a, Graham et al. 2008). Furthermore, high levels of post-settlement mortality can result in a reduction of recruits reaching maturity (Smith 1992, Szmant & Miller 2006, Vermeij & Sandin 2008).

The mode of sexual reproduction exhibited by corals can influence the abundance and composition of coral recruits, and their spatial-temporal distribution (Sammarco & Andrews 1989, Harrison & Wallace

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1990, Sammarco 1994, Atchison et al. 2008, Harrison 2011). Broadcast spawning of large quantities of gametes for external fertilization in the water column is the dominant mode of sexual reproduction in corals, and is commonly a synchronized event during a short annual breeding season (Harrison & Wallace 1990, Harrison 2011). Varying levels of synchronicity occur between and within species depending on their geographic location (Harrison & Wallace 1990). In contrast, brooders release fewer, yet larger, ready-to-settle planulae, which can settle within centimeters of parental colonies (Gerrodette 1981, Richmond 1997, Brazeau et al. 2011) and release planulae throughout extended periods or year round (Harrison & Wallace 1990). Spawned gametes can disperse vast distances before they are competent to settle after approximately 4-6 days (Harrison & Wallace 1990, Richmond & Hunter 1990), however rapid settlement of some species, such as *Platygyra daedalea*, can occur as early as three days (Miller & Mundy 2003). This indicates that the settlement of spawned offspring can occur closer to natal colonies than previously thought (Sammarco 1994, Miller & Mundy 2003). While the maximum competency period of brooders is likely longer than that of spawners due to their greater energy reserves (Richmond 1988), potential maximum competency periods of as much as 100 days have been found for both spawners and brooders (Wilson & Harrison 1998, Harii et al. 2002 respectively). This shows that planulae from both reproductive modes are capable of large scale dispersal. Considerable variation between competency periods within the two reproductive modes indicates that there are other factors which can influence coral settlement patterns.

During planktonic development, coral planulae lose their positive buoyancy and develop a swimming ability with the aid of ciliated epidermal cells (Harrison & Wallace 1990, Raimondi & Morse 2000, Szmant & Meadows 2006). While planulae are considered weak swimmers, and predominantly rely on currents for dispersal (Harrison & Wallace 1990), they can regulate their vertical position within the water column once sufficiently developed by altering swimming patterns and velocity (Pizarro & Thomason 2008). Furthermore, planulae sensory cells detect changes in water temperature (Bassim & Sammarco 2003), barometric pressure (Stake & Sammarco 2003), light availability (Kuffner 2001), water chemistry (Gleason et al. 2009), and even reef noise (Vermeij et al. 2010). These stimuli influence the behavioural response of planulae during the dispersal phase and stimulate planulae to descend back to the reef substratum in search of a suitable settlement surface.

During substratum exploration, planulae swim with their aboral surface in close proximity to the substratum (Harrison & Wallace 1990) as this contains sensory cells which facilitate searching and testing behaviour (Vandermeulen 1974). Once planulae find a suitable settlement surface, they attach and begin secreting a skeleton (Harrison & Wallace 1990), leaving a permanent record of their existence unless they

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become dislodged or overgrown (Richmond 1985). However, if conditions are stressful after settlement, they can dislodge and return to the water column to search for another site (Richmond 1985). Furthermore, planulae can delay skeletal secretion after morphing and actively search the substratum for a suitable microhabitat within a small distance from their initial settlement site (Vermeij 2002). The importance of settlement selectivity by coral larvae is highlighted by the fact that, once settled and morphed, they need to survive conditions at that location in order to reach maturity (Vermeij 2002). Consequently, habitat selection during settlement plays an influential role in their post-settlement survival and the resulting distribution patterns of adult corals on reefs (Mundy & Babcock 1998, Baird et al. 2003).

The settlement and metamorphosis of planulae into sedentary polyps (settlement process) is a crucial step in the life history of corals and is often limited by a lack of suitable surfaces for settlement and subsequent survival (Harrington et al. 2004). The study of this process whereby corals return to a benthic stage is common practice in recruitment studies and has received considerable attention within the last three decades (Bak & Engel 1979, Birkeland 1982, Fitzhardinge 1985, Fisk & Harriott 1990, Baird & Hughes 1997, Edmunds 2000, Green et al. 2010, Brazeau et al. 2011). However, the small size, and slow growth of recruits (Babcock 1985, Edmunds 2007) results in many recruits becoming visible to the human eye on the natural substratum only a year after settlement (Wallace & Bull 1981). As a result, it has become common practice for researchers to attach artificial settlement surfaces, which can be retrieved for microscopic examination, to the reef allowing investigation into the early life stages of coral recruits. By studying the settlement of coral planulae, researchers gain an understanding of the availability of planulae at both spatial and temporal scales (Harriott 1985, Hughes 1985, Wallace 1985a, Glassom et al. 2006), and their behavioural responses to both abiotic (e.g. Babcock & Davies 1991, Mundy & Babcock 1998) and biotic factors (e.g. Birrell et al. 2008b, Arnold et al. 2010). A variety of both biotic and abiotic microhabitat factors have been investigated that have been shown to inhibit or induce coral settlement with the use of settlement plates, both in the field (Harriott & Fisk 1987, Mundy 2000) and laboratory (Harrington et al. 2004).

Several abiotic variables influence the supply of coral planulae and their subsequent settlement at a particular site. For example, local hydrodynamics play an influential role in the supply of planulae (e.g. Oliver et al. 1992) and their attachment (Abelson et al. 1994). Abiotic aspects of settlement surfaces have received considerable attention. These include substratum orientation (Rogers et al. 1984, Tomascik 1991), surface texture (Carleton & Sammarco 1987), color (Mason et al. 2011) and composition (Benayahu & Loya 1984, Harriott & Fisk 1987, Field et al. 2007, Burt et al. 2009, Lee et al. 2009, Green et al. 2010). These studies have shown that settlement onto the undersurfaces and inclined/vertical

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surfaces is usually highest at low latitudes (Rogers et al. 1984, Tomascik 1991). In contrast, a shift in settlement towards the top surfaces has been recorded at high-latitude locations (Harriott & Banks 1995, Fairfull & Harriott 1999, Glassom et al. 2006), possibly due to light limitation (Harriott & Banks 1995, Harriott & Simpson 1997). Corals tend to prefer rough settlement surfaces (Harriott & Fisk 1987, Nozawa et al. 2011), and settle at higher frequencies on red surfaces (Mason et al. 2011).

It has been widely recognized that biologically conditioned settlement surfaces (microbial biofilms) are favorable for coral settlement (Benayahu & Loya 1987, Harrison & Wallace 1990, Johnson et al. 1997, Webster et al. 2004). Thus it has become common practice for researchers to pre-condition settlement surfaces with a biofilm before starting experiments (Nozawa et al. 2006, Erwin et al. 2008, Cohen et al. 2009). Although the principle biotic inducer of coral settlement reported in the literature is crustose coralline algae (CCA) (Morse et al. 1996, Heyward & Negri 1999, Raimondi & Morse 2000, Harrington et al. 2004), substratum preference can be species-specific (Harrington et al. 2004, Golbuu & Richmond 2007). Reportedly, CCA can induce settlement in a variety of coral species due to the presence of large polysaccharides within their cell walls (Morse et al. 1994, Morse et al. 1996). The extraction and attachment of these molecules onto artificial surfaces has resulted in increased settlement in both the laboratory and field (Morse et al. 1994). However, comparatively high levels of settlement have been recorded on both dead and living CCA, which suggests that compounds found beneath the surface layers of CCA can induce settlement (Heyward & Negri 1999). Recruits which settle on CCA can be compromised by dislodgement during the sloughing of CCA epithelial layers (Harrington et al. 2004) and CCA overgrowth (Maida et al. 1994, Dunstan & Johnson 1998); however, post-settlement survival studies of this nature remain scant. In addition, the competitive edge between recruits and CCA is dependent on the prevailing environmental conditions (Sammarco 1980). Aged biofilms lacking CCA have also been shown to induce high levels of settlement (Webster et al. 2004), along with extracts from coral skeletons and coral rubble (Heyward & Negri 1999), indicating that coral larvae receive a variety of cues from reefs.

Following settlement, recruit mortality is generally extremely high (Rylaarsdam 1983, Babcock 1985, Fairfull & Harriott 1999),.due to unfavorable microhabitat selection, the resulting physical conditions, and competition between other biota at the site of settlement (Keough & Downes 1982, Babcock & Mundy 1996). Settlement on ephemeral surfaces increase mortality rates, as recruits can become dislodged (Birrell et al. 2008a). Consequently, settlement on surfaces such as turf algae and macro-algae generally reduces survival of recruits (Birrell et al. 2005, Kuffner et al. 2006, Birrell et al. 2008a). Furthermore, turf algae can limit settlement indirectly by trapping sediment, which has been shown to reduce settlement

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(Babcock & Davies 1991, Hunte & Wittenberg 1992, Babcock & Mundy 1996). It is suggested that intermediate levels of grazing pressure can optimize settlement conditions (Sammarco & Carleton 1981), by reducing algal cover (Mumby et al. 2007) and creating refuges for settlement (Birkeland & Randall 1981). Over and above grazing pressure, the allelopathic effects of other biota such as soft corals can inhibit settlement (Maida et al. 1995). Furthermore, post-settlement survival of recruits can be compromised by competition with other biota which can overgrow and smother new recruits, especially in nutrient-rich environments where competing organisms can thrive (Birkeland 1977).

The degree of selectivity in microhabitat is not always high (Baird & Morse 2004, Erwin & Szmant 2010) and settlement onto ephemeral surfaces have been reported (Nugues & Szmant 2006). Carleton and Sammarco (1987) hypothesized that more common species can be less sensitive to texture. Such variations indicate that a better understanding of cues which induce or inhibit coral planular settlement is needed.

1.2. Motivation for this study

Coral reproduction and recruitment are important components which should be incorporated into adaptive management strategies of coral reefs due to their importance in reef resilience-. Generalizations across recruitment studies are complicated by the use of different methods, as evidence suggests these may influence settlement patterns (Harriott & Fisk 1987, Field et al. 2007, Burt et al. 2009, Burgess et al. 2010). Such differences may be attributed partly to different settlement surfaces (Harriott & Fisk 1987, Harrington et al. 2004, Burt et al. 2009) as planulae can be highly selective during settlement (Harrington et al. 2004, Ritson-Williams et al. 2010). Furthermore, different recruit detection techniques can also yield inconsistent results (Edmunds et al. 1998, Baird et al. 2006). This makes a rapid *in situ* recruit detection technique desirable, which in turn would facilitate the quantification of coral recruitment over greater surface areas (Burgess et al. 2010).

Reportedly, coral recruitment decreases with an increase in latitude (Hughes et al. 2002). Therefore, the high-latitude reefs in South Africa may experience low levels of recruitment. Furthermore, recruitment is a dynamic process, and requires continual monitoring to enable adaptive management. In contrast to other parts of the world, a clear understanding of coral reproduction and recruitment on the high-latitude Maputaland reefs of South Africa remains to be achieved. Maputaland reefs are situated along an exposed, high-energy coastline, making night-diving extremely dangerous (chapter 2.1). As such, coral spawning events on these reefs remain to be documented, and reproductive work has been limited to histological studies of a select few species (see Benayahu & Schleyer 1998, Kruger & Schleyer 1998, Kruger et al.

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1998). Coral recruitment has only been investigated in a single study conducted between 1999 and 2002 (Glassom et al. 2006). Therefore, an updated study, with investigation into additional components of coral recruitment is therefore necessary to provide data to facilitate more effective management of the high latitude reefs of South Africa.

The objectives of this study were to:

1. Assess the degree to which different methods affect the results in coral recruitment studies.

2. Compare the levels of coral recruitment on natural and artificial substrata.

3. Compare coral recruitment at three locations on Two-mile Reef, in the iSimangaliso Wetland Park.
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1.3. Arrangement of thesis

This thesis consists of five chapters. An introductory chapter (chapter 1), Materials and Methods (chapter 2), two chapters prepared for publications in peer-reviewed journals (chapter 3 and chapter 4), and a concluding chapter (chapter 5). The materials and methods in the two journal article chapters (chapter 3 and chapter 4) are presented together in chapter 2 to avoid repetition.

Chapter 2:

Methods

2.1. Study area and monitoring sites

Reefs along the east coast of Africa are predominantly fringing reefs, and extend down the continent from Somalia in the north, to the Maputaland coastline of South Africa. Coral-dominated reefs become less accretive at higher latitudes due to a reduction in factors which are necessary for their growth, namely decreased water temperature and aragonite saturation (Kleypas et al. 1999). This results in the global reduction of coral reefs at high-latitudes. Aside from being at the southern extremity of Africa's east coast, Maputaland reefs are exposed to open ocean swells (Riegl et al. 1995), which can cause physical damage to coral communities (Riegl 2001, pers. obs.). Collectively, these factors contribute to the small size of Maputaland reefs, as they limit accretion. Due to the above, these reefs comprise coral-dominated communities on rock substrata derived from ancient fossilized sand dunes rather than being true accretive reefs (Ramsay & Mason 1990, Riegl et al. 1995, Schleyer & Celliers 2003a). The reefs, are topographically relatively uniform, and occur at a depth range of 9 - 34 m (Ramsay & Mason 1990).

Regardless of the above, the coral communities on these reefs attain high species diversity of both hard and soft Indo-Pacific corals (Schleyer & Celliers 2003a). These collectively constitute the majority of the living epibenthic cover (Spalding et al. 2001). Hard corals are more diverse, with 93 species, compared to 39 soft coral species (Schleyer & Celliers 2003a). However, the latter cover a greater surface area (Schleyer & Celliers 2003a, Schleyer et al. 2008) where they dominate reef-top communities (Riegl et al. 1995), and cover the same surface area as hard corals at the reef-sediment interface (Schleyer & Celliers 2003b).

The local oceanography along the Maputaland coast is influenced by the southward flowing Agulhas Current, which flows along the continental shelf (Hutchings et al. 2002), and is predicted to transport coral planulae from reefs to the north (Morris 2009, Macdonald et al. 2011). Inshore currents predominantly run in a south-westerly direction and are predicted to transport spawned planulae southwards; however, reversal currents do occasionally occur which can retain, and transport planulae northwards (Morris

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2009). The resulting dispersal of coral larvae within the system is largely unknown, however the local scale connectivity of corals within the area is currently under investigation.

Maputaland Reefs have been divided spatially into three complexes (Riegl et al. 1995) and are all situated within the Isimangaliso Wetland Park, a UNESCO World Heritage Site (Fig. 2.1). The protection status of the reefs varies according to their geographical location, with reefs within the southern complex declared no-take areas, and all fishing and boating activities prohibited. Conversely, limited fishing is allowed within the central and northern complexes. A thriving scuba diving industry exists within the central complex at Sodwana Bay, where approximately 80 000 dives are conducted each year (Walters & Samways 2001). Of these reefs, Two-mile Reef (TMR) is the largest, most frequently visited reef and is predominantly covered by the most diverse coral community found on this stretch of coast (Celliers & Schleyer 2008).

Three monitoring sites were selected on TMR due to its large size and importance (Fig. 2.1). At each site, three concrete Y-frames were installed on relatively flat reef areas, thereby creating a spatially nested sampling design. The distance between Y-frames varied between 5m and 15m apart from each other at each site. Each monitoring station varied marginally according to depth and topography and was selected in a north-south direction within the reef-top community on TMR. The northern site was the deepest site (15m - 17m) and was characterized by relatively flat topography with few gullies. Compared to the northern site, the central site was located around a large stand of *Acropora austera,* at a shallower depth (12-15m) in an area where there were more gullies. The southern site was the shallowest (9-12m) and was characterized by variable topography with sharp drop-offs into sand gullies. Due to its shallower depth this site experienced more surge.

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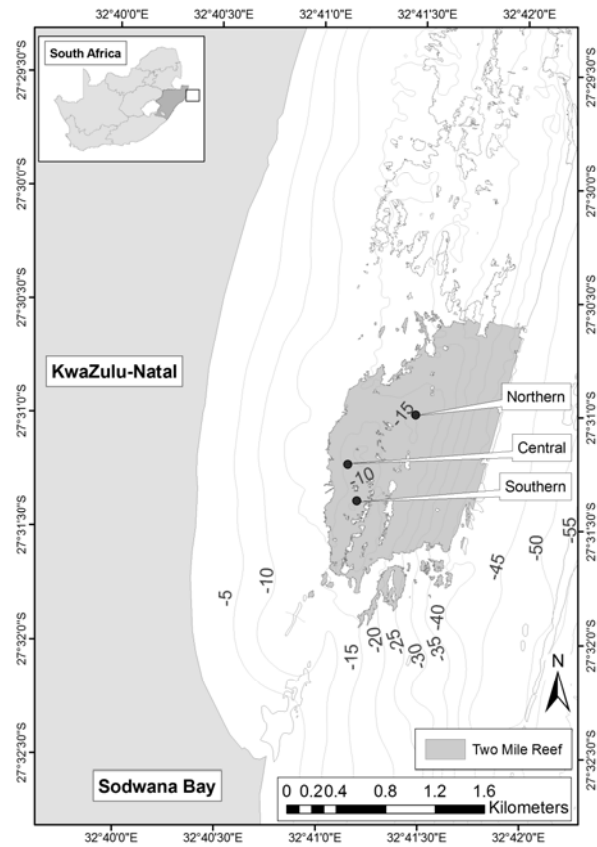
Fig. 2.1. Location of the three study sites on Two-mile Reef (TMR) at Sodwana Bay on the Maputaland coast of KwaZulu-Natal, South Africa.

2.2. A review of settlement surfaces, their attachment, and recruit detection techniques used in coral recruitment studies

2.2.1. Settlement surfaces and attachment techniques

Although some studies have investigated coral recruitment on the natural reef substratum (e.g. Sammarco 1982, Rylaarsdam 1983, Edmunds et al. 2004, Roth & Knowlton 2009), the majority have utilized artificial settlement surfaces. Artificial tiles for settlement studies can be attached individually onto the

reef substratum (Mundy 2000, Burt et al. 2009) or onto settlement frames (Harriott & Fisk 1987, Glassom et al. 2006). Even though artificial settlement surfaces have limitations (see Harriott & Fisk 1987, Mundy 2000, Thomason et al. 2002) and it is debatable whether they are similar to the natural substratum (Mundy 2000, Nozawa 2008), their use has allowed scientists to investigate an array of variables pertaining to coral recruitment. Such variables include the availability and diversity of coral planulae and other sessile organisms which can settle at a particular site. Furthermore, their associated behavioural responses to biotic and abiotic variables can be determined by placing surfaces at desired spatial and temporal scales.

Artificial settlement surfaces can be obtained from the environment, such as dead coral skeletons (Wallace 1985b, Harriott & Fisk 1987, Babcock & Davies 1991, Babcock & Mundy 1996), or can comprise surfaces which are not naturally found on reefs. Such surfaces include cement blocks (Hunte & Wittenberg 1992) and cement slabs (Lee et al. 2009), PVC plates (Maida et al. 1995, Oren & Benayahu 1997, Soong et al. 2003), a combination of granite, gabbro, sandstone and terracotta plates (Burt et al. 2009), formica plastic sheets (Vermeij 2006), plastic petri dishes (Harriott & Fisk 1987) and more commonly, commercially produced tiles (Harriott & Fisk 1987, Tomascik 1991, Hunte & Wittenberg 1992, Maida et al. 1995, Mundy & Babcock 1998, Wilson & Harrison 1998). The majority of substrata used have rough surfaces and range in shape from flat plates to sophisticated three-dimensional structures (Fig. 2.1). The final choice is often based on cost and availability (Field et al. 2007). The development of settlement surface design has evolved with increased understanding of micro-scale influences on coral settlement. These include the preferential settlement of planulae on biologically-conditioned surfaces (Harrington et al. 2004) and micro-scale refuges (Nozawa 2008).
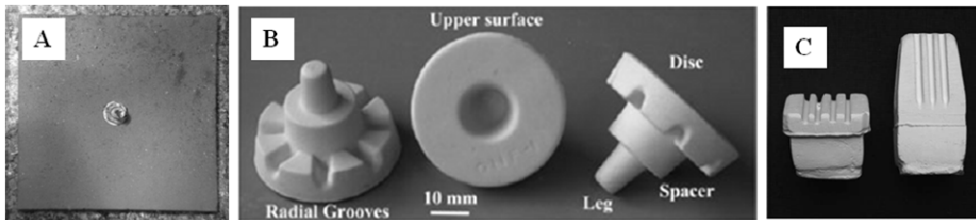
Fig. 2.1. Settlement surfaces used to quantify coral settlement, ranging from standard, unglazed ceramic household tiles, A (chapter 3), to sophisticated three-dimensional structures, B (Okamoto et al. 2008) and C (Petersen et al. 2005).

Aside from the variety of settlement surfaces used, the manner in which the settlement surfaces are attached to the substratum can vary (Fig. 2.2). The attachment of artificial settlement surfaces onto frames anchored on the reef is common practice (e.g. Harriott & Fisk 1987, Maida et al. 1994, Gleason 1996, Baird & Hughes 1997). However, direct attachment of individual tiles onto the reef has been proposed to have statistical superiority by avoiding complications associated with the dependence of tiles attached to frames (Mundy 2000) and is an alternative technique that has been used to attach artificial settlement surfaces (Hughes et al. 2000, Burt et al. 2009). Despite this, direct attachment techniques can be labour-intensive. In contrast, the attachment of multiple tiles can be less labour-intensive and more cost-effective. Furthermore, intense overgrowth on tiles attached directly onto the substratum can make them undetectable, whereas frame structures permit their easy detection. Due to the large variety of methods used by scientists, comparisons of recruitment studies must be made with caution (Harriott & Fisk 1987, Field et al. 2007). However, the need for comparative studies is imperative to identify both regional and global trends (Hughes et al. 2002).
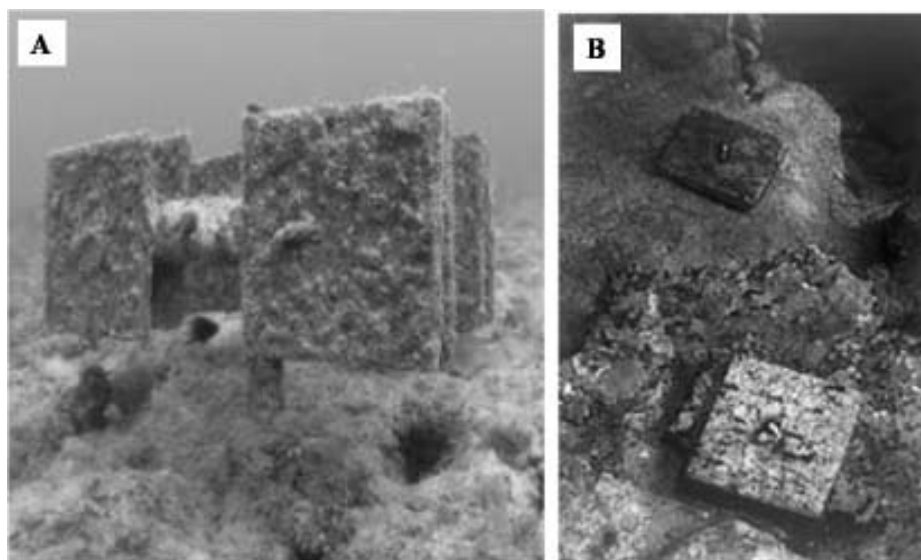
Fig. 2.2. Attachment of multiple tiles onto frames (A) and the direct attachment of independent tiles onto the natural substratum (B) (adapted from Rubin et al. 2008 and Mundy 2000 respectively).

2.2.2. Recruit detection techniques

2.2.2.1. Ex situ

The majority of all artificial settlement surfaces are analyzed under a dissecting microscope after being retrieved from the substratum. This enables researchers to search surfaces for recruits visually and determine their relationship with other surrounding living biota. However, the latter is excluded in the majority of such studies, as tiles are often treated with bleach to remove all living biota and expose the skeletal framework of cryptic recruits to enable identification.

2.2.2.2. In situ

Studies utilizing the natural substratum can be beneficial in that they consist of unaltered settlement surfaces. The detection of recruits on these surfaces can only be done *in situ*, which can limit the questions that can be addressed. Furthermore, recruit identification and associated measurements, such as size, cannot be accurately quantified. *In situ* techniques include unaided visual searches (Edmunds et al. 1998, Miller et al. 2000, Norström et al. 2007), aided visual searches and photographic techniques (Smith 1997, Edmunds et al. 1998, Piniak et al. 2005).

Unaided visual searches are often time-consuming and not effective in detecting early post-settled recruits. While the use of a magnifying glass can enhance the effectiveness of recruit detection, it is also time-consuming. The use of a fluorescence pulsating light has proven to be highly effective at detecting coral recruits <1 mm (Roth & Knowlton 2009). This technique excites fluorescent proteins within coral tissue which fluoresce under blue or UV light (Mazel 1995). However, it is limited to low light conditions and works best at night (Piniak et al. 2005). Thus, it may be unsuitable where night-diving is not possible. Other biota, such as anemones and zoanthids, can also fluoresce (Piniak et al. 2005) and further investigation may be necessary to ensure that fluorescent objects are indeed scleractinian recruits. Not all corals fluoresce and dead recruits go undetected. Consequently, although the use of this technique is considered more effective at detecting smaller recruits than other visual searches, it is ineffective for many post-settled recruits and does not enable the quantification of recruit post-settlement mortality.

Rapid assessments, such as photographic techniques, can be desirable for financial, safety and logistical reasons. Photographic techniques include small-scale, white-light, macro-photography (Smith 1997,

Edmunds et al. 1998) and fluorescence photography (Mazel 2005, Baird et al. 2006). Both are less time-consuming than visual searches and provide a permanent, two-dimensional record of the substratum under investigation. However, recruits are often cryptic and undetectable, even in high-resolution white-light images. Consequently, white-light macro-photography has been shown to be less effective at detecting recruits than unaided visual searches (Burgess et al. 2010). As with fluorescence visual searchers, fluorescence photography has been shown to reveal recruits <1 mm (Baird et al. 2006, Schmidt-Roach et al. 2008) and is extremely effective at detecting small post-settled recruits >1 mm. In contrast to fluorescent visual searches, fluorescent photography can be conducted during daylight with the correct camera settings (Mazel 2005). However, the technique is non-selective and non scleractinian fluorescent biota may be detected. It is impossible to differentiate between these on a camera LCD screen and this can result in overestimation of recruit densities (Piniak et al. 2005). Furthermore, identification of corals to species is not possible (Piniak et al. 2005). Regardless of these limitations, the use of this technique in combination with microscopic analysis can provide a valuable insight into early coral life history processes (Schmidt-Roach et al. 2008).

2.3. Methods used in this study

2.3.1. Settlement surfaces

Three artificial settlement surfaces viz. ceramic tiles, marble tiles, and ceramic tiles conditioned with CCA were used for this study. In addition, recruitment was quantified in replicate quadrats of the surrounding natural substratum at each study site for comparative purposes and were only used in chapter 3 (Appendix 1). All three tile types were of standard size (9.7cm x 9.7cm x 1cm) and were centre-drilled with a 6 mm hole to enable their horizontal attachment onto frames (See 2.3.2 below), exposing the four vertical edges (38.80 cm^2) and horizontal top surfaces (93.58 cm^2) of each tile for coral settlement (a total of 132.89 cm^2 per tile). Hereafter, vertical edge and horizontal top surfaces are referred to as 'edge' and 'top' surfaces of tiles respectively. All surfaces were sandblasted to create uniform rough surfaces.

2.3.1.1. Ceramic tiles

Unglazed ceramic tiles are the most commonly used (e.g. Gleason 1996, Glassom et al. 2006) and recommended (English et al. 1997) artificial settlement surfaces reported in the scientific literature. This can be due to their availability and low cost (Harriott & Fisk 1987). While these tiles are popular, they

may not necessarily result in optimal settlement. Thus they were chosen to compare with other tile types to determine if their popularity is warranted.

2.2.1.2. Marble tiles

Marble tiles are composed of calcium carbonate ($CaCO_3$) in the form of calcite. While the composition of marble is thus dissimilar to the aragonite of coral skeletons, it has nevertheless been shown to constitute a suitable surface for coral settlement (Heyward & Negri 1999). Therefore marble tiles were selected as the second tile surface for this study.

2.2.1.3. Crustose coralline alga-conditioned (CCA) ceramic tiles

 CCA can influence coral settlement (Morse et al. 1988, Morse et al. 1994, Heyward & Negri 1999, Harrington et al. 2004, Price 2010). In order to condition ceramic tiles with CCA, tiles were placed in an aquarium for two months where *Mesophyllum funafutiense* was prolific. *Mesophyllum* spp. have been shown to provide a suitable surfaces for coral settlement (Heyward & Negri 1999) and have been recorded in the study area. Tiles with ≥50% surface cover of CCA were installed in the field.

2.2.1.4. Natural substratum

A square quadrat, the same size as a tile, was used to take 15 replicate fluorescent images of the surrounding natural substratum before the retrieval of tiles (see 2.2.2.1). This enabled the comparison of recruitment on artificial settlement surfaces and the natural substratum. The quadrat was randomly placed in close proximity to tile attachment structures (see 2.3.2) on natural substrata that was suitable for coral settlement (i.e. bare/CCA substrata with minimal macro-algae and sediment).

2.3.2.   Tile attachment technique and study period

Although direct attachment of individual settlement surfaces onto the natural substratum can yield results with statistical advantages over the attachment of multiple tiles on frames (Mundy 2000), conditions at a particular study site can preclude this method of attachment. Additionally, recruitment on tiles attached by the two techniques has been found to be comparable (Mundy 2000). A large body of literature has involved the attachment of multiple tiles onto a single anchored structure (e.g. Harriott & Fisk 1987, Glassom et al. 2004). These structures commonly consist of steel or wire frames and concrete structures.

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The attachment of tiles onto frames is a long-standing technique outlined in a commonly followed manual (e.g. English *et al*. 1997).

Independent placement of tiles was not possible in this study. Previous attempts to drill into the hard fossilized sandstone of the reef substratum in the study area proved unfeasible (M.H. Schleyer pers. com.). Despite this, further attempts were made to attach tiles directly to the substratum in a trial experiment. This was done by cable-tying tiles to electrical push-mounted plugs which were squeezed into cracks on the reef (as done by Field *et al.,* 2007). However, suitable cracks were limited, resulting in inadequate spatial placement of the tiles. Additionally, strong surge during the trial resulted in many of the tiles becoming dislodged. Hence, the attachment of multiple tiles onto anchored frames was deemed more fitting.

In light of the above, nine concrete Y-frame structures were carefully designed to meet the objectives of this study and three replicate Y-frames were installed at three study sites (chapter 2.2). The weight of each Y-frame (75 kg) and flat, three-legged shape provided effective anchorage and stability to the tiles in the turbulence on the reef (Fig. 2.2). The three arms of each Y-frame structure made their construction, transport and installation relatively simple. The edges were chamfered at 60° to minimize turbulence on their upper surfaces. Tiles were attached in a horizontal position and recessed on the Y-frames, as a previous study conducted on the same reef reported higher settlement on the top surfaces of tiles (Glassom et al. 2006). The recessed attachment of tiles created a gap (~7 mm) between each tile edge and the concrete structures or adjacent tiles. After manufacture, the concrete arms were placed in a flow-through aquarium for two weeks to allow for chemicals to be leached out of the structures. Thereafter structures were installed on the reef one month prior to the attachment of tiles. Each Y-frame was installed in gaps between corals on the reef.

Field Code Changed

Fig. 2.2. Concrete Y-frame with the recessed horizontal placement of 15 tiles 10 cm above the natural substratum and the attachment of a sediment trap and a water movement measuring device deployed in a concurrent study. Photo credit: C. Floros.

Five replicates of each type of tile were attached onto each Y-frame in a stratified sampling design (Fig. 2.3). This resulted in the same number of replicates of each tile in the five possible positions on the Y-frame arms, with 45 tile replicates at each of the three study sites. Two consecutive six-month soak periods were applied, from October 2009-April 2010, and April 2010 to October 2010. One tile at the central study site was broken and was replaced half-way through the summer sampling period. Coral recruitment onto these two tiles varied significantly from the remaining tiles on the Y-frame after removal and was therefore eliminated from further analysis. Additionally, a storm flipped one of the Y-frames at the southern study site, one month prior to the completion of the winter sampling period. Likewise, these 15 tiles were excluded from subsequent analyses.
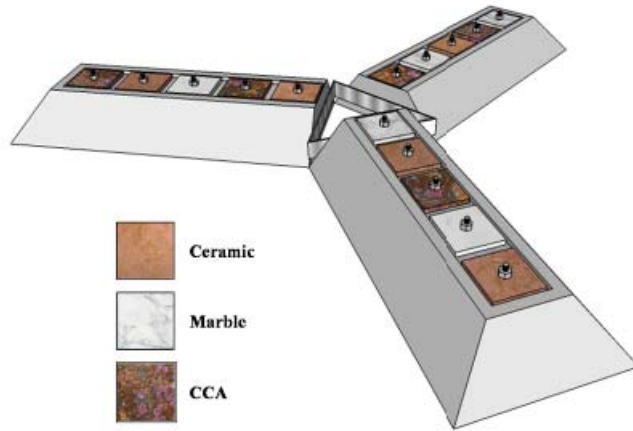
Fig. 2.3. Stratified attachment of the three tile types onto a Y-frame resulting in each tile type represented on the five tile positions on a Y-frame arm. Balanced sampling design resulted in five replicates of each tile type on each Y-frame.

2.3.3. Recruit detection techniques

2.2.2.1. In situ fluorescence photography

Fluorescent images of the top surface of all tiles used in this study, and of the surrounding natural substratum (chapter 2.3.1) were taken prior to their retrieval at the summer sampling period. These were used in chapter 3. The fluorescent apparatus consisted of a modified (Sea & Sea) 1G camera and housing with two Sea & Sea YS-27DX strobes. A (NightSea) barrier filter and two (NightSea) excitation filters were attached in front of the (Sea & Sea) camera lens and strobes respectively. The camera was attached to a stainless steel frame, resulting in a field of view of 19.2 X 14.3 cm. Dives were conducted during the early morning (before 10 a.m.) as low ambient light conditions are beneficial for the successful detection of coral recruits with fluorescence photography (Mazel 2005). Photos were taken perpendicular to the tiles, so only their top surface could be used to determine the effectiveness of this technique (Appendix 2). The approximate XY position of each fluorescent object was determined using ImageJ (http://rsb.info.nih.gov/ij), thereby creating reference points for their identification during microscopic analysis. Only fluorescent objects with a diameter <15 mm in natural substratum images were counted, based on the largest size of a recruit found on a tile.

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2.2.2.2. Ex situ microscopic analyses

Microscopic analysis was used to compare recruitment among the three tile types and to compare the effectiveness of this technique with fluorescent photography (Chapter 3). In addition, recruits detected with microscopy were used to assess spatial and temporal recruitment dynamics (Chapter 4). Once retrieved, tiles from both sampling periods were fixed in 4% formal saline solution and stored for pre-bleaching microscopic analysis. During the pre-bleaching analysis of summer tiles, the percentage cover of biota surrounding each recruit within three millimeters of its corallum was visually estimated under a Zeiss Stemi DV4 stereo-microscope to quantify the microhabitat surrounding each recruit (chapter 4). Surrounding categories consisted of: bare tile substratum, crustose coralline algae (CCA), turf algae and sediment, erect macroalgae, encrusting macroalgae, encrusting bryozoans, scleractinian coral recruits, barnacles, and 'other'. Winter tiles were excluded from such rigorous pre-bleaching analysis; only fluorescent objects detected in *in situ* photographs were re-located on these tiles to determine if they were indeed hard coral recruits (chapter 3).

Following this, both summer and winter tiles were placed in household bleach for 72 hrs to remove living biota and aid in the identification of recruits. During both pre-bleaching and post-bleaching counts, the four vertical edges and the top surface of tiles were searched for scleractinian coral recruits. Individual recruits were recorded if they possessed a complete basal plate and identified to family level (Appendix 3) based on their skeletal structure as per English et al. (1997) and Babcock et al. (2003). Unidentifiable recruits were assigned to an "other" category. The number of polyps per recruit was also counted and the corallum diameter measured with an eye-piece graticule. Each recruit's position was referenced with vernier calipers and the tile number noted. For each tile, additional recruits detected after bleaching were added to those counted from pre-bleaching. The abundance of recruits that settled on the two surface orientations (top and edges) of each tile was standardized per cm^2 to enable direct comparisons for chapter 4.

Chapter 3:

Methods for studying coral recruitment: The influence of settlement surface and recruit detection techniques

3.1. Abstract

The settlement of new corals on reefs has been the focus of numerous studies over the past 30 years. However, methods used to study settlement are likewise bountiful, making many studies incomparable. Here coral recruitment was compared on three settlement surfaces comprising ceramic and marble tiles, and ceramic tiles conditioned with crustose coralline algae (CCA) by microscopic examination. While recruitment differed on the three tile surfaces, with more settlement on CCA tiles, recruitment in this study varied more as a result of differences at spatial scales regardless of tile composition. Fluorescent photography was investigated as a rapid *in situ* technique to detect early post-settled recruits, and its limitations are discussed. It proved suitable to successfully detect many but not all early post-settled recruits as small as 0.75 mm basal disk diameter, and all taxonomic categories used in this study. It was used to compare settlement on the tiles and the natural substratum, which differed markedly. While fluorescent photography has its limitations, it shows promise as a useful tool to assess qualitative, but not quantitative, recruitment.

Keywords

Coral settlement · Fluorescence photography · Natural substrata · Artificial settlement surfaces

3.2. Introduction

Like many sessile marine invertebrates, scleractinian corals rely on passive dispersal, settlement, and survival of offspring to add new individuals to a population. Coral recruitment is recognized as a key demographic process influencing community structure and the decline and recovery of coral populations (Bak & Engel 1979, Harrison & Wallace 1990, Hughes & Tanner 2000). Therefore it is important that recruitment is quantified (Wells 1995, Burgess et al. 2010). Methods of studying this process vary according to the settlement surface used, manner in which settlement surfaces are attached, and the techniques employed to detect recruits. Coral settlement can differ on different settlement surfaces

(Harriott & Fisk 1987, Harrington et al. 2004) due to larval recognition of suitable surfaces for settlement. Furthermore, the detection of recruits can differ among different techniques (Edmunds et al. 1998, Baird et al. 2006). While the effectiveness of various methods has been addressed (Harriott & Fisk 1987, Field et al. 2007, Burt et al. 2009, Burgess et al. 2010), a comprehensive comparison is needed. In addition, an effective, rapid, *in situ* technique to detect coral recruits on the natural substratum would enable the rapid quantification of coral recruitment over greater surface areas (Burgess et al. 2010).

Although studies have quantified coral recruitment on natural substrata by visual searches (Harriott 1985, Mumby 1999, Ruiz-Zarate & Arias-Gonzalez 2004, Glassom & Chadwick 2006), or photographic techniques (Smith 1992, 1997, Edmunds et al. 1998, Burgess et al. 2010), the majority of studies have used artificial settlement surfaces to quantify coral recruitment by microscopic examination (e.g. Hughes et al. 1999, Mundy 2000, Glassom et al. 2004, Glassom et al. 2006, Adjeroud et al. 2007). The investigation of recruitment on natural substrata provides an indication of recruitment under natural conditions. However, the small size, slow growth rate, and cryptic nature of recruits limit their detection *in situ* during early life stages (Miller et al. 2000). This has resulted in the majority of studies only detecting coral recruits >5 mm in size (Roth & Knowlton 2009). Recruits of this size can be several months old (Wallace & Bull 1981, Ruiz-Zarate & Arias-Gonzalez 2004), thereby barring investigation into important early post-settlement stages on the natural substrata.

Standard visual searches of the natural substrata are time-consuming and can underestimate coral recruitment as early post-settled recruits are often too small to be detected by the naked eye. The aid of a magnifying glass allows smaller recruits (as small as 1 mm) to be detected (Tomascik 1991, Glassom & Chadwick 2006, Vermeij et al. 2009). However, this is likewise time-consuming and can therefore be impractical at large spatial scales (Edmunds 2000, Glassom & Chadwick 2006). An alternative visual search method, which is far more rapid and likewise assists with the detection of smaller recruits, is the use of a fluorescent torch (e.g. Baird et al. 2006, Roth & Knowlton 2009). This technique capitalizes on the presence of fluorescent pigments within a broad taxonomic range of corals and symbiotic algae which become visible when stimulated by blue or ultraviolet light (Mazel 1995). Although the precise function of fluorescent pigments is unknown, they can be linked to photoprotection (Salih et al. 1998, Salih et al. 2000) and assisting zooxanthellae photosynthesis (Kawaguti 1969). Their presence within coral planulae even before settlement enables the rapid detection of small coral recruits in contrast to non-fluorescing surfaces. This technique can more accurately detect coral recruits in highly fluorescent taxa (Baird et al. 2006) and is more effective under night conditions when the fluorescent contrast is greater, rendering the recruits more visible (Baird et al. 2006). However, estimations of recruitment can be biased as not all

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scleractinian corals fluoresce, and other cnidarians, such as anemones, also contain fluorescent pigments. It can therefore be necessary to investigate fluorescent objects further to determine if they are indeed scleractinian recruits. Dead recruits which lack tissue also go undetected with this technique but are commonly incorporated into recruitment studies which involve the bleaching and microscopic examination of artificial settlement surfaces.

Photographic techniques are the most rapid *in situ* method to quantify coral recruitment. They enable large surface areas to be sampled and permit small scale macro-photography (e.g. Smith 1992, Smith 1997, Edmunds et al. 1998, Burgess et al. 2010) and fluorescent photography (e.g. Piniak et al. 2005, Schmidt-Roach et al. 2008). While recruits as small as 1 mm have been detected with macro-photography (Smith 1992), comparative studies have shown that recruitment can be underestimated with this technique, and visual searches have been proposed as a better technique (Edmunds et al. 1998, Burgess et al. 2010). Fluorescent photography has been shown to be effective in detecting coral recruits larger than 1 mm in size and a useful method to determine the fine scale temporal variation of recruitment *in situ* (Schmidt-Roach et al. 2008). However, this technique shares the limitations of fluorescent visual searches. Additionally, it is not possible to positively confirm that fluorescent objects are indeed scleractinian coral recruits from images as they are not recorded at a sufficient resolution. Consequently, this technique has been proposed as an effective technique for qualitative surveys rather than quantitative measures of coral recruitment (Piniak et al. 2005).

Regardless of the technique used to detect coral recruits *in situ*, the small size of recruits hinders their taxonomic identification in the natural environment. Consequently, the use of artificial settlement surfaces which can be retrieved for rigorous microscopic examination remains common practice. Although artificial surfaces can vary structurally from natural habitats (Gischler & Ginsburg 1996), they provide valuable insights into short-term, small-scale recruitment dynamics (Keough & Downes 1982). Logistics associated with the use of artificial settlement surfaces limit the surface area of the reef being sampled. After retrieval, artificial settlement surfaces are commonly placed in household bleach to remove living tissue and expose the skeletal structures of coral recruits. This is used for their identification during microscopic examination (English et al. 1997, Babcock et al. 2003). Size-based measurements such as basal disk diameter can be measured with a graticule eye-piece which can then be used to estimate when settlement occurred based on previous time-series work on the growth of recruit basal disks (e.g. Schmidt-Roach et al. 2008).

The use of artificial settlement surfaces in recruitment studies is far from standardized. Various artificial surfaces have been used and these can vary in size, shape, composition, texture, and means of attachment. They also provide substantially different environments to natural substrata (Rylaarsdam 1983), as appropriate chemical cues which can induce coral settlement are often lacking. These can be commonly found on the natural substratum, such as crustose coralline algae (CCA) (Morse & Morse 1996). Recruit mortality has been shown to be higher on artificial substrata than natural substrata. This can result in substantially different levels of recruitment on artificial settlement surfaces and the natural substrata at a particular site (Rylaarsdam 1983).

The aims of this study were twofold. Firstly, we aimed to investigate how coral recruitment varies on three different artificial settlement surfaces and the natural substratum. To do so, we compared the *in situ* settlement of hard corals on ceramic (CER), marble (MAR), and crustose coralline algae conditioned ceramic tiles (CCA) with settlement on the surrounding natural substratum. These were selected as the first is commonly used (e.g. Gleason 1996, Abelson et al. 2005), the second is similar in chemical composition to dead coral skeletons, and the last constitutes an important functional group which "cues" coral settlement (Morse et al. 1996, Harrington et al. 2004). The latter two artificial settlement surfaces have both been shown to induce coral settlement (Harrington et al. 2004, Lee et al. 2009). The second aim of this study was to ascertain the usefulness of fluorescent photography as a rapid *in situ* detection technique. This was done by comparing the detection of coral recruits on tiles from fluorescent photographs followed by pre-bleaching and post-bleaching microscopic analysis. We hypothesized 1) that coral recruitment would vary significantly on the three different tiles 2) that recruitment on the tiles would differ significantly from that on the surrounding natural substrata and 3). that numbers of recruits detected by fluorescent photography and microscopic examination would not differ significantly.

3.3. Materials and Methods

3.3.1. Study area, monitoring sites and methods used in this study

Refer to chapter 2.1 and chapter 2.3.

3.3.2. Statistical analyses

Only the summer dataset (October 2009 – April 2010) was used in this chapter. For statistical comparisons between tile types, the data were $\sqrt{(x + 3/8)}$ transformed for analyses (Zar 1996). The effects of tile

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position on each Y-frame on levels of recruitment were investigated by grouping and comparing all tiles at the same position on the nine Y-frame structures by means of a one-way ANOVA. Where significant differences were found, *post-hoc* Tukey tests were undertaken. The total number of recruits on each tile per tile type, study site, and Y-frame nested within study site was compared by means of a nested ANOVA. A *post-hoc* Tukey HSD test was used to compare settlement onto the three tile types. The effectiveness of fluorescent photography for the detection of scleractinian coral recruits was determined by first confirming that fluorescent objects detected in the associated photographs were indeed corals. As the assumptions for parametric analysis could not be met, even after transformation, the count data of fluorescent corals detected on the top surface of tiles and on the natural substratum were analyzed using a Kruskal Wallis ANOVA and a p*ost-hoc* multiple comparisons of mean ranks for all groups was conducted (see Siegel & Castellan 1988).

3.4. Results

3.4.1. Microscopic examination

In total, 1948 hard corals settled on the 134 tiles used in this study, with the majority of settlement (87%) occurring on the side surfaces of tiles compared to the top, horizontal surface. The placement position of tiles on Y-frames did not yield different levels of recruitment ($F_{4, 129} = 0.76$, $p = 0.56$). The overall settlement on the three tile types differed significantly (Table 3.1), with settlement onto CCA tiles significantly greater than marble tiles (Tukey's HSD: $P < 0.01$) (Fig. 3.1). Regardless of tile type, differences between study sites, Y-frames nested within study sites, and individual tiles on Y-frames, accounted for more of the variance (Table 3.1).

Table 3.1. Nested ANOVA of all recruits detected with microscopy on all exposed settlement surfaces of tiles used during summer (October 2009 – April 2010). Each level of spatial data is nested within greater spatial scales i.e. there are 15 tiles per Y-frame and three Y-frames within each study site. The error term represents individual settlement tiles on concrete Y-frames.

Variance source	df	F	P	Percent of variance
Tile composition	2	9.03	0.0002	5.7352
Study site	2	61.39	0.0000	38.9971
Y-frame	6	8.5	0.0000	16.2026
Error	123			39.0651
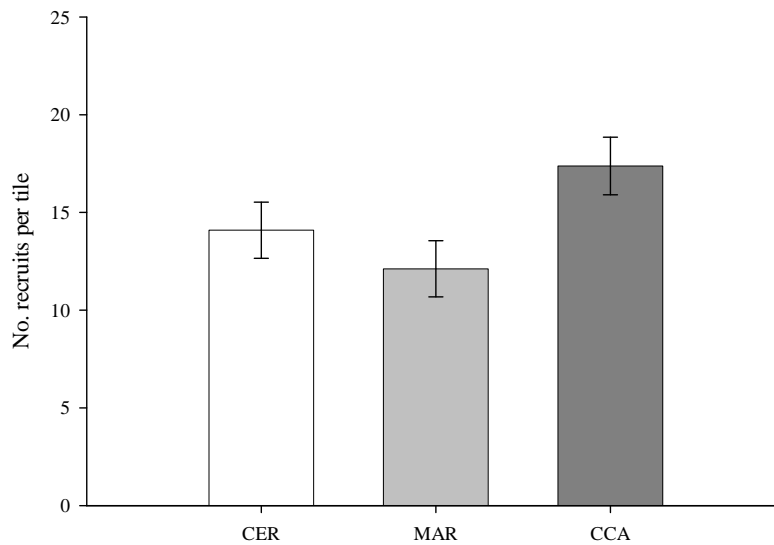
Fig. 3.1. Settlement (mean ± SE) on all exposed surfaces of CER, MAR, and CCA tiles from both sampling periods and at all sites.

3.4.2. Corals detected by fluorescence

In total, 83 fluorescent objects were detected. Eleven of these detections were absent during post-bleaching microscopic examination, suggesting that they must have become dislodged during the bleaching process. An additional fluorescent object proved to be an anemone. Furthermore, two fluorescent objects in close proximity to each other were revealed to be a single recruit that had been partially covered by sediment.

Overall, fluorescent photography detected 27% (70/259) of the corals detected on the top surfaces of tiles during microscopic examination (Table 3.2). All four taxonomic categories were detected, of which some were <1 mm (Table 3.2). Recruit densities in the fluorescent photographs were consistently underestimated (Fig. 3.2). Fluorescent photography was more accurate when recruit densities were low; however accuracy decreased as recruit densities increased (Fig. 3.3).

Table 3.2. Comparison of recruits detected by fluorescence photography and microscopy techniques on the top surfaces of tiles. Fluorescent detections comprised recruits that were confirmed to be corals by microscopic analysis. Microscopic detections constituted recruits that were undetected by fluorescent photography.

Detection technique	Taxa	No. of recruits	Basal disk range (mm)	Basal disk (mean ± SE)	No. of polyps (range)
Microscopy	Pocilloporidae	120	0.760 - 14.688	1.900 ± 0.117	1 – 9
	Acroporidae	54	0.580 - 3.750	1.121 ± 0.065	1 – 5
	Poritidae	14	1.094 - 4.250	2.320 ± 0.241	1 – 12
	Other	1	1.640 - 1.640	1.64	1
Fluorescent photography	Pocilloporidae	64	0.750 - 13.125	2.946 ± 0.266	1 – 69
	Acroporidae	2	0.960 - 1.375	1.167 ± 0.207	1
	Poritidae	2	1.813 - 2.080	1.946 ± 0.134	1 – 2
	Other	2	2.056 - 2.063	2.056 ± 0.006	1
Overall		259	0.580 - 14.688	1.997 ± 0.094	1 – 69
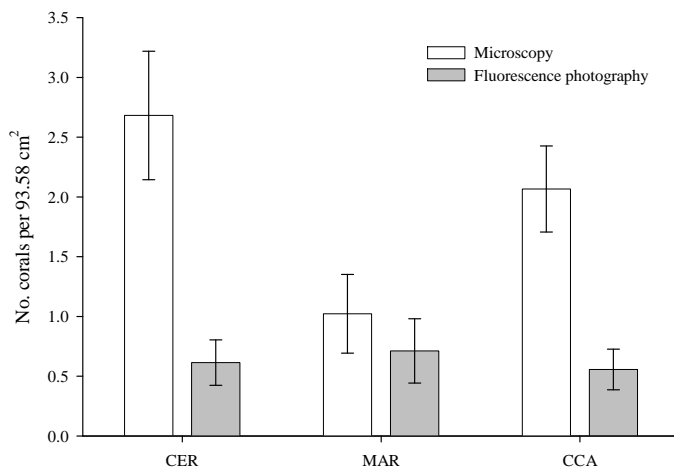
Fig. 3.2. Comparison of coral recruits (mean ± SE) on the top surfaces of tiles detected by microscopic examination and fluorescent photography. Microscopic counts include recruits previously detected with fluorescence.
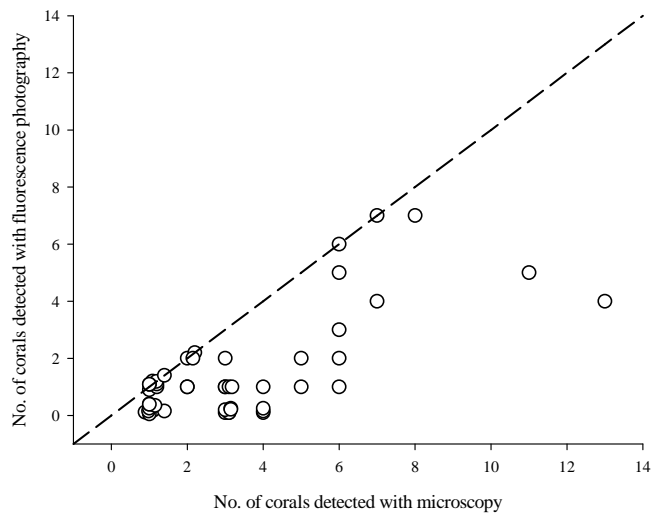
Fig. 3.3. Relationship between the number of coral recruits per tile recorded by fluorescent photography and microscopic analysis. Only tiles with at least one recruit detected by either/both techniques are represented. Data points of the same value were shifted by 0.3 on both axes for graphical representation. Dashed line represents a slope of 1.

The number of corals detected by fluorescence on the top surfaces of the three tile types and the natural substratum differed significantly (Kruskal-Wallis ANOVA: $H_{3,179} = 19.76$, $p < 0.05$). Fluorescent detections on the natural substratum were significantly higher than ceramic, marble, and CCA tiles (Multiple comparisons of mean ranks for all groups: $p = 0.012$, $p = 0.009$, and $p = 0.013$ respectively) (Fig. 3.4).
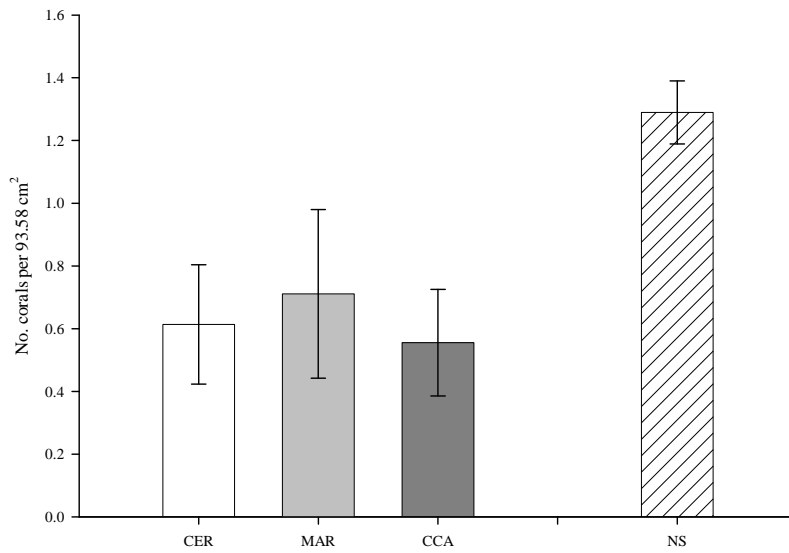
Fig. 3.4. Number of corals per 93.58 cm^2 (mean ± SE) detected with fluorescence on the three tile types and the natural substratum

3.5. Discussion

Overall significant differences were found between recruitment on the three tile types, and between study sites and Y-frames (Table 3.1). However, recruitment in this study varied more as a result of differences between sites and Y-frames than tile surfaces (Table 3.1). This indicates that site-specific differences play more of a role in the levels of recruitment than the different tile surfaces. Burt *et al.* (2009) obtained similar results, with variation in coral recruitment onto tile surfaces more affected by the study sites than the settlement surfaces used.

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Overall, fewer recruits were detected by microscopy on MAR tiles than both the CER and CCA tiles (Fig. 3.1). Although overall recruitment was greatest on ceramic tiles conditioned with *M. funafutiense* CCA, this did not differ significantly from standard ceramic tiles. This indicates that *M. funafutiense* did not enhance coral settlement at Sodwana Bay. The functional role of CCA in inducing coral settlement is well recognized (Morse et al. 1988, Heyward & Negri 1999, Raimondi & Morse 2000, Harrington et al. 2004), due to the detection of polysaccharides within the cell walls of CCA by planulae (Morse & Morse 1991). CCA can further enhance coral settlement by limiting the amount of turf algae and the sediment which can be trapped in it, as well as reducing the settlement of competitors (Babcock & Mundy 1996, Ruiz-Zarate et al. 2000). However, the suitability of CCA for settlement can be species-specific for both corals and algae (Harrington et al. 2004, Ritson-Williams et al. 2010), as certain CCA species can outcompete recruits by overgrowth, or dislodge them by sloughing their epithelial layer. Epithelial sloughing of *M. funafutiense* was observed in this study, which can have limited the suitability of this surface for coral settlement. Further investigation of the functional role that other CCA species can have on coral recruitment on Maputaland Reefs is required. Results from this study support the use of low cost CER tiles for recruitment studies as there was little variation between these and the more expensive MAR tiles.

Conventional methods for measuring coral recruitment in the field, such as standard *in situ* visual searches or artificial settlement surfaces are time-consuming, making their application on a large scale impractical (Edmunds 2000, Glassom & Chadwick 2006). The use of coral fluorescence as a more rapid means to detect small coral recruits has been investigated in fluorescent visual searches (Baird et al. 2006) and fluorescent photography (Piniak et al. 2005, Schmidt-Roach et al. 2008). Searches with a fluorescent torch can reduce search time and enable the detection of small, previously cryptic recruits (Baird et al. 2006, Roth & Knowlton 2009). It has been suggested that photographic techniques can offer an even more rapid *in situ* method to quantify coral recruitment (Burgess et al. 2010). Additional advantages of this technique include data collection by non-specialist divers, the acquisition of a permanent record and decreased observer error during data collection (Burgess et al. 2010). However, comparisons of normal photography and visual searches have shown the latter to be more accurate (Edmunds et al. 1998, Burgess et al. 2010).

In this study, we found that, even the increased contrast provided by fluorescent photography, consistently underestimated coral recruitment (Fig. 3.3). Even though coral recruits <1 mm were detected in fluorescent images, only 28% of corals that settled on the top surfaces of tiles were detected (Table 3.2), a finding similar to that of an earlier study (Schmidt-Roach et al. 2008). Certain factors prevent the detection of settled corals in fluorescent images. Firstly, the abundance of fluorescent pigments in the

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coral recruits is essential for their detection (Papina et al. 2002). Although not found in all corals, most Indo-Pacific reefs are dominated by fluorescent taxa (Baird et al. 2006). In addition, the size at which recruits settle can play a role in their detection (Schmidt-Roach et al. 2008) and dead recruits or living recruits covered by other biota/sediment will not be detected.

Consequently, the remaining 72% of coral recruits which were undetected on the tiles could have been dead, non-fluorescing, or covered by turf/sediment when photographed. Post-settlement mortality could have contributed to a significant proportion of these undetected corals, as this can be extremely high (60-90% mortality) within the initial 3-12 months after settlement (Sorokin 1995). This makes these two methods useful for comparing gross settlement versus net recruitment. Additionally, high levels of sedimentation and turf algae occurred on the top surfaces of tiles, which could have also contributed to the low recruit counts. All taxonomic categories found in this study were observed to fluoresce (Table 3.2). The smaller diameter of acroporid and poritid recruits during settlement (Babcock et al. 2003, Schmidt-Roach et al. 2008), could have contributed to fewer detections with fluorescent photography in this study (Table 2).

The attachment of tiles onto Y-frames meant that only the top surface of tiles could be photographed. Thus, the majority of coral settlement, which occurred in refuges on the edges of tiles, could not be sampled with fluorescent photography. More coral recruits were detected with microscopy, with a greater difference observed on CER and CCA tiles compared with MAR tiles (Fig.3.2). This could be due to the limited detection of corals as the white skeleton of recruits was not easily detected on the white surface of MAR tiles. All three tile types had fewer fluorescent detections than that found on the surrounding natural substratum (Fig. 3.4).

Possible explanations for this trend include:

1. The natural substratum is more suitable for coral settlement as artificial surfaces can lack chemical cues which coral larvae use to recognize suitable surfaces (Morse & Morse 1996).

2. Quadrats were semi-randomly placed on surfaces of the natural substratum that were considered suitable for coral settlement (i.e. minimal turf algae and sediment cover), whereas tiles surfaces generally had both turf and sediment on their top surface, resulting in lower levels of fluorescent detections.
3. Fluorescent detections on the natural substratum of larger recruits, which could have been older than the soak time of tiles, thereby improving their detection.

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4. Certain coral families (such as favids) do not readily settle on tiles.
5. Soft corals, which are likely to be abundant on the natural substratum, invariably detach from tiles before they can be counted.

In summary, we have shown that coral settlement can vary significantly on different artificial settlement surfaces at the reef scale. However, variation in coral settlement appeared attributable more to spatial scale rather than artificial settlement surfaces. Fluorescent photography was found to be useful for the detection of small recruits, in all the coral families encountered. However a large portion of corals which settled on the top surfaces of the tiles were undetected in photographs with this technique. Further research combining the use of fluorescent photography and conventional microscopic examination at finer temporal scales is recommended. While this technique has its limitations, the use of fluorescent photography as a qualitative tool to assess recruitment trends should not be discounted (Baird et al. 2006). A combination of fluorescent visual searches and fluorescent photography of both tile surfaces and the natural substrata is warranted to further investigate the rapid use of coral fluorescence for recruit detection.

Field Code Changed

3.6. Acknowledgements

Chapter 4:

Recruitment dynamics of scleractinian corals on a high latitude reef at Sodwana Bay, South Africa

4.1. Abstract

Maputaland Reefs, situated along the north eastern coastline of South Africa, constitute the most southern distribution of coral communities along the African continent. These high-latitude reefs are receiving increased attention as indicators of future changes on tropical reefs, yet an understanding of key processes involved in their resilience are lacking. Here, we investigated the recruitment dynamics of scleractinian corals within the core community found on these reefs over two six-month sampling periods. Spatial and temporal variation in their abundance and composition indicated that coral recruitment varied significantly between study sites, between attachment devices within sites, and showed preference for the edges of settlement tiles. Additionally, the abundance and composition of recruits varied between the two sampling periods, with pocilloporids found to be dominant throughout the year. The majority of recruits were <3 mm, and their microhabitat was dominated by bare substrata and crustose coralline algae. Results from this study highlight the dynamic temporal and spatial variation of coral recruitment within a heavily utilized reef.

Keywords

Coral recruitment · Microhabitat · Pocilloporidae · Sodwana Bay · South Africa

4.2. Introduction

The introduction and subsequent survival of new coral individuals (coral recruitment) is well recognized for its role in coral reef resilience and structuring coral communities (Harrison & Wallace 1990, Caley et al. 1996, Connell et al. 1997). Consequently, it is important to quantify this demographic process and incorporate it into coral reef management strategies (Hughes et al. 1999, Hughes et al. 2003). This process has been the focus of numerous studies worldwide (Birkeland & Randall 1981, Harriott & Fisk 1988, Babcock & Mundy 1996, Edmunds 2000, Ruiz-Zarate & Arias-Gonzalez 2004, Vermeij 2006), however it

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has received little attention on the high-latitude reefs of South Africa (except for Glassom et al. 2006), where coral-dominated reefs reach their southern limit along the east coast of Africa.

Coral recruitment involves multiple processes, which begin with reproductive output, followed by dispersal, settlement, and metamorphosis of the planulae (Harrison 2011, O'Leary & Potts 2011). Finally, recruits must survive factors such as competition during post-settlement to reach maturity (Harrison & Wallace 1990, Richmond 1997, O'Leary & Potts 2011). The importance of these processes determine the life history strategies of corals (see Harrison & Wallace 1990), and influence the spatio-temporal abundance and composition of coral recruits (Dunstan & Johnson 1998, Glassom et al. 2006, Adjeroud et al. 2007, O'Leary & Potts 2011). Spatially, coral recruitment can vary at a variety of scales, including regional (Fisk & Harriott 1990, Hughes et al. 2002), local (i.e. between or within reefs in the same region) (Dunstan & Johnson 1998, Baird & Hughes 2000, Mundy 2000, Glassom et al. 2006, Adjeroud et al. 2007, O'Leary & Potts 2011), and microhabitat scales (Nozawa 2008, Roth & Knowlton 2009). The supply of coral planulae at a particular location is influenced by physical processes, such as ocean currents and water movement within a reef (Sammarco & Andrews 1988, Oliver et al. 1992). Additionally, behavioural responses of coral planulae, such as modifying their position in the water column by swimming (Pizarro & Thomason 2008), responding to barometric pressure (Stake & Sammarco 2003), chemical cues (Morse et al. 1996, Gleason et al. 2009), and auditory cues (Vermeij et al. 2010) influence the spatial dynamics of coral recruitment, especially at smaller spatial scales. Post-settlement processes such as predation and competition also play an influential role in small spatial scale variation in coral recruitment (O'Leary & Potts 2011)

When released from parent colonies, internally fertilized (brooders) and externally fertilized planulae (broadcast-spawners) enter a planktonic dispersal phase. As they develop, they lose their positive buoyancy and develop the ability to swim (Harrison & Wallace 1990, Raimondi & Morse 2000, Szmant & Meadows 2006). During this time, they encounter a variety of large-scale settlement cues, ranging from chemical water quality (Gleason et al. 2009) to reef noise (Vermeij et al. 2010), which are detected by sensory cells. Once in close proximity to the substratum, planulae actively search for an appropriate surface to settle on, attach, and adopt a sedentary life form (Vermeij 2002).

Appropriate surfaces for planular attachment and survival include encrusting crustose coralline algae (CCA) (Morse et al. 1996, Heyward & Negri 1999, Harrington 2004), dead coral skeletons (Harriott & Fisk 1987), and bare substrata (Harriott 1983, Harrington et al. 2004). In contrast, ephemeral surfaces, such as sediment (Babcock & Davies 1991, Hunte & Wittenberg 1992), fleshy macroalgae, and turf algae

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incur reduced levels of settlement and result in higher levels of mortality as recruits can become dislodged (Kuffner et al. 2006, Birrell et al. 2008a). Appropriate surfaces for coral settlement and survival can be limiting in the natural environment (Harrington et al. 2004), and the degree of microhabitat selection for settlement surfaces can be species specific (Carlon & Olson 1993, Baird & Morse 2004). Additionally, coral mortality can occur from predation by echinoderms (Sammarco 1980) and fish (Christiansen et al. 2009, O'Leary & Potts 2011), or from competition with surrounding biota (Birkeland 1977). Consequently, coral recruitment can show considerable variation at the microhabitat level, (Nozawa 2008, Roth & Knowlton 2009).

Coral reproductive strategies appear to be the main factor that influences both inter- and intra-annual temporal variability in coral recruitment (Fisk & Harriott 1990, Dunstan & Johnson 1998, Glassom et al. 2006). While most corals tend to have well-defined breeding seasons (Harrison & Wallace 1990), peaks in their reproduction, and resulting recruitment, can vary between locations (Harrison & Wallace 1990) and years (Soong et al. 2003). Temporal variation in coral recruitment has been reported in East African countries such as Tanzania (Franklin et al. 1998, Nzali et al. 1998), Kenya (Mangubhai et al. 2007), and the high-latitude reefs of South Africa (Glassom et al. 2006).

While the reproductive dynamics of corals along the Maputaland coastline are largely unknown, preliminary work has shown that corals on these reefs are sexually active with the majority of species being gonochoric, seasonal broadcast spawners (Schleyer et al. 1997). Most spawning occurs in late January (Schleyer et al. 1997, Kruger & Schleyer 1998), with peaks in settlement of acroporids and pocilloporids during March and May respectively (Glassom et al. 2006). Settlement of coral planulae has, however, been recorded year round on Maputaland reefs (Glassom et al. 2006), indicating that additional reproductive events do occur. Mass spawning events, such as those recorded on the Great Barrier Reef (Babcock et al. 1986) have not yet been documented on the Maputaland reefs of South Africa.

In this study, the spatial and temporal variation in coral recruitment on Two-mile Reef (TMR) in South Africa was investigated. This was done by attaching removable settlement tiles for two six-month sampling periods onto Y-frames at three study sites. It was hypothesized that the abundance of coral recruits would differ temporally, between the two sampling periods, and spatially, between and within the three study sites. Additionally, the contribution of coral families was hypothesized to differ. We also predicted that most recruits would be small, due to high post-settlement mortality, with a smaller proportion of large recruits which settled soon after the immersion of tiles. A final aspect of this study was to qualitatively assess the microhabitat of the recruits, including the biota that can compete with them.

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Results of this study were expected to provide valuable insight into the ability of coral communities on TMR to respond to, and replenish populations, after disturbance events.

4.3. Materials and Methods

4.3.1. Study area, monitoring sites and methods used in this study

Refer to chapter 2.1 and chapter 2.3.

4.3.2. Statistical analyses

Due to violations of the assumptions for a parametric t-test on both raw and transformed data, the overall count of recruits per tile used during the two sampling periods, and on the top surface and edge surfaces of tiles, was compared with Mann Whitney U t-tests. Due to the unbalanced spatial design of the winter sampling dataset, only the summer dataset was used to ascertain patterns in overall spatial variation in coral recruitment on TMR. Counts of corals per tile from tiles used during the summer sampling period were $\sqrt{(x + 3/8)}$ transformed and analyzed using a nested ANOVA, with Y-frames nested within study sites. Where significant differences were found, *post-hoc* Tukey HSD tests were conducted. The overall composition of recruit families was compared between study sites, Y-frame at each study site, on the two tile surface orientations, and between the two sampling periods with chi-square tests. The mean corallum diameter of pocilloporid recruits found on summer tiles was compared with those used in winter by mean of a Mann–Whitney Rank sum t-test. The mean corallum diameter of pocilloporid recruits on summer tiles was compared between the three study sites with a nested ANOVA. The size of pocilloporid recruits which settled on the top surface and edges of tiles were compared with a Mann–Whitney Rank sum t-test. Descriptive statistics were used to compare the percentage cover of each surrounding category for all recruits. All statistical tests in this study were done in STATISTICA (StatSoft, Version 7, Tulsa, USA), with significant differences defined as $P < 0.05$.

4.4. Results

4.4.1. Abundance

Over the two six-month sampling periods, a total of 2205 recruits were counted, an overall settlement of 8.68 ± 9.59 (mean $\pm$ S.D.) recruits per tile (equivalent to 653 recruits m^{-2}). The number of recruits on

summer tiles differed significantly from winter tiles (Mann–Whitney U: Z = 12.10, P < 0.001). Most (88%) settlement occurred on summer tiles, with a 6.6-fold decrease in the mean abundance of recruits on winter tiles, 14.5 ± 9.9 and 2.2 ± 2.3 respectively.

Aside from differences between sampling periods, analysis on spatial settlement patterns from summer tiles showed that the abundance of coral recruits varied considerably (Fig. 4.1). The abundance of coral recruits differed significantly between the three study sites and between Y-frames nested within study sites (Table 4.1). Mean recruitment was significantly higher at the northern site compared to both the central and southern sites (Tukey's HSD: $P < 0.001$), and accounted for 54% of all recruits. Settlement also differed significantly between Y-frames at the central and southern study sites where settlement was generally lower (10.45 ± 6.56 and 9.78 ± 6.15 respectively), but did not differ at the northern site (23.27 ± 9.78) (Fig. 4.1). Settlement differed markedly between the top and edge surfaces of tiles (Mann–Whitney U: Z = 15.35, $P < 0.001$), with the mean settlement on vertical edges 14 times greater than on top surfaces, (0.23 ± 0.19 and 0.02 ± 0.03 respectively) (Fig. 4.2).
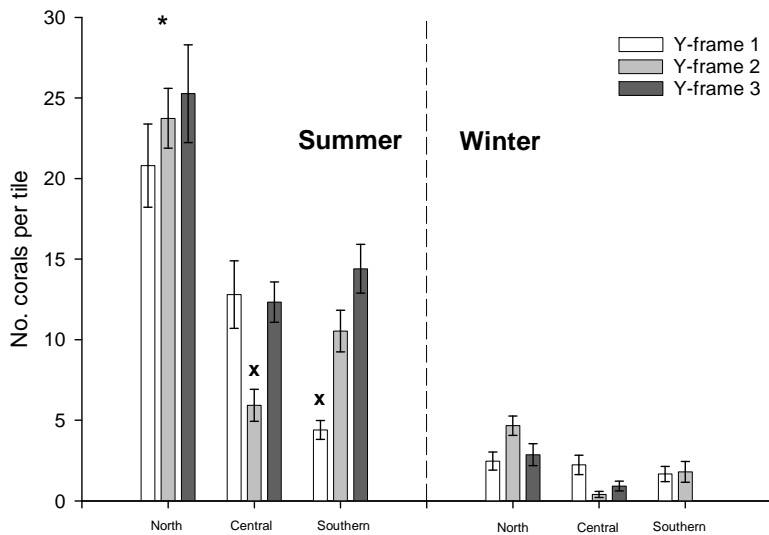
Fig. 4.1. Abundance of coral recruits (Mean ± SE) on tiles attached to the three Y-frames at each study site from the two sampling periods (Summer = October 2009 – April 2010, Winter = April 2010 – October 2010). Significantly different levels of settlement between study sites and between Y-frames within study sites during summer are marked (*) and (x) respectively where $P < 0.05$.

Table 4.1. Variation between recruitment at the three study sites and between Y-frames nested within study sites from the summer sampling period. * = P <0.0001.

Variance source	*Df*	MS	*F*	*P*
Study site	2	2.12	48.44	*
Y-frame	6	0.45	10.33	*
Error	125	0.04		
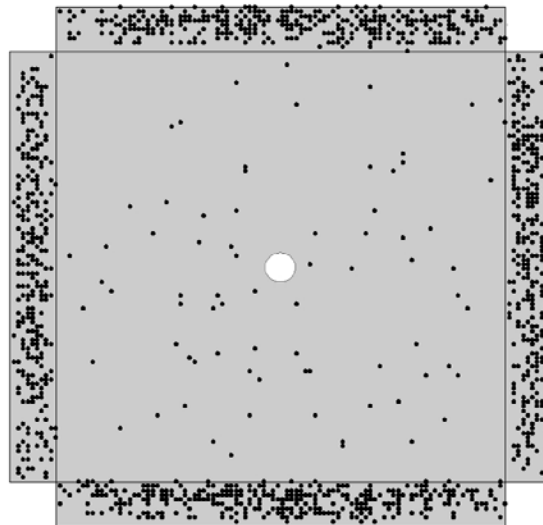
Fig. 4.2. Tile template illustrating the settlement location of the 2205 recruits detected in this study.

4.4.2. Recruit composition

The overall recruit composition in both summer and winter was dominated by pocilloporids (87.98%), with the remainder consisting of acroporids (10.29%), poritids (1.13%) and 'others' (0.59%) (Fig. 4.3). The composition of coral recruits differed between the two sampling periods (chi-square test χ^2 = 39.91, *df*

= 3, $P < 0.001$) (Fig. 4.3). While all four taxonomic categories were detected on summer tiles, the only taxon found during the winter sampling period was Pocilloporidae (Fig. 4.3).
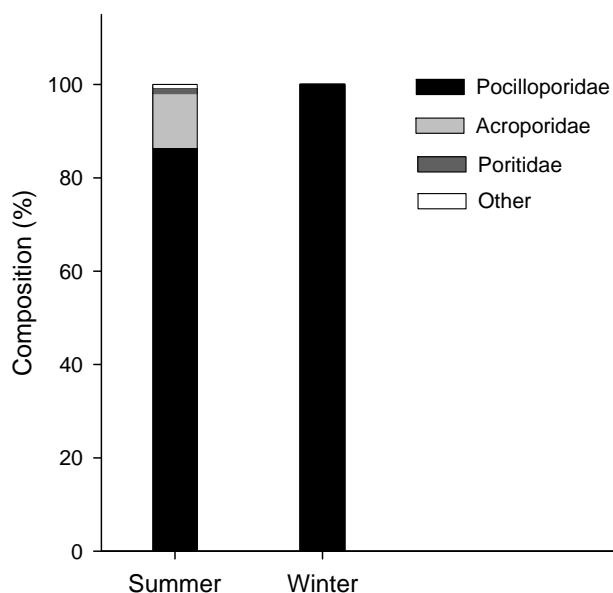
Fig. 4.3. Composition of coral recruits on settlement tiles deployed at Sodwana Bay in summer and winter

Pocilloporid, acroporid, and poritid recruits were found at each of the three study sites during summer. However, their contribution varied between study sites (chi-square test $\chi^2 = 61.69$, $df = 6$, $P < 0.001$) and Y- frames at the northern (chi-square test $\chi^2 = 13.60$, $df = 6$, $P < 0.05$) and central sites (chi-square test $\chi^2 = 23.21$, $df = 6$, $P < 0.001$), but not the southern site (chi-square test $\chi^2 = 8.01$, $df = 4$, $P > 0.05$) (Fig. 4.4). The contribution of acroporid recruits was greatest at the central site (Fig. 4.4). The contribution of coral taxa on the tops and edges of tiles also differed significantly (chi-square test $\chi^2 = 63.84$, $df = 3$, $P < 0.001$), with acroporids and poritids comprising a greater proportion on the top surface (Fig. 4.4).
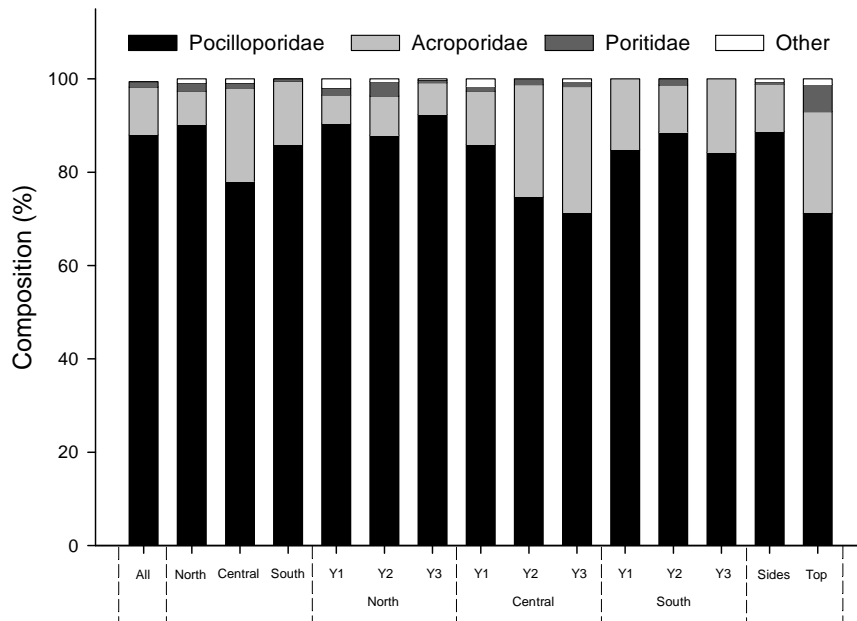
Fig. 4.4. Overall composition and variation of recruits during summer, at the three spatial scales investigated in this study (between study sites, Y-frames at study sites, and the top surfaces compared to edge surfaces of tiles).

4.4.3. Size frequencies

The mean corallum diameter of the 2205 recruits in this study was 2.1 mm, and ranged from the smallest size of 0.5 mm (an acroporid) to 14.7 mm (pocilloporid). The size frequency distribution of these 2205 recruits was positively skewed, with 87.8% of recruits <4.5 mm, recruits 1.5-3 mm constituting the largest proportion (Fig. 4.5). The size frequencies of pocilloporids and acroporids were likewise positively skewed; however, acroporids were generally smaller than pocilloporids (1.2 ± 0.4 SD and 2.2 ± 1.1 respectively). Acroporids were predominantly <1.5 mm (83.7%), the largest acroporid recruit being 3.8 mm in diameter.
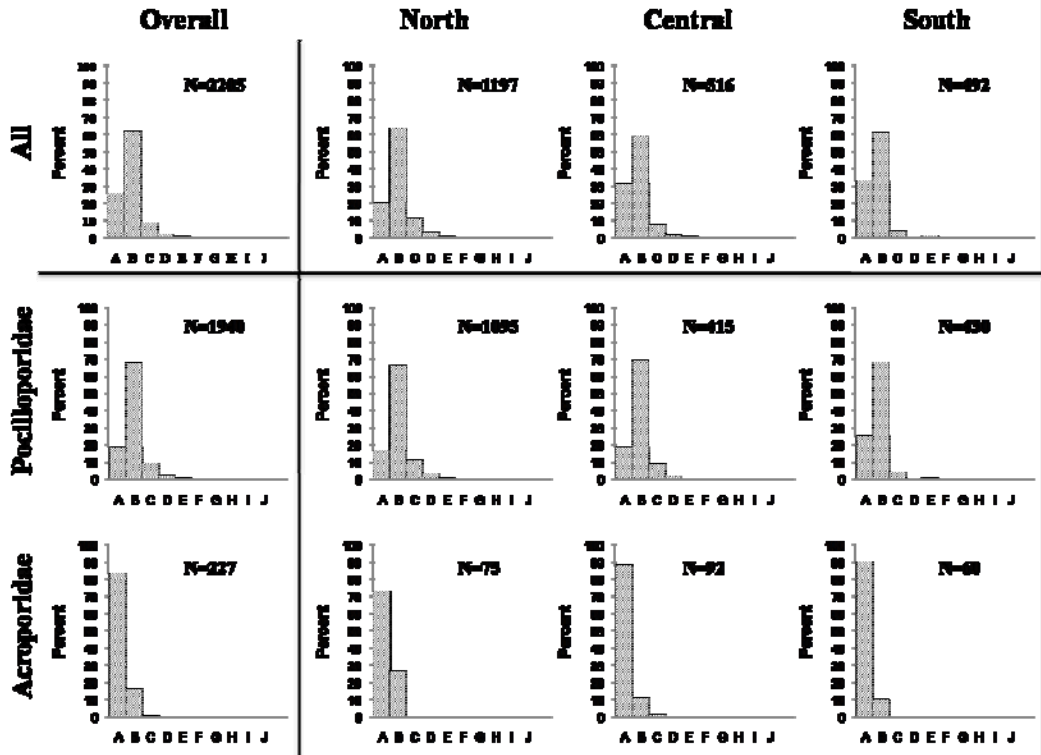
Fig. 4.5. Overall percent of size frequencies of all recruits at the three study sites, between the two most dominant taxa and the spatial variation thereof. Size classes: A = 0-1.5 mm, B = 1.5- 3 mm, C = 3-4.5 mm, D = 4.5-6 mm, E = 6-7.5 mm, F = 7.5-9 mm, G = 9-10.5 mm, H = 10.5-12 mm, I = 12-13.5 mm, J = 13.5-15 mm).

Although the majority of pocilloporids were within the 1.5 - 3 mm size class at each of the three sites, the mean corallum diameter of pocilloporids differed significantly at the three study sites (nested ANOVA: $F_{(2,124)} = 6.18$, $P < 0.01$), and between study periods (Mann–Whitney U: $Z = 7.31$, $P < 0.001$). Pocilloporids were significantly larger at the northern site compared to the southern site (Tukey's HSD: $P < 0.01$) (2.3 and 2.0 mm respectively) (Fig. 4.6), and increased from 2.2 mm in summer to 3.0 mm during winter. The size increase was relatively consistent across the three study sites (Fig. 4.6). The overall mean size of Pocilloporidae that settled on top surfaces was significantly larger than the edges of tiles (Mann–Whitney U: $Z = 3.81$, $P < 0.001$).

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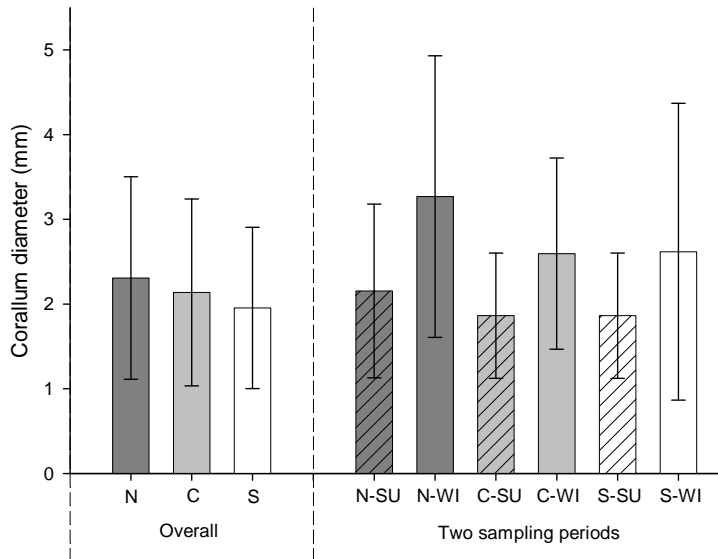
Fig. 4.6. Overall and sample period mean (±SD) corallum size of pocilloporid recruits at the three study sites (N = northern, C = central, S = Southern, SU = October 2009-April 2010, WI = April 2010 – October 2010).

4.4.4. Surrounding microhabitats

In total, 77.6% of recruits were detected prior to bleaching of the tiles and were used to assess their surrounding biota. Overall, the percentage cover of microhabitat categories within 3 mm of recruits was not equal, with CCA contributing the greatest (39.65 ± 0.84%) cover at all three study sites (Fig.4.7). Bare tile surface was the second highest category (25.84 ± 0.76%), with a greater contribution at the northern site. The remaining categories each contributed <10% to the surrounding habitat of recruits and were present at all three study sites except for barnacles which were absent at the southern site. Overall, other coral recruits comprised 3.58 ± 0.26% of the microhabitat, these being more prevalent at the northern study site (4.48 ± 0.38%).
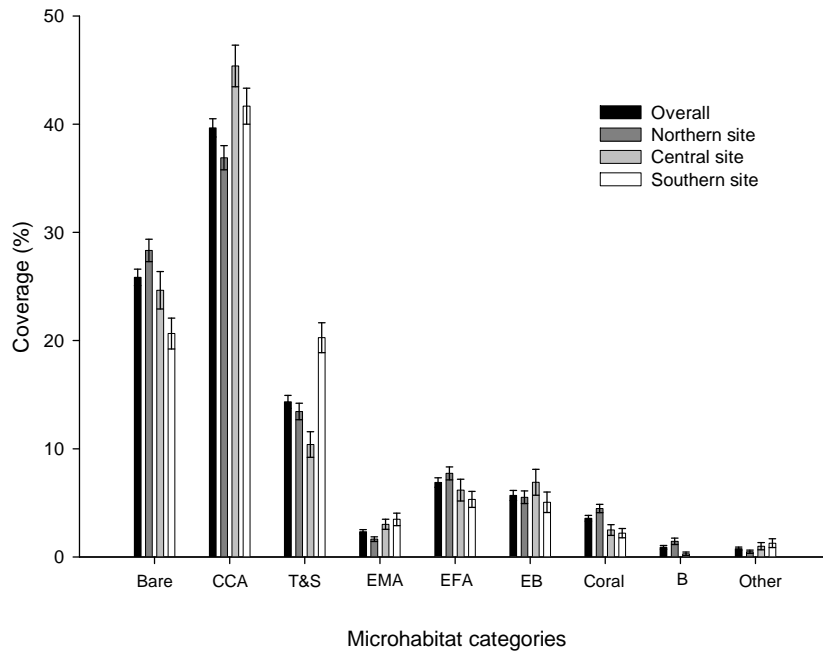
Fig. 4.7. Overall mean ± SE cover of microhabitat categories surrounding each recruit within three millimeters at the three study sites. CCA = Crustose coralline algae, T&S = Turf and sediment, EMA = Erect macro-algae, EFA= Encructing fleshy algae, EB = Encrusting bryozoans, B = Barnacles.

The contribution of microhabitat categories was likewise different on the tops and edges of tiles (Fig. 4.8). Turf and sediment (40.92 ± 3.93%) dominated the top surfaces, followed by bare tile substrata (28.38 ± 3.78%) and encrusting fleshy algae (18.03 ± 3.37%). The remaining categories each accounted for <6.6 % of the cover on the top surfaces. In contrast, the surrounding biota on the edges of tiles was dominated by CCA (41.29 ± 0.86%). followed by bare tile substrata (25.72 ± 0.78%), and turf and sediment (13.03 ± 0.57%). The remaining accounted for <6.3% on the edges of tiles.
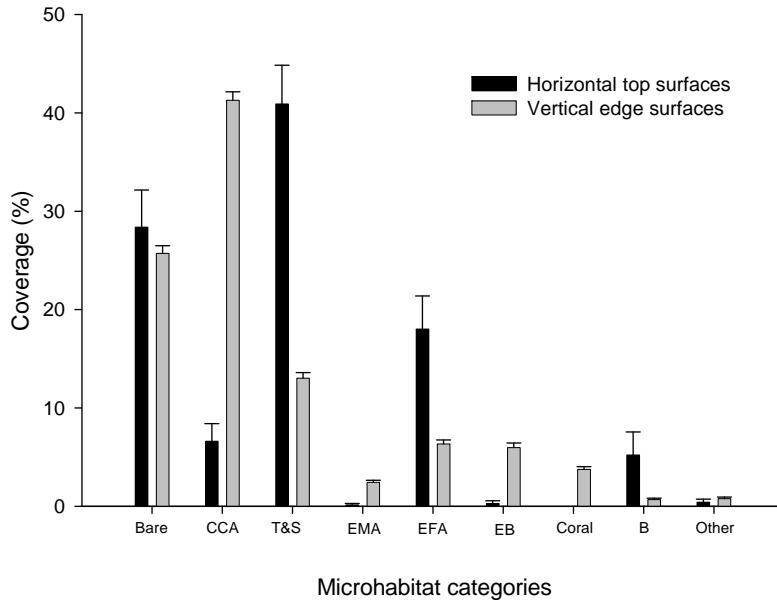
Fig. 4.8. Overall mean ± SE cover of recruit surrounds on the top and edges of tiles. CCA = Crustose coralline algae, T&S = Turf and sediment, EMA = Erect macro-algae, EFA= Encructing fleshy algae, EB = Encrusting bryozoans, B = Barnacles.

4.5. Discussion

The overall recruitment rate of 653 coral recruits m^{-2} obtained in this study is lower than that reported for the central Great Barrier reef in Australia (Hughes et al. 1999, 2000), but higher than southern Australia (Banks & Harriott 1996, Dunstan & Johnson 1998), the Caribbean (Hunte & Wittenberg 1992, Smith 1992), Tanzania (Franklin et al. 1998, Nzali et al. 1998), and Kenya (Tamelander 2002, O'Leary & Potts 2011). The overall mean rate of coral recruitment obtained in this study was considerably lower than a previous study (1004 recruits m^{-2}) conducted between November 1999-2002 on four Maputaland reefs (Glassom et al. 2006). While it is tempting to make direct comparisons between recruitment rates from different studies, differing methods, which influence recruitment rates, prohibit such comparisons (Harriott & Fisk 1987, Field et al. 2007), even during concurrent studies (Glassom et al. 2004, Abelson et al. 2005). Inter-annual variation could also account for the differences between studies at the same location.

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The life history strategies exhibited by corals have a profound influence on the production, supply, and settlement of coral planulae and, as a result, can contribute to significant variations in the spatial and temporal dynamics of coral recruitment (Hughes & Tanner 2000). The overall abundance and composition of coral recruits in this study was not evenly spread between the two sampling periods. Coral recruitment verified the general seasonal trend for reefs along the east African coastline (Franklin et al. 1998, Nzali et al. 1998, Glassom et al. 2006, Mangubhai et al. 2007), with peaks occurring during the first half of the year. Glassom et al. (2006) found a bimodal peak in recruitment in March and May during each of the three years in their study, with broadcast spawners dominating recruitment in March, and brooders being more abundant in May. Most brooding coral species have multiple gametogenic cycles, whereas broadcast spawning species tend to have one annual gametogenic event (Petersen 2005). Consequently, recruitment from brooders can occur throughout the year, with broadcast spawners being absent at certain times of the year.

Results from this study and others (Banks & Harriott 1996, Fox 2005) concur with such a trend, as pocilloporid recruits (which contain brooding species) were present year round. Acroporids, which are predominantly broadcast spawners (Harrison 2011), were totally absent on tiles used during the winter sampling period of this study. Recently, research on *Acropora austere* has shown that these spawn during January (L. Masse unpublished data), and are predicted to have contributed to acroporid colonies on tiles collected in April. The presence of pocilloporid recruits year round can be explained by their reproductive strategies, as *Pocillopora verrucosa* broadcast-spawns in late January (Kruger & Schleyer 1998), and *Pocillopora damicornis* broods either sexually or asexually (Stoddart 1983, Ayre & Miller 2004, Sherman et al. 2006). The smaller mean size of acroporids compared to pocilloporids is to be expected as the latter are generally larger at the time of settlement (Babcock et al. 2003, Schmidt-Roach et al. 2008). While Schmidt-Roach (2008) predicted that acroporids settle at ~1.14 mm, Babcock et al (2003) report that Acroporidae recruits can be as small as 0.53 mm. A growth study of the early stages after settlement of corals found on the Maputaland Reefs of South Africa, as done by Babcock et al (2003) in Australia, is necessary to provide greater taxonomic resolution on coral recruitment on these reefs.

The overall composition of coral recruits obtained in this study was strikingly similar to that obtained in a previous, larger spatial scale recruitment study on four reefs within the central complex (Glassom et al. 2006). Here, pocilloporids were also found to be predominant at all spatial scales, which can be attributable to a change in the relative abundance of families of coral spat from acroporid dominance at low latitudes, to pocilloporid dominance at higher latitudes (Hughes et al. 2002). Additionally pocilloporids are less selective during settlement (Richmond 1985). The contribution of acroporids was

also similar as was the seasonal variation in the composition of recruits was found in this study and Glassom et al (2006). While aproporids constitute a much greater proportion than pocilloporids to the mature community structure on Maputaland reefs, this is not reflected in the composition of recruits found in this study, and that of Glassom et al. (2006).

The significant difference in the abundance of recruits at the three study sites, and within study sites over both sampling periods indicates that recruitment could be patchy on TMR, with certain areas receiving low levels of recruitment. However, long-term studies are required to determine if recruitment trends obtained in this study are consistent. If so, areas with low recruitment are predicted to have limited recovery potential following high levels of disturbance. Low recruitment rates in a particular area can be a result of limited larval supply, inadequate surfaces for settlement or high post-settlement mortality (Szmant & Meadows 2006). The southward flowing Agulhas Current is predicted to transport coral planulae from reefs to the north (Morris 2009, Macdonald et al. 2011), and retain larvae during occasional reversal inshore currents (Morris 2009). While genetics work on *Pocillopora verrucosa* has revealed no genetic differentiation between populations on Maputaland Reefs (Ridgway et al. 2001), genetic isolation of *Acropora austera* between a northern Maputaland reef and reefs to the south indicates that reef connectivity within the area is yet to be fully understood (Macdonald et al. 2011). Consequently, further research into the supply of coral larvae and investigation into their post-settlement survival on Maputaland Reefs is necessary.

While consistently greater levels of recruitment occurred on Y-frames at the deeper northern site, a reduction occurred at the shallower sites. Such a trend has been observed elsewhere (Rogers et al. 1984, Smith 1997). In contrast, intermediate depths have been found to have higher recruitment rates (Roth & Knowlton 2009). Future studies with replicate sites at different depth intervals are necessary to ascertain trends in recruitment associated with water depth. Coral planulae have been shown to exhibit phototactic behaviour (Morse et al. 1988, Carlon & Olson 1993, Babcock & Mundy 1996), but the role of this behaviour in coral settlement remains poorly understood. Besides reduced light availability, lower levels of surge were characteristic of the northern site compared to the other sites. Higher flow rates have been shown to adversely influence the settlement success of other benthic biota (Boxshall 2000) and could have contributed to the lower settlement rates obtained at the shallower sites of this study.

Aside from differences between study sites, other studies have shown that coral recruitment can vary at a smaller scale (Dunstan & Johnson 1998, Baird & Hughes 2000, O'Leary & Potts 2011). Recruitment on tiles on the three Y-frames at the central and southern study sites during the summer sampling period

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corroborated such a trend. Small-scale patchiness of larvae and biotic interactions could contribute to differences in recruitment between Y-frames. These can include grazing pressure by fish (Adjeroud et al. 2007, Christiansen et al. 2009, O'Leary & Potts 2011) and variability in suitable settlement surfaces (Vermeij et al. 2011). While both these parameters were not quantified in this study, sedimentation and high levels of encrusting macroalgae could have contributed to different recruitment on Y-frames (pers. obs).

The settlement preference of coral recruits for the vertical tile surfaces in this study is an interesting result. Due to greater light availability in the tropics, coral settle on the undersurfaces of tiles, which contrasts with settlement on the upper surfaces of tiles at higher latitudes where light is limiting (Harriott & Banks 1995, Harriott & Simpson 1997, Glassom et al. 2006). While such a trend has previously been observed on the high-latitude reefs of South Africa (Glassom et al. 2006), the settlement preferences from this study show otherwise. The majority of coral settlement was on the vertical surfaces of tiles regardless of depth. This indicates that other factors aside from light availability could be more important for coral settlement, such as microhabitat refuges created in this study. Increased light availability on the top surfaces of tiles could have influenced growth rates, thereby resulting in larger recruits observed on these surfaces.

Settlement tiles were rapidly colonized by sessile epibentic organisms in the field. This resulted in the reduction of free space for coral planula settlement. Additionally, once settled, larvae had to compete with high levels of living biota. Such competition has been proposed as a possible explanation for reduced levels of recruitment in other studies (e.g. Banks & Harriott 1996, Holmes et al. 1997), particularly at higher latitudes (Holmes et al. 1997). Surface cover categories which are commonly known to be less suitable for coral settlement, such as turf algae and encrusting macroalgae, contributed to a greater proportion of biotic cover on top surfaces of tiles. In contrast, categories such as CCA which can enhance coral settlement (e.g. Harrington 2004, Erwin et al. 2008, Neo et al. 2009, Vermeij et al. 2011),were more abundant on the vertical edges of tiles. The lack of competition by turf algae on the vertical edges of tiles could explain why both CCA cover and coral settlement was highest here. Turf algae and sediment entrapment was commonly found on the top surfaces of tiles in this study. Turf algae often accumulate sediment (Steneck 1997, Purcell 2000), which inhibits coral settlement directly by pre-emption of space, and indirectly by smothering and killing recruits (Babcock & Mundy 1996). Consequently increased rates of coral recruitment can occur when sedimentation rates are low (Nzali et al. 1998).

Encrusting macro-algae cover in this study was dominated by *Lobophora variegata*. *Lobophora* spp. can contain compounds that inhibit settlement and metamorphosis of both *Acropora millepora* and *Stylophora*

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pistillata (Baird & Morse 2004).. In contrast, Roth and Knowlton (2009) found surprisingly high levels of settlement onto *Lobophora* although lower than CCA and bare substratum. This indicates that our current understanding on the influence of macroalgae on coral recruitment is incomplete. While this study has considered the immediate surrounds of coral recruits, further studies investigating large-scale biota assemblages are required.

In conclusion, this study has shown that both the abundance and composition of coral recruits is not uniform throughout the year. Furthermore, it corroborates other studies which have shown both local (between study sites), and within site variation (between Y-frames) in the abundance of coral recruits. As found in the majority of other studies, pocilloporids dominated recruitment composition throughout the year. Finally, the qualitative assessment of the microhabitat surrounding recruits sheds new insights on biota which can influence coral recruitment on TMR.

4.6. Acknowledgements

Chapter 5:

Conclusion

Settlement studies provide insight into the availability of planulae at both spatial and temporal scales (Harriott 1985, Hughes 1985, Wallace 1985a, Glassom et al. 2006). On the natural substratum, recruits can be up to a year old before they are visible to the human eye, due to their small size, and slow growth (Wallace & Bull 1981). In this study, implications associated with the use of varying methods to study coral recruitment were addressed (chapter 3), followed by an investigation into the dynamics of this ecological process on the high-latitude reefs of South Africa in (chapter 4).

Study methods

While a significant difference was found between recruitment on the three tile types at the reef scale, spatial variability accounted for more variation in recruitment than settlement surface type (chapter 3). Similar trends have been observed elsewhere (Burt et al. 2009). The majority of coral settlement occurred on the edges of tiles, regardless of tile type, further corroborating the importance of spatial scale (chapter 4).

Settlement surface type can affect the detectability of recruits, as was found in this study with white calcium carbonate skeletons of bleached recruits on the white surfaces of marble tiles (chapter 3). This could explain why fewer recruits were detected on marble tiles. Aside from influencing detectability, colour has been shown to affect settlement (Mason et al. 2011). It is thus recommended that surface colour be considered in the choice of settlement surfaces in future studies.

Results from this study support the use of low cost CER tiles for recruitment studies as there was little variation between these and the more expensive MAR tiles. Although overall recruitment was greatest on ceramic tiles conditioned with *M. funafutiense* CCA, it did not differ significantly from standard ceramic tiles. This indicates that *M. funafutiense* did not enhance coral settlement at Sodwana Bay. Although the functional importance of CCA in inducing coral settlement has long been recognized, *in situ* studies of the influence of CCA are lacking (Price 2010).

An investigation into fluorescent photography as a rapid, *in situ* technique to detect post-settled recruits indicated that, although coral recruits <1 mm were detected, coral recruitment was consistently underestimated, with only 28% of settled recruits detected. This underestimation could be attributed to microscopic examination of tiles quantifying both living and dead skeletons, whereas fluorescent images only capture living recruits. However, post-settlement mortality of coral recruits on tiles was not quantified during pre-bleaching microscopic examination, which should be incorporated into future studies. Fluorescence analysis of settlement tiles and the surrounding natural substratum at each study site indicated that fluorescent objects did not differ significantly between the three tile surfaces, but fewer corals were detected on all three tile surfaces than on the surrounding natural substratum. This could be attributed to the natural substratum providing refuges for coral settlement which were absent on the top surfaces of tiles.

Dynamics

Seasonal variation was observed in the overall abundance and composition of coral recruits in this study (chapter 4) and concurred with general seasonal trends for reefs along the east African coastline (Franklin et al. 1998, Nzali et al. 1998, Glassom et al. 2006, Mangubhai et al. 2007). Brooders can recruit year round, while broadcast spawners only do so at certain times of the year. Locally, this study and work by Glassom et al (2006) provides evidence that broadcast spawners and brooders could contribute to temporal variations in settlement. In this study, pocilloporid recruits (which contain brooding species) were present year round (chapter 4), which has also been observed elsewhere (Banks & Harriott 1996, Fox 2005). Acroporids, which are mostly broadcast spawners (Harrison 2011), were absent during the winter period (chapter 4).

The overall composition of coral recruits obtained in this study was similar to that obtained by Glassom et al. (2006). Pocilloporids, which are considered a pioneering taxa (Endean & Cameron 1990), and less selective during settlement (Richmond 1985), dominated at all spatial scales (chapter 4). Acroporid contribution to recruitment in this study (chapter 4) was also similar to Glassom et al. (2006). In this study coral recruit size differed between acroporids and pocilloporids (chapter 4), a trend observed elsewhere (Babcock et al. 2003, Schmidt-Roach et al. 2008). This can be explained by differences in life history strategies (Babcock et al. 2003, Schmidt-Roach et al. 2008), however further taxonomic resolution on size differences of recruits at settlement remains to be achieved. Post-settlement mortality can be high (Babcock 1985, Babcock & Mundy 1996, Wilson & Harrison 2005), which can explain the skewed size

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distribution towards smaller recruits in this study (chapter 4). This aspect of coral recruitment requires further investigation on Maputaland reefs.

In this study more recruits were found at the deepest site, and fewer at the shallower sites (chapter 4), a trend observed elsewhere (Rogers et al. 1984, Sammarco 1994, Smith 1997). Local studies investigating associations between recruitment rate and water depth with replicate sites at depth intervals are required. Lower levels of surge, which were characteristic of the deepest site, can also explain these trends as flow rates affect settlement success (Boxshall 2000). Areas with low recruitment were found in this study (chapter 4) and may be a result of limited larval supply, inadequate surfaces for settlement or high post-settlement mortality (Szmant & Meadows 2006). Long-term studies determining whether or not low levels of recruitment are persistent or transient are necessary. Coral recruitment was observed to vary at small spatial scales in this study (chapter 3; chapter 4) and can be attributed to biotic interactions (Adjeroud et al. 2007, Christiansen et al. 2009, O'Leary & Potts 2011) and variability in suitable settlement surfaces (Vermeij et al. 2011).

Results from this study suggest that microhabitat can play an influential role in coral settlement (chapter 4). Surface growth on the tops of tiles was dominated by turf algae and encrusting macroalgae (chapter 4). Turf algae accumulate sediment (Steneck 1997, Purcell 2000), which can smother settled recruits and limit the space available for settlement (Babcock & Mundy 1996). Most coral recruits settled on the vertical edges in refuges of tiles, which were dominated by CCA (chapter 4). This could have enhanced coral settlement, yet further studies investigating biota assemblages and their interaction effects on recruitment are needed.

Coral recruitment has important implications for reef resilience, thereby influencing the strategies employed in reef management. There is evidence that Maputaland reefs are self-sustaining (Schleyer et al. 1997), and high levels of settlement have been recorded (Glassom et al. 2006, and this study). The need for long-term monitoring and the careful consideration of both spatial and temporal replication in future studies is elucidated by the highly dynamic and variable recruitment trends observed on Two-mile Reef. Furthermore, this study highlights the need for the careful selection of the methods used to assess coral recruitment, both in terms of settlement surfaces and recruit detection techniques.

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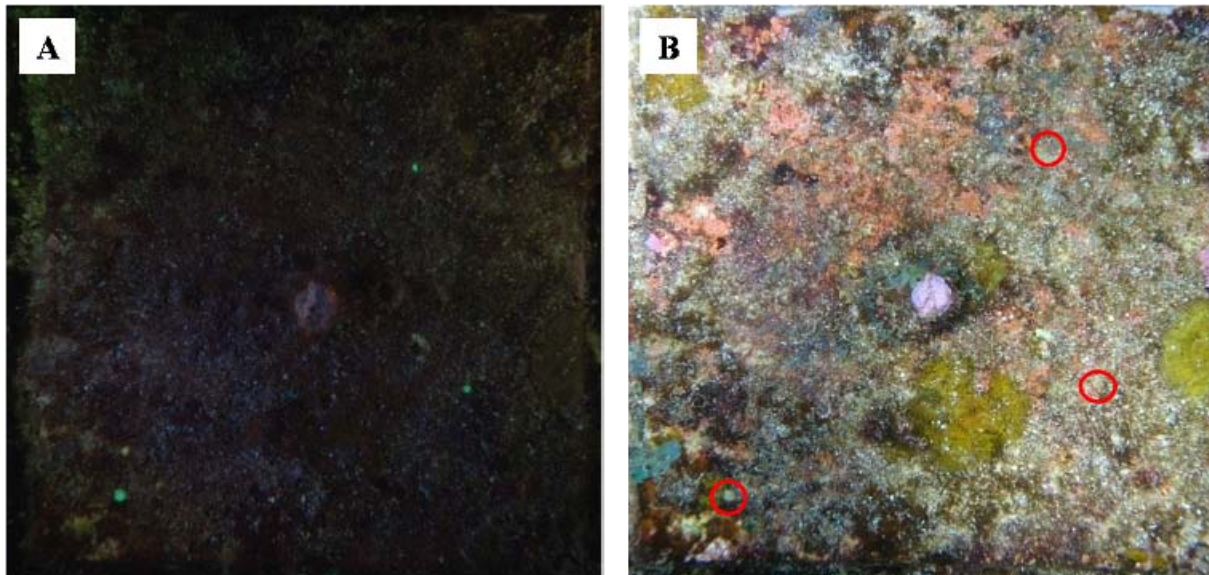
Appendix 1

In situ images of the three artificial settlement surfaces (A = ceramic tile; B = marble tile; C = crustose coralline algae conditioned ceramic tile) and the natural substratum (D) investigated in this study.
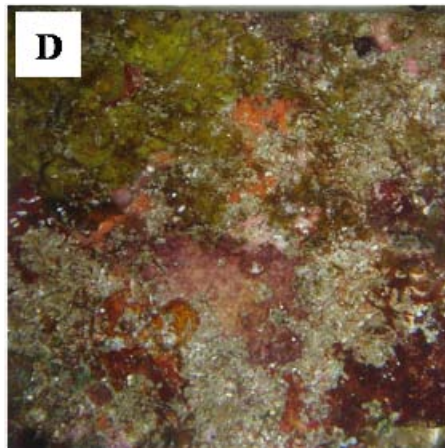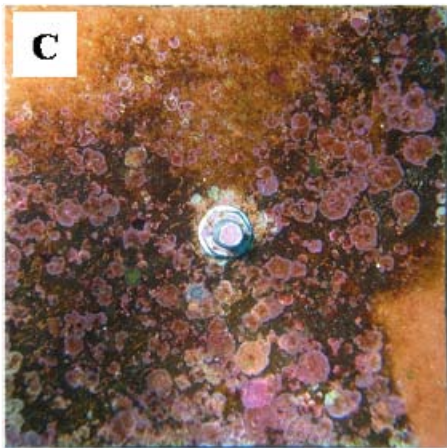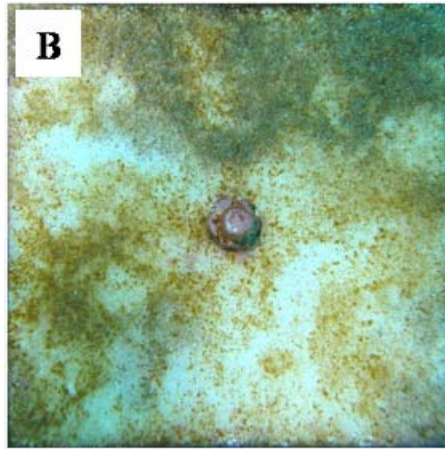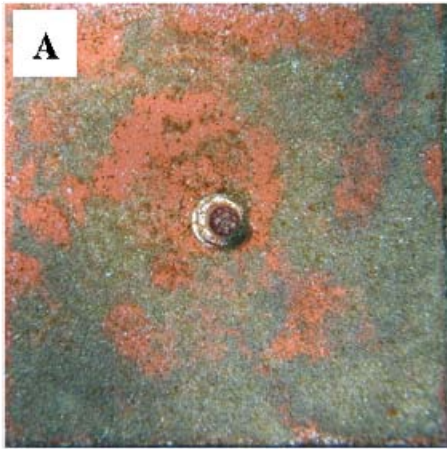
Appendix 2

In situ images taken of the top surface of a ceramic tile with fluorescence photography (A) and standard flash photography (B). Fluorescent detections in A are circled in red in B.

Appendix 3

Skeletal structure of Pocilloporidae (A), Acroporidae (B) and Poritidae (C) recruits identified in this study.