Factors affecting coral recruitment and calcium carbonate accretion rates on a Central Pacific coral reef

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Abstract

Coral recruitment and calcium carbonate ($CaCO_3$) accretion are fundamental processes that help maintain coral reefs. Many reefs worldwide have experienced degradation, including a decrease in coral cover and biodiversity. Successful coral recruitment helps degraded reefs to recover, while $CaCO_3$ accretion by early successional benthic organisms maintains the topographic complexity of a coral reef system. It is therefore important to understand the processes that affect coral recruitment and $CaCO_3$ accretion rates in order to understand how coral reefs recover from disturbances.

The aim of this thesis was to determine how biophysical forcing factors affect coral recruitment, calcification and bioerosion on a pristine coral reef. I used artificial settlement tiles to measure coral recruitment and $CaCO_3$ accretion at ten sites (four on the fore reef, four on the Western Reef Terrace and two at the Entrance Channel) at Palmyra Atoll. *Fungia* skeletons and pieces of dead coral rock were used to measure bioerosion rates, which were combined with the $CaCO_3$ accretion rates to obtain a net $CaCO_3$ budget of the reef substratum. Interactions between coral recruits and other benthic organisms on the settlement tiles were recorded to determine the settlement preferences and competitive strength of coral recruits. The settlement preference of *Pocillopora damicornis* for divots shaped like steephead and bumphead parrotfish bites marks was determined by adding *P. damicornis* larvae to a container with a settlement tile with the aforementioned divots.

I found that coral recruitment and $CaCO_3$ accretion are influenced by biophysical forcing factors. Most pocilloporids likely recruit close to their parents while the origin of poritid larvae is much more distant. Pocilloporid recruitment rates were also significantly correlated with the successional stage of the benthic community on the settlement tiles, especially the cover of biofilm and bryozoa. Biofilm and crustose coralline algae (CCA) were preferred as settlement substrata by coral larvae, however both pocilloporids and poritids settled on a large number of different benthic substrata. *P. damicornis* larvae showed a significant settlement preference for divots shaped like parrotfish bite marks over a flat settlement surface. Coral recruits were good competitors against encrusting algae but were often outcompeted by filamentous and upright algae. Settlement tiles were almost entirely colonised by benthic organisms within three to

twelve months of deployment. The mass of $CaCO_3$ deposited onto the settlement tiles negatively correlated with herbivore grazing pressure on the benthic community. Bioerosion rates within pieces of coral (internal bioerosion) increased over time but overall bioerosion rates (internal and external) rarely exceeded $CaCO_3$ deposition by CCA.

My results show how variability in biophysical forcing factors leads to natural variation in coral recruitment and $CaCO_3$ accretion. This thesis highlights the importance of measuring herbivore grazing, CCA and turf algae cover to gain a better understanding of reef resilience. I conclude that models constructed for Caribbean reefs may not be suited to predict resilience in Pacific reefs and that within the Pacific, two different kinds of resilience models need to be constructed, one for human-inhabited coral reefs and one for uninhabited coral reefs.

Hanau ka ‘Uku-ko’ako’a, hanau kana, he ‘Ako’ako’a, puka

(Born was the coral polyp (as the first organism on earth), born was the coral, came forth)

- Kumulipo, a Hawaiian creation chant

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Structure of this thesis

This thesis consists of a General Introduction, four data chapters and a General Discussion. An additional research project undertaken during this PhD is included as Appendix 1. Chapters 2, 3, 4 and 5 were written as independent manuscripts intended for publication, which leads to some degree of overlap and repetition between these individual chapters and/or the General Introduction. These chapters are papers in progress which have not yet been submitted for publication.

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CHAPTER 1

General Introduction

1.1 CORAL REEFS AND ATOLLS

1.1.1 Importance of coral reef and atolls

Coral reefs occur in tropical and semi-tropical waters between 32° North and 30° South (Barnes 1987) and currently cover about 284'300 km^2 of the Earth's surface, an area smaller than the land mass of Italy (de Groot et al. 2012). Despite their small size, they have a large effect on Earth's physical, chemical, biological and social appearance. Corals and crustose coralline algae (CCA), have constructed the largest structures built by organisms including humans. They created limestone structures as tall as 1300 m and as long as 2000 km (Birkeland 2015a). Coral reefs greatly affect oceanic and atmospheric chemistry as they take up about half of the calcium that enters the sea and fix roughly 700 billion kg of carbon each year (Birkeland 2015a). Coral reefs are biodiversity hotspots hosting up to 30 animal phyla (Paulay 1997) and sustaining up to six trophic levels (Grigg et al. 1984). Atolls formed by coral reefs act as stepping stones for species dispersal, enabling species to be distributed across extensive spatial barriers, for example from the Indo-Pacific to the Eastern Pacific (Dana 1975; Grigg and Hey 1992). Coral reefs also provide millions of people with ecosystem services such as shoreline protection from wave action and erosion, generation of coralline sands, fisheries, tourism revenue, raw material for construction, raw natural products for pharmaceuticals, recreational and cultural values (Conservation International 2008; Wilkinson 2008). Their total economic value has been estimated at $352,249 per hectare per year; higher than any other biome on earth (de Groot et al. 2012).

Many of the reefs in the Pacific Ocean are atolls; ring-shaped reefs located in mid-ocean that enclose a shallow lagoon. Atolls form from coral reefs growing on the side of a volcanic island. As the island begins to sink, the reef builds itself upwards for thousands or millions of years to stay at the water surface (Nunn 2009a). *Motu*, islands within the atoll, form either when the reef is exposed by falling sea levels or through the accumulation of sediments and grow through the accumulation of sediment from the fore reef (Nunn 2009a). Many *motu*

are inhibited as they contain freshwater and soil (Nunn 2009a). The people living on these *motu* are very dependent on coral reefs as a source of food, for storm protection and income. Furthermore, reefs also have a stabilizing effect on their social structure. Fishing is often a cooperative activity involving all family members and helps solidify the roles and importance of individuals within the family (Birkeland 2015a).

1.1.2 Stressors affecting coral reefs and atolls

Between 1997 and 2011, 55% of the coral reef area worldwide was lost due to a combination of natural and anthropogenic stressors (Costanza et al. 2014) such as over-harvesting, pollution, disease and the effects of increased sea surface temperatures and ocean acidification (Hoegh-Guldberg et al. 2007). The reef ecology and geomorphology of most coral reefs have been modified by these stressors and do not resemble their natural or pristine state anymore (Jackson and Sala 2001; Halpern et al. 2008). Long-lasting changes in community composition and structure (Nyström et al. 2008), reduction of topographic complexity (Alvarez-Filip et al. 2009), and alterations in the abundance of key reef-associated species (Hughes et al. 2003; Mumby et al. 2006a) are common on many coral reefs.

Human occupation of *motu* (atoll islands) affects corals reefs through increased sedimentation and nutrient levels, overfishing and exploitation of limestone for building purposes (Barnett and Adger 2003; Woodroffe and Biribo 2011). Furthermore, climate change affects atolls through rapid sea level rise, increased frequency and intensity of storms and coral reef degradation through increasing ocean acidification and frequent coral bleaching, threatening the existence of *motu* and food sources of their inhabitants (Nurse et al. 2001; Bleakley 2004). Despite widespread belief, complete drowning of their island due to sea level rise is not the principal climate change-induced challenge faced by people living on *motu*, which are rarely situated more than 2-3 meters above sea level (Webb and Kench 2010; Kench et al. 2015; Mann et al. 2015; McLean and Kench 2015). Coral reef degradation and inundation and salinization of land are a larger threat (Nunn 2009b).

1.1.3 Addressing coral reef degradation

With coral reef degradation comes a decline in the ecosystem functions that reefs provide (Hoegh-Guldberg et al. 2007; Knowlton and Jackson 2008), affecting the livelihood of reef-dependent communities. Stressors on coral reefs act both on local and global scales.

Global threats such as climate change can generally not be managed at a local scale and are likely to increase in the future (Frieler et al. 2013). However, it is generally believed that reducing local stressors will help coral reefs deal with impacts of global stressors (Ateweberhan et al. 2013; Anthony et al. 2015). To counteract reef degradation on a local scale, two major strategies have been employed: conservation and restoration. Coral reef conservation tools include Marine Protected Areas (MPAs, Halpern 2003; Rodrigues et al. 2004), fish aggregation devices to aggregate pelagic fish for local fisheries and thereby reducing fishing pressure on nearby coral reefs (Bell et al. 2013) and fisheries management such as fishing bans (Rogers et al. 2015a). Coral reef restoration tools include deployment of artificial reef structures on reefs that have lost their topographic complexity (Bohnsack and Sutherland 1985; Baine 2001) and coral restoration through transplantation of asexually produced fragments or sexually produced coral recruits (Rinkevich 2005, 2014). The best tool to sustain the ecosystem services provided by a coral reef depends on the status of the reef. Reefs with high topographic complexity profit from MPAs the most, while reefs with low topographic complexity can profit from artificial reef structures, coral restoration, fish aggregation devices and managed herbivore fisheries more than from MPAs (Rogers et al. 2015a).

Inhabitants of remote atolls depend highly on their local reefs (Barnett and Adger 2003; Turner et al. 2007) and are extremely vulnerable to their degradation (Watson et al. 2016). It is therefore not surprising that locally managed marine areas (LMMA) are the most common used conservation tool in independent island states in the Pacific. In 2008, over 500 communities and 15 countries were involved in LMMAs in the Pacific Islands (Govan et al. 2009). Locally, these LMMAs are successful at increasing the abundance of targeted species and likely also increase the livelihood of the local communities that manage them (Govan et al. 2009). Reef restoration has hardly been considered in the Pacific Islands region (Nunn 2009b) but may be suited for areas that have lost their topographic complexity (Rogers et al. 2015a) and could lead to significant socio-economic and cultural benefits for local communities (Kittinger et al. 2013). Hope for coral reef recovery and adaptive changes in human behaviour on Pacific Islands exists given that constant change has been an integral part of both coral reef ecosystems (Birkeland 2015a) and atoll-dwelling communities (Lindstrom 2008; Gough et al. 2010; McMillen et al. 2014).

1.2 CORAL REEF RESILIENCE

1.2.1 Resilience

Despite climate change and local stressors affecting coral reefs worldwide (Halpern et al. 2008), some reefs thrive while others degrade (West and Salm 2003; Cheal et al. 2010; Gilmour et al. 2013; Johns et al. 2014). This difference in response to disturbance maybe caused by differences in reef resilience (Birkeland 2015a). Ecological resilience (hereafter referred to as resilience) is the capacity of a system to absorb disturbance and reorganise while undergoing change yet still retaining essentially the same function, structure, identity, and feedbacks (Walker et al. 2004). Resilience combines two processes: "resistance" which refers to tolerance, acclimatisation and adaptation, and "recovery" which refers to reproduction, successful recruitment, repair and healing (Birkeland 2015b). Chronic human stressors such as fishing pressure, nutrient input and increased sea temperatures decrease the resilience of coral reefs (Hughes et al. 2010; Anthony et al. 2015). These drivers act in a slow and continuous manner and may lead to chronic disturbances including coral diseases. Reefs with low levels of chronic human stressors are resilient to event-driven acute disturbances such as tropical cyclones, coral bleaching events, destructive fishing and crown-of-thorns starfish outbreaks and regain their living coral cover and species richness within 10-15 years in the absence of further acute disturbances (Hughes et al. 2010; Anthony et al. 2015).

Until the 1970s, coral reef communities were resilient (for examples see Birkeland 2015a) but since the mid-1970s, coral communities have struggled to recover from disturbances (Hughes and Tanner 2000; Gardner et al. 2003; Birkeland 2015a). From the mid-1960s until the mid-1990s, 54% of coral reefs located in the Pacific Ocean and 83% of coral reefs in the Caribbean Sea were not able to recover after a disturbance event (Connell 1997). Future scenarios indicate that the resilience of tropical coral reefs will decline due to climate change and ocean acidification (Anthony et al. 2011). This is both driven by an increase in frequency and severity of acute disturbance events such as coral bleaching (Van Hooidonk and Huber 2009; Van Hooidonk et al. 2013) and storms (Emanuel 2005; Knutson et al. 2010; Gardner et al. 2014) as well as a decrease in the potential of coral reefs to recover from these disturbances due to reduced coral growth (Reynaud et al. 2003) and recruitment (Hoegh-Guldberg et al. 2007; Albright and Langdon 2011).

Reducing pressures and exposures to stress is therefore not sufficient to prevent or reverse coral reef declines. Managers of coral reef ecosystems also must focus on supporting the system's resilience to these threats (Nyström et al. 2008; McClanahan et al. 2012; Kennedy et al. 2013; Anthony et al. 2015). Coral reef resilience incorporates aspects of the entire ecosystem, which makes management decisions based on resilience extremely complex. Furthermore, global and local stressors often act synergistically (Tompkins and Adger 2004) and management decisions often have unintended or unanticipated negative effects (Tallis and Polasky 2009). Lastly, due to the close coupling between coral reefs and society, most conservation challenges are embedded in socio-ecological systems (Game et al. 2014). This calls for the implementation of system approaches to coral reef management and conservation (Chapin et al. 2010; McCook et al. 2010; Anthony et al. 2015). Attention is now focused on identifying indicators for reef resilience and constructing system models based on resilience to assist coral reef ecosystem managers with decision making.

1.2.2 Indicators of resilience

A loss of resilience often results in a rapid and broad-scale change in an ecosystem, a so called regime shift (Done 1992). These regime shifts may not be reversible and have a large impact on the ecosystem services a coral reef provides (Mumby et al. 2013; Kennedy et al. 2013). One goal of coral reef conservation is to prevent such regime shifts or predict them early enough (Carpenter and Brock 2006). The major challenge the resilience concept poses is that we are currently unable to measure resilience directly due to it being multidimensional and context dependent (Holling 2001). For this reason, new indicators of resilience are being developed. The two general indicators of low resilience that hold true over different ecosystems: (1) increasing standard deviations and changes in skewness; and (2) slower recovery rate from small perturbations, fail to detect regime shifts in marine ecosystems (Brock and Carpenter 2006; Carpenter and Brock 2006; Van Nes and Scheffer 2007; Guttal and Jayaprakash 2008; Lindegren et al. 2012; Dakos et al. 2015). Therefore other indicators of resilience are required that are able to predict regime shifts on coral reefs (Nyström et al. 2008).

To capture the multitude of aspects influencing resilience, several indicators rather than just one are necessary (Carpenter et al. 2005). Nyström et al. (2008) identified six potential areas where resilience indicators are likely. Firstly, a **functional groups** approach measuring

species richness and relative abundance of species determines the redundancy level of the ecosystem and with it its potential to maintain ecosystem processes in the face of change. Secondly, measuring size-class distributions of organisms provides information on **demographic skewness in species population**, an important indicator of the past, present and future of the ecosystem. Thirdly, if aggregated patterns of body mass are found within the system, it likely has **discontinuities** (a sharp difference in characteristics between areas)**.** These discontinuities are caused by a relatively small set of dominant processes that act on the ecosystem. Identifying discontinuities can therefore shed more light on these processes. Fourthly, the **good versus bad colonisers** approach measures the ratio between key positive organisms/processes versus key negative organisms/processes. The ratio between calcifying and non-calcifying benthic organisms will, for example, predict which species are more likely to colonize freed space on the reef. Fifthly, **local regime shifts** act as indicator of impending catastrophic regional regime shifts. Lastly, **potential space availability versus grazing capacity** measures the ratio between available space for benthic recruitment and grazing capacity. This approach focuses on determining if herbivore grazers will be able to crop macroalgae and turf algae if more space becomes available for the algae. Obura and Grimsditch (2009) identified 61 basic resilience indicators for coral reef systems that can be quantified using rapid assessment methods. Each indicator is assigned a level on a semi-quantitative scale ranging from one to five. This therefore represents a simple method to provide a first assessment of coral reef conservation outcomes employable in a variety of developing country settings. However, McClanahan (2012) identified two problems with such a large number of indicators: (1) it lowers the importance of each individual indicator in the end result, and (2) surveys become more expensive and resource intensive, which decreases the likelihood that they will be used in practice. He proposed a set of 11 weighted resilience indicators instead (see Appendix 2 for list of indicators). These were chosen based on perceived importance, scientific evidence and feasibility.

1.3 SYSTEM MODELS OF RESILIENCE

A main focus of many resilience models and theories is the regime shift between the coral and the macroalgal dominated state of coral reefs in the Caribbean (Mumby et al. 2006b, 2007; Elmhirst et al. 2009; Baskett et al. 2010; Anthony et al. 2011; Mumby et al. 2014). The

term regime shift describes a marked change in the structure of a community (Figure 1.1b, c, d, Done 1992) and differs from a gradual change in benthic cover on a coral reef (Figure 1.1a). If a second stable state is present (Figure 1.1c, d), then a reversal of the regime shift is less likely, especially if the system shows hysteresis (Figure 1.1d). Hysteresis refers to a system that does not return to its former state even if the stressor drops below the level that induced the regime shift (Mumby et al. 2013). Scientists have used empirical data and theoretical modelling to determine whether the coral and macroalgal dominated states of coral reefs in the Caribbean represent two separate stable states of the ecosystem (Mumby et al. 2013) and if and how a system can return from an algal-dominated state to a coral-dominated state (Mumby et al. 2007). Currently, most evidence supports the theory that coral reefs naturally have only one stable state (Figure 1.1a) but that the loss of *Acropora* spp. and herbivorous urchins has led to coral reefs in the Caribbean displaying two stable states with hysteresis (Figure 1.1d) (Mumby et al. 2013). This knowledge helps coral reef managers in the Caribbean to gain a better understanding of the risks of a regime shift and how to manage it.

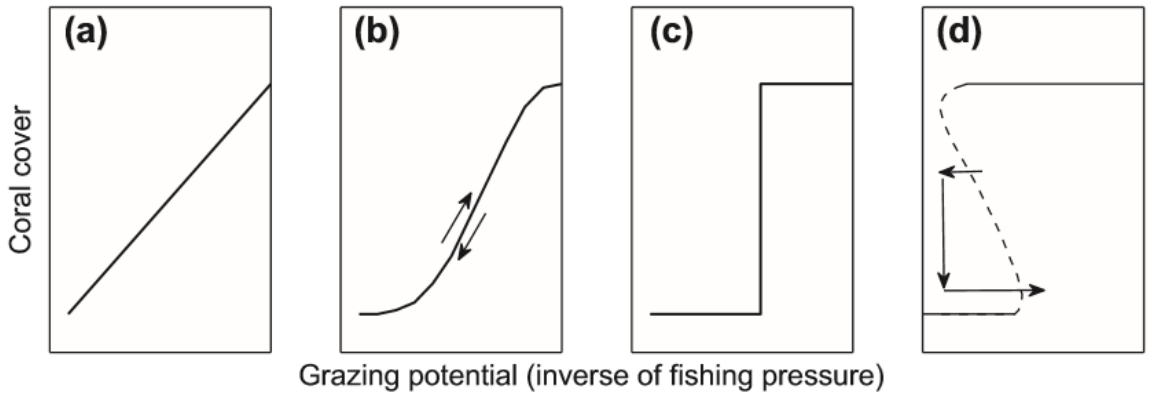

Figure 1.1. Possible relationships between ecosystem state (coral cover) and an external driver (grazing potential). (a) Linear, (b) threshold monotonic increase , (c) severe threshold with alternate states, and (d) alternate states with hysteresis. Arrows indicate that reversals of the ecosystem state are simple in (b) but complex in (d) where a small decline in grazing can shift the system into coral cover decline but a much larger increase in grazing is needed to restore coral cover to its previous value. Dashed line denotes unstable equilibrium. Figure from Mumby et al. (2013).

Pacific reefs are also affected by increasing human stressors. For example, this year's worldwide record sea surface temperatures led to large scale bleaching events at locations such as the NorthernGreat Barrier Reef and Kiribati. Aerial coral bleaching surveys of the Northern Great Barrier Reef conducted by Terry Hughes revealed that 93% of the reefs surveyed showed signs of bleaching (ARC Centre of Excellence for Coral Reef Studies 2016), while 95% of the corals in Kiribati were found dead or bleached in March 2016 by Julia Baum and her research team (Washington Post 2016). However, resilience studies on Pacific coral reefs are rare (Roff and Mumby 2012). This then leads to the question of whether knowledge about resilience of Caribbean coral reef ecosystems can be applied to the Pacific – that is, given the suite of different species/genera and the different status of reefs in the two regions, is it reasonable to extrapolate from one to the other? Roff and Mumby (2012) concluded that many of the general principles of resilience, such as the need to control macroalgal blooms, are likely universal and therefore apply to both the Caribbean and the Pacific. However, the biodiversity of Pacific reefs is higher than that of Caribbean reefs, and this phenomenon includes herbivorous species, which are key indicators of reef community resilience (McClanahan et al. 2012). The Caribbean lacks many species and a whole taxonomic group of herbivores (genus *Naso*) that are present in the Pacific (Bellwood et al. 2004; Roff and Mumby 2012). Furthermore, Pacific and Caribbean reefs differ in benthic cover (Done 1992; Gardner et al. 2003; Bellwood et al. 2004; Mumby et al. 2007) and concentration of bioavailable iron (Fe^{2+}) (Duce and Tindale 1991). These differences likely lead to reefs of the two regions responding differently to disturbances and decrease in herbivore abundance. Coral-macroalgal regime shifts and the existence of two stable states, for example, are reached more easily on Caribbean than on Indo-Pacific reef systems (Cheal et al. 2010; Roff and Mumby 2012).

1.3.1 Studying resilience on pristine reefs

The Pacific contains a wide range of coral reefs, from pristine to severely degraded reefs (Smith et al. 2016). For coral reefs, the term pristine refers to reefs that are subject to minimal human impact due to their remote location and the (relative) lack of human inhabitants in proximity to the reef. The term pristine therefore refers to intact, natural ecosystems which likely also have high levels of resilience. Williams et al. (2015) found that natural biophysical drivers can explain differences in hard coral, CCA and macroalgae cover between uninhabited islands in the Pacific while these natural biophysical relationships were not present on

populated islands in the Pacific. The drivers acting on uninhabited pristine coral reefs are therefore different from those on more degraded inhabited reefs. Research on how biophysical forcing factors affect resilience of pristine coral reefs will (1) help the conservation of these important last remaining pristine coral reefs, (2) provide a baseline against which future change may be judged, and (3) improve our understanding of how other reefs used to function before they became degraded.

1.4 REEFS TOMORROW INITIATIVE

Palmyra Atoll, is a sparsely inhabited atoll that has been studied extensively. Until recently, scientists conducting research on Palmyra Atoll collaborated loosely. To shed light on mechanisms of reef resilience however, a system approach is needed. For this reason, several institutions working on Palmyra Atoll started the Reefs Tomorrow Initiative (RTI). Members of RTI include The American Museum of Natural History, The Coral Reef Alliance, The Nature Conservancy, Scripps Institution of Oceanography, Stanford University, University of California Santa Barbara, University of North Carolina Wilmington, and Victoria University of Wellington (http://reefstomorrowinitiative.org/). The mission of this collaboration is to advance coral reef science, management and conservation through interdisciplinary study of reef resilience, and to work with managers to apply this new understanding to reef conservation. This involves a tight coupling of empirical research, theoretical modelling and applied research. My PhD research is part of the first phase of the RTI (Figure 1.2). In this first phase we examined how biological and physical forcing factors that naturally differ within Palmyra Atoll affect the ecology of the atoll. These new empirical insights were combined with existing knowledge to develop a new suite of mathematical models of reef resilience. Lastly, active engagement with resource managers across the Pacific ensures that the work of RTI addresses the most pressing management needs. This last step addressed the issue that on Pacific Atolls, scientific information often does not reach or is not used at the local level where communities make local decisions (Barnett 2001; Nunn 2009b; Barnett and Campbell 2010). Community-based engagement in the entire process from problem assessment to implementation is therefore key to assure that the scientific findings from the healthy reefs surrounding Palmyra can be translated into useful information for reef conservation on other inhabited Pacific atolls (Hernández-Delgado 2015).

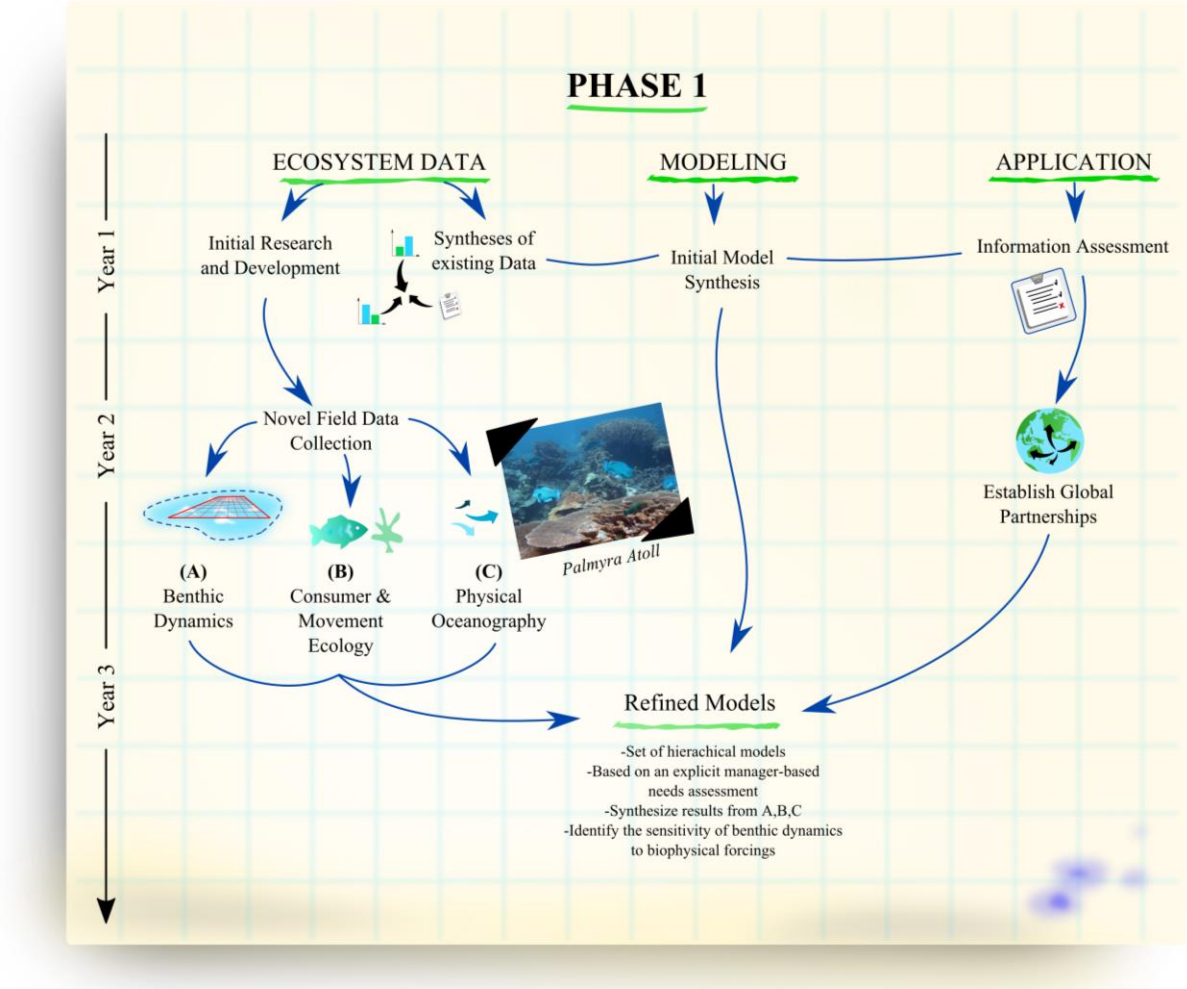

Figure 1.2. Phase one of the Reefs Tomorrow Initiative (RTI). The conducted research is split into field research (ecosystem data), modeling (modeling), and collaboration with managers and local communities (application). *Blue arrows* indicate the chronological order the research was conducted. *Blue lines* show that information interchange happened between the different parts of the RTI research. The time line of phase one is on the left. Diagram drawn by David Young.

The empirical research of RTI focused on the reef benthos and the processes that shaped it. The different reef states between the Caribbean and Indo-Pacific regions are due to differences in their overall benthic states (Done 1992; Gardner et al. 2003; Bellwood et al. 2004; Mumby et al. 2007). Recent advances in benthic monitoring such as structure-from-motion 3 D benthic modelling facilitate the collection of high resolution empirical benthic data (Javernick et al. 2014; Burns et al. 2015), which until now was often simplified in reef resilience models (e.g. Anthony et al. 2011; Rogers et al. 2015). At the heart of the empirical

research of RTI are high-resolution photographs of the reef floor stitched together to photomosaics which cover 200 m^2 of continuous reef floor. These photomosaics were used to quantify coral cover and species composition. Resurveying of the same plots in consecutive years made it possible to track the fate of individual organisms, their battle for space on the reef floor and changes in their patterns of abundance. Spatial and behavioural patterns of six herbivorous species of parrotfish, surgeonfish and tangs (*Acanthurus nigricans*, *A. lineatus*, *Chlorurus sordidus*, *C. microrhinos*, *Ctenochaetus striatus*, and *C. marginatus)* were measured to provide insight into how herbivores affect interactions between corals and macroalgae on reefs. This included a study on how parrotfish bite marks on the reef structure affect coral recruitment rates. My role in this multi-team and multidisciplinary program was to record coral recruitment, calcification and bioerosion rates within ten photomosaic plots to describe two important processes that often serve as indicators for coral reef resilience: coral recruitment and $CaCO_3$ accretion/erosion. Lastly, a detailed water circulation model using the COAWST modelling suite was developed to gain a better understanding of how physical factors, like temperature and waves, cause changes in the benthic communities and, therefore, how they may impact on reef resilience. For example, McClanahan et al. (2012) identified weather-driven water mixing as a potential physical factor influencing coral reef resilience that requires further research attention. Parallel to the empirical research at Palmyra Atoll, partnerships with coral reef managers were established to determine what information they need in order to manage their resources. All of these findings were then synthesised in a suite of ecological models that describe the details of benthic dynamics. The goal of these models was to determine which biophysical forcing factors have the strongest effect on the benthos and thus which affect the resilience of coral reefs across natural and human-made gradients of forcings. This strategy is based on the currently forming consensus that, despite their complexity, ecosystems and their resilience are frequently controlled by just a few strong variables (Holling 1996; Scheffer et al. 2009; McClanahan et al. 2012).

1.5 PALMYRA ATOLL

Palmyra Atoll is a U.S. National Wildlife Refuge (NWR) and part of the Pacific Remote Islands Marine National Monument, situated approximately 1700 km southwest of Hawaii in the Northern Line Islands, central Pacific Ocean. Palmyra Atoll serves as an

important baseline for remote Central Pacific reef systems as it is located approx. 5 degrees north of the equator (Sandin et al. 2008). It is among the most remote coral reefs on Earth and has never had an indigenous human population. Its major human impact was the substantial modification of the atoll during WWII. The U.S. military reclaimed land, built several airstrips and dredged an eight meter deep channel for ship access into the lagoon (Dawson 1959), modifying Palmyra Atoll's lagoon in a similar way to lagoons on many inhibited Pacific Atolls (Gardner et al. 2010). However, in 1945 humans stopped modifying the atoll's shoreline and lagoon and natural processes started acting on them again (Collen et al. 2009). Current local impacts on the reefs of Palmyra Atoll are limited to occasional fine lagoon sediment deposition on the reef and iron-leakage from shipwrecks (Work et al. 2008; Collen et al. 2009; Williams et al. 2013), which were removed in January 2014. Nevertheless, the reef systems are still influenced by global effects resulting from climate change like coral bleaching and acidification and suffer from naturally occurring coral and CCA diseases (Brainard et al. 2005; Williams and Miller 2005; Vargas-Angel 2009; Vargas-Ángel 2010; Price et al. 2012). In a regional and global context, the reefs of Palmyra Atoll are considered exceptionally healthy (Knowlton and Jackson 2008), with a large biomass of fishes, an intact food web, high live coral cover, high coral settlement and recruitment rates and diverse algal assemblages (Sandin et al. 2008; Roth and Knowlton 2009; Tsuda et al. 2012). Furthermore, biodiversity of corals is higher on the reefs of Palmyra Atoll and its neighbour Kingman Reef than on the other Line and Phoenix Islands (Williams et al. 2008a). This is likely the result of them being positioned in the eastward moving North Pacific Equatorial Counter Current (NECC) (Williams et al. 2008a).

1.5.1 Natural variation in coral reef benthos and associated processes on Palmyra Atoll

Both back reef and fore reef habitats can be found on Palmyra Atoll. These two habitats differ significantly in hard coral cover, coral recruitment, the prevalence of coral disease, the composition of early benthic successional communities, the biomass of herbivorous fish and their grazing frequency (Williams et al. 2008, 2011a, 2013; Roth and Knowlton 2009; Price et al. 2012; Hamilton et al. 2014). While part of the these differences are caused by differences in depth between the fore reef and the back reef, it is also likely that differences in physical and/or biological forcing factors affect the benthic communities found at Palmyra Atoll.

The strength of physical forcing factors differs within regions at Palmyra Atoll. Regular flushing of the lagoon onto the reef terrace occurs through a dredged channel (the Entrance Channel). This is of ecological concern because it is a likely cause of an increased load of fine sediment at the Western Reef Terrace, especially close to the channel (Maragos et al. 2008; Collen et al. 2009; Williams et al. 2011b). This increase in fine sediment likely has implications for coral community structure and macroalgal abundance (Williams et al. 2011b; Gove et al. 2015). Northern fore reef sites experience high wave energy (1-3 m wave heights) during the Northern hemisphere winter whereas the mean wave energy hitting the Southern sites is only moderate (1-2 m) and mainly occurs during the Southern hemisphere winter (Williams et al. 2013; Rogers 2015; Gove et al. 2015).

A recent study found that the benthic community composition on Palmyra Atoll was significantly correlated with wave energy (Gove et al. 2015). Turf algal abundance increased as bed shear stress increased, following the pattern found on topographically more uniform Kingman Reef, where turf algal abundance increased with wave energy (Williams et al. 2013). Gove et al. (2015) found that the system undergoes a naturally induced regime shift between CCA and turf algae at a mean bed shear stress threshold of 18 Nm^{-2}. The relative dominance of different coral morphologies (i.e. encrusting, plating and branching) was also dependent on thresholds in wave forcing, adding to the evidence that regime shifts from calcifying (i.e. hard corals and CCA) to non-calcifying regimes (i.e. turf algae) occur on Palmyra Atoll in the absence of local human impacts (Gove et al. 2015). These studies could not identify the mechanism that lead to the differences in physical oceanography they observed. The authors believe that further research on current variability, such as a more detailed nearshore hydrodynamic model, would potentially be able to capture these physical forcing factors (Williams et al. 2013; Gove et al. 2015). The water circulation model developed by RTI is a very detailed model of nearshore currents at Palmyra Atoll. It can therefore be used with the other empirical data collected by RTI to determine if natural differences found in biophysical forcing factors within Palmyra affect benthic composition and benthic processes such as coral recruitment and net $CaCO_3$ accretion on Palmyra Atoll.

1.6 CORAL RECRUITMENT

McClanahan et al. (2012) concluded that hard coral recruitment rates and macroalgal abundance are the strongest indicators of a coral reef's recovery potential. Coral recruitment is a critical process that helps maintain coral populations and facilitates recovery after a disturbance (Vermeij and Sandin 2008; Graham et al. 2011; Gilmour et al. 2013). Hard corals have a bipartite life cycle consisting of a pelagic dispersive larva and a sessile benthic adult stage. During this life cycle they pass through three demographic bottlenecks that influence coral recruitment: (1) larval supply, (2) settlement, and (3) post-settlement survival (Arnold et al. 2010; Chong-Seng et al. 2014). In this thesis, coral recruitment makes combined reference to larval supply, settlement and post-settlement processes (Harrison and Wallace 1990). The number of fecund adult corals and their reproductive output define larval production. Coral larvae travel on the water surface and have to survive a "wall of mouths" consisting of planktivorous fishes during the day and hard corals, zoanthids and anemones at night (Hamner et al. 1988; Fabricius and Metzner 2004). Coral larvae generally settle within several hours to weeks (reviewed by Ritson-Williams et al. 2009). Certain larvae are competent to settle minutes after being released (Best and Resing 1987; Carlon and Olson 1993), whereas others survive for over 244 days before settlement. While some larvae will settle close to their parent colony (Swearer et al. 2002), others will be dispersed by currents and waves before they are ready to settle (Raimondi and Morse 2000). The number of available larvae for settlement (larval supply, Harrison and Wallace 1990) therefore depends both on local larval availability and the number of larvae that arrive from more distant sources and is a combined result of reproduction, fecundity and larval dispersal. Different cues can induce coral larvae to descend in the water column and start probing the benthos for a suitable nursery habitat (Raimondi and Morse 2000). Settlement refers to the metamorphosis process during which the coral larvae undergo morphological changes and attach to the substratum. Settlement is completed once the coral settler has formed a calcium carbonate calyx; I hereafter referred to the coral as a coral recruit (Kuffner et al. 2006). Finding the right nursery habitat is crucial for post-settlement survival. The larvae of many coral species have therefore developed specific habitat preferences for settlement (Arnold et al. 2010). Post-settlement survival generally refers to the survival rate of corals not visible in the field with the naked eye (<0.5 cm in diameter or approximately 6 months after settlement), whereas recruit survival generally refers to visible

corals (> 0.5 cm in diameter and more than 6 months after settlement) (Birrell et al. 2008). In this thesis, post-settlement survival refers to survival of coral recruits up to 15 months after settlement. Post-settlement survival to the size of a juvenile coral (>1 cm, Penin et al. 2010) is low for hard corals and depends on direct and indirect competition with the benthic community surrounding the coral settler (Birrell et al. 2008). The term adult refers to reproductive corals. Corals of many families are non-reproductive if their diameter is ≥ 5 cm (Harrison and Wallace 1990). In this thesis, I therefore refer to corals with diameters of ≥ 5 cm as adult corals.

1.6.1 Difference in coral recruitment between resilient and degraded reefs

Pristine/resilient reefs have a greater variability in benthic composition, higher topographic complexity and a more complex food web than degraded reefs. This has important implications for coral recruitment. A complex food web with an elevated abundance of fishes and corals increases the likelihood of being consumed during the larval phase. Coral larvae encounter a greater diversity of settlement substrata and surfaces on resilient reefs and their settlement choice likely influences post-settlement survival (Harrington et al. 2004; Golbuu and Richmond 2007; Ritson-Williams et al. 2010). This likely lead to some coral species adapting by showing a strict settlement preferences for either certain benthic substrata or crevices (Nozawa 2008; Arnold et al. 2010). Post-settlement survival is influenced by both competition with other benthic organisms and predation by herbivores. Resilient reefs generally have less turf and macroalgal cover than degraded reefs (Smith et al. 2016), with the result that competition between corals and other benthic organisms may be reduced. However, the greater abundance of larger herbivores (e.g. urchins, fishes) on resilient reefs is likely to increase coral post-settlement mortality due to indirect predation (grazing). Larval and recruit mortality are therefore likely similar resilient and non-resilient reefs, which means that the ability of resilient reefs to recover from substantial damage (up to 100% coral mortality) within 10-15 years (Birkeland 2015a) is attributed to other factors that differ between resilient and non-resilient reefs (Pearson 1981; Hughes and Connell 1999). The difference in recruitment success between resilient and degraded reefs is likely due to degraded reefs experiencing chronic stress. Fecundity of adult corals decreases when they are stressed, allowing adults to retain extra energy for survival (Kojis and Quinn 1984; Veghel and Bak 1994). This reduction of fecundity can last for several months up to several years after the stress event (Szmant and Gassman 1990; Cox and Ward 2002; Levitan et al. 2014). Under chronic stress, this reduction

in resource allocation towards reproduction in favour of survival becomes a permanent state (Birkeland 2015b). On several Caribbean reefs, for example, a decrease in abundance of reproductive adult coral colonies and lower coral fecundity rates have led to a decline of coral recruitment and with it the ability of the coral reef ecosystem to recover after a disturbance (Hughes and Tanner 2000; Bak et al. 2005).

1.7 CALCIUM CARBONATE ($CaCO_3$) ACCRETION

Despite having an average higher topographic complexity than Pacific reefs (Graham and Nash 2013), many Caribbean reefs are currently becoming flatter (Alvarez-Filip et al. 2009) and 21% now have a negative net $CaCO_3$ budget (Kennedy et al. 2013). The physical three-dimensional structure of the reef ecosystem and its topographic complexity are possible indicators of resilience on coral reefs (Mumby et al. 2014). A topographically complex reef supports a rich fauna of fishes and invertebrates (Graham and Nash 2013 and references within) by providing newly settled juvenile fish with hiding places and appropriate food (Caley et al. 1996). The available habitat for reef-associated species thus depends largely on the structure of the reef framework rather than on live coral cover (Newman et al. 2006; Alvarez-Filip et al. 2009; Friedlander et al. 2014). Topographic complexity is also vital for ecosystem services such as tourism and shore line protection. However, topographic complexity is still understudied and further research is needed to determine how topographic complexity affects coral reef resilience and if it is suited to be used as a strong indicator of resilience (McClanahan et al. 2012).

$CaCO_3$ budgets quantify the mass of $CaCO_3$ deposited on a reef and take both $CaCO_3$ production and erosion into account. $CaCO_3$ accretion and destruction is mainly influenced by three key functional groups: (1) the main primary $CaCO_3$ producers, corals, (2) the main secondary $CaCO_3$ producers, calcareous encrusters, and (3) the destructive group of bioeroders (Perry et al. 2008). $CaCO_3$ is deposited by organisms as small as a single coral polyp, however the structures that emerge out of this process can be as tall as 1300 m and as long as 2000 km (Birkeland 2015a). $CaCO_3$ accretion can therefore be studied at different temporal (seconds to 10’000 years) and spatial scales (coral polyp to reef system) (Perry et al. 2008). Biologists often study $CaCO_3$ production on an ecological time scale (hours to 100 years) and at an intra-

reef spatial scale. Their questions revolve around shifts in $CaCO_3$ production, topographic complexity changes, and coral-macroalgal regime shifts (Perry et al. 2008).

1.7.1 Calcification

Coral reefs and landforms created by sediments derived from coral reefs are unique because they are predominately composed of $CaCO_3$ derived almost entirely from ecological processes. Calcification refers to the production of $CaCO_3$. Main calcifiers on reefs include hard corals, molluscs, CCA, bryozoans, tube worms and foraminifera. Calcification is important for the growth of the individual calcifying organism as well as for overall reef accretion. For example, larger corals have been shown to have lower mortality rates, especially in the very early post-settlement period (Rylaarsdam 1983; Hughes and Jackson 1985; Babcock and Mundy 1996; Hughes and Tanner 2000; Wilson and Harrison 2005). Furthermore, once coral colonies reach a certain age, fecundity increases with coral size (Hughes 1984; Babcock 1991). Therefore, growth rates have an indirect influence on recruitment through the number of larvae released by adult corals.

Primary framework builders

Hard corals are the most important primary framework builders on modern coral reefs (Scoffin 1992). They create a hard substratum with high topographic complexity, including many small and large cavities.

Secondary framework builders

Secondary framework building refers to $CaCO_3$ accretion on top of this primary framework. This includes encrusting of the primary framework and accumulation of sediment in cavities (Scoffin 1992). Whilst all calcifiers found on the reef, including corals, can act as secondary framework builders, CCA has been identified as the main secondary framework builder (Perry et al. 2008). CCA reinforces the skeletal structures of dead corals and fills cracks in the reef substratum (Barnes et al. 1990; Bjork et al. 1995). Secondary framework builders can contribute significant amounts of $CaCO_3$ to the reef structure to an extent where they actually dominate calcium carbonate accumulation (e.g. on algal ridges) (Steneck and Adey 1976; Bosence 1984). Even on other parts of the reef, non-coral calcifiers are often more abundant than live corals (Vroom et al. 2006; Vroom 2010). CCA has calcification rates similar

to corals (0.5 - 20 kg of $CaCO_3$ m^{-2} y^{-1} for CCA versus 1.4 and 18 kg of $CaCO_3$ m^{-2} y^{-1} for corals) (reviewed by Harney and Fletcher 2003) and has therefore the potential to contribute significantly to $CaCO_3$ accretion.

1.7.2 Bioerosion

The $CaCO_3$ produced on a reef is constantly being reworked by macroborers, microborers and grazers, a process named bioerosion by Neumann (1966). Microborers consist of algae, bacteria and fungi, while polychaete worms, sipunculids, vermetids, gastropods, sponges and bivalves are classified as macroborers (Chazottes et al. 1995; Edinger 2001). Grazers include echinoids, gastropods and a wide variety of fish (Hutchings 1986; Edinger 2001). Bioerosion can be both chemical and mechanical. Grazers, including some polychaetes and molluscs mechanically bioerode the substratum while chemical boring is common in bacteria, fungi, algae, coelenterates and some polychaetes (Ruetzler and Rieger 1973; Pomponi 1977; Bromley 1978; Pomponi 1979; Hutchings 1986). Other species like sponges, molluscs and some polychaetes combine chemical and mechanical boring (Bromley 1978; Risk and MacGeachy 1978; Hutchings 1986). Bioerosion is important for the coral reef ecosystem because it produces sediments, helps propagate fragments of branching corals (Tunnicliffe 1981), facilitates the formation of characteristic reef structures and increases biodiversity by creating habitats for sessile and mobile cryptic organisms as well as caverns for larger animals (Warme 1975; Hutchings 1986; Hubbard et al. 1990). But it also reduces reef accretion (Hutchings 1986) and weakens the reef framework, which makes the reef more vulnerable to storm damage and slumping (Ginsburg 1954; Goreau and Hartman 1963; Hein and Risk 1975; Warme 1975; Jaap et al. 1984; Hutchings 1986).

1.7.3 Net $CaCO_3$ budgets

Net $CaCO_3$ bugets of coral reefs are calculated by summing up the gross carbonate productions from corals and calcareous encrusters and the $CaCO_3$ sediment that is deposited on the reef (produced within or imported). From that sum the loss through biological or physical erosion, dissolution or sediment export are subtracted (Chave et al. 1972). The balance between $CaCO_3$ production and erosion strongly influence both coral reef accretion and sediment availability for adjacent land constructions (e.g. growth or formation of *motu*). On healthy coral reefs, for example, herbivore grazing removes $CaCO_3$ and produces sediment.

These reefs will therefore have low net reef accretion (because herbivores are so abundant) despite having a high rate of $CaCO_3$ production (Kleypas et al. 2001). $CaCO_3$ production and erosion therefore need to be studied in combination with each other in so called net $CaCO_3$ budgets. Net $CaCO_3$ budgets give insights into net reef accretion and net sediment production, but also show the relative contribution of each of the underlying processes.

In order to determine the net $CaCO_3$ budget of coral reefs, detailed measurements of calcification rates and cover data for calcifiers are needed. This need for detail is one reason why net $CaCO_3$ budgets exist for only a few reefs (see Kench et al. 2009 and Figure 1.3 for examples). This lack of knowledge is particularly concerning for coral reef atolls, which need both reef accretion and sediment production to prevail (Hart and Kench 2007; Kench et al. 2009). Perry et al. (2008) showed that, at the most fundamental level, $CaCO_3$ budget is mainly influenced by the $CaCO_3$ producers (corals and calcareous encrusters) and the bioeroders. These three key biogenic component groups are also most directly impacted by environmental and ecological change. They proposed a ternary plot approach (Figure 1.3) toward net $CaCO_3$ budgets, which is well suited to identify the relative importance of these three key functional groups and shows whether or not a reef is accreting or eroding. This approach can also be used to track temporal variation in net $CaCO_3$ budgets (Perry et al. 2008, Figure 1.3b, c). It therefore has the potential to be a predictive tool for management purposes. The ternary approach to assess and predict the geomorphic condition of the reef is an important addition to ecologically focussed reef assessment and prediction tools. The geomorphic condition and ecological condition of a coral reef often differ from each other (Kleypas et al. 2001; Perry et al. 2008), but at the same time influence each other. A shift in the reef ecological status can impact its $CaCO_3$ production and reef framework development (Eakin 1996; Tomascik 1997; Edinger et al. 2000; Riegl 2001). Reef ecology and island sedimentology are tightly linked (Perry et al. 2015). $CaCO_3$ accretion on the other hand influences the topographic complexity of the reef, which is needed to support a rich fauna of fishes and invertebrates (Graham and Nash 2013).

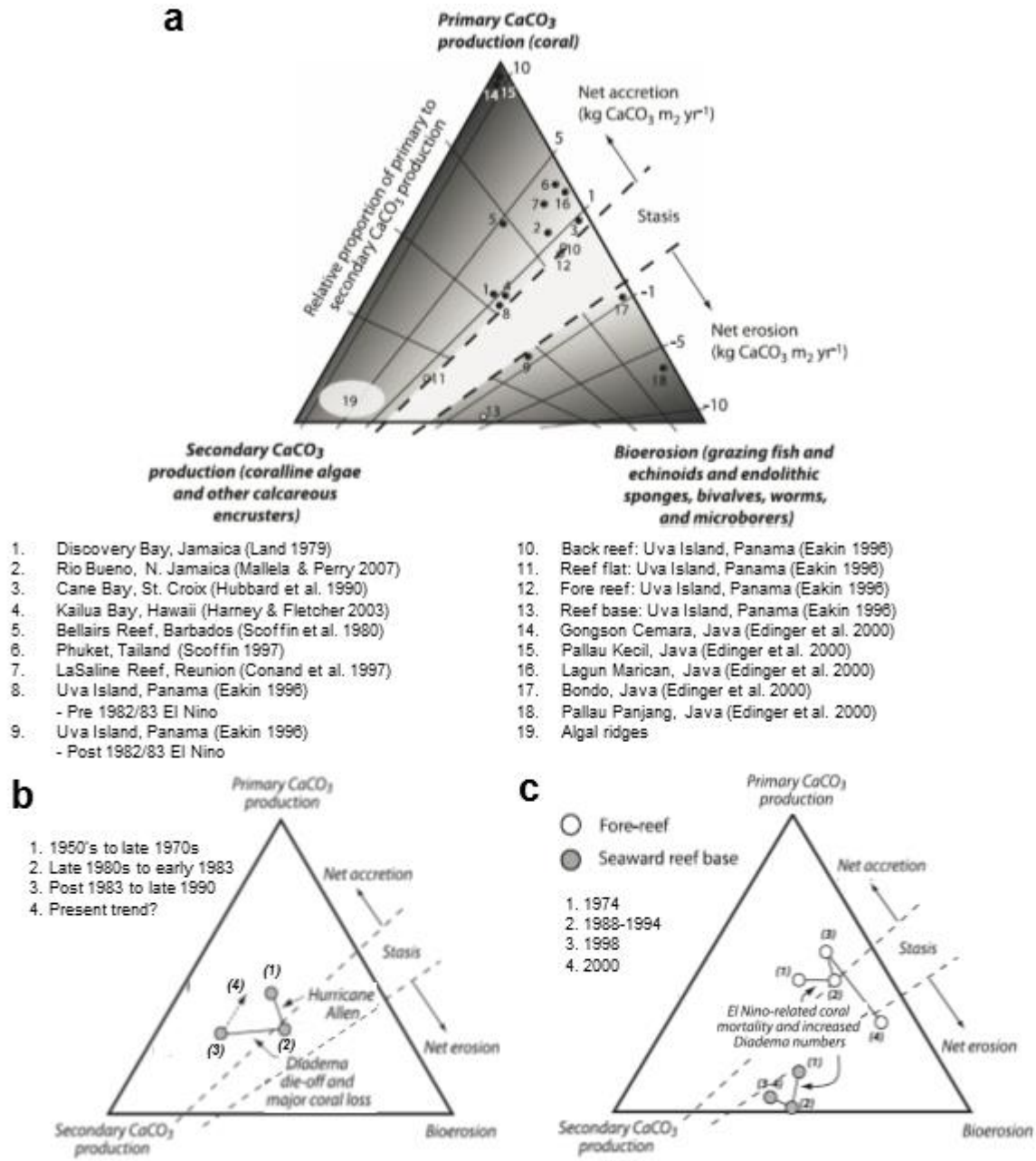

Figure 1.3. Different biogenic $CaCO_3$ production states derived from primary and secondary $CaCO_3$ production, and bioerosion. $CaCO_3$ production can be read from the scale running from the bottom of the triangle to the left side. The scale running from the bottom of the triangle to the right side show the relative importance of primary and secondary $CaCO_3$ producers. (a) Budget state points occupied by different reefs at the reef-wide scale (*closed circles*) and the reef sub-environment scale (*open circles*). (b) + (c) Temporal trends in the net $CaCO_3$ production regime at (b) Discovery Bay, Jamaica and (c) Uva Island, Panama. Net $CaCO_3$ budget (*circles*) are numbered in chronological order. They are linked by *lines* that show how the net $CaCO_3$ budget changed due to the disturbance listed next to the lines. Figure from Perry et al., 2008.

1.8 IMPACT OF HERBIVORES ON RECRUITMENT AND NET $CaCO_3$ ACCRETION

Key species are species that influence ecosystem diversity and functionality so immensely that the removal of these species leads to pronounced ecological and geomorphological change of their environment (Wootton 1997; Wright et al. 2002; Terborgh and Estes 2013; Eddy et al. 2014). Protection of these species is often thought to result in the protection of the ecosystem itself (Bellwood et al. 2003; Soulé 2005). Herbivores are key reef-associated species that have a large impact on the benthic community composition of coral reefs (Steneck 1997; Mumby et al. 2006a). Herbivorous species on coral reefs are often classified into functional groups based on either foraging range, e.g. 1-100 cm^2, 0.5-1 m^2 or up to 0.5 ha (Carpenter 1986), or feeding methods, e.g. scrapers/excavators, grazers/detritivores, and algal browsers (Cheal et al. 2010). While foraging ranges give insight into how frequently a patch of benthos is grazed (frequent for organisms with small ranges), feeding methods describe the outcome for the benthos, from being completely cleared and excavated to being cropped. Echinoids (urchins) can be major herbivores on coral reefs (Hay 1984; Alcoverro and Mariani 2004; Mumby et al. 2006b), but on Palmyra, herbivorous echinoid density is extremely low, which makes herbivorous fishes the primary large-bodied grazers in this system and the focus of this section (Sandin et al. 2008).

Herbivores affect coral recruitment in several ways. They control macroalgal abundance (Burkepile and Hay 2006; Sotka and Hay 2009; Burkepile and Hay 2010), influence competitive interactions between macroalgae and corals (Jompa and McCook 2002; Hughes et al. 2007) and provide resilience following disturbances (Hughes et al. 2007). Herbivore removal, for example through fishing, can lead to cascading effects, including the lowering of coral recruitment rates through an increase of macroalgal cover and a decrease of CCA cover (Hughes et al. 2007; O'Leary et al. 2012). Bumphead parrotfish (*Bolbomethopon muricatum*) not only consume algae and coral rock, like other parrotfish but also prey on live corals, which obviously negatively affects adult corals, especially pocilloporids and acroporids. However, Bumphead parrotfish also increases asexual reproduction in these coral species by creating approximately 14 fragments per hour of feeding (McCauley et al. 2014). These large parrotfish also produce crevices that are free of algae and which may be beneficial for coral settlement (McCauley et al. 2010). However, bumphead parrotfish and other herbivores also affect post-settlement survival of coral recruits via predation on them (Arnold et al. 2010).

Herbivores impact the $CaCO_3$ budget both positively and negatively. They have been associated with both decreased and increased coral growth rates (Rotjan and Lewis 2008; Sotka and Hay 2009; Burkepile and Hay 2010). The decreased growth rates may be due to tissue damage and loss through grazing scars (Rotjan and Lewis 2008), while the increased growth rates could be caused by the presence of grazers leading to less tissue damage from competing algae (Jompa and McCook 2002). Herbivores are major bioeroders (Chazottes et al. 1995; Tribollet et al. 2002) and therefore their abundance and community composition has a direct effect on bioerosion. Furthermore, they influence other bioeroders (such as algae and sponges) by grazing on them. For example, parrotfish grazing reduces the population of the bioeroding sponge *Cliothosa* spp. (Sammarco et al. 1987).

The scale of the effect of herbivores on the benthic composition and topographic complexity of a reef depends both on the availability of algae and the species and size class composition of herbivores (Cheal et al. 2010). When algae are rare on coral reefs, herbivores keep them in the early stages of succession with rapid turnover (Klumpp et al. 1987). An abundant array of algae leads to herbivores becoming more selective, avoiding macroalgae with anti-herbivore defences, which facilitates the takeover by macroalgae (Birkeland et al. 1985). A diverse guild of herbivores graze more effectively on macroalgae than a single species assemblage (Duffy 2003; Burkepile and Hay 2006). More diverse herbivore assemblages also increase coral reef resilience through functional redundancy. Palmyra Atoll has a high level of functional redundancy as many herbivorous species overlap in their resource use or even graze on the same algal types (especially turf algae) and have similar bite rates and impact on the benthos (Hamilton et al. 2014). However, Palmyra Atoll is also home to the bumphead parrotfish which occupy a functionally unique role in coral reef communities as outlined above (Bellwood et al. 2003; McCauley et al. 2010), this makes it vitally important to ecosystem stability and resilience. Lastly, the size class composition of herbivores is also likely to affect resilience. In many fish species fecundity increases exponentially with size (Birkeland 2015b), which makes large individual fish extremely valuable for sustaining fish populations.

1.9 AIMS AND OBJECTIVE OF THIS THESIS

A better understanding of coral recruitment, calcification, bioerosion and the impact of herbivores on these processes is needed to determine the mechanisms behind coral cover

decline. While these processes have been studied widely on reefs that are moderately to severely degraded (Knowlton and Jackson 2008) only a few studies have looked at them on pristine reefs (e.g. Pari et al. 1998; Roth and Knowlton 2009; McCauley et al. 2010; Price 2010). For the early recognition and detection of declining reef health on pristine reefs, these processes need further investigation. This will also benefit moderately to severely degraded reefs by providing a baseline for recruitment, calcification and bioerosion, giving conservation efforts new guidelines and goals. Lastly, it will increase the understanding of reef resilience by investigating key resilience-forming processes on a highly complex and resilient coral reef.

The overall objective of this thesis is to increase the understanding of how natural biophysical forcing factors influence benthic recruitment and $CaCO_3$ accretion at Palmyra Atoll and to provide baselines for recruitment, calcification and bioerosion at central Pacific reefs. Specific aims include:

- To determine if different areas of the reef (fore reef, Western Reef Terrace and Entrance Channel) differ in their rates of recruitment (of corals, CCA, algae and bryozoans), calcification, bioerosion and reef accretion and if any biophysical forcing factors, especially physical oceanography and herbivore grazing, are responsible for these differences.
- To determine if pocilloporid and poritid recruits are produced locally or arrive from a distant source by investigating correlations between coral recruit presence/absence and density with local adult coral cover and the volume of water arriving at each study site on Palmyra.
- To measure the succession of benthic recruitment on Palmyra Atoll over time and investigate the interactions between coral recruits and other benthic organisms, including the identification of inhibitor and facilitator substrata for coral settlement.
- To determine the influence of parrotfish grazing on coral settlement by measuring settlement patterns of *Pocillopora damicornis* larvae and their post-settlement survival.
- To determine the net $CaCO_3$ budget of early successional benthic communities on Palmyra Atoll by quantifying bioerosion and secondary calcification rates.

CHAPTER 2

Influence of localised currents, benthic cover and composition on pocilloporid and poritid recruitment rates

2.1 ABSTRACT

Successful recruitment is vital for the maintenance and recovery of coral populations. Recruitment refers to the processes of larval dispersal, settlement and post-settlement survival. Little is known about the processes that shape hard coral recruitment because coral larval dispersal and settlement rates are rarely measured in the field. In this study, appropriate measurable proxies for distant coral larval supply, local larval supply and suitability of the reef substratum were identified with the aim of modelling pocilloporid and poritid recruitment. This study combined recruit counts with a water flux model and measures of coral and non-coral benthic cover to determine if coral recruitment is driven by distant larval supply (water flux), local larval supply (coral cover) and/or the availability of suitable benthic substratum for settlement and post-settlement survival (non-coral benthic cover). The study was conducted at Palmyra Atoll (central Pacific Ocean), a remote reef complex with high coral cover which shows variation in coral composition, flow regimes and wave energy. Most pocilloporid larvae settle within 200 m^2 of their parent colony, whilst most poritid larvae arrive from other reefs within Palmyra Atoll. The presence of other benthic organisms (especially CCA and bryozoans) had a negative influence on pocilloporid recruitment rates. Poritid larvae reach settlement competency later than pocilloporid larvae. I also found that a network of healthy reefs connected via tidal flow ensure successful recruitment within the Palmyra Atoll reef system. Tidal flow connections should therefore be considered when areas are selected for marine protected areas, and a network of areas rather than a single area should be protected.

2.2 INTRODUCTION

Coral recruitment is a critical process that helps maintain coral populations and facilitates recovery after a disturbance (Vermeij and Sandin 2008; Graham et al. 2011; Gilmour et al. 2013), by ultimately influencing abundance and species composition (Hughes et al. 2010). Corals have a bipartite life cycle consisting of a pelagic dispersive larval phase and a sessile benthic adult stage. During this life cycle, they pass through three demographic bottlenecks that influence coral recruitment: (1) larval supply, (2) settlement, and (3) post-settlement survival (Arnold et al. 2010; Chong-Seng et al. 2014). Part of this life cycle, the journey of coral larvae from being released from their parent colony to becoming an established coral recruit is described in detail in chapter one. The number of fecund adult corals and their reproductive output define larval production. While some larvae will settle close to their parent colony (Swearer et al. 2002), others will be dispersed by currents and waves before they are ready to settle (Raimondi and Morse 2000). The number of available larvae for settlement at any one site therefore depends both on local larval availability and the number of larvae that arrive from more distant sources. Finding the right nursery habitat is crucial for post-settlement survival, which depends very much on direct and indirect competition with the benthic community surrounding the coral settler (Birrell et al. 2008).. The larvae of many coral species have therefore developed specific habitat preferences for settlement (Arnold et al. 2010). In this study, coral recruit refers to a coral larvae that underwent complete metamorphosis, including formation of a calcium carbonate calyx; following the definition by Kuffner et al. (2006). Coral recruitment makes combined reference to larval production and dispersal, settlement and post-settlement survival to the size of a juvenile coral.

Several processes can decrease the number of successful hard coral recruits found on a reef. Fecundity, local adult coral population, larval mortality and hydrodynamics influence larval availability. Settlement preference of the larvae combined with available benthic substrata will affect settlement, while competition, predation, facilitation and disturbance can lead to differences in post-settlement survival. There are three main theories about the relative contribution of these processes to the success of coral recruitment (Elmhirst et al. 2009; Arnold et al. 2010): (1) low recruitment rates are mainly caused by a reduction of adult corals resulting in a reduced larval pool (Hughes and Tanner 2000; Hughes et al. 2000; Gilmour et al. 2013); (2) low recruitment rates are mainly due to decreased fecundity of adult corals (Kojis and

Quinn 1984; Hughes et al. 2000; Birkeland 2015b); and (3) the main cause of low recruitment is that the reef substratum is less suitable for recruitment (Connell et al. 1997; Bellwood et al. 2004; Carpenter and Edmunds 2006; Vermeij 2006; Hughes et al. 2007). Commonly used methods to study coral recruitment census coral recruits that are several months old. By that time the recruits have passed through the three bottlenecks of recruitment. Consequentially, surprisingly little is known about the relative importance of these three hurdles on coral recruit survival. It is therefore difficult to formulate conclusions on what causes low recruitment rates. Additional studies accounting for all three processes (larval supply, settlement and post-settlement survival) are needed to determine what drives coral recruitment.

Settling larvae can either originate from close by (closed population) or from a more distant reef (open population). Currently, there is clear evidence that populations of marine species with a larval dispersive phase vary between fully open and fully closed, with self-recruitment commonly making up 30- 60% of the larval supply (Jones et al. 2009). For corals, several studies have found positive correlations between adult hard coral cover and recruitment (Harriott and Fisk 1988; Vermeij 2005; Gilmour et al. 2013; Salinas-de-León et al. 2013; Chong-Seng et al. 2014; Kayal et al. 2015), while others have found no evident correlation (Edmunds et al. 2010; Penin et al. 2010; O'Leary and Potts 2011; Penin and Adjeroud 2013).

Hydrodynamic models have been used to estimate larval dispersal within a system (Black 1993; Cowen et al. 2000; Paris and Chérubin 2008; Treml et al. 2008; Kool et al. 2010; Alberto et al. 2011; Coleman et al. 2011; Treml et al. 2012; Mora et al. 2012; Coleman et al. 2013; Coscia et al. 2013; Sunday et al. 2014). Seascape genetic models, for example, use hydrodynamic models to explain genetic differences between populations (Riginos and Liggins 2013). Hydrodynamic models were used to explain genetic differences in four coral species within the Caribbean (Galindo et al. 2006). Baums et al. (2006) investigated one of the genetic barriers in the Caribbean at a smaller spatial scale using particle trajectory simulations obtained from a Regional Oceans Modelling System. They identified that the Mona Passage between Puerto Rico and Hispaniola acts as a filter to larval dispersal of the coral *Acropora palmata*. Even on a spatial scale below 30 km, the oceanographic distance (probability of larval dispersal) is better suited to explain genetic differences than the Euclidian distance (actual spatial distance) between sites: ocean currents explained 50% of the seemingly chaotic genetic

patchiness of *Kelletia kelltii*, a subtidal whelk with a 40–60 day pelagic larval duration and an overall genetic distance between populations of $F_{ST} \approx D_{est} \approx 0.001$ (White et al. 2010).

Coral larvae disperse at a range of spatial scales, from meters to hundreds kilometres, while settlement substratum selection and processes influencing post-settlement survival happen at a much smaller spatial scale of millimetres to centimetres (Penin and Adjeroud 2013). The induction of settlement and subsequent post-settlement survival are largely dependent on the reef substratum. Laboratory and field studies have shown that crustose coralline algae (CCA) and bare space covered in biofilm promote coral larval settlement (reviewed by Birrell et al. 2008) while other substratum types, *Dictyota* spp. for example, have a negative effect on settlement through pre-emption of space (Kuffner and Paul 2004; Kuffner et al. 2006). Algae also influence coral post-settlement survival via processes such as sloughing, overgrowing and shading (Birrell et al. 2008). The main effect of macroalgae, cyanobacteria, *Peyssonnelia* spp. (red algae) and bryozoans on coral recruitment is negative (Birrell et al. 2008; Diaz-Pulido et al. 2009; Arnold et al. 2010; Hauri et al. 2010; Venera-Ponton et al. 2011; Sin et al. 2012), while CCA and biofilms tend to promote coral settlement (Golbuu and Richmond 2007; Birrell et al. 2008; Arnold et al. 2010; Tran and Hadfield 2011). Furthermore, turf algae have been found to both inhibit and facilitate coral recruitment (Birrell et al. 2008; Arnold et al. 2010; Diaz-Pulido et al. 2010; Venera-Ponton et al. 2011).

Corals of the families Acroporidae, Pocilloporidae and Poritidae can be reliably identified at recruit level (Babcock et al. 2003). The majority of studies worldwide found recruit compositions dominated by pocilloporids (examples e.g., Baird and Hughes 2000; Reyes and Yap 2001; Soong et al. 2003; Glassom et al. 2004; Mangubhai et al. 2007; Perkol-Finkel and Benayahu 2007). However, acroporids or poritids dominate recruit composition in some locations (Baird and Hughes 2000; Nozawa et al. 2006; López-Pérez et al. 2007). Pocilloporids make up the majority of early recruits in French Polynesia (Penin et al. 2010; Penin and Adjeroud 2013), the only Central Pacific location where recruit composition has been previously described. These three families not only differ in their recruitment rates but also in their potential and realised larval dispersal distances, settlement substratum preferences and post-settlement survival rates. Correlations between recruit abundance and adult abundance/fecundity have been reported for the acroporids and pocilloporids (Harriott and Fisk

1988; Hughes et al. 2000; Gilmour et al. 2013; Chong-Seng et al. 2014; Kayal et al. 2015), while no such correlations have been documented for the poritids (Penin et al. 2010; Penin and Adjeroud 2013; Chong-Seng et al. 2014; Kayal et al. 2015). This indicates that the poritids have a greater minimal larval dispersal distance than the other two families. These three families also differ in their settlement preferences, with the acroporids preferring certain CCA species as settlement substratum, while the pocilloporids and poritids do not exhibit any specific substratum preferences (Harrigan 1972; Lewis 1974; Goreau et al. 1981; Morse et al. 1988; Heyward and Negri 1999; Baird and Hughes 2000; Baird and Morse 2004; Harrington et al. 2004; Golbuu and Richmond 2007; Ritson-Williams et al. 2010, 2014). Post-settlement mortality is also believed to differ amongst the families, with the pocilloporids often displaying a higher post-settlement mortality rate than the poritids and acroporids (Penin et al. 2010; Penin and Adjeroud 2013). Studies focussed on the relative importance of larval supply, settlement rate and post-settlement survival should therefore distinguish between different coral families because the relative importance of these processes is likely to differ between them.

The reefs surrounding Palmyra Atoll are particularly interesting for investigating recruitment processes. Palmyra Atoll is one of the most remote coral reefs on the planet and is separated from neighbouring reefs in the Northern Line islands by deep oceanic water. A very clear population subdivision was found between Palmyra Atoll and its closest neighbour Kingman Reef (67 km distance) for the tropical sea cucumber species *Holoturia atra* (Skillings et al. 2010). Their larvae require at least 18-25 days to reach competency, two weeks longer than most coral larvae. It is therefore likely that coral larval exchange between Kingman Reef and Palmyra Atoll is also limited. Outside the lagoon, the back reef and fore reef areas have high coral cover and has low impact from anthropogenic stressors (Work et al. 2008; Knowlton and Jackson 2008; Collen et al. 2009; Williams et al. 2013). Both rapid settling brooding (*Pocillopora damicornis*, *Stylophora pistillata*) and broadcast spawning pocilloporidae (*Pocillopora eydouxi*, *P. meandrina*, *P. veruucosa*) are found on Palmyra Atoll (Hirose et al. 2000; Harii et al. 2002; Nishikawa et al. 2003; Williams et al. 2008a; Baird et al. 2009). Whilst no specific information is available on the reproductive mode or competency period of the poritidae at Palmyra Atoll (*Porites superfusa* and massive *Porites* spp.) (Williams et al. 2008a), it is likely that they are broadcast spawners because 64% of all poritidae species are broadcast

spawners (Baird et al. 2009). Palmyra Atoll exhibits differences in coral composition, flow regimes and wave energy between sites (Williams et al. 2008, 2013; Rogers 2015: Chapter 4). Palmyra Atoll is therefore well suited for a study investigating processes that shape settlement and recruitment on a spatial scales of mm to km.

In this study, a combination of methods was used to evaluate the influence of distant (derived from other area within the atoll) and local (derived from the same study site and therefore equivalent to self-recruitment) larval supply and the availability of suitable substratum for settlement and post-settlement survival on the recruitment rates of corals pocilloporids and poritids at Palmyra Atoll. My hypothesis was that recruitment rates correlate significantly with both larval supply (distant and local) and the availability of suitable settlement substrata. I hypothesised that pocilloporids would dominate the recruit composition and that the larvae of pocilloporids and poritids would originate from different sources, with pocilloporid recruitment rates correlating with local coral cover and poritid not. Lastly, I hypothesised that recruitment rates would decline as the total deployment duration of the settlement tile increases, due to enhanced competition with other benthic organism.

2.3 METHODS

2.3.1 Study sites

This study was carried out on Palmyra Atoll (see General Introduction for further information about this study area). The Reefs Tomorrow Initiative (RTI) choose ten sites on the reef surrounding Palmyra Atoll for our collaborative work (Figure 2.1), the different groups within RTI therefore all worked on the same sites or a subset of these sites. RTI choose four sites on the fore reef at a depth of 10 m (FR3, FR5, FR7, FR9), and six sites on the back reef at a depth of 3-5m (RT1, RT4, RT10, RT13, EC1, EC2). These were chosen based on an earlier study which found significant differences in benthic cover between the fore reef and the back reef as well as between the Western Reef Terrace (RT) and the Entrance Channel (EC). The back reef is characterised by corals from the genera *Montipora*, *Astreopora* and *Acropora* and the fore reef by the genera *Pocillopora, Hydnophora, Leptoseris, Gardineroseris, Fungia, Favites* and *Favia* (Williams et al. 2008). Sandin et al. (personal communication) measured percentage coral cover for RTI using 200 m^2 photomosaics. On the fore reef, photomosaics were collected

each year at 2 different depths (10 m, 30 m) at four different sites. On the back reef, 6 sites were monitored yearly using photomosaics (~ 5 m depth). These photomosaics were created by taking continuous photographs with a twin Nikon D7000 SLR set up (Focal length = 18 mm & 55 mm) whilst swimming parallel lines within the plots. The camera used to generate processed photomosaics is equipped with a wide-angle 18 mm focal length lens to ensure high overlap among adjacent images. The second camera is equipped with a 55 mm focal length lens to capture images with ≤1 mm resolution. These pictures were stitched together to a single high-resolution picture {Citation} covering the entire \ plot and each adult coral colony was identified to genus. Examples of the 3-D photomosaic end products and videos of the in water data collection can be found under http://100islandchallenge.org/photos-videos/.

Waves and tides, currents, near bottom temperatures, and bottom stresses were also measured at several of the study sites (Monismith et al. 2015; Rogers et al. 2015b, 2016). As described in Rogers (2015), this data was used to calibrate and validate a 3D circulation model using the COAWST modelling suite (Warner et al. 2010). This modelling effort shows that Palmyra Atoll experiences regular tide and wave-driven flushing of the interior lagoons through the main dredged channel (Entrance Channel) located next to EC1 and EC2 and by flows over the reef crest around the atoll. Flows on the fore reef are also more weakly influenced by the prevailing flow past the atoll in the North Equatorial Counter Current (Rogers et al. 2015b). Moderate wave energy (1-2 m wave heights) was found on the southern side of the fore reef (FR3, FR5) while the northern side of the fore reef (FR7, FR9) had higher wave energy (1-3 m wave heights) (Williams et al. 2013; Rogers et al 2015). The two western fore reef sites receive large volumes of water from the Western Terrace (FR9) and the Lagoon (FR3), respectively (Rogers, 2015).

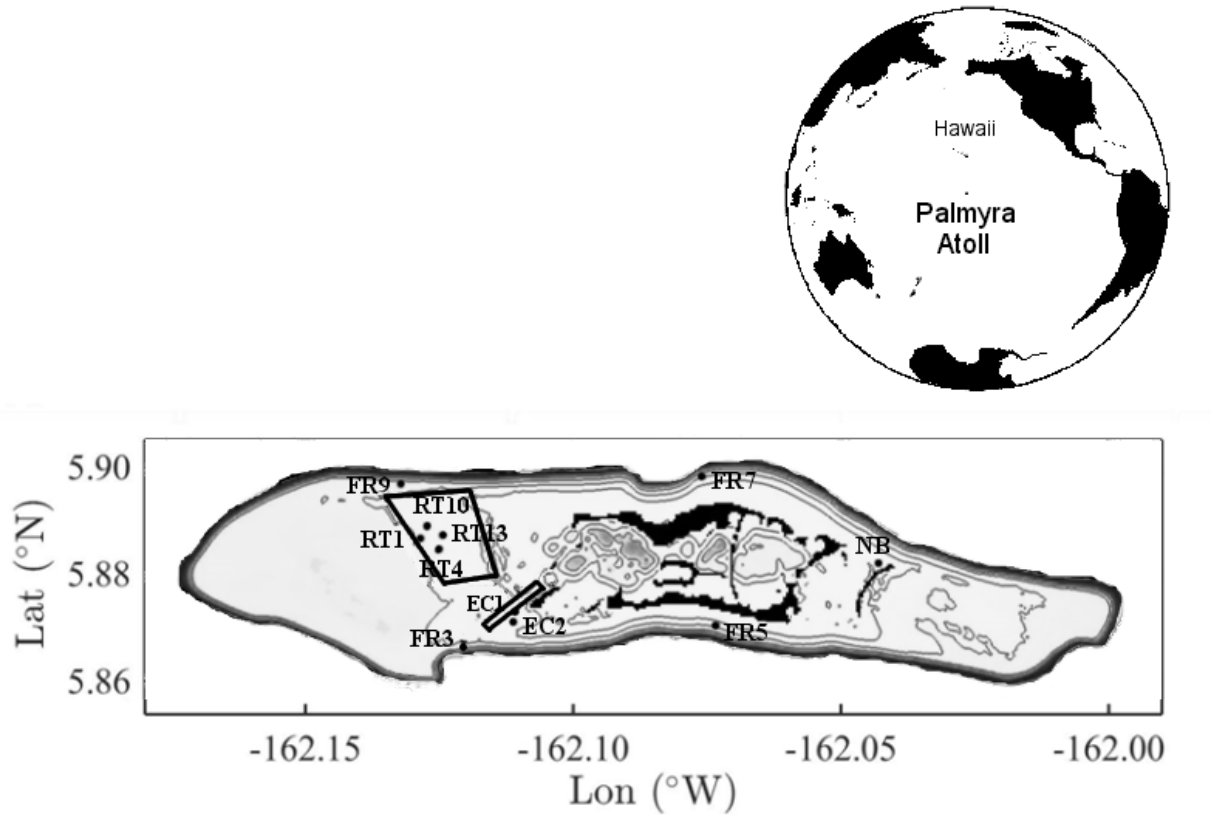

Figure 2.1. Location of Palmyra Atoll and the study sites. The location of Palmyra Atoll in the Pacific Ocean is indicated by a dot (not to scale to the size of the Atoll) on the globe. Sites FR3, 5, 7 and 9 are located on the fore reef. RT1, 4, 10, 13, EC1, 2 and NB are located on the back reef. The *black areas* represent land mass; the water depth is shown in grey scale with the lightest areas being the shallowest water depths. The *grey isobars* are at 5, 10, 50, and 100 m depth. The *black rhomboid* around RT1, 4, 10, 13 represents the location of the Western Reef Terrace. The *black rectangle* next to EC1 and 2 shows the location of the Entrance Channel. EC = Entrance Channel, FR = Fore reef, RT = Reef terrace, NB = North Barren (Site used in Chapter 5 only).

2.3.2 Experimental design

Figure 2.2 shows a diagram of the experimental design which integrates the main aspects of these three drivers on coral recruitment. For each site, distant larval supply was measured in the number of particles that arrived from different areas within Palmyra Atoll according to the COAWST model. The retention of larvae at a particular site was estimated through the loss of particles (measured in outward water flow) with retention increasing as loss decreases. Local larval supply was estimated using adult cover of pocilloporid, poritid and adult hard coral cover. Settlement tiles were deployed at each site to measure coral settlement and recruitment

rates. The benthic cover on each settlement tile was assessed to determine the abundance of suitable substrata for settlement and post-settlement survival. Tiles were deployed for different time periods (length of white arrows in Figure 2.2) and some tiles were returned to the reef after analysis (Tiles without asterisk in Figure 2.2), enabling the measurement of post-settlement survival rates. Redeployment of settlement tiles made it also possible to determine if coral recruitment rates declined as the benthic community develops on the settlement tiles (thickness of benthic cover on settlement tiles in Figure 2.2), by comparing recruitment rates on redeployed tiles (Tile group C, Figure 2.2) with recruitment rates on newly deployed tiles (Tile group A and B, Figure 2.2).

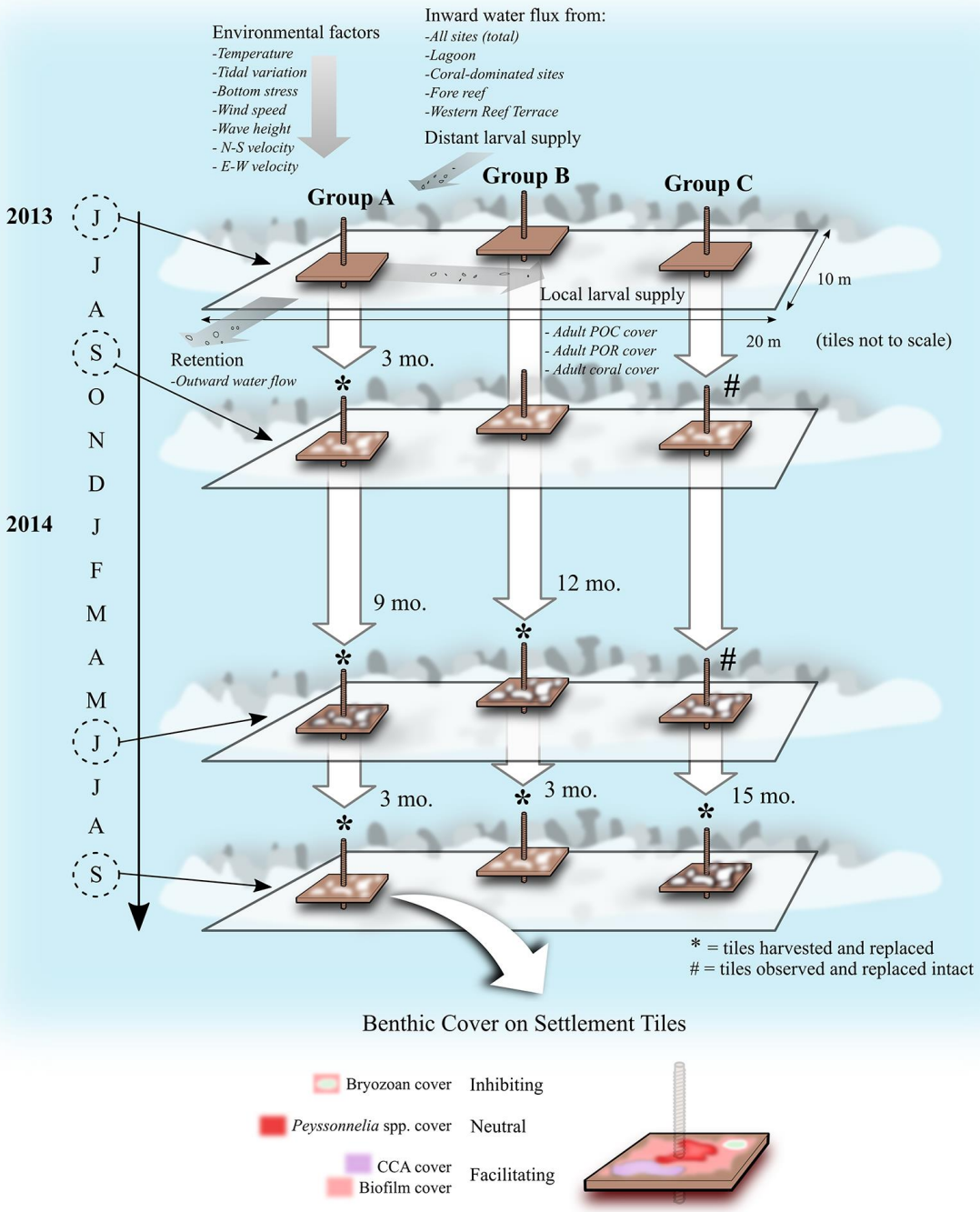

Figure 2.2. Possible factors influence coral settlement and recruitment. At each time point, 15 tiles (5 for each group) were deployed at each of the 10 sites. *The white arrows* indicate how long tiles were deployed between analysis. *Asterisks* indicate that tiles were replaced by new tiles after analysis, *Hashtags* indicate that tiles were returned to the same stake after analysis in the lab. The time line on the left (unit: starting letter of the months) starts at June (*J*) 2013 and ends in September (*S*) 2014. *Large font text* was used to categorize factors, the factors themselves are shown in *small font text*. POC: pocilloporids and POR: poritids. Diagram drawn by David Young.

2.3.3 Measurement of dependent variable and covariates

Coral recruitment rates and time

Coral recruitment rates were used as the dependent variable in my correlation analysis and model. To measure coral recruitment, clay settlement tiles (10 cm x 10 cm x 1 cm) were deployed in May/June 2013 at 10 different sites on the reefs surrounding Palmyra Atoll (Figure 2.1). They were deployed onto stainless steel stakes with a 1 cm high plastic spacer being placed between the tile and the reef benthos to create a cryptic space below the tile (Figure 2.3). The stakes were located at a depth of 3-5 m at the reef terrace and entrance channel sites and at a depth of 10 m at the fore reef sites. At each site fifteen tiles were deployed, which were divided randomly into three groups. The first group of tiles (Tile group A, Figure 2.2) was collected in September 2013 after 3 months of deployment and fresh (new) tiles were deployed onto the same stakes. These new tiles were collected and exchanged for fresh tiles in May/June 2014 after 9 months of deployment. The second group of tiles (Tile group B, Figure 2.2) was collected and exchanged in May/June 2014 after one year of deployment. The third group of tiles (Tile group C, Figure 2.2) was collected both in September 2013 (3 months of deployment) and May/June 2014 (12 months of deployment). These tiles were not exchanged for new tiles but returned to their original stakes after analysis. A final tile collection for all three groups was conducted in September 2014. The tiles collected at this time were deployed for three (Tile groups A and B) or fifteen months (Tile group C). Redeploying one set of tiles back onto the reef made it possible to track coral recruits over time and determine post-settlement survival rates. Furthermore, it also created two sets of data for both the nine and three-month deployment period in 2014: Tile group C was deployed with an established benthic community present on them, while Tile groups A and B were deployed completely clean. For tiles deployed for nine months, it will be possible to determine if recruitment rates differ between the clean tiles of tile groups A and tiles from group C with a three-month old benthic community. For tiles deployed for 3 months in 2014, it will be possible to determine if recruitment rates differ between the clean tiles of tile group A and B and tiles from group C with a twelve-month old benthic community. This is schematically represented in Figure 2.2, with the benthic community composition changing over time. Time is represented in the correlation analysis and model by three different variables: collection date, deployment duration (length of white arrows) and benthic successional stage (thickness of benthic cover

on tiles) (Figure 2.2). Using the correlations and model I was able to differentiate amongst coral recruitment that was significantly variable due to (1) years or seasons (2) tiles deployed for different lengths of time and (3) tiles with different benthic successional stages.

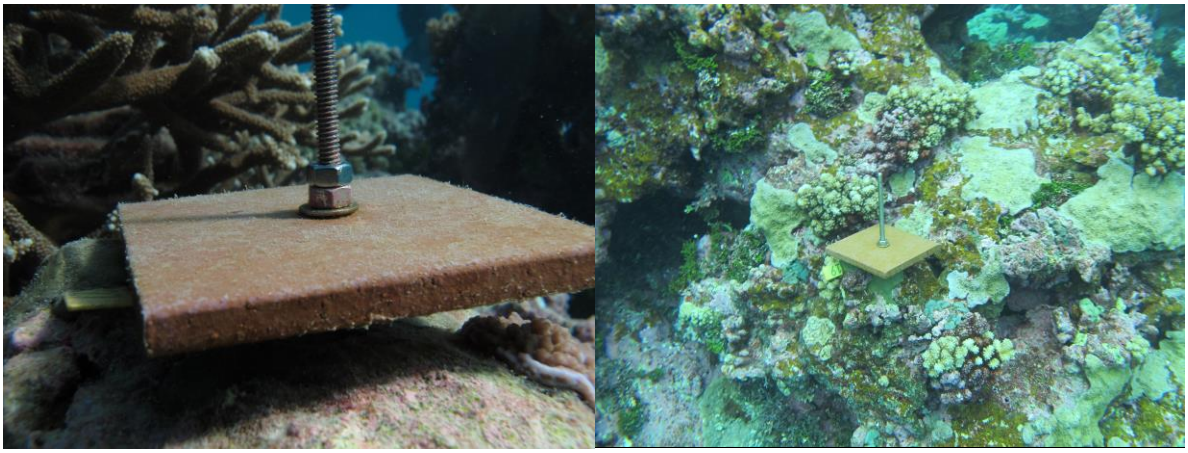

Figure 2.3. Close up and overview picture of the set up and placement of settlement tiles on the reef. A 1 cm wide spacer was placed between the reef and the tile to create a cryptic habitat on the underside of the settlement tiles.

After collection the tiles were kept in a temperature controlled aquarium with bubblers to keep the benthic community on the tiles alive. The exposed (top) and cryptic (underside) surfaces of the tiles were photographed. The tiles from groups A and B were then air dried and transported to Victoria University in Wellington. There they were examined for coral recruits under a dissecting microscope. Recruits were categorised to each of the three major families (Acroporidae, Pocilloporidae and Poritidae) or to an 'other' families category (Babcock et al. 2003). The age of pocilloporid recruits with one polyp was determined by comparing their skeleton to skeletogenesis patterns found in Baird and Babcock (2000). Pocilloporid recruits of the age of ~12 hours, ~24 hours, ~48 hours and 3 days or older could be identified. The *Pocillopora damicornis* recruits surveyed in Chapter 4 developed a second polyp after 11 to 15 days. Schmidt-Roach (2008) found that pocilloporid recruit size is constant during the first week after settlement and increases thereafter, supporting my result that a second polyp is formed after 11-15 days. I therefore assume that the maximal age of pocilloporid recruits with

a single polyp is 15 days. All coral recruits were photographed and their positions on the tiles were mapped on the exposed and the cryptic side of all tiles.

Tiles from group C were examined for coral recruits at Palmyra under the compound microscope. They were placed in a container of water to keep the benthic community on the tile alive during microscopy. A first examination was performed using a NIGHTSEA Blue lights and filter, while the second examination was conducted under ambient light. Certain coral recruits fluoresce under blue light, which increases their detectability. Not all individual coral recruits fluoresce however, and absence or presence of fluorescence does not correlate with taxonomy (Manica and Carter 2000; Salih et al. 2000; Vermeij et al. 2002). All coral recruits were categorised according to Babcock et al. (2003), photographed and mapped as with the recruits examined at Victoria University. For coral recruits found after the second and third deployment of the same settlement tiles onto the reef (May/June 2014 and in September 2014), it was noted if the individual had recruited to the tile during the last deployment period or if they were recruits that were found on the tile earlier. The tiles were then returned to the aquarium and returned to their site-specific stakes on the same or next day.

Suitable substratum for settlement and post-settlement survival

Since the large majority of coral recruits were found on the cryptic (underside) of the tiles, the availability of favourable substratum for settlement and post-settlement survival was estimated using the cover of the four most abundant benthic taxonomic groups on the cryptic side of the settlement tiles. This included CCA, bryozoans, bare substratum with a biofilm (hereafter referred to as biofilm) and the thalloid red alga *Peyssonnelia* spp., which together made up 85.3% of the total benthic cover found on the cryptic side of all settlement tiles. CCA and biofilm were identified as facilitating substrata, bryozoans as inhibiting substratum and *Peyssonnelia* spp. as neutral substratum concerning pocilloporid and poritid settlement (Chapter 3 of thesis). Each time coral recruits counts were conducted, pictures of the entire settlement tile (cryptic and exposed) were also taken. Percentage cover data for the benthic organisms and bare substratum covered in biofilm found on the tile was determined by overlaying 200 random points onto the picture of the settlement tiles and identifying the substrate that laid below them in coral point count program CPCe 4.0 (Kohler and Gill 2006) as outlined in detail in Chapter 3.

Local larval supply

Correlation between coral recruitment rates and adult cover of the same coral family can be used to determine if larval supply is mainly local (derived from the same study site) (Vermeij 2005; Gilmour et al. 2013). Furthermore, Nozawa (2011) advised the measurement of adult pocilloporid cover when conducting coral recruitment studies as he found a significant correlation between pocilloporid recruitment and adult pocilloporid cover. While a significant positive correlation between coral recruitment rates and adult coral cover indicates a high possibility of the presence of local larval supply, one cannot automatically conclude that larvae are supplied from distance sources if such a correlation is absent. The lack of correlation can for example be caused by differences in fecundity of adult corals rather than absence of local larval supply (Hughes et al. 2000). In this study I used percentage adult coral cover data of pocilloporids and poritids (colonies >5 cm diameter) (Harrison and Wallace 1990) obtained from the RTI photomosaics, to test if recruit abundance/presence correlated with adult coral cover. These photomosaics spanned a 10 by 20 meter area at each site, with the settlement tiles being deployed inside that area. I also looked at correlations between coral recruitment and the cover of adult hard corals in general and the cover of the other coral family (Porites adult cover for pocilloporid recruitment) to determine if a significant relationship between adult cover and recruitment is likely caused by larval supply or by larvae preferring to settle close to corals.

Distant larval supply, currents, wind, waves and environmental factors

Whilst a significant positive correlation between coral recruitment and adult coral cover indicates a high possibility of local larval supply, one cannot automatically conclude that larvae are only supplied from distance sources if such a correlation is absent. For example, a lack of correlation may be caused by differences in fecundity of adult corals rather than absence of local larval supply (Hughes et al. 2000). In the present study, distant larval supply refers to larvae that are derived from sites within the atoll that differ from the site at which they settle. Its extent depends on spatial and temporal variations in water mass transport associated with mean currents due to tides, waves and wind, and due to the Stokes drift associated with the surface wave field (see Monismith and Fong 2004). To model the effect of distant larval supply and environmental factors I used hydrographic data (e.g. near-bottom velocities and temperatures) and a connectivity matrix based on the COAWST model describing water flux rates and pathways within and around Palmyra Atoll. The horizontal grid resolution of the

COAWST model was 50 m, which is adequate to resolve the major flow paths on the atoll. The model was run for four separate runs, each of 14 days duration. The four model runs were selected to represent different forcing conditions in wave height, direction, tidal phasing, offshore flow speed and direction: the average connectivity results are presented. The model assumes that larvae can settle immediately after being released, which is adequate for *P. damicornis* and *S. pistillata*, but could lead to an overestimation of retention for the other pocilloporid and poritid species at Palmyra. The COAWST model used to generate the water flux connectivity matrix and the methods used to measure physical oceanographic forcing factors are discussed in detail in Rogers (2015).

Because coral larvae are generally dispersed at the water surface I expect that their transport will be more strongly influenced by winds and waves than they would be by scalars like temperature that are generally uniformly distributed over the water column by mixing. Near-surface transport is caused by wind and Stokes drift (which acts in the direction of wave propagation), and its direction and strength can therefore differ variably from depth-averaged currents. For this reason, wave height and wind speed were also included as covariates along with depth-averaged currents (Fig. 2.2). For the depth-averaged currents, I included measures of the average strength and direction of the currents during each settlement tile deployment period (N-S and E-W current velocities), as well as the variance of these current velocities over the same time periods (standard deviation of N-S and E-W current velocities). Due to the variability in direction of flow, the variances of the current velocities are better suited as an approximation of the average flow velocity over that time period than the average current velocity itself. Much of the flow variability is the result of oscillating tidal flows (Rogers et al. 2016b), which typically results in low average velocity but high velocity variance. Distant larval supply was approximated using the total number of tracer particles arriving at the site (inward water flux) as modelled by the COAWST circulation model. I divided the 22 points of origin within the COAWST circulation model into four areas that represent potential coral larval dispersal hubs within Palmyra Atoll: (1) coral-dominated, (2) the Western Reef Terrace, (3) the fore reef and (4) the lagoon. Using the matrix (Supplementary Material 1) I calculated the number of water particles that originated from these four areas that arrive at each study site, according to the COAWST circulation model.

Because water parcels from sites with low coral cover will likely contain small numbers of coral larvae I included water flux from four potential coral larval dispersal hubs into the model. As first potential larval dispersal hubs I identified all coral-dominated sites at Palmyra Atoll (yellow, green, red areas in Fig. 2.4). However, the fore reef and the back reef vary significantly in their coral community composition (Williams et al. 2008a), indicating possible limited larval exchange between the back reef (green and yellow) and the fore reef (red). The fore reef could therefore be mainly self-seeding and was identified as a larval dispersal hub. However, the fore reef site with the highest coral recruitment (FR9) receives a large volume of water from the Western Reef Terrace (green), identifying the latter as a potential larval dispersal hub. The water flux model showed that the retention time of water at Palmyra Atoll is greatest in the lagoon, with water parcels (and therefore larvae) leaving the reef system (coloured areas) within 10 hours of being released from their parent colony unless they pass through the lagoon. For many larvae, failure to spend time passing through the lagoon would mean that they reach offshore waters (white area) before they reach settlement competency (that is, they are lost to the atoll's reef system). The lagoon could therefore act as an important retention mechanism by allowing extra time for larval development before competent coral larvae are moved over the back and fore reef sites where they can settle.

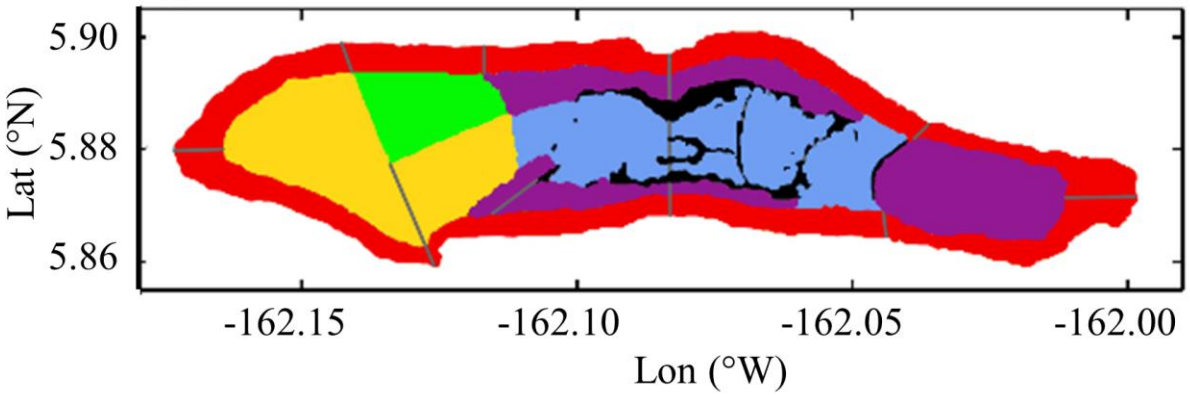

Figure 2.4. The different areas between which water flux was measured. The *black areas* in the centre represent the land mass of Palmyra Atoll. The COAWST model measured water flux between 22 points of origin, which are separated in this diagram by *grey lines*. Some points of origin where grouped together (*same background colour*). *Green*: Western Reef Terrace (1 point of origin); *red*: Fore reef (9 points or of origin); *blue*: lagoon (4 points of origin). *Green, red and yellow combined*: Coral dominated site (substantial part of the entire area has > 50 % coral cover, 12 points of origin). Total water influx and out flux were calculated using all areas (*blue, green, yellow, red, purple,* 22 points of origin/destination).

Retention time is a measure of the time a larva or parcel of water spends at a certain site and is positively correlated with coral recruitment (Sammarco and Andrews 1989). Larval retention was estimated using the amount of water that left the site, hereafter referred to as outward water flow (Fig. 2.2). This is likely to be a good proxy for larval retention because it has been shown that flushing rates can be used to predict coral larvae residence times on coral reef (Black et al. 1990). Near bottom temperature, tidal variation, N-S and E-W current velocities and their standard deviations and bottom stress were included as environmental covariates in the correlation analysis (Fig. 2.2). Near bottom temperature was also included as an environmental covariate in the binary logistical and linear regression modelling (see subsequent section).

The hydrographic data (near-bottom velocities, tidal variation, N-S and E-W current velocity, water temperature) and a connectivity matrix based on the COAWST model describing water flux rates and pathways within and around Palmyra Atoll were provided by the Stanford University group. The COAWST model used to generate the water flux connectivity matrix and the methods used to measure physical oceanographic forcing factors are discussed in detail in Rogers (2015).

2.3.4 Statistical analysis

The recruitment data were skewed and contained many zeros. For this reason I split the data into two subsets: presence/absence of coral recruits and positive abundance of coral recruits (Fletcher et al. 2005). Positive abundance data includes only tiles that received coral recruits, so the zero values are omitted from that data set. This approach of data splitting is sometimes also called a hurdle model (Mullah 1986; Arulampalam and Booth 1997). One major advantage of this combined approach is that I can model presence/absence and positive abundance of the data separately. This makes it possible to determine whether presence/absence and/or positive abundance are being influenced by the covariates in different ways. A single settlement tile served as an individual observation. For each coral family (pocilloporid and poritid) two data sets were created: 'presence/absence data' and 'log-abundance data'. The log-abundance data contained fewer observations than the presence/absence data, because it excluded tiles that were not colonised by coral recruits (i.e., absences).

First I calculated the Pearson's correlation coefficient between the 'presence/absence data', the 'log-abundance data' and the covariates (collection date, deployment duration, benthic succession stage, adult hard coral cover, adult pocilloporids cover, adult poritids cover, inward water flux, outward water flow, water received from coral-dominated sites, water received from fore reef, water received from the reef terrace, water received from the lagoon, temperature, north-south velocity, east-west velocity, north-south velocity standard deviation, east-west velocity STD, bottom stress, surface tidal variation, wave height and wind speed) and then also between the 'log-abundance data' and the covariates. Then I modelled the 'presence/absence data' using a binary logistic regression, whereas the 'log-abundance data' was modelled with an ordinary regression. For both types of models main effects and 1st order effects were considered. Factors within the categories distant larval supply, local larval supply and benthic substratum were not combined with each other for 1st order effects, because they represented different ways of measuring the same biophysical forcing factor. I checked model adequacy for the ordinary regression by plotting the residuals. These indicated no obvious problems with the model. The Hosmer and Lemeshow goodness of fit test was used to determine model adequacy for the binary logistic model. Many of the covariates had missing values (Appendix 3, Table A3.1). This leads to exclusion of cases during model generation.

For this reason, I decided to limit the data modelled to settlement tiles located on the fore reef. This had multiple advantages: (1) no missing values for covariates describing adult hard coral cover, (2) independent measurements of water flux for each site, (3) uniform depth for all sites. Surface tidal variation, bottom stress, wind speed, E-W & N-S velocity and their standard deviations still had missing values even in the reduced data set. I therefore decided to not include them as covariates into the models.

No statistically significantly well fitted models for presence/absence and abundance were found for poritids. For this reason, I did not combine the two models for the poritids. For the pocilloporid recruits, the best fitting models for presence/absence and log-abundance data were combined to predict the expected number of pocilloporids recruits as follows. Let Y (*benthic succession stage, peyssonnelia, temperature, adult hard coral cover, adult poritids cover)* be the number of pocilloporids recruits found on a tile when Benthic successional stage = *benthic succession stage*, Peyssonnelia = *peyssonnelia,* Temperature = *temperature,* Adult hard coral cover = *adult hard coral cover*, Adult poritids cover = *adult poritids cover.* Also let Z (*benthic succession stage, peyssonnelia, temperature, adult hard coral cover, adult poritids cover*) be a binary variable, equal to 1 if pocilloporids recruits are present on the tile and zero otherwise.

The expected value of Y is given by:

$$E(Y) = Pr(Z=1)E(Y|Z = 1) + PR(Z = 0)E(Y|Z = 0)$$

$$= Pr(Z=1)E(Y|Z = 1)$$

$$= \pi\mu$$

where π = Pr(Z=1) and μ = E(Y|Z = 1). A natural estimate of the expected density of pocilloporids recruits is given by (Stefánsson 1996; Welsh et al. 1996):

$$\hat{E}(Y) = \hat{\pi}\hat{\mu} \qquad (1)$$

where

$$\hat{\pi} = \frac{1}{1+ e^{-(\beta * x')}} \qquad (2)$$

and

$$\hat{\mu} = e^{w'\theta + \sigma 2/2} \qquad (3)$$

are the estimates of $\hat{\pi}$ and $\hat{\mu}$ obtained from the two regression model with

β = vector of estimates of the coefficients in the presence/absence logistic regression model
x = vector of explanatory variables in the presence/absence logistic regression model
θ = vector of estimates of the coefficients in the log abundance ordinary regression model
w = vector of explanatory variables in the log abundance ordinary regression model
σ^2 = residual mean square in the log abundance ordinary regression model.

A confidence interval for the estimate in equation (1) was obtained using parametric bootstrapping (Davison and Hinkley, 1997). Bootstrapping was performed for each part of the model (equations 2 & 3) separately using a 95% confidence interval from 9999 bootstrap samples. This generated a confidence interval for β and θ from which the confidence interval for E(Y) was calculated.

Each covariate included in the model was checked for strong correlations ($R^2 > 0.85$) to other covariates. Strongly correlated covariates tend to affect the dependent variable in a very similar way. A covariate in the model could therefore easily be replaced by a covariate with

which it is strongly correlated. Testing for strong correlations within covariates therefore helps to draw conclusions from the model output as it shows which other covariates could also be responsible for the pattern found in coral recruitment rates.

2.4 RESULTS

I successfully retrieved 391 out of 400 tiles from the reef. A total of 870 coral recruits were found on the settlement tiles. Seventeen coral recruits settled on the top of the tiles whereas 853 settled on the bottom of the tiles. Pocilloporids made up 77.6%, poritids 11.4%, acroporids 0.4% and other corals 1% of all recruits while 9.6% of all recruits could not be identified to family and were therefore grouped in "unknown corals". Of the pocilloporid recruits found on 3 month old settlement tiles in September 2013 (n= 136), 11.8% survived for an additional 9 months and 5.1% survived for an additional 12 months. 15% of the newly recruited pocilloporids in May 2014 (n =29) were still alive 3 months later in September 2014. Only three poritid recruits were found on settlement tiles that were subsequently redeployed and one of them survived for a year after it was first found, while the other two died within 3 months of detection. Not a single one of the eight coral recruits that were found on the top side of the settlement tiles that were reanalysed survived until the next tile analysis. Of the pocilloporid recruits, 31% were less than 15 days old, with 6.6% being less than 2 days old.

2.4.1 Correlation analysis

The full results of the correlation analysis can be found in Table 2.1 and 2.2. Below I summarise the results by stating the significant correlations found ($p < 0.05$).

All sites

The presence of pocilloporid recruits on the tiles correlated with the cover of biofilm (+), CCA (-), bryozoans (-) and the successional stage of the benthic community (-). It also correlated with proxies for local and distant larval supply and larval retention (Table 2.1). The log abundance of pocilloporid recruits on the tiles correlated positively with proxies for local and distant larval supply. Furthermore, it correlated negatively with the successional stage of the benthic community (Table 2.1). The presence of poritid recruits correlated with proxies for distant larval supply and larval retention, while the log abundance of poritid recruits only correlated with the standard deviation of the north-south current velocity (-) (Table 2.1).

Table 2.1. Correlation between pocilloporid and poritid recruitment and biophysical forcing factors on Palmyra Atoll. Column 2 & 3 show the Pearson's correlation and its test statistic for correlations between the presence data (P/A) and the covariates described in Table A3.1. Columns 4 & 5 show the Pearson's correlation and its test statistic for correlations between the log abundance data of pocilloporid (POC) and poritid (POR) recruits and the covariates described in Table A3.1 Data derived from all settlement tiles deployed at the 10 study sites were used in this analysis.

		P/A POC	**P/A POR**	**Log abundance POC**	**Log abundance POR**
Time					
Deployment duration	Pearson's Correlation	-0.054	0.059	-0.068	-0.114
	Sig. (2-tailed)	0.295	0.254	0.441	0.534
	N	379	379	131	32
Collection date	Pearson's Correlation	-0.077	-0.082	-0.029	-0.192
	Sig. (2-tailed)	0.133	0.112	0.741	0.294
	N	379	379	131	32
Successional stage of benthic community	Pearson's Correlation	**-0.200****	0.025	**-0.216***	-0.254
	Sig. (2-tailed)	**<0.001**	0.627	**0.013**	0.160
	N	**379**	379	**131**	32
Proxies for suitable substratum for settlement and post settlement survival					
CCA cover	Pearson's Correlation	**-0.129***	-0.042	-0.004	-0.065
	Sig. (2-tailed)	**0.013**	0.421	0.967	0.725
	N	**366**	366	128	32
Peyssonnelia spp. cover	Pearson's Correlation	0.067	-0.050	-0.072	0.167
	Sig. (2-tailed)	0.199	0.342	0.419	0.361
	N	366	366	128	32
Bryozoan cover	Pearson's Correlation	**-0.178****	0.092	-0.131	-0.239
	Sig. (2-tailed)	**0.001**	0.078	0.140	0.188
	N	**366**	366	128	32
Biofilm cover	Pearson's Correlation	**0.162****	0.071	0.082	0.149
	Sig. (2-tailed)	**0.002**	0.174	0.356	0.415
	N	**366**	366	128	32
Proxies for local larval supply					
Adult hard coral cover	Pearson's Correlation	**0.548****	0.062	**0.505****	-0.034
	Sig. (2-tailed)	**<0.001**	0.454	**<0.001**	0.871
	N	**150**	150	**50**	25
Adult pocilloporid cover	Pearson's Correlation	**0.538****	0.150	**0.529****	0.017
	Sig. (2-tailed)	**<0.001**	0.066	**<0.001**	0.937
	N	**150**	150	**50**	25
Adult poritid cover	Pearson's Correlation	-0.049	-0.091	-0.272	-0.029
	Sig. (2-tailed)	0.553	0.269	0.056	0.889
	N	150	150	50	25

Table 2.1 continued

		P/A POC	P/A POR	Log abundance POC	Log abundance POR
Proxies for distant larval supply					
Inward water flux	Pearson's Correlation	**0.276****	0.000	0.047	-0.171
	Sig. (2-tailed)	**<0.001**	0.997	0.592	0.349
	N	**379**	379	131	32
Water received from lagoon	Pearson's Correlation	**0.302****	**-0.129***	0.007	-0.176
	Sig. (2-tailed)	**<0.001**	**0.012**	0.941	0.334
	N	**379**	**379**	131	32
Water received from fore reef	Pearson's Correlation	0.004	0.087	0.118	0.016
	Sig. (2-tailed)	0.931	0.089	0.178	0.929
	N	379	379	131	32
Water received from Western Reef Terrace	Pearson's Correlation	**0.346****	**0.203****	**0.324****	0.017
	Sig. (2-tailed)	**<0.001**	**0.002**	**0.001**	0.936
	N	**227**	**227**	**95**	25
Water received from coral-dominated sites	Pearson's Correlation	**0.263****	0.090	**0.235****	-0.100
	Sig. (2-tailed)	**<0.001**	0.080	**0.007**	0.586
	N	**379**	379	**131**	32
Proxy for retention					
Outward water flow	Pearson's Correlation	**0.195****	**-0.167****	-0.122	-0.151
	Sig. (2-tailed)	**<0.001**	**0.001**	0.165	0.410
	N	**379**	**379**	131	32
Environmental factors					
Tidal variation	Pearson's Correlation	0.018	-0.040	0.086	-0.284
	Sig. (2-tailed)	0.787	0.538	0.459	0.225
	N	237	237	76	20
Temperature	Pearson's Correlation	**-0.130***	-0.050	-0.024	-0.129
	Sig. (2-tailed)	**0.013**	0.338	0.790	0.481
	N	**364**	364	126	32
Wave height	Pearson's Correlation	-0.034	**0.239****	0.065	-0.145
	Sig. (2-tailed)	0.579	**<0.001**	0.554	0.479
	N	261	**261**	85	26
E-W Velocity	Pearson's Correlation	**-0.374****	0.106	0.030	0.142
	Sig. (2-tailed)	**<0.001**	0.139	0.795	0.550
	N	**198**	198	76	20
N-S Velocity	Pearson's Correlation	**-0.322****	0.034	0.000	-0.076
	Sig. (2-tailed)	**<0.001**	0.636	0.998	0.749
	N	**198**	198	76	20

Table 2.1 continued

		P/A POC	P/A POR	Log abundance POC	Log abundance POR
Environmental factors					
E-W Velocity Standard deviation	Pearson's Correlation	**0.458****	**0.176***	**0.328****	0.087
	Sig. (2-tailed)	**<0.001**	**.013**	**0.004**	0.715
	N	**198**	**198**	**76**	20
N-S Velocity Standard deviation	Pearson's Correlation	-0.029	**-0.164***	-0.054	**-0.490***
	Sig. (2-tailed)	0.690	**0.021**	0.641	**0.028**
	N	198	**198**	76	**20**
Wind speed	Pearson's Correlation	0.105	-0.011	0.127	0.065
	Sig. (2-tailed)	0.074	0.850	0.194	0.732
	N	290	290	107	30
Bottom Stress	Pearson's Correlation	0.035	**0.248****	0.052	-0.097
	Sig. (2-tailed)	0.546	**<0.001**	0.594	0.610
	N	292	**292**	107	30

Bold numbers = significant correlations
* = p-value between 0.01 and 0.05
** = p-value < 0.01.

Fore reef sites

Due to coral cover measurements only being available for fore reef sites, I did a separate correlation analysis using only the tiles at the fore reef sites.

The presence of pocilloporid recruits on the tiles correlated significantly with the cover of bryzoans (-) and *Peyssonnelia* spp. (+) and the successional stage of the benthic community (-). It also correlated with proxies for local and distant larval supply and larval retention (Table 2.2). The log abundance of pocilloporid recruits on tiles with recruits had significant negative correlations with bryozoan cover and proxies for local and distant larval supply (Table 2.2). The presence of poritids recruits correlated negatively with proxies for larval retention and positively with adult pocilloporids cover. The log abundance of poritids recruits on tiles only correlated with the standard deviation of the north-south current velocity (-) (Table 2.2).

Table 2.2. Correlation between pocilloporid and poritid recruitment and biophysical forcing factors on the fore reef of Palmyra Atoll. Column 2 & 3 show the Pearson's correlation and its test statistic for correlations between the presence data (P/A) and the covariates described in Table A3.1. Columns 4 & 5 show the Pearson's correlation and its test statistic for correlations between the log abundance data of pocilloporid (POC) and poritid (POR) recruits and the covariates described in Table A3.1. Data derived from all settlement tiles deployed at the 4 fore reef sites were used in this analysis.

		P/A POC	**P/A POR**	**Log abundance POC**	**Log abundance POR**
Time					
Deployment duration	Pearson's Correlation	-0.049	0.051	-0.044	-0.149
	Sig. (2-tailed)	0.563	0.542	0.764	0.478
	N	143	143	49	25
Collection date	Pearson's Correlation	-0.087	-0.126	0.151	-0.201
	Sig. (2-tailed)	0.299	0.134	0.300	0.335
	N	143	143	49	25
Successional stage of benthic community	Pearson's Correlation	**-0.253****	0.003	-0.062	-0.248
	Sig. (2-tailed)	**0.002**	0.969	0.672	0.233
	N	**143**	143	49	25
Proxies for suitable substratum for settlement and post settlement survival					
CCA cover	Pearson's Correlation	0.109	0.077	0.254	-0.096
	Sig. (2-tailed)	0.194	0.361	0.078	0.647
	N	143	143	49	25
Peyssonnelia spp. cover	Pearson's Correlation	**0.190***	0.103	-0.009	0.072
	Sig. (2-tailed)	**0.023**	0.223	0.950	0.734
	N	**143**	143	49	25
Bryozoan cover	Pearson's Correlation	**-0.326****	-0.030	**-0.320***	-0.307
	Sig. (2-tailed)	**<.001**	0.721	**0.025**	0.136
	N	**143**	143	**49**	25
Biofilm cover	Pearson's Correlation	0.159	0.004	-0.099	0.228
	Sig. (2-tailed)	0.057	0.966	0.497	0.273
	N	143	143	49	25
Proxies for local larval supply					
Adult hard coral cover	Pearson's Correlation	**0.560****	0.072	**0.511****	-0.034
	Sig. (2-tailed)	**<0.001**	0.395	**<0.001**	0.871
	N	**143**	143	**49**	25
Adult pocilloporid cover	Pearson's Correlation	**0.538****	0.150	**0.529****	0.017
	Sig. (2-tailed)	**<0.001**	.066	**<0.001**	0.937
	N	**150**	150	**50**	25
Adult poritid cover	Pearson's Correlation	-0.032	-0.087	-0.277	-0.029
	Sig. (2-tailed)	0.702	0.301	0.054	0.889
	N	143	143	49	25

Table 2.2 continued

		P/A POC	P/A POR	Log abundance POC	Log abundance POR
Proxies for distant larval supply					
Inward water flux	Pearson's Correlation	**0.269****	-0.119	**-0.380****	-0.223
	Sig. (2-tailed)	**0.001**	0.157	**0.007**	0.283
	N	**143**	143	**49**	25
Water received from lagoon	Pearson's Correlation	**0.229****	-0.129	**-0.403****	-0.224
	Sig. (2-tailed)	**0.006**	0.125	**0.004**	0.282
	N	**143**	143	**49**	25
Water received from fore reef	Pearson's Correlation	**--0.454****	-0.030	**-0.359***	0.043
	Sig. (2-tailed)	**<0.001**	0.725	**0.011**	0.840
	N	**143**	143	**49**	25
Water received from Western Reef Terrace	Pearson's Correlation	**0.573****	0.164	**0.550****	0.017
	Sig. (2-tailed)	**<0.001**	0.051	**<0.001**	0.936
	N	**143**	143	**49**	25
Water received from coral-dominated sites	Pearson's Correlation	**0.518****	-0.014	0.029	-0.157
	Sig. (2-tailed)	**<0.001**	0.868	0.846	0.453
	N	**143**	143	49	25
Proxy for retention					
Outward water flow	Pearson's Correlation	0.014	**-0.166***	**-0.487****	-0.197
	Sig. (2-tailed)	0.866	**0.047**	**<0.001**	0.344
	N	143	**143**	**49**	25
Environmental factors					
Tidal variation	Pearson's Correlation	0.131	0.080	0.315	-0.284
	Sig. (2-tailed)	0.166	0.398	0.090	0.225
	N	114	114	30	20
Temperature	Pearson's Correlation	-0.018	-0.113	0.163	-0.104
	Sig. (2-tailed)	0.829	0.179	0.264	0.621
	N	143	143	49	25
Wave height	Pearson's Correlation	**0.213***	0.125	0.180	-0.196
	Sig. (2-tailed)	**0.023**	0.188	0.293	0.408
	N	**113**	113	36	20
E-W Velocity	Pearson's Correlation	**-0.570****	-0.035	-0.032	0.142
	Sig. (2-tailed)	**<0.001**	0.745	0.846	0.550
	N	**90**	90	38	20
N-S Velocity	Pearson's Correlation	**-0.343****	-0.016	-0.062	-0.076
	Sig. (2-tailed)	**0.001**	0.883	0.710	0.749
	N	**90**	90	38	20

Table 2.2 continued

		P/A POC	P/A POR	Log abundance POC	Log abundance POR
Environmental factors					
E-W Velocity Standard deviation	Pearson's Correlation	**0.558****	0.138	**0.317***	0.087
	Sig. (2-tailed)	**<0.001**	0.176	**0.049**	0.715
	N	**97**	97	**39**	20
N-S Velocity Standard deviation	Pearson's Correlation	**-0.265****	-0.083	0.223	**-0.490***
	Sig. (2-tailed)	**0.009**	0.421	0.173	**0.028**
	N	**97**	97	39	**20**
Wind speed	Pearson's Correlation	**0.245***	0.088	0.166	0.165
	Sig. (2-tailed)	**0.014**	0.384	0.299	0.451
	N	**99**	99	41	23
Bottom Stress	Pearson's Correlation	**0.210***	0.110	-0.166	-0.093
	Sig. (2-tailed)	**0.024**	0.243	0.300	0.666
	N	**115**	115	41	24

Bold numbers = significant correlations
* = p-value between 0.01 and 0.05
** = p-value < 0.01.

2.4.2 Modelling

To determine which combinations of predictors were best suited to model pocilloporid and poritid recruitment I modelled the presence/absence data from the fore reef sites with a binary logistics model. The log abundance data from the fore reef sites was modelled using an ordinary regression. For pocilloporids, I combined the best model of both these analyses into a single model.

Binary logistic model

The binary logistic model that predicted the measured pocilloporid presence/absence data the best using the fewest covariates included the succession stage of the benthic community, the cover of *Peyssonnelia* spp. on the tile, temperature, adult hard coral cover and adult poritids at the site (χ^2 = 83.924, df = 5, p < 0.001, Table 2.3). This model correctly predicted the presence of pocilloporid recruits in 90.2% of the cases. The binary logistic models which predicted the presence of poritid recruits the best, increased the prediction power by 4.9%, from 81.1% (prediction: no recruitment to all tiles) to 86.0% (χ^2 = 27.278, df = 13, p = 0.011, Table 2.4).

Table 2.3. Estimates of coefficients for best fitting binary logistic model of presence/absence of pocilloporid recruits on settlement tiles. B = coefficient for the constant in the null model. S. E. = Standard error around the coefficient for the constant. Wald = Wald χ^2 test statistics (tests null hypothesis that the constant equals to 0). df = Degrees of freedom for Wald χ^2 test. Sig. = P-value of Wald χ^2 test. Exp(B) = Exponentiation of the B coefficient, which is an odds ratio.

	Coefficients					
Model	**B**	**S.E.**	**Wald**	**df**	**Sig.**	**Exp(B)**
Adult poritid cover	-0.325	0.160	4.138	1	0.042	0.723
Temperature	-3.629	1.831	3.928	1	0.048	0.027
Adult hard coral cover	0.338	0.058	34.187	1	<0.001	1.402
Succession stage of benthic community	-0.257	0.069	13.971	1	<0.001	0.774
***Peyssonnelia* spp. cover**	0.049	0.023	4.313	1	0.038	1.050
Constant	98.014	52.111	3.538	1	0.060	3.691E+42

Table 2.4. Estimates of coefficients for best fitting binary logistic model of presence/absence of poritids recruits on settlement tiles. B = coefficient for the constant in the null model, S. E. = Standard error around the coefficient for the constant, Wald = Wald χ^2 test statistics (tests null hypothesis that the constant equals to 0), df = Degrees of freedom for Wald χ^2 test, Sig. = P-value of Wald χ^2 test, Exp(B) = Exponentiation of the B coefficient, which is an odds ratio.

	Coefficients					
Model	**B**	**S.E.**	**Wald**	**df**	**Sig.**	**Exp(B)**
CCA	2.765	1.647	2.818	1	0.093	15.876
Bryozoan cover	3.595	2.170	2.744	1	0.098	36.402
Adult hard coral cover	0.561	0.189	8.799	1	0.003	1.753
CCA by Temperature	-0.090	0.058	2.447	1	0.118	0.914
Adult hard coral cover x CCA cover	-0.009	0.004	5.303	1	0.021	0.991
Adult hard coral cover x Bryozoan cover	0.275	0.163	2.836	1	0.092	1.316
Adult pocilloporid cover x Bryozoan cover	-1.110	0.672	2.731	1	0.098	0.329
Adult Porites cover x Bryozoan cover	-0.817	0.486	2.828	1	0.093	0.442
Biofilm by Temperature	0.006	0.002	7.287	1	0.007	1.006
Adult hard coral cover x biofilm cover	-0.007	0.003	6.366	1	0.012	0.993
Adult hard coral cover x succession stage of benthic community	-0.101	0.046	4.879	1	0.027	0.904
Adult pocilloporid cover x succession stage of benthic community	0.197	0.078	6.328	1	0.012	1.218
Adult poritid cover x succession stage of benthic community	0.201	0.098	4.249	1	0.039	1.223
Constant	-13.423	4.063	10.915	1	0.001	0.000

Log-abundance model

The ordinary regression that best described the log-abundance data of pocilloporid recruits has an adjusted R^2 value of 0.306 and a p value of < 0.001. The covariates in this model were adult hard coral cover and the volume of water received from coral-dominated sites (Table 2.5). Other models also had a p-value < 0.001, but a lower R^2 value (A list of these models can be found in Table 2.6).

Table 2.5. Estimates of coefficients for best fitting log positive abundance model of pocilloporid recruits on settlement tiles. B = unstandardized coefficients, Std. Error = Standard error of unstandardized coefficients. Beta = standardized coefficients, t = t-test statistic (tests null hypothesis that the constant equals to 0), Sig. = p-value of t-test.

Coefficients

Model	Unstandardised Coefficients		Standardised Coefficients	t	Sig.
	B	Std. Error	Beta		
(Constant)	0.187	0.429		0.437	0.664
Adult hard coral cover	0.062	0.013	0.674	4.808	<0.001
Water received from coral-dominated sites	-0.135	0.060	-0.317	-2.264	0.028

Table 2.6. List of ordinary regression models for pocilloporid recruit rates that had a p value < 0.001. Models that differed from these models by adding an additional covariate were only included if including them increased the adjusted R^2 value (e.g. adding water received from coral-dominated sites to adult hard coral cover).

Adjusted R^2	ANOVA p-value	Covariates included in model
0.306	< 0.001	Adult hard coral cover,Water received from coral-dominated sites
0.287	< 0.001	Water received from Western Reef Terrace
0.264	< 0.001	Adult pocilloporid cover
0.245	< 0.001	Adult hard coral cover

Modelled pocilloporid recruitment rate

The number of pocilloporid found on a single settlement tile ($\hat{E}(Y)$) was modelled by combining the binary logistical model described in Table 2. with the ordinary regression model described in Table 2.. The binary logistic model determined whether or not pocilloporid recruits were present on a settlement tile ($Pr(Z=1)$) while the ordinary regression model was used to predict the number of pocilloporid recruits ($E(Y|Z = 1)$) found on the tiles which had pocilloporids recruit to them. The equation of the full model was

$$E(Y) = Pr(Z=1)E(Y|Z = 1)$$

The full model was a function of *Peyssonnelia* spp. cover, benthic succession stage, adult poritid cover, temperature, water received from coral-dominated sites and adult hard coral cover. Figure 2.5a shows a graphical representation of $\hat{E}(Y)$ on a tile with mean *Peyssonnelia* spp. cover (23.28% ± 13.58 (SE)) that was deployed on the fore reef for 3 months at a site with mean adult poritid cover (4.49% ± 2.03 (SE)) and mean temperature (28.59 °C ± 0.15 (SE)). All upper and lower values of the bootstrapping analysis (including the constant) of the ordinary regression model were included into the 95% confidential confidence interval.

In this combined model, the probability of pocilloporid larvae settling on a tile increased as the cover of *Peyssonnelia* spp. increased. The longer the tile was deployed on the reef the less likely it was to be settled by pocilloporid larvae (Figure2.5b). Furthermore, tiles at sites with higher near bottom temperatures or higher adult poritids cover were less likely to be settled on. The number of tiles with pocilloporid recruits as well as the number of pocilloporid recruits per tile was higher on sites with high adult hard coral cover (Figure 2.5). Tiles located at sites that received a large volume of water from coral-dominated areas had fewer pocilloporid recruits on them than tiles receiving a small volume of water from that area (Figure 2.5).

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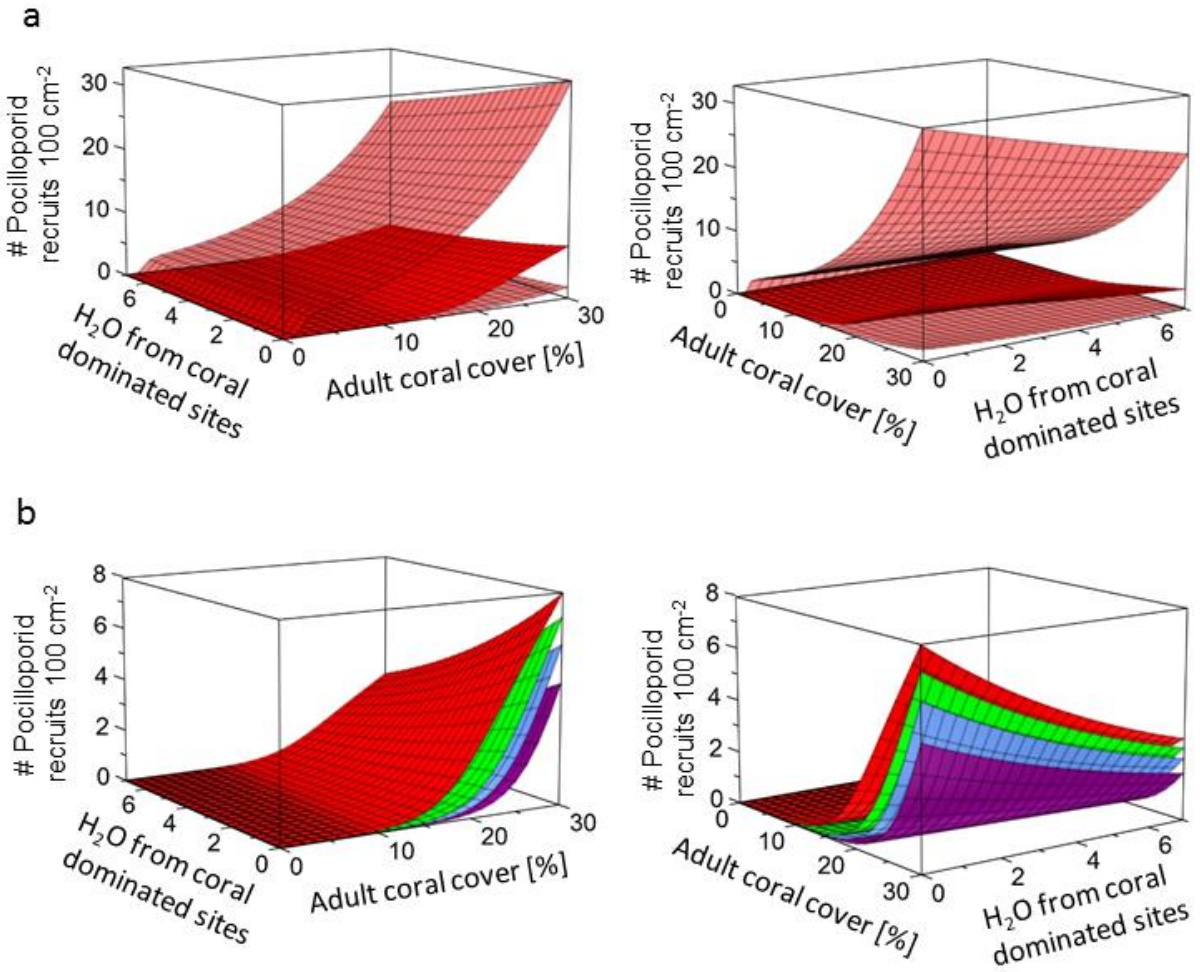

Figure 2.5. Estimates of expected pocilloporid recruit abundance depending on adult hard coral cover and water received from coral-dominated sites. The predictions are for a settlement tile with average *Peyssonnelia* spp. cover, at a site with average poritid cover and average near bottom temperature. (a) shows the estimates for tiles that were deployed for a total of 3 months (*red area*) including a 95% confidence limit (*transparent red area*) which was obtained through bootstrapping. (b) shows the estimates for tiles that were deployed for a total of 3 months (*red = red area in (a)*), 9 months (*green*), 12 months (*blue*) and 15 months (*purple*). Each graph (a and b) is shown from two different angles.

Correlation between covariates

The covariates used to model pocilloporid recruit density correlated strongly ($R^2 > 0.85$) with other covariates not present in the model. Adult hard coral cover correlated negatively to water received from the fore reef (with $R^2 = 0.915$) and adult pocilloporid cover had a strong positive correlation with the volume of water received from the Western Reef Terrace ($R^2 = 0.954$).

2.5 DISCUSSION

Coral recruitment is dependent on (1) larval supply, (2) settlement and (3) post-settlement survival. However, knowledge about the relative importance of these three processes for recruitment success is limited, although each of these processes can act independently as the main driver influencing recruitment (Vermeij 2005; Penin and Adjeroud 2013; Gilmour et al. 2013). The main aim of this study was to determine how local and distant larval supply and the availability of suitable substratum for settlement and post-settlement survival (hereafter referred to as suitable substratum) influence recruitment rates. Pocilloporid and poritid recruitment rates were modelled using proxies for local and distant larvae larval supply, as well as the availability of suitable substratum. Pocilloporid recruitment rates correlated with proxies for larval supply (local and distant) and the availability of suitable substratum. Poritid recruitment was more difficult to predict with the chosen proxies and correlated only with proxies of distant larval supply and larval retention.

2.5.1 Local larval supply

The extent to which coral reefs are self-seeding is a hotly debated topic (see Harrison and Wallace 1990; Harrison 2006; Graham et al. 2008). The current consensus is that the importance of local and distant larval supply differs between locations, with coral populations varying from completely closed to completely open (Jones et al. 2009). In this study, the presence and abundance of recruits correlated positively with adult cover for pocilloporids, while no such correlation could be found for poritids. Positive correlation between adult cover and recruitment rates have previously been found for pocilloporids, while these two parameters have never been found to correlate for poritids (Harriott and Fisk 1988; Penin et al. 2010; Penin and Adjeroud 2013; Chong-Seng et al. 2014; Kayal et al. 2015). More than 50% of the larvae of the two brooding pocilloporid species found on Palmyra Atoll (*P. damicornis* and *S.*

pistillata) are expected to settle within a day of being released (Harii et al. 2002; Nishikawa et al. 2003). They are therefore likely to settle close to their parent colony (Figueiredo et al. 2013) as demonstrated by the relatively weak connection of *S. pistillata* populations on the Great Barrier reef (Ayre and Hughes 2000). The correlation between adult pocilloporid cover and pocilloporid recruitment in this study is therefore likely to be caused by the rapid settlement rates of *P. damicornis* and *S. pistillata*. The other pocilloporids species found on Palmyra Atoll are broadcast spawners (Baird et al. 2009), whose larvae are expected to be located away from their natal reef when they reach settlement competency (Hughes et al. 2000). The results from the correlation analysis suggest that poritid species on Palmyra are broadcast spawners with a longer competency period than *P. damicornis* and *S. pistillata*. The presence of poritid recruits on the settlement tiles was positively correlated with wave height and negatively with outward water flow, a proxy for retention time. However, the results from the binary logistical model suggest that larval retention does not play a role in poritid recruitment and that it is mainly influenced by adult coral cover and benthic cover. Due to these contradictary results it is hard to draw any clear conclusions on what influences poritid recruitment.

2.5.2 Distant larval supply - direction of currents matter as much as strength

Both pocilloporid and poritid recruitment correlated with the standard deviation of current velocities, a measure of how much the current velocity varied during the study period. Tidal flow, and to a lesser extent winds and waves, are responsible for much of this variation (Rogers et al. 2016b). Sites with higher standard deviations of current velocity are therefore likely to have greater flow variability (within the E-W or N-S directions). Pocilloporid recruitment (presence and abundance) and poritid recruitment (presence) correlated positively with the standard deviation of the E-W current velocity. The presence and abundance of poritid recruits correlated negatively with the standard deviation of the N-S current velocity. Because of the east-west elongated geometry of Palmyra Atoll, the E-W tidal currents generally transport coral larvae from one reef to another and therefore supply sites with larvae. The N-S tidal currents generally either transport larvae offshore (from the north shore) or toward the interior of the atoll (from the south shore), both areas where larvae are unlikely to find a suitable settlement substratum. These offshore or lagoon areas do not contain many hard corals, and therefore N-S currents generally do not supply reefs with additional coral larvae. The exception to this is the reef system located on the Western Reef Terrace and the adjacent fore

reef sites, which are connected via N-S currents. It is therefore not surprising that both pocilloporid and poritid recruitment on the fore reef correlated positively with the volume of water received from the Western Reef Terrace, and pocilloporid and poritid recruitment on the back reef correlated positively with the volume of water received from the fore reef. Unfortunately, I was not able to include the standard deviations of the E-W and N-S current velocities in the modelling as data for these covariates were only available for approximately half of my study sites for each deployment time (Table S2.1). It would however, be interesting to see how strong their influence is on pocilloporid and poritid recruitment compared to the other covariables. Other studies (Sammarco and Andrews 1989; Adjeroud et al. 2007) have reported that recruitment increased as flushing rates decreased, as was found for the N-S currents on Palmyra, or that recruitment increased with swell exposure (Adjeroud et al. 2007; Penin and Adjeroud 2013), as was found for the E-W currents on Palmyra. It is important to determine not only the magnitude, but also the direction and source of currents, as these are likely to influence the supply or removal of larvae from a site.

2.5.3 Availability of suitable substratum for settlement and post-settlement survival

Settlement tiles placed in cryptic habitat have been found to be dominated by CCA and *Peyssonnelia* spp., which reflects the natural community of that habitat (Matsuda 1989). The abundant benthic substrata found on the cryptic side of the settlement tiles deployed in this study therefore likely reflect the benthic community on cryptic reef habitat at Palmyra. Poritid recruitment rates did not correlate with substratum availability on the settlement tiles while the presence and abundance of pocilloporid recruits correlated negatively with the succession stage of the benthic community. This was likely due to an increase in post-settlement competition between recruits and other benthic organisms. There was a positive correlation between pocilloporid recruits and percentage biofilm cover but negative correlation with percentage CCA and bryozoan cover. Bryozoans compete with coral recruits via space pre-emption while CCA is a major post-settlement competitor of coral recruits at Palmyra Atoll (Chapter 3). CCA also facilitates coral settlement at Palmyra Atoll and elsewhere (Chapter 3, (Morse et al. 1996; Baird and Morse 2004; Vermeij 2005; Golbuu and Richmond 2007; Birrell et al. 2008; Arnold et al. 2010; Price 2010; Tran and Hadfield 2011; O'Leary et al. 2012), however this positive effect of CCA on coral recruitment, is not able to outbalance the negative effects of post-

settlement competition. My results show evidence that pocilloporids are early recruiters with high settlement rates onto biofilm (Harrigan 1972; Baird and Morse 2004).

2.5.4 Environmental factors

Wind speed, wave height and bottom stress correlated positively with the number of tiles that received recruits. This indicates that settlement is influenced by water and wind movement. Bottom shear stress was estimated by taking the square root of the bottom wave velocity; increased bottom shear stress therefore refers to currents pulling harder on the benthos. High bottom stress increased recruitment, which could indicate that more larvae successfully settle on the underside of settlement tiles, as this cryptic habitat provides a shelter from currents for encrusting organisms (Martindale 1992). Coral larvae disperse at the water surface and sink/swim to the bottom once they are ready to settle (Willis and Oliver 1990). Wind and waves therefore likely influence their movement and may counteract currents that push them away from their natal reef or supply larval from distant sources. The number of settlement tiles containing pocilloporid recruits decreased as temperature increased. The average temperatures measured for each deployment period varied between 28.35 and 28.91 °C and did not show any seasonality. It is however unlikely that such small temperature differences directly affected recruitment rates, even if a significant correlation has been found (Edmunds et al. 2010). Temperature was included in the model because it showed a significant effect ($p = 0.048$), but a strong effect on recruitment at Palmyra Atoll in unlikely.

2.5.5 Limiting and regulating factors

Recruitment is influenced by factors that limit settlement and post-settlement survival and factors that regulate them (Caley et al. 1996). It is important to distinguish between limiting and regulating factors when predicting population size fluctuations. Limiting factors determine whether or not recruitment is present while regulating factors increase or decrease the number of recruits found. In this study, limiting and regulating factors were distinguished by splitting the data into (1) presence/absence and (2) abundance of recruits. Proxies for larval supply (distant and local) and suitable substratum affected the presence of pocilloporid recruits on the tiles. Larval supply also correlated with pocilloporid abundance: sites with higher pocilloporid larval supply did not only have more tiles with pocilloporid recruits on them, they also generally had more pocilloporid recruits per tile than other sites. The only significant

correlation between recruit abundance and suitable substratum was found was between the abundance of pocilloporid recruits and the benthic successional stage. The only regulatory factor for poritid recruitment was N-S flow variability. Poritid recruitment was further limited by distant larval supply, wave energy and retention time. I therefore conclude that the availability of suitable substratum for settlement and post-settlement survival acts mainly as a limiting factor on pocilloporid recruitment, while larval supply acts as a limiting factor on both pocilloporid and poritid recruitment and as a regulating factor on pocilloporid recruitment at Palmyra Atoll. Vermeij (2005) and Carlon (2001) came to a similar conclusion for reefs in the Florida Keys and British Virgin Islands, identifying habitat availability as a limiting factor and presence of adult coral colonies as a regulatory factor. Recruitment rates to the reefs of Palmyra Atolls are therefore limited and regulated in a similar way as less pristine reefs.

2.5.6 Overall Conclusion

The results of this study indicate that pocilloporid larvae reach settlement competency faster than poritid larvae. Pocilloporid recruitment is likely strongly dependent on the local production of pocilloporid larvae, which could lead to slow recovery rates after high local pocilloporid cover loss. Poritid recruitment likely relies on larvae being retained within a reef network until they reach settlement competency, changes in current flow direction and velocity and wave height will therefore likely result in changes of poritid recruitment rates.

I also found that oscillating tidal flows strongly influence coral recruitment rates and that the direction of the flow determines whether or not this influence is positive or negative. My results imply that reefs that are connected through tidal flow to neighbouring reefs on this atoll have higher pocilloporid and poritid recruitment rates. I therefore did not find a single area that acts as a larval dispersal hub but rather identified that a network of healthy reefs connected via tidal flow ensure successful recruitment within the Palmyra Atoll reef system. Tidal flow connections should therefore be considered when areas are selected for marine protected areas and a network of areas rather than a single area should be protected.

2.5.7 Limitations of this approach

Proxies for distant and local larval supply as well as for suitable substratum for settlement and post-settlement survival were used in this study. Such an approach leads to many uncertainties and limitations. Larval supply is ideally measured by observing the number

of larvae that arrive at a site, which is practically impossible. In this study, detailed data on adult hard coral cover and hydrodynamic processes were used as proxies for larval supply. This approach assumes constant fecundity rates between the study sites. Fecundity rates can vary between sites (Hughes et al. 2000). An improvement to this approach would therefore be to measure fecundity rates rather than adult hard coral cover. Coral recruits in this study were between twelve hours and 15 months old. The older recruits are at first detection, the harder it is to formulate a conclusion about the relative contribution of larval supply, successful settlement and post-settlement survival rates to the observed patterns of recruitment (Vermeij and Sandin 2008). In my study, 31% of the pocilloporid recruits were less than 15 days old and 6.6% were two days or younger. The pattern seen in these groups of recruits, especially the latter, can be contributed to a large part to larval supply and settlement success. The other 69% of the pocilloporid recruits were likely heavily affected by post-settlement mortality according to the low post-settlement survival rates found for pocilloporid recruits in this study. Differences in post-settlement survival rates between the individual settlement tiles and sites could distort the initial settlement rates. This is a limitation many recruitment studies face. In this study, proxies for post-settlement survival were included into the analysis, for example the successional stage of the settlement tiles and their benthic cover. I therefore tested whether or not the recruitment pattern found correlated with larval supply and suitable substratum for settlement and post-settlement survival. To better distinguish the effect of post-settlement survival from the effect of larval supply and settlement success on coral recruitment, a first recruit count should be conducted about two weeks after settlement tiles are deployed. Unfortunately, due to the remoteness of my study location, I was not able to sample the settlement tiles earlier than 3 months after deployment.

CHAPTER 3

Possible origin of settlement preference adaptation seen in coral species: a close up view on interactions between coral recruits and benthic organisms.

3.1 ABSTRACT

Spatial competition is intense in benthic reef communities because bare space is rapidly colonised. Corals therefore settle into a hostile world with immediate space competition. Little is known about how the succession stage of a benthic community affects coral recruitment rates but they have been found to correlate negatively on Palmyra Atoll. To determine what causes this negative correlation, this study investigated the interactions of coral recruits with their immediate benthic neighbour. Settlement tiles were deployed on both the fore reef and the back reef for 3, 9, 12 and 15 months. The percentage cover of different benthic taxonomic groups was determined on each tile and coral recruits were counted and photographed under the microscope. Interactions between coral recruits and other benthic organisms were recorded to determine competitive strength and settlement preference leading to successful settlement of coral recruits. Filamentous and upright algae outcompeted coral recruits, while the recruits had a competitive advantage over encrusting algal species. Corals avoided settlement on bryozoans, which lead to these two groups rarely interacting with each other. Coral recruits settled on a variety of substrata but preferred to settle on bare substratum covered in biofilm and crustose coralline algae (CCA). As biofilm became scarce, successful settlement on top of CCA increased significantly. Overgrowth competition was higher on tiles deployed for 9 – 15 months than on tiles deployed for 3 months. The simultaneous decrease in biofilm cover, increase in bryozoan cover and overgrowth competition is the likely cause of the negative correlation between pocilloporid recruitment rates and the succession stage of the benthic community reported in Chapter 2. Successful settlement on top of CCA or bare substratum covered in biofilm of many coral species may be an adaptation to avoid overgrowth in a very competitive environment.

3.2 INTRODUCTION

Coral recruitment refers to the cumulative processes of larval dispersal, settlement and post-settlement mortality of corals onto the reef benthos. It helps to maintain coral populations and facilitates recovery after a disturbance (Vermeij and Sandin 2008; Graham et al. 2011; Gilmour et al. 2013). Often coral larvae have to settle on top of an already established benthic community as bare space on the reef is rare (Birrell et al. 2008). They thus have to compete for space with other benthic invertebrates and algae immediately after settlement. Because the earliest life stages of most benthic organism are generally bad competitors (Sebens 1982; Vermeij and Sandin 2008) it is not surprising that post-settlement survival and therefore coral recruitment rates are largely influenced by other benthic organisms.

Space is often the major limiting resource in marine benthic communities (Connell 1961; Dayton 1971; Paine 1974). Bare space, opened up by perturbations, is quickly colonised by benthic organisms. Solitary organisms generally dominate the early succession stage of the marine benthic community. This is typically followed by a more developed benthic community consisting of a near complete cover of colonial sheets and encrusting species (Jackson 1977; Arnold and Steneck 2011). On tropical coral reefs, solitary polychaete worm tubes are very abundant during the early successional stage, while the surface is dominated by encrusting calcified algae, non-coralline algae and invertebrates (bryozoans, ascidians and sponges) in the later successional stages (Arnold and Steneck 2011). Overgrowth is common in more developed benthic communities, indicating that competition for space is intense (Jackson 1977).

Very little is known about how the difference successional stages of the benthic community affect recruitment of hard corals. Harger and Tustin (1973) found that on newly available substratum, substratum complexity influences coral recruitment, while interactions with other benthic organisms shape coral recruitment rates once a community dominated by encrusting organisms is established. Coral recruitment rates decrease when coral larvae encounter well developed benthic communities (Jackson and Buss 1975). On terracotta tiles, coral larvae often settle more frequently on early successional species such as biofilm, the thin coralline alga *Titanoderma prototypum*, and calcareous polychaete tubes (Arnold et al. 2010; Arnold and Steneck 2011). Arnold and Steneck (2011) found that in Belize, the substratum on

which most small coral recruits are found change as the benthic community on the reef develops. While most coral recruits settle successfully on biofilm when it is abundant on terracotta tiles, the settlement rate onto biofilm cover drops below 10- 20%. Instead they increase their settlement onto crustose coralline algae (CCA), *Peyssonnelia* spp. and invertebrate crusts (sponges, bryozoan and polychaete worm tubes).

Once an almost complete cover of benthic organisms is established, competition with other benthic organisms becomes a major factor influencing post-settlement survival of coral recruits (Harger and Tustin 1973). Algae compete with newly settled coral recruits through overgrowth/smothering, the release of chemicals, abrasion, and epithelial sloughing (Birrell et al. 2008). They also indirectly affect coral recruit survival through shading/overtopping, sediment accumulation and changes in hydrodynamics due to algal morphology (Figure 3.1) (Birrell et al. 2008). The predominant effect of macroalgae, cyanobacteria and *Peyssonnelia* spp. (red algae) on coral recruitment is mostly negative (Birrell et al. 2008; Diaz-Pulido et al. 2009; Arnold et al. 2010; Hauri et al. 2010; Venera-Ponton et al. 2011; Sin et al. 2012) while CCA and biofilms tend to promote coral recruitment (Golbuu and Richmond 2007; Birrell et al. 2008; Arnold et al. 2010; Tran and Hadfield 2011). The effect of turf algae on coral recruitment varies considerably between inhibition or facilitation (Birrell et al. 2005, 2008, Vermeij 2005, 2006; Kuffner et al. 2006; Arnold et al. 2010; Diaz-Pulido et al. 2010; Venera-Ponton et al. 2011) This is likely due to algal turf consisting of several different algae species. Turf algae assemblies therefore often vary in height and sediment trapping, which explains the variation in effects found between studies (Birrell et al. 2008; Diaz-Pulido et al. 2010). Only a few studies examined the influence of benthic invertebrates on coral recruitment. Negative correlations have been found between the number of coral recruits on settlement tiles and bryozoan cover on the tiles in the Northern Red Sea (Glassom et al. 2004) and the combined cover of oysters and bryozoans on the tiles at Heron Island on the Great Barrier Reef (Dunstan and Johnson 1998). However, in Kenya no correlation was found between coral recruitment and bryozoan cover on settlement tiles (Mangubhai et al. 2007). Sponges and bivalves have been found to negatively influence coral recruitment onto settlement tiles in the British Virgin Islands through space pre-emption (Carlon 2001). Furthermore, sponges were identified as the main substratum that leads to coral recruit death through overgrowth (Arnold and Steneck 2011).

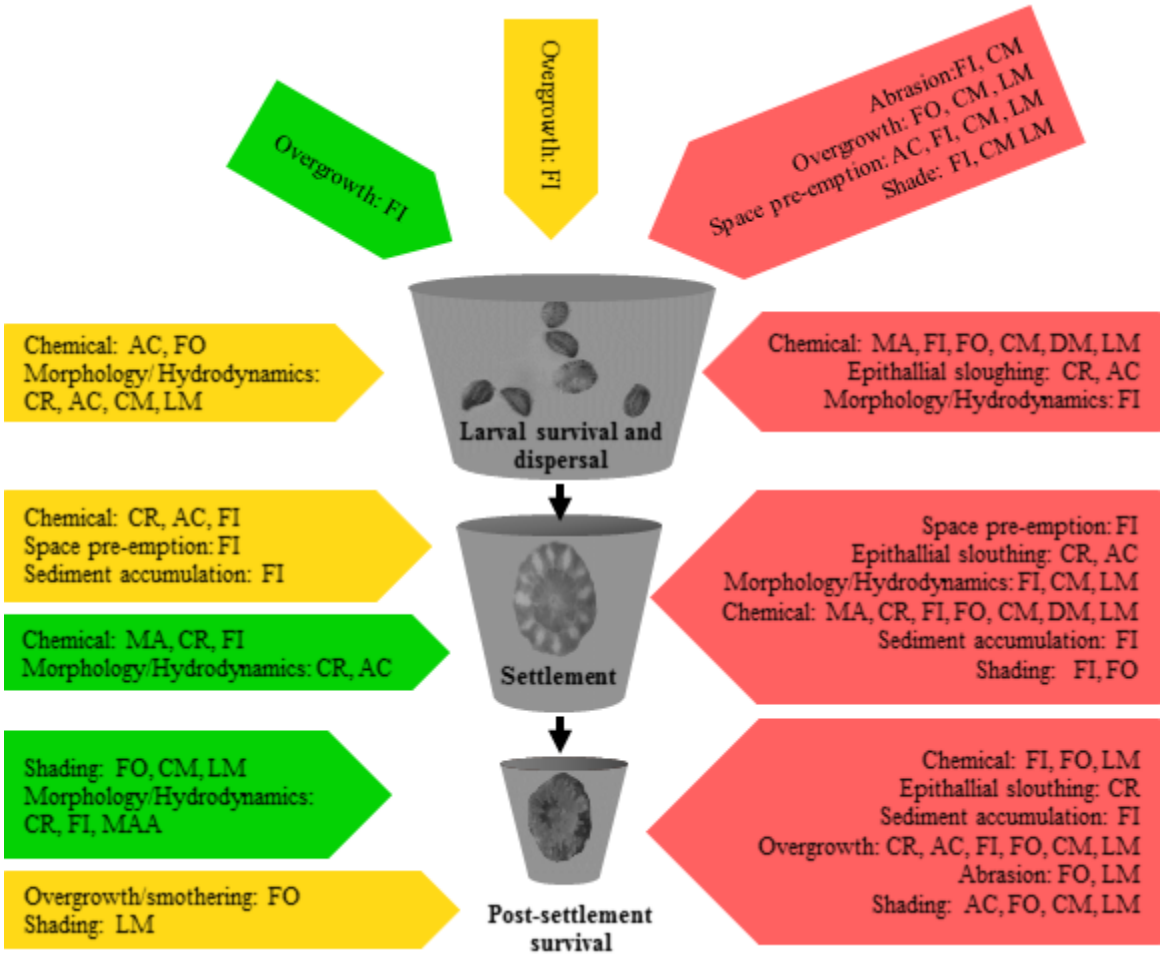

Figure 3.1. Effects of algae on coral recruitment. Algal-coral interactions are shown for recruitment in general (*arrows on top*), larval survival and dispersal (*first cone*), coral settlement (*second cone*) and post-settlement survival (*third cone*). *Red arrows* represent negative effects or inhibition, *green arrows* positive effects or enhancement and *yellow arrows* ambiguous interactions. The different algal functional groups are abbreviated as following: microalgae (MA), crustose (CR), articulated calcareous (AC), filamentous and diminutive forms (<2 cm) including epilithic algal community (EAC) and turf (FI), foliose and corticated foliose (creeping and upright) (FO), corticated macrophytes (CM), leathery macrophytes (LM) and macroalgae in general (MAA). This figure is based on Table 3 in Birrell et al., (2008) incorporating results from Arnold et al. (2010), Diaz-Pulido et al. (2010), Rasher and Hay (2010), Paul et al. (2011), Rasher et al. (2011), Venera-Ponton (2011),Morrow et al. (2012), Sin et al. (2012), Ritson-Williams et al. (2014), Olsen et al. (2014), Webster (2015).

One way coral recruits can avoid being outcompeted by other benthic organisms is by settling on bare substratum covered in biofilm or on benthic organisms that are weak competitors. The larvae of some coral species are very specific in terms of where they settle and metamorphose (Golbuu and Richmond 2007). *Agaricia tenuifolia* and *A. agaricites danai* prefer to settle on CCA (Harrigan 1972; Lewis 1974; Goreau et al. 1981; Morse et al. 1988; Baird and Hughes 2000; Baird and Morse 2004). Other coral species (including *Agaricia agaricites humilis*, *Acropora cervicornis*, *A. millepora*, *A. nasuta, A. palmata*, *A. tenuis*, *A. digitifera, Goniastrea retiformism* & *Montastrea faveolata*) even differentiate among CCA, recruiting only to certain CCA species (Morse et al. 1988, 1996; Heyward and Negri 1999; Harrington et al. 2004; Golbuu and Richmond 2007; Ritson-Williams et al. 2010, 2014). *Stylaraea punctata* on the other hand shows a strict preference for biofilms (Golbuu and Richmond 2007). These settlement preferences seem to reflect survival probabilities as well as recruitment strategies. Sloughing is the most efficient way for several CCA species to clear themselves of coral recruits. Coral species that differentiate between CCA species for settlement, settle on top of CCA species that slough less frequently than others (Harrington et al. 2004; Ritson-Williams et al. 2010). These CCA species are mostly found in cryptic environments, which protects them from herbivore grazing (Price 2010; Ritson-Williams et al. 2010), therefore coral recruits could also use their presence as a cue for suitable habitat (Buenau et al. 2012). *S. punctata*, unlike most adult corals, can become overgrown by CCA even in its adult stage: Golbuu and Richmond (2007) therefore proposed that the avoidance of CCA during settlement by *S. punctata* leads to a higher survival rate.

While acroporids prefer certain CCA species as settlement substratum, pocilloporids and poritids do not exhibit any specific substratum preference (Harrigan 1972; Lewis 1974; Goreau et al. 1981; Morse et al. 1988; Heyward and Negri 1999; Baird and Hughes 2000; Baird and Morse 2004; Harrington et al. 2004; Golbuu and Richmond 2007; Ritson-Williams et al. 2010, 2014). Pocilloporids and poritids respond to CCA in a similar way to acroporids (Morse et al. 1996; Baird and Morse 2004; Price 2010; O'Leary et al. 2012) but also have the ability to recruit to many different substrata. Therefore, pocilloporids and poritids have either a facultative response to CCA or the settlement responses to CCA vary between species in these families (O'Leary et al. 2012). Pocilloporid and poritid recruits therefore interact more frequently than acroporids with benthic organisms avoided by acroporids for settlement.

Studying these interactions can provide insights into why acroporids avoid settling on these substrata. Pocilloporid often recruit to bare substrata covered in biofilm and *Stylophora pistillata* is even able to recruit to surfaces that have not yet been biologically conditioned, and therefore do not contain a biofilm (Baird and Morse 2004). This is likely one reason for the success of pocilloporids as an r-selected pioneer species and may give them an advantage over species that are K-selected, thus superior competitors as adults (Baird and Morse 2004).

Coral recruitment rates increased as either the cover of CCA or the availability of bare substratum increased and decreased with an increase of turf algae or bryozoans (Connell et al. 1997; Carlon 2001; Vermeij 2005; Vermeij and Sandin 2008; Arnold and Steneck 2011). These studies compared coral recruitment rates with benthic cover on a spatial scale of >100 cm^2. Many of the processes that influence coral recruitment act on an even smaller scale of millimetres to centimetres (Vermeij 2006). It is therefore important to investigate the relationship between coral recruits and other benthic organisms on a millimetre to centimetre scale because this is the scale at which individual to individual interactions occur. Only a few field studies have looked at settlement preference of coral recruits on a millimetre scale (Sammarco et al. 1981; Roth and Knowlton 2009; Arnold et al. 2010; Arnold and Steneck 2011; O'Leary et al. 2012). Several studies recorded overgrowth and shading on a millimetre to centimetre scale (Bak and Engel 1979; Sammarco et al. 1981; Van Moorsel 1985; Sammarco 1991; Gleason 1996; Harrington et al. 2004; Vermeij 2006; Arnold and Steneck 2011). Of these studies only three simultaneously investigated which benthic species were being overgrown by coral recruits and which overgrew coral recruits (Sammarco et al. 1981; Gleason 1996; Arnold and Steneck 2011). Further studies examining the full suite of interactions between coral recruits and other benthic organisms on a millimetre to centimetre scale are therefore needed.

The settlement preference of various coral species mentioned above seem to reflect survival probabilities as well as recruitment strategies (Harrington et al. 2004; Golbuu and Richmond 2007; Nozawa 2008; Ritson-Williams et al. 2010). This indicates that settlement preference may be an adaptive trait in coral species. The community composition of coral reefs has been relatively stable during the Pleistocene (Jackson 1992) but many coral reefs have changed drastically in the last decades due to reef degradation (D'Elia et al. 1991; Gardner et

al. 2003; Bruno and Selig 2007). Only a few coral reefs exist in the almost pristine state in which settlement preference of coral larvae for substrata likely evolved (Knowlton and Jackson 2008). Palmyra Atoll is located in the Central Pacific and currently experiences minimal human impact, its outer reef is in a nearly pristine state with a healthy benthic community dominated by corals and CCA (Smith et al. 2016). Historical documentations of nearby inhabited atolls imply that the current coral reef ecosystem found on Palmyra Atoll resembles those of nearby atolls a few decades ago (Sandin et al. 2008). Palmyra Atoll is thus well suited to study the effects of benthic organisms on hard coral recruitment under the environmental conditions that likely lead to the settlement preference adaptations seen today. A study investigating settlement of coral recruits on natural substrata on Palmyra Atoll reported an unusual high number of recruits (12%) settling on the brown alga *Lobophora* spp. (Roth and Knowlton 2009). Unfortunately, the authors were not able to determine if this behaviour was due to *Lobophora* spp. being very abundant at Palmyra Atoll or coral larvae showing a settlement preference for *Lobophora* spp. In Chapter Two, I found that coral recruitment rates correlated significantly with the successional stage of the benthic community on the settlement tiles as well as with cover of CCA, bryozoans and bare substratum covered in biofilm. Further studies on the interactions between benthic organisms and coral recruitment on Palmyra Atoll are therefore needed to gain a better understanding of the trends found by Roth and Knowlton (2009) and in Chapter Two. This will also increase our understanding of possible mechanisms that lead to the settlement preference found in coral larvae today.

The aim of this study was to investigate interactions between coral recruits and their direct benthic neighbours on a millimetre to centimetre scale level. First, I quantified the number of interactions between coral recruits and their direct benthic neighbours and classified these interactions into corals winning, corals losing or stand-offs. I hypothesised that the number of interactions between a benthic taxonomic group and the coral recruits is proportional to the cover of this taxonomic group. However, I also hypothesised that the ratio between winning and losing interactions varies according to the competitive abilities of benthic taxonomic groups. Secondly, I investigated successful settlement (settlement and subsequent early post-settlement survival up to 2 weeks) of coral larvae by determining which benthic substratum the earliest life stage of coral recruits (1 polyp) settled upon. I distinguished between pocilloporid and poritid recruits to determine if settlement preferences varied between

families. My hypothesis was that coral recruits of both pocilloporids and poritids are found on various different substrata but that they show clear preferences for bare substratum covered in biofilm and CCA while avoiding bryozoans and strong competitors identified through the second sub aim of this study. I also hypothesised that the successful settlement onto different benthic substrata changes as the benthic community on the settlement tiles matures. Lastly, I measured percentage cover of all benthic organisms on the settlement tiles deployed on the reef for different lengths of time to determine (1) the patterns of ecological succession and (2) any spatial differences in the benthic coral reef community found on Palmyra Atoll. I hypothesis that benthic organisms cover increases over time on the cryptic tile surface. I also hypothesise that the back reef and front reef will differ in the composition of the benthic organisms found on the settlement tiles.

3.3 METHODS

3.3.1 Site

This study was carried out on Palmyra Atoll (see General Introduction and Chapter Two for further information about the study area). All of the data used in this chapter was collected from settlement tiles deployed at ten sites (EC1, EC2, FR3, FR5, FR7, FR9, RT1, RT4, RT10, and RT13) following the methods described in Chapter Two.

3.3.2 Recruitment

The first group of tiles (Tile group A, Figure 2.2) was collected after 3 months in September 2013 and fresh (new) tiles were deployed onto the same stakes. These new tiles were collected and exchanged for fresh tiles in May/June 2014, after 9 months of deployment. The second group of tiles (Tile group B, Figure 2.2) was collected and exchanged in May/June 2014, after one year of deployment. The third group of tiles (Tile group C, Figure 2.2) was collected both in September 2013 and May/June 2014. These tiles were not exchanged for new tiles but returned to their original stakes after analysis. A final tile collection for all three groups of tiles was conducted in September 2014.

Settlement tiles were examined for coral recruits following the methods described in Chapter Two. A recruit was defined as a coral larva that underwent complete metamorphosis,

including formation of a calcium carbonate calyx (Kuffner et al. 2006). For each coral recruit, I noted the number of polyps it contained, the family it belonged to, and its position on the tile.

3.3.3 Interactions between coral recruits and benthic substrata

The benthic community on the settlement tiles changed too rapidly to investigate interactions between benthic organism over a time series of images taken of the reanalysed settlement tiles. Interactions were therefore investigated on static images, following the contact matrices approach (Turner and Todd 1994; Bell and Barnes 2003). I recorded all interactions between coral recruits on the cryptic (under) side of the settlement tiles and their immediate neighbours. Only 17 coral recruits were found on the top side of the settlement tile, for this reason I did not investigate interactions between coral recruits and benthic substrata on the top of the settlement tiles. Interactions were classified as (1) won by the coral (coral overgrows other benthic organism), (2) won by the other benthic organism (other benthic organism overgrows coral) or (3) a stand-off, where the coral recruit and the benthic organism were touching but no dominance was apparent (Figure 3.2a). Interactions were counted on the colony level: for example, a coral recruit overgrowing two colonies of CCA would count as two winning interactions. Furthermore, to weight the interactions, I determined how much of the coral-benthic border each interaction type entailed (Figure 3.2b), giving an interaction type that only takes up 5% of the border a smaller weight than an interaction type that takes up 50% of the border. For example, if a coral recruit overgrew two colonies of CCA, then the length of the coral-benthic border of both these interactions would be added together to determine the length of the coral-benthic border taken up by coral winning over CCA. To determine the proportion of the coral-benthic border each interaction type entailed, I loaded a picture of each coral recruit into the image analysis software ImageJ. The length of each interaction type (i.e., extent of colony border interaction) was measured in ImageJ and recorded. All interactions (counts and proportion of coral-benthic border) were recorded in a contact matrix (Table 3.1).

Table 3.1. Example of a cell of the contact matrix.

	Benthic group	
Coral recruits	stand-offs	won by the benthic organism (coral overgrown)
	won by the coral (coral overgrowth)	Total

The matrix produced in this survey is similar to contact matrices used in previous studies on inter- and intra-species interactions of bryozoans and sponges (Turner and Todd 1994; Bell and Barnes 2003). One significant difference is that in this study I also recorded the length of the coral-benthic border for each interaction as described above.

I also recorded the level of overgrowth on the coral recruits. For each taxonomic group that overgrew a coral recruit I determined if it only overgrew the edge of the recruit or if it overgrew the coral recruit partially (Figure 3.2a). Each overgrowth interaction was therefore put into one of the categories: (1) overgrowth of the edge and (2) partial overgrowth.

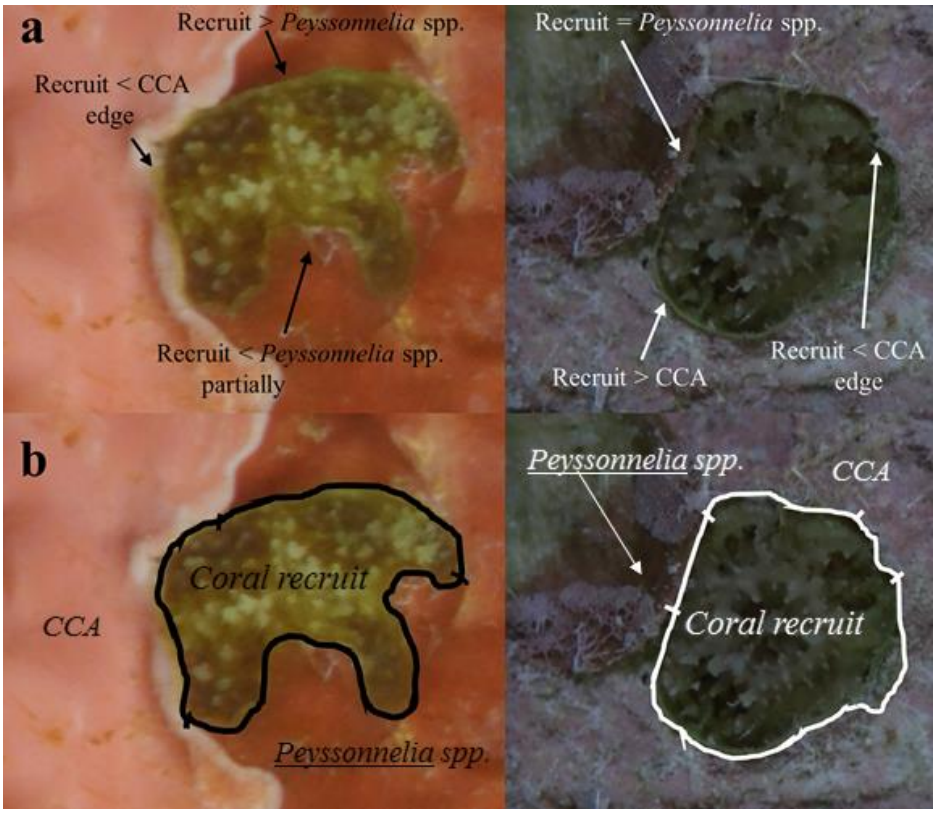

Figure 3.2. Classification of winning, losing and stand-off interactions. (a) Examples of winning (>), losing (<) and stand-off (=) interactions. For each interaction lost by the coral recruit, the level of overgrowth was also recorded: *edge* or *partially*. (b) Coral-benthic border measurements for the two examples in (a). The *closed loop* shows the total coral-benthic border, *Lines/dividers* on the coral-benthic border show where the interactions identified in (a) start and end.

3.3.4 Benthic cover

Pictures taken of the settlement tiles after collection were analysed in Coral Point Count with Excel extension (CPCe v. 4.1; Kohler and Gill 2006). A trial using 16, 32, 48, 64, 80, 96, 128, 160, 192, 208 and 256 stratified points was conducted on 10 settlement tiles to determine the number of stratified points needed for an accurate percentage cover results. The difference between random and stratified random points is that for stratified random points the analysed area is sub-divided into m rows and n columns and each cell is popluted with k random points. This reduces the potential clumping of the random points using the simple random method, and ensures that some random points are present in each image cell region. Two hundred stratified points were identified to yield reliable percentage cover data (Appendix 1). These points were placed on the cryptic side of the settlement tiles in a 10 x 10 grid. Two points were therefore placed randomly in every 1 cm^2 segment of the cryptic side of the settlement tile. Using the benthic cover information for these 200 points, the program calculated the percentage cover data for the benthic organisms and bare substratum found on the tile. I identified different taxonomic groups of algae (CCA, cyanobacteria, *Dictyota* spp., *Lobophora* spp., *Peyssonnelia* spp., green encrusting algae, turf algae and macroalgae) and invertebrates (amphipod tubes, bryozoans, foraminifera, hydrocorals, hydroids, sponges, polychaete worm tubes, tunicates, vermetids and other invertebrates). Only bryozoans were identified to species level. First, the settlement tiles were examined under the microscope to identify the bryozoans to genus level. Between one and three individuals of each genus of bryozoan present on the tiles was then examined under the Scanning Electron Microscope to identify them to species level.

3.3.5 Data analysis

Factors other than benthic cover also influence coral recruitment rates. Some of these factors (oceanic currents, local coral cover) act on a larger scale than benthic cover (see Chapter Two for in depth information). It is therefore likely that these factors are constant on a spatial scale of 100 cm^2. For this reason, I used the individual settlement tiles (100 cm^2) as a unit of measurement. This study also only included the cryptic side of the tile, which eliminates settled sediment accumulation and grazing as factors that influenced coral recruitment (no grazing scars found on cryptic side). Coral recruitment rates within the scale of a settlement tile are

therefore either driven by the benthic cover on the settlement tile or differences in light availability within a tile (Maida et al. 1994).

Interactions between coral recruits and the benthic substratum

Two analysis were performed to determine if the number of interactions between coral recruits and a specific benthic substratum group was dependent on the availability of that substratum. First, I compared the mean percentage cover of the substratum on the settlement tiles to the mean percentage of the length of the coral-benthic border involved in the interactions. This gives an indication of whether interactions are more/less frequent than expected if settlement of coral larvae was random and therefore following the abundance of the substratum on the tile. In a second step, I performed a correlation analysis between the percentage cover of each taxonomic group and the percentage of the length of the coral-benthic border involved in interactions between coral recruits and that taxonomic group. This analysis plots the length of the coral-benthic border involved in interactions with a specific taxonomic group against that taxonomic group's abundance for each individual settlement tile. This analysis was performed for taxonomic groups that had in total more than 30 interactions with coral recruits. This analysis will show in more detail how abundance of the taxonomic group affects the number of interactions between coral recruits and that group.

Successful settlement

To determine successful settlement of coral larvae (settlement and subsequent early post-settlement survival up to 2 weeks), I looked at winning interactions between coral recruits with a single polyp and other benthic organisms. I assumed that the substratum these coral recruits are currently overgrowing is the same substratum they settled on a few days or weeks earlier. I also assumed that coral larvae do not show an age-related settlement preference and that therefore all differences in successful settlement found on the tiles were related to the tiles' benthic community. Not all substrata found on the settlement tiles were included in this analysis. Substrata were included if at least one coral recruit settled on them or they cover more than 25% of one or more settlement tiles.

Using the proportional length data from the coral-benthic interaction border, I determined the proportion of substratum type i in all winning interactions between single polyp coral recruits and other benthic organisms for each tile ($r_{i,s}$). Then I calculated Manly's alpha

preference index (Manly et al. 1972; Krebs 1989; Price 2010) for each substratum type on each tile. This is a simple measure of preference that is often used for diet preference in animals. It compares the probability that a coral larva encounters a certain substratum ($n_{i,s}$) with the rate that coral larvae settle on this substratum ($r_{i,s}$). The Manly's alpha selectivity index was calculated using the following equation:

$$\alpha_{i,s} = \frac{r_{i,s}}{n_{i,s}} \frac{1}{\sum_{j=1}^{m} \frac{r_{j,s}}{n_{j,s}}}$$

where: $\alpha_{i,s}$ = Manly's alpha (preference index) for substratum *i* on settlement tile *s*

$r_{i,s}$, $r_{j,s}$ = Proportion of substratum *i* or *j* in interactions won by single polyp coral recruits on settlement tile *s* (*i* and *j* = 1,2,3, …., *m*)

$n_{i,s}$, $n_{j,s}$ = Proportion of substratum *i* or *j* available on settlement tile *s*

m = Number of benthic substrata types available on settlement tile *s*

alpha values are normalised so that

$$\sum_{i=1}^{m} \alpha_{i,s} = 1 \text{ for each settlement tile } s$$

and

$\alpha_{i,s} > \frac{1}{m}$ substratum *i* is preferred for settlement on settlement tile *s*

$\alpha_{i,s} < \frac{1}{m}$ substratum *i* is avoided for settlement on settlement tile *s*

For each settlement tile, $\alpha_{i,s}$ were compared to the expected Manly's alpha index for no difference in settlement preference and early post-settlement mortality between substrata ($\frac{1}{m}$). $\frac{1}{m}$ differs between settlement tiles due to differences in availability of settlement substrata. For

each substratum I determined the number of tiles for which $\alpha_{i,s} > \frac{1}{m}$ and $\alpha_{i,s} < \frac{1}{m}$. Furthermore, I calculated the mean difference (Δ) between $\alpha_{i,s}$ and $\frac{1}{m}$ for each substratum

$$\Delta = \alpha_{i,s} - \frac{1}{m}.$$

For substrata that were present on five or more settlement tiles, I used the Shapiro-Wilk test for normality to determine if Δ was normally distributed ($p>0.01$). For normally distributed data, I performed a paired t-test between $\alpha_{i,s}$ and $\frac{1}{m}$ to determine if the mean Manly's alpha index value differed from the expected Manly's alpha value if the coral recruits showed no difference settlement preference and early post-settlement mortality did not differ between substrata ($\frac{1}{m}$). Because the non-normally distributed data were not symmetrically distributed around zero, I used a sign test to analyse these data. This test compares the median of the differences (Δ) between the measured Manly's alpha value and the expected Manly's alpha value for no difference in settlement preference and early post-settlement mortality between substrata ($\frac{1}{m}$).

Benthic succession

Pairwise PERMANOVAs were used to determine if the composition of the benthic community differed between sites and deployment durations. Percentage cover data recorded for the cryptic side of settlement tiles were compared using the following benthic groups: Bare substratum covered in biofilm, CCA, cyanobacteria, *Dictyota* spp., green encrusting algae, *Lobophora* spp., *Peyssonnelia* spp., turf algae, other macroalgae, thin layer of unidentifiable algae, polychaete worm tubes, tunicates, the three bryozoan taxa *Pleurocodonellina microperforata*, *Parasmittina hastingsae*, *Turbicellepora ampla*, and other invertebrates. Bray Curtis similarity analysis was used on the untransformed data to obtain the resemblance matrix for the PERMANOVA. The first test design compared sites with each other and the second tested deployment durations. The settlement tiles were then grouped according to the PERMANOVA results: sites and deployment durations that did not differ significantly from each other were grouped together. An MDS plot was used to visualise how the benthic

community of these groups differed from each other. PERMANOVA and MDS analyses were conducted in PRIMER v6 (Clarke and Warwick 2001).

3.4 RESULTS

3.4.1 Interactions between coral recruits and benthic substratum

I recorded 2123 interactions between coral recruits and other benthic organisms: 1320 on the tiles deployed for three months (515 on the fore reef and 805 on the back reef) and 803 on the tiles deployed for 9 - 15 months (433 on the fore reef and 370 on the back reef) (Table 3.2). Pocilloporid recruits were involved in 1748 interaction and poritid recruits in 195 interactions, while 180 interactions were between other coral recruit families and benthic organisms. Coral recruits found on tiles deployed for 3 months had a mean of 3.29 ± 0.09 (SE) interactions per tile with other benthic organisms on the back reef and 3.17 ± 0.10 (SE) on the fore reef. After 9 - 15 months of deployment, the average number of interactions was 3.16 ± 0.12 (SE) on the back reef and 2.92 ± 0.11 (SE) on the fore reef. The percentage of the coral-benthic border involved in interactions with other benthic organisms increased over time (Figure 3.3).

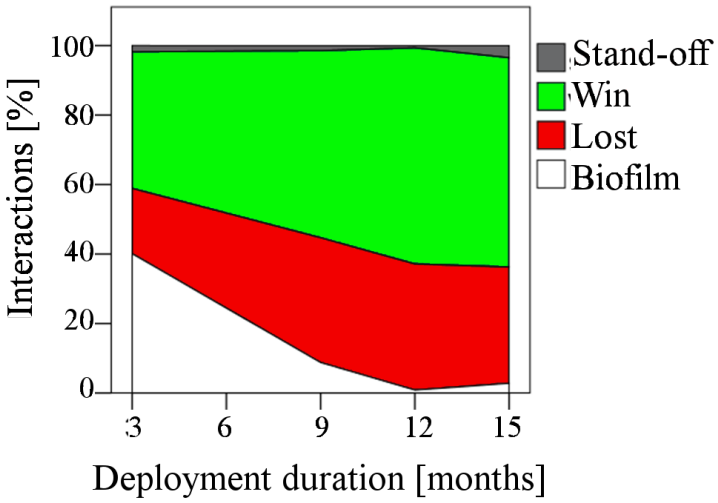

Figure 3.3. Percentage of the coral-benthic border involved in interactions with other benthic organisms. For each deployment duration the lengths of the coral-benthic borders of all coral recruits (fore reef and back reef) were summed and split up into stand-off interactions, interactions won or lost by the coral recruit and interactions with bare substrata covered in biofilm.

Coral recruits won more interactions with their benthic neighbours than they lost (Figure 3.3). Overall all deployment times combined, 46% of the coral-benthic border was occupied by corals overgrowing other benthic organisms. This changed over time from 46% on the back reef and from 31% on the fore reef on tiles deployed for 3 months to 59% on tiles deployed for 9 - 15 months on both the fore reef and back reef. Over all deployment times combined, 25% of the coral-benthic border was occupied by benthic organisms overgrowing corals. This increased over time from 21% (3 months deployment) to 39% (9 - 15 months deployment) on the back reef and from 16% to 33% on the fore reef. Stand-off interactions were generally rare but more common between corals and other invertebrates than between corals and algae.

Table 3.2. Contact matrix for interactions between coral recruits found on tiles deployed for 3 to 15 months and other benthic taxonomic groups. The first column for each interaction type (won, lost, stand-off, total) shows the number of interactions recorded. The second column shows how much of the total coral-benthic border was covered by these interactions. Under lost interactions, a third column shows the percentage of lost interactions where the coral recruit was partially overgrown (mean for all settlement tiles ± SE).

	Coral recruits								
	Won		**Lost**			**Stand-off**		**Total**	
	#	%	#	%	Partially Overgrown	#	%	#	%
Algae									
CCA	840	31%	357	12%	33.2% ± 3.8	36	1%	1233	44%
Cyanobacteria			6	0%	100.0% ± 6.9			6	0%
Dictyota spp.	1	0%	9	0%	80.0% ± 20.0	1	0%	11	0%
Green encrusting algae	117	2%	2	0%	0.0% ± 0.0			119	2%
Lobophora spp.	49	2%	18	1%	44.1% ± 12.0	3	0%	70	3%
Peyssonnelia spp.	191	7%	106	5%	57.9% ± 5.8	11	0%	308	12%
Turf	117	4%	184	6%	62.1% ± 6.9	7	0%	308	10%
Invertebrates									
Bryozoans	2	0%	3	0%	33.3 % ± 33.3	1	0%	6	0%
Coral	7	0%	7	0%	42.9 % ± 20.2	15	0%	29	0%
Foraminifera	1	0%	2	0%	100% ± 0.0			3	0%
Polychaete worm tubes	11	0%	2	0%	100% ± 0.0	6	0%	19	0%
Vermetids			1	0%	100% ± 0.0			1	0%
Other									
Biofilm	443	28%						443	28%
Unknown	9	0%	1	0%	0.0% ± 0.0			10	0%

Most of the interactions between coral recruits and other benthic taxonomic groups involved CCA species (Figure 3.4, Table 3.2). Coral recruits won 68% of these interactions. Recruits were also often found overgrowing bare substratum covered by a biofilm (referred to as biofilm hereafter) or interacting with *Peyssonnelia* spp. and turf algae. Turf algae often outcompeted coral recruits while *Peyssonnelia* spp. was frequently overgrown by them. Of all the algae species, green encrusting algae was the weakest competitor against coral recruits with only 1 in 60 interactions being won by the algae (Figure 3.5). Interactions between corals and other invertebrates were rare (Table 3.2). With the exception of bryozoans, this mirrored the low abundance of other invertebrates on the settlement tiles (Figure 3.4).

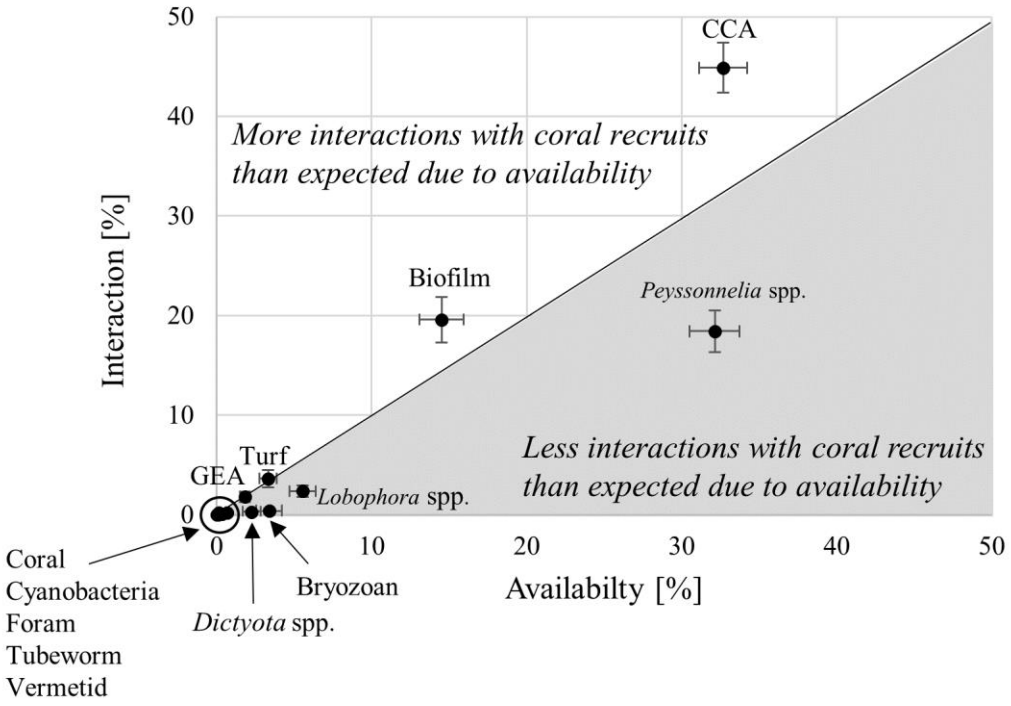

Figure 3.4. Mean percentage of coral-benthic borders involved in interactions with different benthic substrata in relation to the mean availability of those substrata on the settlement tiles. CCA = Crustose coralline algae, GEA = Green encrusting algae.

For each interaction lost by a coral recruit, the overgrowth level was recorded. Two levels of overgrowth were differentiated: only on the edge of the recruit and partial (more than just the edge) overgrowth. Algae that won more interactions against coral recruits were also more likely to partially overgrow the recruits (Figure 3.5).

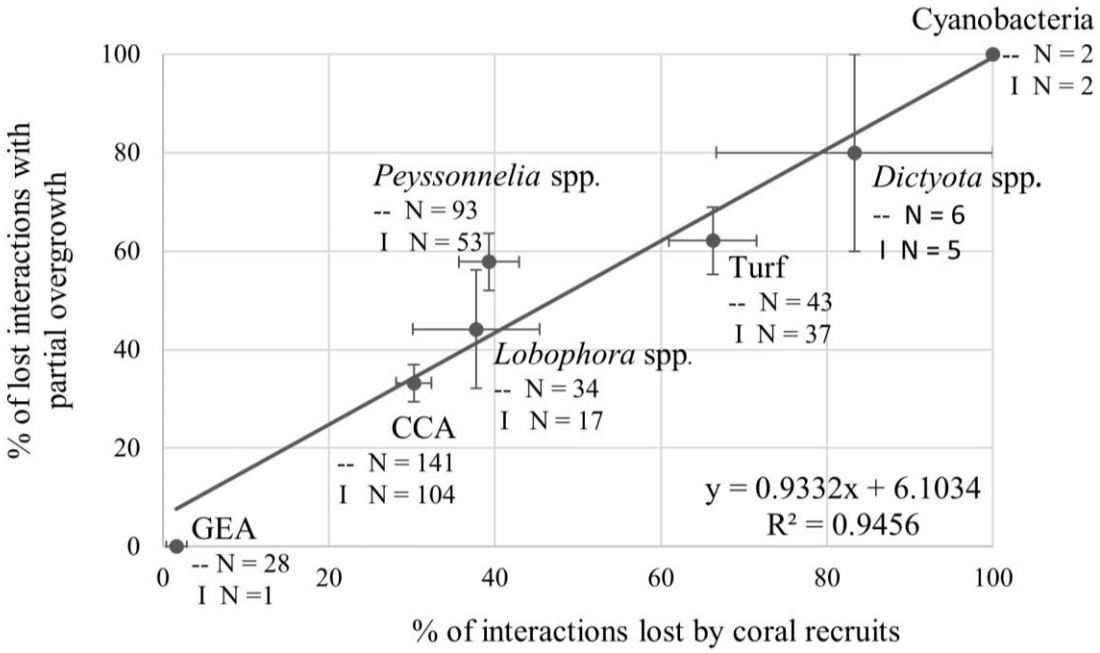

Figure 3.5. Comparison between level of overgrowth and competitive strength of algae taxonomic groups. In this graph the percentage of lost interactions where the coral recruit was partially overgrown (out of all losing interactions) is plotted against the percentage of interaction lost by the coral recruit (out of all winning or losing interactions). Means for the x-axis are calculated from tiles with interactions between the algal taxonomic group and the coral recruit (N displayed in graph) while the means for the y-axis were calculated from tiles which had at least one interaction lost by the coral recruit to that algal taxonomic group (N displayed in graph). Error bars: ±SE. CCA = Crustose coralline algae, GEA = Green encrusting algae.

On settlement tiles deployed for three months on the fore reef, most interactions were between coral recruits and either CCA (272 out of 515 interactions with other benthic organisms) or biofilm (198 interactions). Coral recruits overgrowing biofilm made up 52% of the coral-benthic border on these settlement tiles. On tiles deployed for three months on the back reef, coral recruits overgrowing biofilm only made up 31% of the coral-benthic border,

placing it as the second most frequent substratum coral interacted with. Most interactions on these tiles were between coral recruits and CCA (442 of 805 interactions with other benthic organisms, 38% of coral benthic-border). On the fore reef, coral recruits on tiles deployed for nine to fifteen months interacted mainly with CCA (306 of 433 interactions with other benthic organisms). On the back reef, coral recruits also interacted the most with CCA (213 of 370 interactions with other benthic organisms), but less frequently than on the fore reef. Many of the interactions on the back reef were between coral recruits and *Peyssonnelia* spp. (118 of 370 interactions), possibly due to *Peyssonnelia* spp. being more abundant on the back reef (51%) than on the fore reef (25%).

pocilloporid recruits differed from poritids recruits in their ability to outcompete *Peyssonnelia* spp. Pocilloporids won almost twice as many interactions as they lost against *Peyssonnelia* spp. (N = 245), while poritids won about the same number of interactions as they lost against *Peyssonnelia* spp. (N = 26).

Coral recruits did not interact with all the taxonomic groups found on the settlement tiles. No interactions were recorded between coral recruits and macroalgae, amphipod tubes, hydrocorals, hydroids, sponges or tunicates. The combined cover for these groups was less than 1% of the cryptic surface of the settlement tiles, on which coral recruits were found. The lack of interactions between coral recruits and these groups is therefore likely due to these groups being rare overall.

The percentage of the coral-benthic border taken up by a substratum was not always comparable to the cover of that substratum on the settlement tile (Figure 3.4). CCA and biofilm covered a larger part of the coral-benthic border than expected from their cover. *Peyssonnelia* spp., *Lobophora* spp., bryozoans and *Dictyota* spp. were less frequently involved in interactions with coral recruits than expected based on their cover. The percentage of the coral-benthic boarder involved in interactions between coral recruits and turf algae and green encrusting algae, respectively was similar to the cover of these algae on the settlement tiles (Figure 3.4).

An increase in cover of CCA, biofilm or *Peyssonnelia* spp. was significantly correlated with an increase in length of the coral-benthic border involved in interactions between coral recruits and these substrata (Figure 3.6). No such significant correlations were found for corals

interacting with green encrusting algae, *Lobophora* spp., or turf algae. Interactions between coral recruits and cyanobacteria, *Dictyota* spp., bryozoans, other coral recruits, foraminifera, polychaete worm tubes, and vermetids were too infrequent for a correlation analysis.

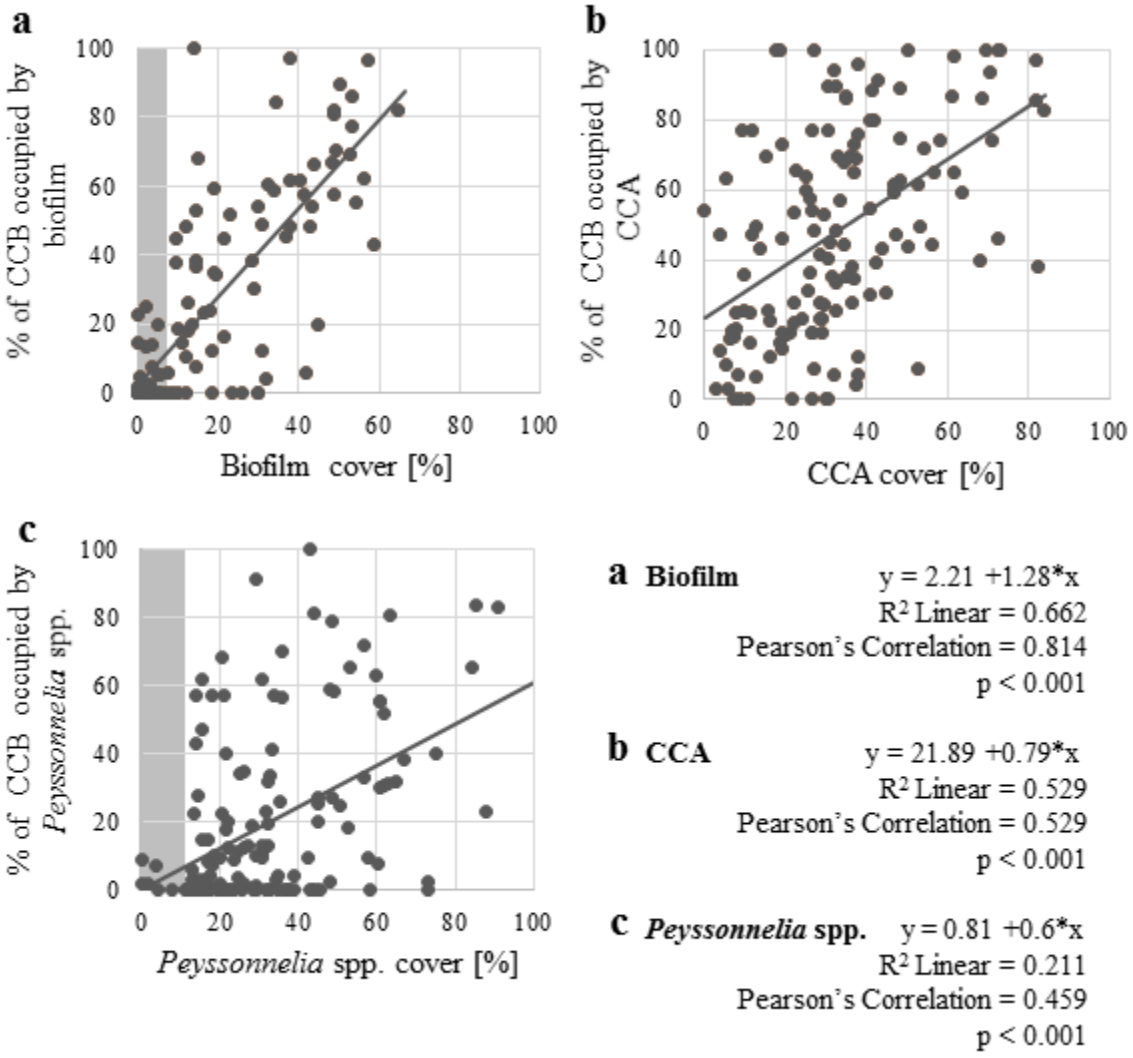

Figure 3.6. Correlation between the percentage of the coral-benthic border (CCB) occupied by interactions between coral recruits and a substratum and the percentage cover of that substratum. The *dots* represent each individual tile, the *line* shows the linear trendline. The equation of each trendline and the statistical results can be found in the list on the right side of the figure. The *grey areas* have a low amount of interactions compared to the rest of the graph. Graphs show correlation for interactions between coral recruits and (a) biofilm, (b) CCA, (c) *Peyssonnelia* spp.

3.4.2 Successful Settlement

Successful settlement (settlement and subsequent early post-settlement survival up to 2 weeks) of 299 coral recruits containing only one polyp were determined. These recruits settled on 91 different settlement tiles: 23 tiles deployed on the back reef for three months, 34 tiles deployed on the fore reef for three months, 8 deployed on the back reef for 9 - 15 months and 26 deployed on the fore reef for 9 - 15 months.

Coral recruits settled significantly more often successfully on CCA and biofilm than other substrata. Settlement success on top of CCA and biofilm substrata was significantly different on settlement tiles deployed for 3 months compared with settlement tiles deployed for 9 - 15 months (CCA: $t = -0.4188$, df = 89, $p < 0.001$, biofilm: $t = 3.231$, df = 79, $p = 0.002$, Figure 3.7). Successful settlement on top of CCA was higher than expected from CCA cover on tiles that were deployed for 9 - 15 months while successful settlement on top of biofilm was higher than expected from its cover on tiles that were deployed for 3 months (Table 3.3). On tiles deployed for three months, the measured Manly's alpha index for settlement success on top of CCA did not differ significantly from the Manly’s alpha index that was expected if the coral recruits showed no difference settlement preference and early post-settlement mortality did not differ between substrata. This indicates that coral recruits responded neutrally to CCA on these tiles. On tiles deployed for 9 - 15 months less coral recruits successfully settled on biofilm than expected from its cover. This was the only substratum for which settlement success was not consistent over time and switched from a high success rate to a rather low success rate.

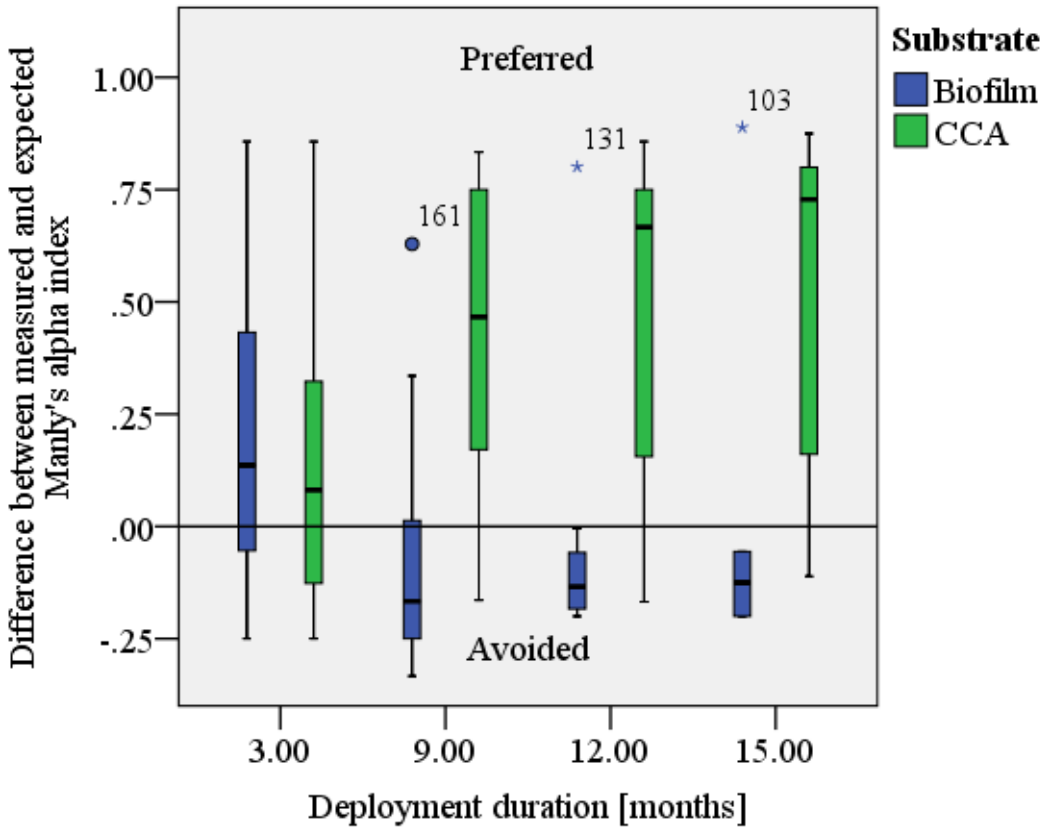

Figure 3.7. Successful settlement rates of coral recruits on top of biofilm and CCA on tiles deployed for different lengths of time. This graph shows the mean difference between the measured Manly's alpha index for CCA and biofilm and the expected Manly's alpha index for these substrata (no differences in preference for substrata or difference in early post-settlement mortality between substrata). Negative values indicate avoidance, while positive values indicate preference. The box plots include all tiles which had CCA or biofilm cover. The box of the box plot includes all data points between the 1st and 3rd Quartile, the median is indicated by a bolt line within the box. The whiskers extend to the highest and lowest values that are no greater than the 1.5 times the interquartile range (size of the box). Outliers (circles) are within the range of 1.5 and 3 times the interquartile range, while extremes (*) are values with more than 3 times the interquartile range.

Coral recruits avoided settling on algae other than CCA. Settlement rates onto *Dictyota* spp., green encrusting algae, *Peyssonnelia* spp., *Lobophora* spp. and turf algae were, on average, lower than expected based on the cover of these algae (Table 3.3).

Ten coral recruits settled partly on top of other invertebrates (bryozoans, foraminifera, polychaete worm tubes and other coral recruits, Table 3.3). Settlement onto these invertebrates

was rare, which was reflected in the measured Manly's alpha index being lower than expected for no difference in settlement preference and early post-settlement mortality between substrata ($\frac{1}{m}$) (Table 3.2). Bryozoans were abundant on settlement tiles deployed for nine or more months on the fore reef; it is therefore likely that the significant result observed here corresponds to coral recruits avoiding bryozoans as settlement substratum or early post-settlement survival being low for coral recruits that settled on bryozoans. Foraminifera, polychaete worm tubes and other coral recruits each never covered more than 5.8% of the settlement tiles.

Coral recruits never settled on top of *Dictyota* spp., which was present on ten tiles and covered over 25% on three of them. No settlement was found on top of cyanobacteria and tunicates either; these substratum types were less common than *Dictyota* spp. but each still reached a cover of over 25% on at least one settlement tile (Table 3).

Pocilloporid and poritid recruits settled on a wide range of algal taxonomic groups including CCA, green encrusting algae, *Lobophora* spp., *Peyssonnelia* spp., and turf algae. Poritid recruits had a significantly higher settlement success on CCA than expected by its cover (Table 3.3). Pocilloporids also showed a trend towards successfully settling more often on top of CCA settlement but this trend was not significant. Both pocilloporids and poritids successfully settled on biofilm more frequently than expected from its availability; this was however, not significant. Poritid recruits were less likely than pocilloporid recruits to settle successfully onto green encrusting algae, *Lobophora* spp. or turf algae . Pocilloporids settled on top of other coral recruits, foraminifera and polychaete worm tubes, while one poritid recruit settled on top of a bryozoan.

Table 3.3. Comparison between measured Manly's alpha index and the expected Manly's alpha index (no preference for settlement substratum exist and early post settlement mortality is uniform across all substrata). The first column under each deployment time (3 months, 9-15 months) and coral type (pocilloporids, poritids, total) shows the number of settlement tiles with a measured Manly's alpha index above the expected ($> \frac{1}{m}$) and below the expected ($< \frac{1}{m}$) Manly's alpha index. The mean difference (Mean Δ), its standard error (±SE) and median difference (Median Δ) between the measured and expected Manly's alpha index values is listed in the second column for each group.

	3 months		**9-15 months**		**pocilloporids**		**poritids**		**Total**	
	$> \frac{1}{m}$ $< \frac{1}{m}$	Mean Δ ±SE, Median Δ	$> \frac{1}{m}$ $< \frac{1}{m}$	Mean Δ ±SE, Median Δ	$> \frac{1}{m}$ $< \frac{1}{m}$	Mean Δ ±SE, Median Δ	$> \frac{1}{m}$ $< \frac{1}{m}$	Mean Δ ±SE, Median Δ	$> \frac{1}{m}$ $< \frac{1}{m}$	Mean Δ ±SE, Median Δ
Algae										
CCA	31	0.16 ± 0.04	28	0.54 ± 0.11	35	0.22 ± 0.05	23	**0.37 ± 0.07***	59	0.27 ± 0.04
	26	**0.08**	6	**0.59***	30	**0.17**	10	0.5	32	**0.23***
Cyanobacteria	0	-0.13 ± 0.02	-	-	0	-0.05 ± 0.06	-	-	0	-0.13 ± 0.02
	3	-0.13			3	-0.02			3	-0.13
Green encrusting algae	8	-0.01 ± 0.05	0	**-0.16 ± 0.02***	7	-0.03 ± 0.05	1	-0.08 ± 0.7	8	-0.04 ± 0.04
	27	**-0.14***	7	-0.13	27	**-0.14***	11	**-0.14***	34	**-0.14***
Lobophora spp.	7	-0.03 ± 0.04	11	-0.13 ± 0.03	7	-0.04 ± 0.04	1	-0.14 ± 0.04	8	-0.08 ± 0.03
	26	**-0.14***	2	**-0.13***	32	**-0.125***	23	**-0.17***	47	**-0.14***
Peyssonnelia spp.	4	-0.14 ± 0.01	5	-0.07 ± 0.1	5	-0.11 ± 0.02	4	**-0.10 ± 0.05***	9	-0.12 ±0.02
	53	**-0.17***	29	**-0.17***	60	**-0.17***	29	-0.17	82	**-0.17***
Turf	3	-0.12 ± 0.02	3	-0.10 ± 0.03	7	-0.09 ± 0.02	1	**-0.12 ± 0.03***	6	-0.11 ±0.02
	40	**-0.14***	15	**-0.13***	40	**-0.14***	20	-0.14	55	**-0.14***

Table 3.3 continued

	3 months		9-15 months		pocilloporids		poritids		Total	
	$> \frac{1}{m}$ $< \frac{1}{m}$	Mean Δ ±SE, Median Δ	$> \frac{1}{m}$ $< \frac{1}{m}$	Mean Δ ±SE, Median Δ	$> \frac{1}{m}$ $< \frac{1}{m}$	Mean Δ ±SE, Median Δ	$> \frac{1}{m}$ $< \frac{1}{m}$	Mean Δ ±SE, Median Δ	$> \frac{1}{m}$ $< \frac{1}{m}$	Mean Δ ±SE, Median Δ
Invertebrates										
Bryozoans	0	-0.14 ± 0.01	1	-0.11 ± 0.04	0	**-0.14 ± 0.01***	1	**-0.13 ± 0.03***	1	-0.13 ±0.02
	13	**-0.14***	18	**-0.13***	18	-0.125	15	-0.15	31	**-0.14***
Corals	2	-0.05 ± 0.06	1	-0.025 ± 0.2	3	-0.04 ± 0.06	0	-0.13 ± 0.01	3	-0.04 ±0.07
	7	**-0.14**	3	-0.13	8	**-0.125**	4	-0.13	10	**-0.17**
Foraminifera	1	0.02 ± 0.14	0	-0.12 ± 0.01	1	-0.05 ± 0.06	0	-0.14 ± 0.02	1	-0.08 ±0.05
	3	-0.11	8	**-0.12***	8	**-0.11***	4	-0.13	10	**-0.11(*)**
Polychaete worm tubes	4	-0.07 ± 0.04	1	-0.12 ± 0.02	5	-0.05 ± 0.04	0	**-0.15 ± 0.01***	5	-0.09 ±0.03
	27	**-0.14***	11	**-0.13***	30	**-0.13***	13	-0.14	39	**-0.14***
Tunicates	-	-0.13 ± 0.01	0	-0.13 ± 0.01	0	**-0.13 ± 0.01***	0	**-0.13 ± 0.01***	0	-0.13 ±0.01
	-	-0.13	1	-0.13	13	-0.125	7	-0.13	17	**-0.13***
Other										
Biofilm	14	0.22 ± 0.04	0	-0.02 ± 0.06	35	0.15 ± 0.04	10	**0.15 ± 0.08**	41	0.14 ± 0.04
	8	**0.21***	3	**-0.13***	26	**0.05**	16	-0.08	40	**0.04**

* $p < 0.01$ (tested for means in bold using paired t-test and for medians in bold using paired sign test)

(*) $0.01 < p < 0.05$ (tested for means in bold using paired t-test and for medians in bold using paired sign test)

3.4.3 Benthic succession

The benthic community on the settlement tiles differed between tiles deployed for 3 months and tiles deployed for 9, 12 and 15 months, respectively ($p = 0.001$ for 3 mo vs 9 mo, 3 mo vs 12 mo and 3 mo vs 15 mo). A significant difference in benthic community composition was also observed between tiles deployed for 3 months in 2013 and in 2014 ($p = 0.0054$). Tiles deployed for 9 - 15 months did not differ significantly in their benthic community composition (9 mo vs 12 mo: $p = 0.5217$, 9 mo vs 15 mo: $p = 0.1824$, 12 mo vs 15 mo: $p = 0.2025$). The benthic community composition on tiles at the back reef sites was significantly different from that at the fore reef sites. The benthic community found on settlement tiles deployed at FR9 differed significantly ($p < 0.05$) from all other sites except RT10 ($p = 0.0627$), while the benthic community observed on tiles at RT1 differed from all other sites. The settlement tiles deployed at EC2 had a significantly different benthic community composition from tiles deployed at the fore reef sites and RT4 ($p = 0.0226$) and RT10 (0.0053). The MDS plot showed no apparent difference between tiles deployed for 3 months in 2013 and 2014 (Figure 3.8). I therefore divided the settlement tiles into two groups: deployed for 3 months and deployed for 9 - 15 months. Within these groups I differentiated between tiles deployed at RT1, other back reef sites, FR9 and other fore reef sites.

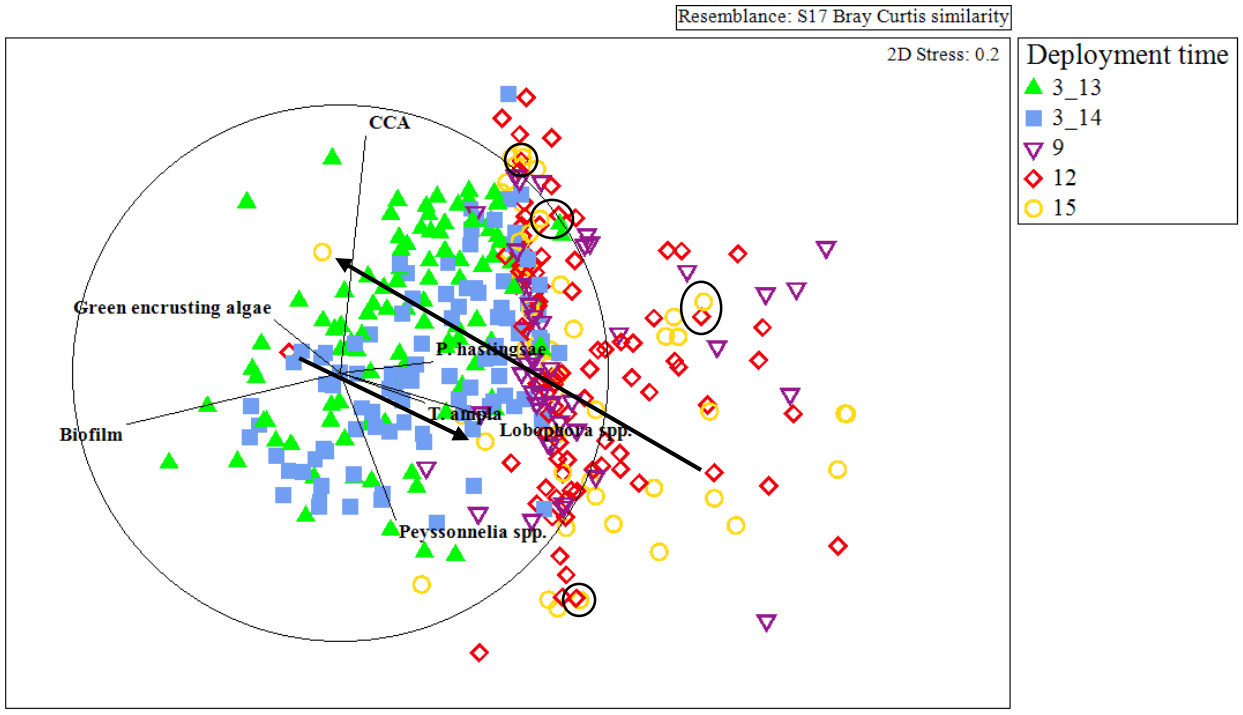

Figure 3.8. Benthic community composition on the cryptic side of settlement tiles deployed for 3, 9, 12 and 15 months. The vectors in this MDS plot show Pearson's correlations with a value > 0.3. Each symbol represents a single tile. Tiles are grouped according to their deployment duration: 3_13: 3 months in 2013, 3_14: 3 months in 2014, 9: 9 months, 12: 12 months and 15: 15 months. The chosen resemblance measure and 2D stress value of the MDS analysis can be found on the top right corner of the MDS plot. *Black arrows* show the change in benthic community composition between 12 months (*red diamond*) and 15 months (*yellow circle*) of deployment for two tiles that had a large change in benthic community composition. *Black ovals* were drawn around benthic community composition data for tiles that had very little change in benthic community composition between 12 months (*red diamond*) and 15 months (*yellow circle*) of deployment.

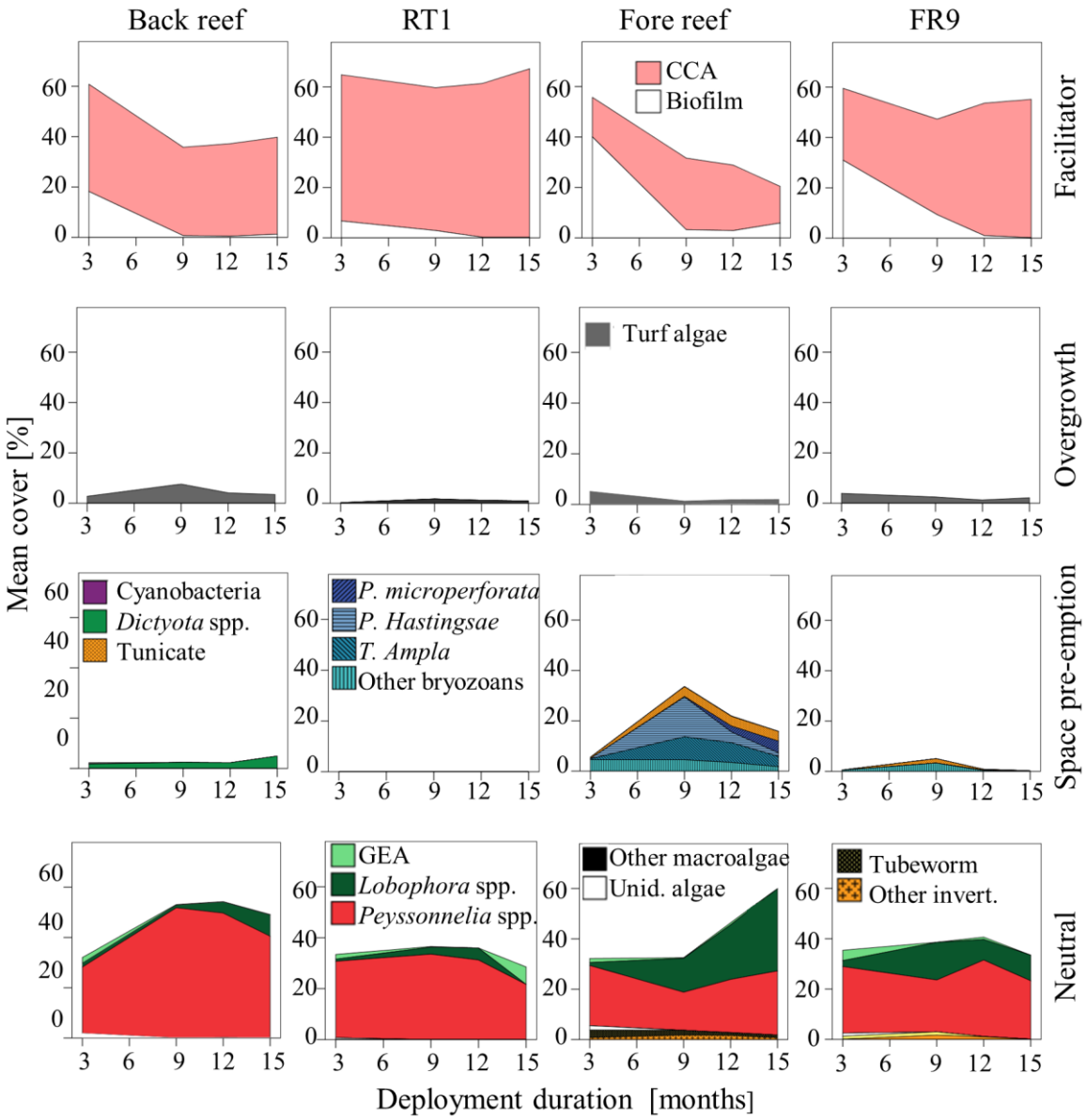

Figure 3.9. Change in mean percentage cover of substrata found on the settlement tiles over time. Substrata are grouped together according to how they affect coral recruitment (Facilitators, overgrowth, space pre-emption, neutral). Sites were grouped together if the benthic composition on settlement tiles did not differ significantly between them (PERMANOVA). Back reef: RT4, RT10, RT13, EC1, EC2. Fore reef: FR3, FR5, FR7. CCA = Crustose coralline algae, GEA = Green encrusting alage, unid. algae: unidentified algae, other invert. = other invertebrates.

The benthic community composition on tiles deployed for 3 months differed from that on tiles deployed for 9 - 15 months, mainly in the cover of biofilm on the settlement tiles (Figure 3.8 & Figure 3.9). Tiles deployed for 3 months on the fore reef had a greater biofilm cover than tiles on the back reef (Figure 3.10 & Figure 3.9). Tiles deployed for 3 months at RT1 had almost as little biofilm on them as tiles deployed for 9 - 15 months (Figure 3.10 & Figure 3.9). The main difference between tiles deployed for 9 - 15 months at FR3, FR5 and FR7 (fore reef) and FR9 and the back reef was the abundance of bryozoans (*P. hastingsae*, *T. ampla*) and *Lobophora* spp. (Figure 3.10 & Figure 3.9). For tiles deployed for 3 months and 9 - 15 months there was a large within-area variability of CCA and *Peyssonnelia* spp. cover. This was especially pronounced for tiles deployed for 9 - 15 months on the back reef (Figure 3.10).

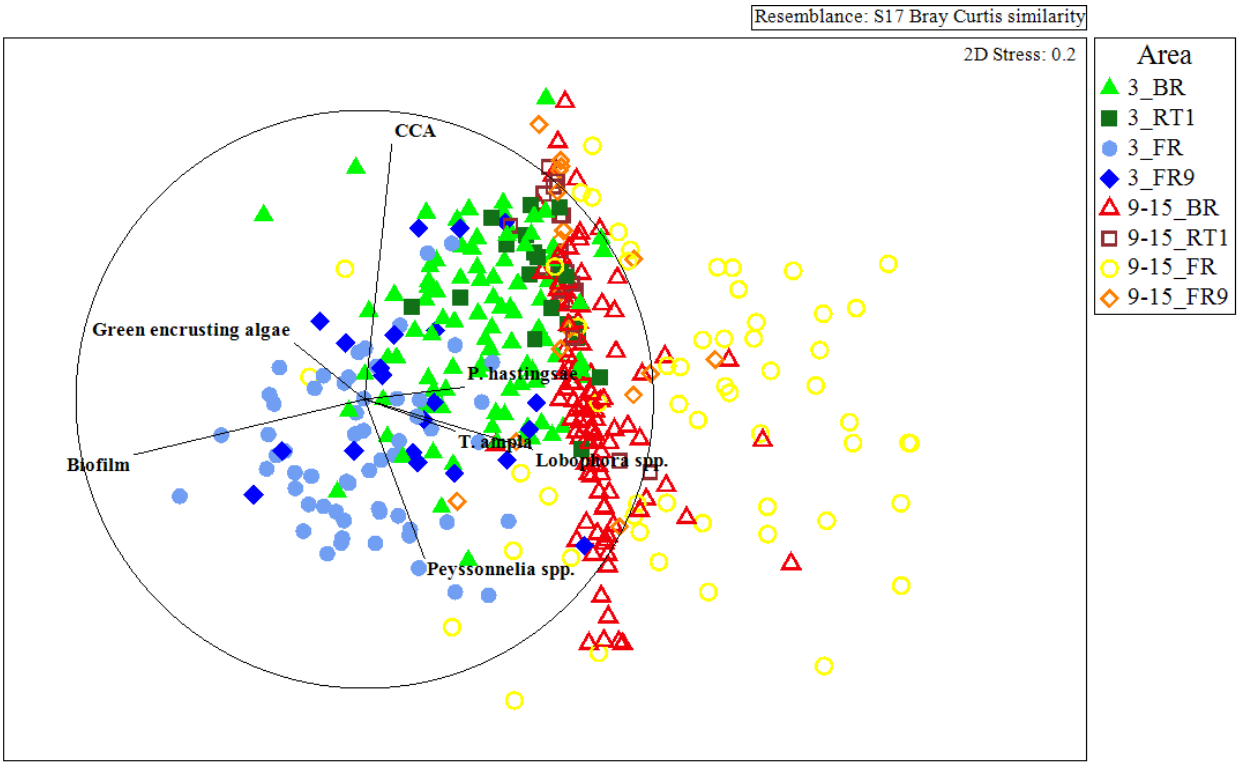

Figure 3.10. Benthic community composition on the exposed side of settlement tiles deployed for 3, 9, 12 and 15 months. The vectors in this MDS plot show Pearson's correlations with a value > 0.3. Each symbol represents a single tile. Tiles are grouped according to their deployment duration (3 and 9 – 15 months) and area on the reef they were deployed at: BR: back reef not including RT1, FR: fore reef not including FR9. The chosen resemblance measure and 2D stress value of the MDS analysis can be found on the top right corner of the MDS plot.

On the back reef, benthic mean cover increased from 93.3 ± 1.9% (SE) (RT1) and 81.8 ± 1.3% (SE) (other back reef sites) on tiles deployed for 3 months to a mean cover of over 99% on tiles deployed for 9 - 15 months (Figure 3.9). During the same time period, benthic cover on settlement tiles on FR3, FR5, and FR7 increased from 59.1 ± 2.2% (SE) to a mean cover over 96%. Benthic cover increased more slowly at FR9 from 69.0 ± 3.4% (SE) on tiles deployed for 3 months to 90.7 ± 4.0% (SE) on tiles deployed for 9 months, to a mean cover of over 98% on tiles deployed for 12 or 15 months (Figure 3.8).

Algae were more abundant than invertebrates on the settlement tiles. Algal taxonomic groups on the settlement tiles included: CCA, Cyanobacteria, *Dictyota* spp., green encrusting algae, macroalgae, *Lobophora* spp., *Peyssonnelia* spp. and turf algae. The algal layer deposited on tiles deployed for 3 months was in certain cases so thin that it was not possible to identify the algal type. These algae were classified as a thin layer of unidentifiable algae. CCA and *Peyssonnelia* spp. were the most abundant algal taxonomic groups present on the settlement tiles (Figure 3.9).

Invertebrates never reached a mean cover above 1% on tiles deployed on the back reef. On fore reef tiles deployed at FR3, FR5 and FR7 mean invertebrate cover ranged from 9.32 ± 1.53% (SE) on tiles deployed for 3 months, to 37.26 ± 6.37% (SE) on tiles deployed for 9 months. Bryozoans were less abundant on tiles deployed at FR9; invertebrate cover therefore ranged from 1.87 ± 1.53% (SE) on tiles deployed for 3 months, to 8.14 ± 1.53% (SE) on tiles deployed for 9 months. Invertebrate taxonomic groups on the settlement tiles included: amphipod tubes, bryozoans, foraminifera, hydrocorals, hydroids, sponges, polychaete worm tubes, tunicates, vermetids and corals. Bryozoans were the most abundant invertebrate group found on settlement tiles deployed on the fore reef. Their abundance peaked on tiles deployed for 9 months. Thirty three species of bryozoan were found, the most abundant being *Turbicellepora ampla* (Kirkpatrick 1888), *Parasmittina hastingsae* (Soule and Soule 1974) and *Pleurocodonellina microperforata* (Tilbrook 2006). *T. ampla* and *P. hastingsae* reached maximal abundance after 9 months of tile deployment. While *P. hastingsae* cover decreased sharply after this peak, *T. ampla* maintained its maximal cover on tiles deployed for 12 months. *P. microperforata* recruited later to the settlement tiles and steadily increased its cover from tiles deployed for 9 months to tiles deployed for 15 months. Other invertebrates with substantial tile cover included tunicates, polychaete worm tubes and sponges.

The different substrata found on the settlement tiles were classified into four categories: Facilitators included CCA and biofilm, which were preferred as settlement substratum by coral recruits, Space pre-emption competitors which included all substrata on which no more than one coral recruited despite high cover of that substratum (*Dictyota* spp., cyanobacteria, bryozoan, and tunicates). Turf algae was placed in the overgrowth competitor category because it had a competitive advantage over coral recruits and overgrew more than 10 recruits. The remaining substrata did not have a very clear relationship with coral recruits and were placed in the neutral category.

3.5 DISCUSSION

In this study the interactions between coral recruits and their benthic neighbours were investigated on a millimetre to centimetre scale. Green encrusting algae and turf algae followed my hypothesis that the number of interactions between a benthic taxonomic group and the coral recruits is proportional to the cover of that particular taxonomic group. Other benthic taxonomic groups had fewer or more interactions with coral recruits than expected. For CCA, biofilm and *Peyssonnelia* spp. a positive correlation was found between their cover and the number of interactions coral recruits had with them. Coral recruits won a majority of the interactions with green encrusting algae, CCA, *Lobophora* spp., and *Peyssonnelia* spp., but lost many interactions with turf algae. Interactions with cyanobacteria and *Dictyota* spp. and invertebrates were rare, as were stand-off interactions. As I hypothesised, both pocilloporids and poritids recruited onto many different substrata. The high successful settlement rate of poritid larvae onto CCA was significantly higher than expected from the available CCA cover. On tiles deployed for 3 months, successful settlement onto biofilm was significantly greater than expected from the available biofilm cover. On tiles deployed for 9 - 15 months, recruits did not settle more successfully than expected onto biofilm, but settled very successfully on top of CCA instead. Lastly I investigated if the percentage cover of benthic organisms on the settlement tiles different spatially and temporarily. Spatial differences were found between the fore reef and the back reef, with invertebrates being almost absent on the back reef while being common on the fore reef, especially on tiles deployed for more than 9 months. Settlement tiles deployed for 3 months had lower overall benthic cover than tiles deployed for 9 – 15 months. CCA and *Peyssonnelia* spp. were the most abundant algal taxonomic groups present on the settlement tiles.

3.5.1 Succession of benthic organisms

On tiles deployed for 3 months, benthic organisms were still in the process of colonising bare space and covered 81.8% ± 1.28 (SE) of the tile surface on the back reef and 69.03% ± 3.41 (± SE) on the fore reef. Tiles deployed for 9 - 15 months had a mean benthic cover that exceeded 96%, which indicates that benthic organisms have to compete for space with each other in order to increase their cover on these settlement tiles. There were two exceptions to this trend: settlement tiles deployed at the back reef site RT1 reached a mean benthic cover of 93.31% ± 1.85 (SE) after only three months while tiles deployed at the fore reef site FR9 did not reach a mean benthic cover over 91% until twelve months of deployment. The benthic cover on the settlement tiles deployed at RT1 did not change profoundly, after 3 months of deployment which indicated that these tiles completed their benthic succession after 3 months. Price et al. (2012) found a similar succession trajectory on the sandwich tiles they deployed on Palmyra Atoll (2 tiles deployed on one stake with a spacer between them) : After three months, the average benthic cover was <80% but increased to >96% for each tile by seven months of deployment. On Palmyra Atoll, cryptic bare space is therefore almost entirely colonised by benthic organism within three to twelve months of it becoming available.

Settlement tiles deployed on the fore reef were colonized slower than settlement tiles deployed on the back reef. This was mainly due to the quickly establishment (within 3 months) of high CCA and *Peyssonnelia* spp. cover on the settlement tiles deployed on the back reef. CCA growth rates are dependent on water temperature, desiccation, availability of light and intensity of grazing (Littler and Doty 1975; Littler and Littler 1984; Steneck 1997; Figueiredo et al. 2000; Bôas et al. 2005). Mean bottom water temperature was very uniform within the whole reef system as well as within the study period. Grazing also did not affect the CCA colonies in question, as they were located on the cryptic side of the settlement tiles. It is however very likely that the higher light levels found on the back reef sites lead to faster CCA growth on the settlement tiles deployed there. Even though they are adapted to lower light levels, cryptic CCA species grow faster under higher irradiance levels (Bôas et al. 2005). The vertical distribution of Rhodophyta, the phyla to which *Peyssonnelia* spp. belong to, is mainly controlled by light levels (Lüning 1985). It is therefore likely that the *Peyssonnelia* spp. found on the settlement tiles at Palmyra Atoll are better adapted to the light levels found on the back reef and grow faster there than on the fore reef.

On the back reef, the composition of the benthic cover was dominated by CCA and *Peyssonnelia* spp. after nine, twelve and fifteen months (linear cluster of red squares and purple diamonds in Figure 3.9). Overall benthic cover on tiles deployed for nine to fifteen months on the fore reef was comparable to the back reef, but its composition was less stable. This was mainly due to a decrease in bryozoan cover and an increase in *Lobophora* spp., which were both hardly found on the back reef. I conclude that both on the back reef and fore reef, a community dominated by encrusting organisms establishes within nine months of substratum becoming available. In the Caribbean, benthic succession also ended in a community dominated by encrusting organisms (Vermeij 2006; Arnold and Steneck 2011). However, the composition of the encrusting organisms varied between Palmyra Atoll and the Caribbean and bare substratum was colonised faster on Palmyra at a rate that was comparable to Split Solitary Island in Australia (Fairfull and Harriott 1999). Settlement tiles deployed at Kaneohe Bay, Hawaii (Chapter 4) also showed high turf and green encrusting algae cover after just 1 month of deployment. It is therefore likely that benthic recruitment occurs slower on Caribbean reefs than Pacific reefs, despite Caribbean reefs being more often algal dominated than Pacific reefs (Roff and Mumby 2012). My results are in line with the findings of Jackson and Buss (1975) that coral recruitment rates decrease as the benthic community develops. Overall coral recruitment (all sites combined) was highest three months after tiles were deployed and decreased as deployment duration became longer. The three sites with the highest recruitment rates (EC1, EC2 and FR9) all followed this trend with a single exception: recruitment rates onto tiles deployed for 12 months at FR9 were higher than recruitment rates onto tiles deployed for 9 months or tiles deployed for 3 months in 2014.

The back reef and fore reef differed in their benthic community composition and the rate of benthic succession. Benthic organisms recruited faster onto bare substratum on the back reef. Furthermore, *Lobophora* spp. and tunicates were more abundant on the fore reef than the back reef. Lastly, bryozoans were almost completely absent on the back reef while they were abundant on the fore reef. At Heron Island and Pelorus Island both situated on the Great Barrier Reef, bryozoan abundance has been found to be higher at sites located at a depth of 9-12 meters than sites located at a depth of 2-3 meters (Dunstan and Johnson 1998; Baird et al. 2003). Price et al. (2012), however, found that bryozoan cover was similar between fore reef and back reef sites on Palmyra. The difference between my result and that of Price et al. (2012) may be due to Price et al. (2012) deploying their tiles as a staked pair (sandwich technique) while single tiles were

deployed in this study. The sandwich technique may lead to lower light levels compared to single tiles, encouraging bryozoans to settle at shallower depth.

3.5.2 Interactions between coral recruits and other benthic organisms

The length of the coral-benthic border occupied by bare substratum covered in biofilm decreased over time as biofilm became rarer on the settlement tiles. On tiles deployed for nine months or longer, 99% (back reef) and 94% (fore reef) of the coral-benthic border was involved in interactions with benthic organisms other than biofilm. This indicates that competition for space becomes more intense as a benthic community develops, consistent with the suggestion of Jackson (1977). Nevertheless, coral recruits won most of the interactions with other benthic organisms even when they were almost completely surrounded by competitors. This supports the results of Barott et al. (2012) who showed that in the Northern Line Islands, small corals (diameter = 5 cm) were able to outcompete other benthic organisms despite being surrounded by them. Barott et al. (2012) offered two explanations why small corals were observed to be better than large corals at competing with other benthic organisms: (1) interactions where small corals lose to other benthic organisms were harder to detect and are therefore under-represented in the results, which means that small corals were actually not better competitors than large corals and (2) young corals grow quickly and do not have to allocate energy to reproduction (Babcock 1991; Soong and Lang 1992; Soong 1993) giving them an advantage when competing with other benthic organisms. My results suggest that it is unlikely that most interactions between coral recruits and other benthic organisms were not detected due to the coral recruits being overgrown fully. Most of the coral recruits which were overgrown by other benthic substrata where overgrown just at the edge of the recruit. If overgrowth happened rapidly, then this stage of overgrowth would be less commonly found than partial or almost total overgrowth. Ferrari at al. (2012) also found evidence that small coral colonies are good competitors: the effect of macroalgae on small coral colonies (diameter = 10 cm) did not significantly differ between coral colonies that interacted with algae on 25% of their border and colonies which were completely surrounded by algae. The recruits in my study were even smaller than the smallest size class used by Barott et al. (2012). My study therefore complements their study on competition between corals and other benthic organisms in the Northern Line Islands as it adds an additional (smaller) size class and results from an additional island not surveyed by Barott et al. (2012).

The length of the coral-benthic border involved in interactions with a benthic taxonomic group was not always similar to the cover of that group on the settlement tiles. Barott et al. (2012) reported a similar result for coral-algal interactions of adult corals in the Northern Line Islands. They did not survey Palmyra Atoll, but my results followed the patterns they found on Palmyra Atoll's closest neighbour Kingman Reef, where corals interacted more frequently with CCA than expected by its cover. This may be caused by the coral recruits settling more often on CCA than other substrata. Frequent settlement of coral recruit onto CCA and biofilm likely determined the number of interactions between coral recruits and the three most common settlement substratum types: CCA, biofilm, and *Peyssonnelia* spp. For each of these three substrata the number of coral interactions with the substratum increased as the substratum cover increased. However, the intercept and slope of this relationship varied between the substratum types. Coral recruits interacted more frequently with CCA and biofilm than expected by their cover alone, while the opposite was true for *Peyssonnelia* spp. This is reflected in the corals' successful settlement - they showed high successful settlement rates on top of CCA and biofilm but struggled to settle onto *Peyssonnelia* spp. Each recorded settlement counts as an interaction between coral recruits and that substratum, leading to an increase in recorded positive interactions. The substratum that corals settle on will also immediately become their most likely competitor as it is located next to and underneath the coral. Settlement preference for a substratum therefore leads directly to an increased likelihood of interaction, both positive and negative, with the taxon forming the substratum. I therefore suggest that if coral recruits preferred to settle on CCA and biofilm, they also interacted more frequently with these two substrata, while avoidance of settlement onto *Peyssonnelia* spp. resulted in fewer interactions with *Peyssonnelia* spp. than expected from its cover.

I found a highly significant linear relationship between the ability of algae to outcompete coral recruits and their ability to partially overgrow coral recruits. This suggests that both measures of competitive strength (number of winning interactions and ability to partially overgrow coral recruits) are strongly related. Algal taxonomic groups that win a large number of the interactions with coral recruits will also partially overgrow the recruit in most of the interactions that they win. Since the slope of the linear trend line is close to 1, I conclude that coral recruits use the same defensive strategies to deter algae from overgrowing their edge and from overgrowing them partially. Further studies on this relationship are needed to determine if this true at other locations.

If this is a globally typical relationship then the ability of algae to outcompete coral recruits can be used to estimate their ability to partially overgrow coral recruits and vice versa. Furthermore, results from studies using either of these two measurements of competitive strength become directly comparable.

Some algal taxonomic groups were better at overgrowing coral recruits than others. This may be the result of differential growth rates, sensitivity to allelochemicals, interference competition for food, the ability to produce specialised overgrowth and defensive structures, the angle of the attack, and colony surface conditions (Jackson and Buss 1975; Jackson 1979; Palumbi and Jackson 1982; Buss 1986; Lidgard and Jackson 1989). Two different CCA species from the Great Barrier Reef for example employed distinctly different strategies to overgrow coral recruits in a lab based study. *Porolithon onkodes* grows up and over the coral recruit while *Titanoderma prototypum* first surrounds the recruit and then reaches around the basal plate of the recruit until it completely overgrows it (Harrington et al. 2004). Algae taxonomic groups with a competitive advantage over coral recruits included cyanobacteria, *Dictyota* spp., and turf algae. These are all filamentous or upright growing algae which overgrow coral recruits by loosely creating shade and abrasion rather than completely covering them. Encrusting algal species (green encrusting algae, CCA, *Lobophora* spp., *Peyssonnelia spp.*) were all inferior competitors to coral recruits and often were not able to overgrow coral recruits further than the edge of the recruit. Coralline algae grow slowly (Adey and Vassar 1975) and are often fouled by fast growing and highly productive filamentous algae (Steneck 1983a). It is therefore not surprising that faster growing filamentous algae are better at overgrowing coral recruits than are slow growing encrusting algae. Adult corals in the Northern Line Islands showed the same pattern in competitive strength against algae as the coral recruits in this study: while they could not outcompete turf algae, they have a competitive advantage over CCA (Barott et al. 2012). Coral recruits in the Dutch Antilles, are easily overgrown by CCA species (Bak and Engel 1979; Van Moorsel 1985). However, Harrington et al. (2004) found in a lab study that CCA rarely overgrew coral recruits and observed similar post-settlement survival rates for recruits on *T. prototypum* as on terracotta tiles covered by a biofilm. Overgrowth by macroalgae, turf algae, *Dictyota* spp. and *Lobophora* spp. on the other hand is detrimental to coral recruits (Box and Mumby 2007; Hauri et al. 2010; Venera-Ponton et al. 2011). Box and Mumby (2007) found that negative effects of *Lobophora variegata* and *Dictyota pulchella* were caused in large part by shading and abrasion rather than allelochemical inhibition.

3.5.3 Successful settlement

The substrate onto which coral larvae could settle the most successfully changed significantly over time as the benthic community developed. Corals expressed an increased in successful settlement on top of CCA between tiles deployed for three months and tiles deployed for nine to fifteen months. In the same time frame, the settlement success on biofilm decreased drastically. This can also be observed in Figure 3.6 where the amount of interactions with biofilm drops suddenly when biofilm cover drops below ~8%. Arnold and Steneck (2011) found the same trend in Belize: when biofilm became scarce (< 10 - 20%), coral recruits started to avoid settling on it and instead showed an augmented preference for settlement onto CCA, *Peyssonnelia* spp. and invertebrate crusts. In Arnold and Steneck's study, biofilm cover did not drop under 20% until the settlement tiles were deployed for two years; the change in settlement preference or early post-settlement survival therefore occurs at different times at Palmyra Atoll and Belize. Nonetheless, the results from these two studies show that coral recruits in the Caribbean and the Pacific respond to changes in biofilm availability in the same way. This change in settlement response is likely due to a change in the biofilm composition. Metamorphosis (settlement) rate on biofilm increased from two week old microbial films to four to eight week old biofilms (Webster et al. 2004). Furthermore, particulate carbon levels change the community composition of biofilms and with it the settlement response of coral to biofilms (Prescott 2015). It is, however, still unclear why settlement success of coral larvae on top of biofilm decreases as the successional stage of the benthic community (availability of biofilm) changes. I hypothesise that when bare substratum covered in biofilm is abundant, coral recruits benefit from settling on this substratum as it is likely that they canreach an adequate size before they have to start competing with other algae. Once bare substratum covered in biofilm becomes scarces, the distance between the newly settled coral recruit and other benthic organisms on the edge of the bare substratum becomes shorter. Coral recruits likely have to compete with other benthic organisms earlier than when bare substratum is abundant. The growth period until the coral recruit has to compete with other benthic organisms therefore decreases and uncertainty exists on what kind of organisms they have to compete with. It may therefore be advantageous for coral larvae to settling on well-established benthic communities to decrease the uncertainty of their competitor species by choosing to settle on CCA, which has a competitive disadvantage to coral recruits.

I found that pocilloporid and poritid recruits settled on a wide range of algal taxonomic groups. Both pocilloporids and poritids settled on CCA more often than expected from the percentage cover of CCA. This trend was significant for poritids. This finding supports previous studies that reported that pocilloporids and poritids respond to CCA in similar ways, indicating that both groups require the presence of CCA for settlement (Morse et al. 1996; Baird and Morse 2004; Price 2010; O'Leary et al. 2012) despite being able to recruit to many different substratum types.

3.5.4 Role of other benthic organisms in coral recruitment

Benthic organisms have been found to influence coral recruitment through promotion of settlement, space pre-emption and post-settlement competition, which includes overgrowth and shading (reviewed by Birrell et al. 2008). My results support the general consensus that CCA and biofilm promote coral larval settlement.

Turf algae, cyanobacteria, *Dictyota* spp., tunicates and bryozoans have a negative effect on coral recruitment. Turf algae have a competitive advantage over coral recruits and have been found to often partially overgrow them. Turf algae therefore influence coral recruitment negatively on Palmyra Atoll. The interaction zones between corals and turf or macroalgae are hypoxic and associated with coral tissue damage and are therefore more "toxic" than the interaction zone between corals and CCA (Barott et al. 2009). The effect of turf algae on coral recruitment varies considerably with studies reporting either inhibition or facilitation (Birrell et al. 2005, 2008, Vermeij 2005, 2006; Kuffner et al. 2006; Arnold et al. 2010; Diaz-Pulido et al. 2010; Venera-Ponton et al. 2011). This is likely caused by algal turf consisting of several different algae species. Turf algae assemblages therefore often vary in height and sediment trapping (Birrell et al. 2008; Diaz-Pulido et al. 2010). Generally, well-grazed algal turf will only overgrow the smallest recruits and provide little effective shade. Thick algal mats on the other hand are capable of overgrowing all sizes of recruits and their height will have major shading effects on the recruits (Birrell et al. 2008). Cyanobacteria, *Dictyota* spp. and bryozoans overgrew more coral recruits than *vice versa*. Interactions between these benthic taxonomic groups and coral recruits were however rare even on settlement tiles on which these benthic taxonomic groups were abundant. Coral recruits avoid settling on these substrata and for this reason they affect coral recruitment mainly through space pre-emption. The same is true for tunicates, which have never been found to interact with coral

recruits. I propose that the negative correlations between coral recruitment and bryozoan cover reported in Chapter Two and by Glassom et al. (2004) and Dustan and Johnson (1998) are mainly due to coral larvae avoiding settlement on bryozoans. Other studies also found that cyanobacteria and *Dictyota* spp. affect coral recruitment through space pre-emption. Cyanobacteria have been found to negatively affect recruitment rates of pocilloporids and were avoided as settlement substratum by poritids (Kuffner and Paul 2004; Kuffner et al. 2006). *Dictyota* spp. both decreased recruitment rates of poritids and changed their recruitment location (Kuffner et al. 2006).

3.5.5 Overall conclusion

Many of the benthic taxonomic groups found on the settlement tiles deployed at Palmyra neither promoted coral settlement nor outcompeted coral recruits once they had settled on the tiles. Coral recruits interacted often with the more abundant substrata in this group: *Peyssonnelia* spp., *Lobophora* spp. and green encrusting algae. I therefore did not find any evidence for the often stated negative effects of *Peyssonnelia* spp. on coral recruitment (Birrell et al. 2008; Diaz-Pulido et al. 2009; Arnold et al. 2010; Hauri et al. 2010; Venera-Ponton et al. 2011; Sin et al. 2012). Furthermore, in Chapter Two I found a positive relationship between *Peyssonnelia* spp. and the presence of pocilloporid recruits on the fore reef. *Lobophora* spp. have been found to decrease poritid recruitment (Kuffner et al. 2006). A previous study on Palmyra Atoll has however identified *Lobophora* spp. as an often chosen substratum for coral settlement (Roth and Knowlton 2009). I found that 18% of all coral recruits with a single polyp settled at least partly on *Lobophora* spp., confirming Roth and Knowlton's (2009) observation. However, this did not reflect a settlement preference of coral recruits for *Lobophora* spp. but was more likely the result of *Lobophora* spp. being abundant and coral larvae on Palmyra Atoll settling on many different substrata.

In Chapter Two, a significant negative correlation between the presence and abundance of pocilloporid recruits on settlement tiles and the total deployment duration of the tiles (succession stage of benthic community) was found. In this chapter it was shown that overgrowth competition intensifies as the succession of the benthic community progresses. Coral larvae furthermore changed which substrata they preferred to settle on when they encountered settlement tiles deployed for over nine months. The simultaneous decrease in biofilm cover, increase in bryozoan

cover and overgrowth competition is the likely cause of the negative correlation between pocilloporid recruitment rates and age of the benthic community found in Chapter Two.

3.5.6 Importance

The results of this chapter identify important interactions between corals and other benthic organisms on both the coral settlement and coral post-settlement level. These new insights together with the findings on benthic succession on the settlement tiles provides the modellers of the Reefs Tomorrow Initiatives reef resilience model with detailed information on how bare substratum is colonised on Palmyra's reefs. Palmyra Atoll is a quasi-pristine coral reef that likely resembles coral reefs of the Central Pacific in absence of anthropogenic disturbances (Jackson 1992; Sandin et al. 2008). The interactions found between coral recruits and other benthic organisms in this study therefore gives insight into how coral settlement preference is established. I found that coral larvae show high successful settlement rates on to bare substratum covered in biofilm and CCA. Settlement preference for these two substrata decreased the possibility of being overgrown by other benthic organisms. The benthic community on Palmyra covered a larger part of the settlement tiles more quickly than in studies conducted in the Caribbean (Vermeij 2006; Arnold and Steneck 2011), which resulted in coral recruits interacting with other benthic organisms on almost their entire border. It is therefore not surprising that overgrowth avoidance likely played a role in the adaption of settlement preference for bare substratum covered in biofilm and CCA species.

CHAPTER 4

Parrotfish bite marks – a refuge for coral recruits?

4.1 ABSTRACT

Settlement of coral larvae and post-settlement survival are two key steps for successful coral recruitment. Coral larvae prefer cryptic habitat for settlement because such habitat often leads to higher post-settlement survival rates. Parrotfish create cryptic habitat through their bite marks. Despite extensive studies on the effects of herbivores on coral recruitment, none has investigated if the presence of herbivore bite marks affect settlement rates of coral larvae. This study investigates if *P. damicornis* larvae show a settlement preference for parrotfish bite marks and if this preference leads to higher post-settlement survival rates. Terracotta tiles with divots shaped like parrotfish bite marks (*Bolbometopon muricatum* and *Chlorurus microrhinos*) were seeded with *P. damicornis* larvae and deployed in the field. *P. damicornis* larvae preferred to settle in divots shaped like *C. microrhinos* bite marks and also preferred divots shaped like *B. muricatum* bite marks to flat tile surfaces. In the laboratory, *P. damicornis* recruits inside the divots had higher survival rates than their counterparts on the flat surfaces. In the field, survival was higher on flat surfaces than inside the divots. Thus, the settlement preference for bite mark-shaped divots observed for *P. damicornis* larvae did not lead to a higher post-settlement survival rate in the field. Overall, the presence of bite marks induced a higher settlement rate and increased the abundance of coral recruits at the end of the study. These results suggest that herbivores like *B. muricatum* and *C. microrhinos* have a positive influence on coral recruitment as their bite marks are a preferred settlement topography for *P. damicornis* larvae. This adds to the already high value these parrotfish species have for reef health. Protection and promotion of their populations should therefore be a target in coral reef conservation.

4.2 INTRODUCTION

Coral reefs worldwide are experiencing a decrease in live coral cover (Gardner et al. 2003; Bruno and Selig 2007; De'ath et al. 2012). Many studies on coral cover decline focus on coral mortality, often ignoring the possibility that declines could be caused by recruitment failure (Hughes et al. 2011). Regardless of what caused the decline in coral cover, successful coral recruitment is needed to increase coral cover after a decline. Arnold et al. (2010) suggested that coral recruitment consists of three sequential steps - (1) production of larval and their dispersal, (2) coral settlement, and (3) post-settlement survival. The number of available larvae for settlement depends both on local larval availability and connectivity. To settle on a substratum, larvae need to encounter conditions that induce metamorphosis and settlement, which include certain depth, light and chemical cues. Once metamorphosis is induced, a suitable nursery habitat is needed for post-settlement survival. Survival is mainly influenced by the benthic cover and availability of cryptic habitat (refuges) on the reef (Arnold et al. 2010). Corals prefer to settle in small crevices which shelter them from pressures such as parrotfish grazing and overgrowth competition (Vermeij 2005).

While the larvae of some coral species appear to settle randomly on the available substratum, others are very specific in terms of where they settle and metamorphose (Golbuu and Richmond 2007). Next to preference for settlement on crustose coralline algae (CCA) or bare substratum covered in biofilm, coral larvae also display a preference to settle in crevices. Nozawa et al. (2011) found recruitment rates to micro-crevices to be an order of magnitude higher to those to flat surfaces. This settlement preference reflects coral survival probabilities with coral recruits inside micro-crevices showing higher survival rates, especially for slow growing coral species (Nozawa 2008, 2010). Other experimental studies showed that settling in refuge structures helped coral recruits to survive under high grazing pressures from sea urchins (Sammarco 1980) or parrotfishes (Brock 1979). A study examining recruitment on natural reef substratum on Palmyra Atoll contradicts these findings (Roth and Knowlton 2009). Not only were more coral recruits found on convex surfaces, but the distribution of microhabitat substrata settled on was identical for corals of ≤ 1 mm and 4-5 mm, implying that microhabitat has no influence on recruit survivorship. Weak correlations between microhabitat and coral recruit survivorship have also been found in the Caribbean and on the Great Barrier Reef (Babcock and Mundy 1996; Edmunds et al. 2004). Furthermore, it has been shown that smooth surfaces like terracotta tiles that are routinely

employed as experimental units experience a shorter succession time to dominance by CCA compared to dead coral substratum, therefore leading to faster recruitment of coral recruits (Adey and Vassar 1975; Arnold et al. 2010). While substratum complexity affects the community structure of the coral recruits shortly after substratum becomes available, its effect diminishes later on with biological structuring forces dominating (Harger and Tustin 1973).

The presence of herbivores has been found to influence coral recruitment. Herbivore removal, for example through fishing, can lead to cascading effects, lowering coral recruitment rates through an increase of macroalgal cover and a decrease of CCA cover (Hughes et al. 2007; O'Leary et al. 2012). However, herbivores, both vertebrate and invertebrate, also negatively influence post-settlement survival of coral recruits by grazing indirectly on them (Arnold et al. 2010). Some herbivore species leave grazing marks on the reef. These crevices cleared of algae fit the settlement preferences of coral larvae and could lead to higher survival of coral recruits. Even though the effects of herbivores on coral have been studied in depth and it has been found that some coral larvae prefer to settle in crevices, no study has investigated the effect that herbivore grazing marks have on coral settlement preferences and recruitment success.

This study focusses on the settlement preference of *Pocillopora damicornis* recruits for parrotfish bite marks and whether this preference leads to higher post-settlement survival rates. *P. damicornis* larvae seem to be non-selective in settlement substratum choice (Harrigan 1972; Lewis 1974; Goreau et al. 1981; Morse et al. 1988; Baird and Hughes 2000; Baird and Morse 2004). Despite preferring micro-crevices for settlement, pocilloporids were the only recruits also found on plain (no crevice) tiles in Nozawa's study (2011). This makes *P. damicornis* a suitable species for recruitment studies as settlement to flat surfaces is needed to determine if early post-settlement survival differs between crevices and flat surfaces. Pocilloporids are a pioneer species (Harrison and Wallace 1990), and as such are important for both coral reef protection and coral reef restoration.

A settlement tile was designed with divots shaped like bite marks of *Bolbometopon muricatum* (Bumphead Parrotfish – large bite marks) and *Chlorurus microrhinos* (Steephead Parrotfish – small bite marks). The divots made up about half of the tile surface area while the rest of the tile was flat. In a laboratory experiment, *P. damicornis* larvae were given these divoted tiles

and flat (no divots) control tiles of the same size – 10.5 × 10.5 cm) as settlement substrata to test the following hypotheses:

- On divoted tiles, *P. damicornis* larvae prefer to settle in smaller than larger divots and on the same tiles they prefer to settle in divots than on the flat tile surface.
- *P. damicornis* recruitment rates to the flat tile surface are the same on divoted tiles and control tiles.

The newly settled *P. damicornis* larvae were monitored to determine early post-settlement mortality rates both in the laboratory and in the field. Coral recruits were maintained in the laboratory for 4 – 17 days before being placed in the field for a month. For the field placement, half the divoted and half the control tiles were caged to exclude herbivores greater than 1 cm^2. Comparison was then made between the caged and uncaged tiles to determine if divots can protect coral recruits from herbivore grazing. The following hypotheses concerning early post-settlement coral mortality were tested:

- On divoted tiles, survival rates for newly settled corals are highest inside small divots, followed by large divots and highest on flat surfaces.
- Survival rates for newly settled corals on flat surfaces are the same on the flat surfaces of divoted tiles and on control tiles.
- Field survival rates for newly settled corals are higher for caged (herbivores excluded) than non-caged tiles (herbivores not excluded).

4.3 METHODS

4.3.1 Study site

This experiment was conducted at the Hawai'i Institute of Marine Biology on Coconut Island, Oahu, Hawaii. 10 adult *Pocillopora damicornis* colonies were collected from the reef surrounding Coconut island (Point Reef, 21°26'00.7"N 157°47'10.6"W) and place in a shaded water table. In August 2014, 1626 *P. damicornis* larvae were collected from these 10 adult colonies. After the larvae settled onto settlement tiles, the settlement tiles were deployed on the edge of the reef terrace of the Point Reef at a depth of 3 meters. The chosen location had a high cover of *Porites* and was often visited by schools of juvenile herbivorous fish. It was chosen due to the high abundance of herbivorous fish compared to other locations on the Point Reef. It has

also been described as a more 'healthy' reef structure than other reefs surrounding Coconut Island (Lawrence et al. 2015). This made it possible to test if the divots provide recruits with a refuge from herbivore grazing. Both the collections of the adult colonies and larvae were carried out under the Special Activity Permit 2015-18 issued by the Department of Land and Natural Resources in Hawai'i.

4.3.2 Laboratory set up

Settlement containers (39 in total) were placed in a flow-through water table with constant water temperature of 25 ºC. The water table was situated under a roof, which reduced natural light levels and prevented rainwater intrusion. The seawater entering the water table was filtered using a 100 µm mesh and trickled through 30 holes (7 mm ø) out of a bucket 25 cm above the water level into the water table (Figure 4.1). The water left the water table through an overflow discard pipe. Water flow into the containers was ensured through 5 holes in the containers. A round hole (7 mm ø) was placed in the middle of the container lid and square holes (1 cm^2) were placed at each corner of the bottom of the container. These were covered in 100 µm mesh to prevent larvae from escaping the containers. The containers were placed on top of egg crate plastic, to ensure water flow below the containers. A 100 µm mesh band was wrapped around the tile and held in place with a rubber band. The result is a mesh wall around the tile that touched the top of the container the tile was placed in. The larvae were added inside the space created by this mesh wall, which kept most of the coral larvae in the water space between the tile and the lid (Figure 4.1).

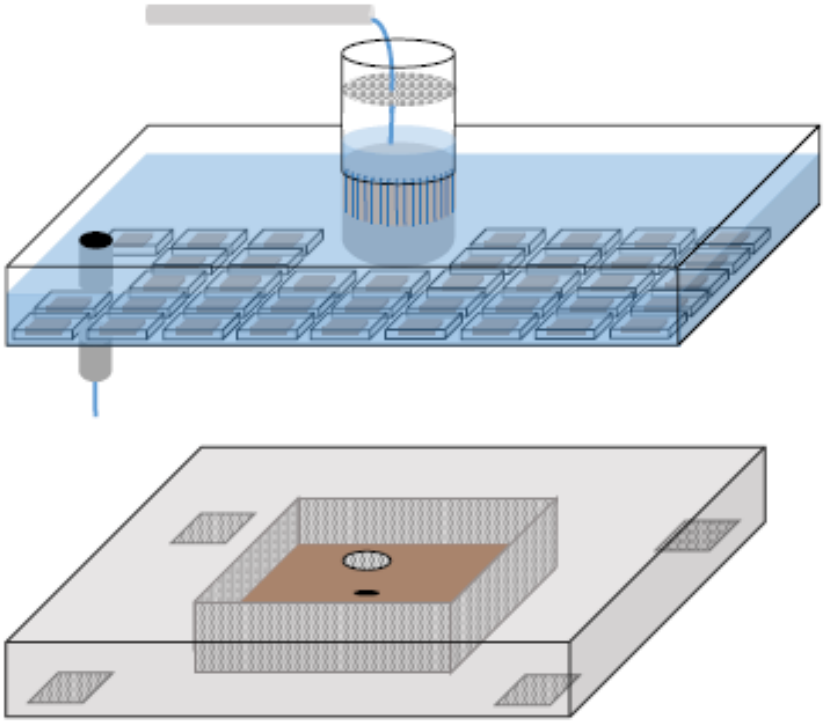

Figure 4.1. Experimental set up for settlement study. The top drawing shows the water table. Water enters the water table through a 25 l bucket with a 100 µm mesh filter (*grey hashed area*) and 30 holes (7 mm ø). Thirty-nine containers with settlement tiles and larvae were placed in the water table. The bottom drawing shows one of the containers. It contains a tile, five holes for water flow (*small hashed squares* and *small hashed circle*) and a mesh band (*hashed band around tile*) around the tile to retain larvae in the water column above the tile. The tile has a hole in the middle (*black circle*). 19 control tiles (tile in bottom drawing of this figure) and 20 divoted tiles (Figure 4.2) were used in this experiment.

Two types of tiles were used in this experiment: divoted and control (flat, no divots) tiles. Both tile types were made out of natural terracotta, 10.5 x 10.5 x 0.8 cm in size and had a 7 mm ø hole in the middle. This hole was used for placement of the tile on a stainless steel rod on the reef. The tiles were conditioned in a flow through water table with seawater for a month to permit development of a natural biofilm prior to being used in the experiment. The control tiles had an entirely flat surface while the divoted tiles contained two large divots (~3.7 L x 2.6 W x 0.4 D cm) and nine small divots (~1.8 L x 1.1 W x 0.13 D cm). Each small divot had four shallow 1 mm deep grooves running length-wise inside them. The large divots were modelled after *B. muricatum* bite marks and the small divots resembled *C. microrhinos* bite marks, according to field measurements from Palmyra Atoll. For this reason, the divots differed in size and the presence of grooves. The

divots were carved into the soft clay before the tiles were hardened in the oven. We (my collaborators and I) tried to design a tile where half of the tile surface was made up by divots, providing coral larvae with equal areas of flat and cryptic (divoted) surface to settle on. Due to the pre-set size requirement for the divots, it was not possible to create a tile where divots made up exactly 50% of the tile surface, but on average, all divots together made up 42% of the tile surface (Figure 4.2). The percentage of area covered by divots was determined by measuring the 3D ellipsoid hemisphere of each divot for 12 divot tiles.

Figure 4.2. Photograph of divot tile with 2 large divots (~3.7 L x 2.6 W x 0.4 D cm), nine small divots (~1.8 L x 1.1 W x 0.13 D cm) and a central hole for placement onto stakes on the reef. Each small divot had four shallow 1 mm deep grooves running length-wise inside them. The large divots were modelled after *B. muricatum* bite marks and the small divots resembled *C. microrhinos* bite marks according to measurements taken at Palmyra Atoll. Divots were carved into the soft clay before the tiles were hardened in the oven.

4.3.3 Settlement experiment

Each morning, larvae were collected by emptying a larval collector placed under the outfall of the water table containing 10 adult *P. damicornis* colonies. The larvae were counted and added to one or several containers with a terracotta tile. On days when fewer than 50 larvae were collected, all larvae were added to a single container. These containers received between 5 and 49 larvae. When more than 50 larvae were collected, the larvae were distributed equally to several containers alternating between containers containing a control tile and containers containing divoted tiles (two containers for 51-100 larvae, three containers for 101-150 larvae, and four containers for 151- 200 larvae). These tiles received between 27 and 50 larvae. On the last two days, 74 - 77 larvae were added to each container. Twelve pairs of containers, where a pair is one divoted tile plus one control tile, were seeded with the same number of larvae (±1) on the same day. The data collected from these containers were used for pairwise comparison while the data from all containers were used for the other statistical tests. In total, 802 larvae were added to control tiles and 824 larvae were added to divoted tiles.

During the laboratory study, settled, swimming and crawling coral larvae were counted every evening on each tile using a NIGHTSEA BlueStar UV flashlight. This flashlight induces fluorescence in the larvae and new recruits and makes them very visible. During this count, larvae situated outside the mesh band but still inside the plastic container were collected with a pipette and returned to the water column above the tile enclosed by the mesh band. The behaviour of the larvae (settled, swimming, crawling) and their position (small divot, large divot, flat tile surface, floating) was recorded. The results was daily counts of (1) newly settled recruits, (2) settled recruits that survived, (3) settled recruits that died and (4) living larvae that have not yet settled. These counts were recorded for each area of each tile (small divot, large divot, flat tile surface). The first count was conducted about 14 hours after seeding the tile with larvae. The last counts were done between 4 and 17 days after tile seeding. This variation was due to staggered tile seeding. The sum of all daily counts of newly settled corals was used to calculate the recruitment density for each area (small divots, large divots and flat surface) of each tile.

Active crawling of a coral larva from the flat part of a tile into a divot was observed during the experiment. For this reason, 37 larvae were placed on the flat part of a divoted tile to observe their movement. 13.5 hours after the placement, the positions of the larvae were noted.

4.3.4 Survival rate in the field

Eight control and 16 divoted tiles from the laboratory experiment described above contained at least one coral recruit at the end of the laboratory phase of the experiment. After examining the tiles for coral recruits under the microscope and mapping their location on a schematic drawing of the tile, these tiles were placed on the Point reef for a month to determine survival rates of the 78 newly settled coral recruits in the field. The tiles were individually placed in horizontal orientation on to stainless steel rods that were cable tied to dead or artificial substratum on the reef. One half of the tiles (4 control and 8 divoted tiles) were individually caged with chicken wire (1 cm mesh size) which protected 41 recruits from herbivore grazing (Figure 4.3). The other tiles (4 control and 8 divoted tiles) were left uncaged which left 37 recruits on the tiles and unprotected from herbivore grazing. Each caged tile was paired with an uncaged tile and the pair was deployed within 50 cm of each other. After retrieval, tiles were examined under the microscope for coral recruits. The status (survival, death) of each coral recruit mapped before the deployment was determined. Survival rates for recruits in divots, on the flat tile surface and on the side of each tile, with or without cage treatment, were calculated. Tiles were visually examined and classified depending on main benthic cover (turf dominated or green encrusting algae dominated) and presence of grazing marks (Figure 4.4).

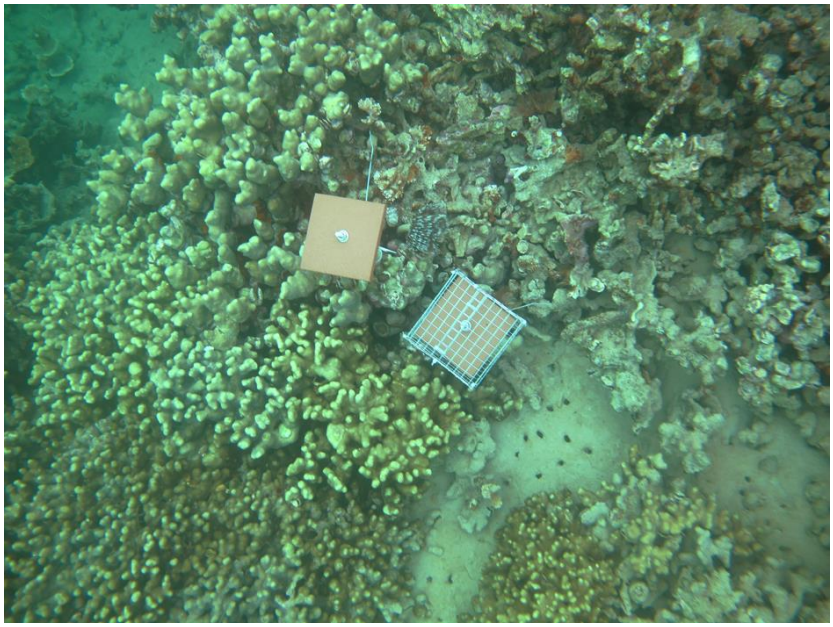

Figure 4.3. Placement of settlement tiles in the field. Tiles were fixed to a stainless steel rod using stainless steel nuts. The rods were cable tied to dead or artificial substratum. Half of the tiles were caged with a 1 cm metal mesh (chicken wire).

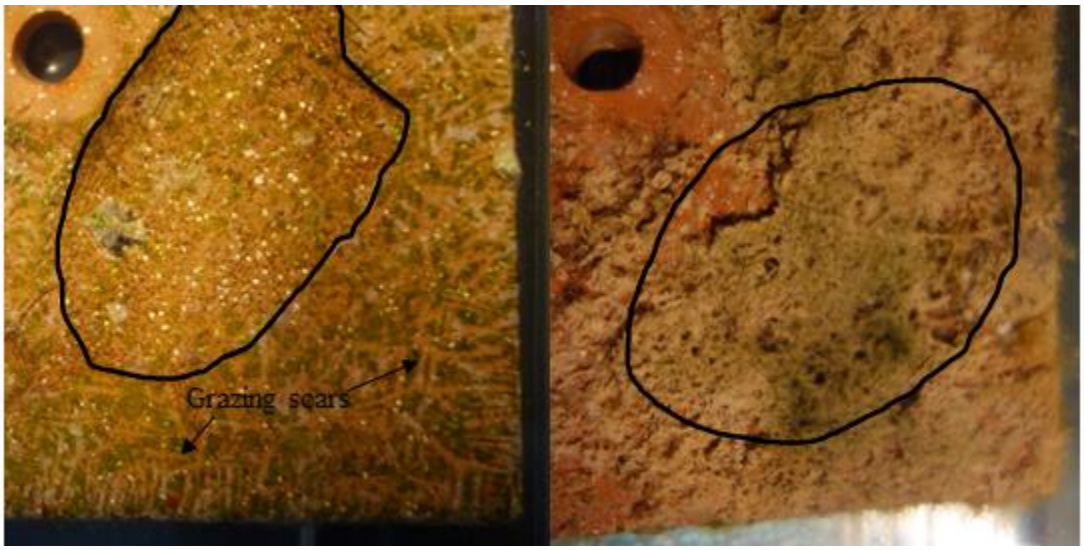

Figure 4.4. Pictures of two tiles after 1 month of deployment in the field. Both tiles show the same tile corner with one large divot (outlined in *black*). The benthic community on the left tile is dominated by green encrusting algae and small grazing scars are visible. The benthic community on the right tile is dominated by turf algae, which covers the divot almost completely.

4.3.5 Statistical analysis

Settlement and laboratory survival experiment

Recruitment density on flat surfaces was highly skewed towards zero and for this reason non-parametric statistical tests were employed. To determine if *P. damicornis* larvae preferred small divots, large divots or flat tile surface to settle on, recruitment densities to these areas were compared for data collected from the divoted tiles. Wilcoxon signed rank tests were performed comparing recruitment densities on small divots to large divots, large divots to flat surface and small divots to flat surface. To test if recruitment was significantly greater on divoted tiles than on control tiles, total recruitment density and recruitment density on the flat surface was compared between data collected from the divoted and the flat tiles. This was done to determine if (1) total recruitment density differed significantly as well as (2) the recruitment density to flat surfaces. The latter makes it possible to determine if the presence of divots on tiles changes the recruitment density to flat surfaces. Two kinds of tests were performed. First, a Mann Whitney U test was employed to test data collected from all tiles to compare total recruitment density and recruitment density on the flat surfaces between divoted and control tiles. On certain days, enough larvae were collected to seed more than one tile. This made it possible to compare data gathered from pairs of divoted and control tiles. For this reason, recruitment density on 12 divoted and 12 control tiles, which were seeded on the same day with the same number of larvae (±1), were compared in the second test. The recruitment densities were square root-transformed to meet the assumption of normality. Divoted and control tiles were paired together according to the date they were seeded with larvae. On three days, enough larvae were collected to seed a total of four tiles. On these days two divoted and two control tiles were seeded with the same number of larvae. Each divoted tile therefore had two possible control tiles it could be paired with for this analysis. Instead of pairing them randomly, the analysis was conducted using all possible pairings. A paired t-test was run for each combination of pairings that was possible in the whole data set. This resulted in eight paired t-tests. The test statistic of the least significant paired t-test was used as result.

During the laboratory placement, numbers of live coral recruits were counted every day for each tile. This makes it possible to determine survival rates of single coral recruits. Survival of each coral spat was assumed to be independent from all others. The survival rates of recruits in divots and on flat surfaces were compared using the Kaplan-Meier (K-M) estimate, because it incorporates censored data. Therefore, coral recruits that survived the laboratory experiment were

considered censored data in the data set. The number of days between settlement and the end of the laboratory treatment was calculated for these coral recruits while for the other recruits the number of days between settlement and their death was noted. This method was adopted because it deals with the fact that the tiles were seeded on different days due to the daily variation in larval availability. The estimated K-M survival curves for recruits in divots and on flat surface were compared using a log-rank test. To determine if survival differed between divoted and control tiles, two sets of estimated K-M survival curves were compared: One curve for all recruits found on divoted and control tiles and a second curve for recruits that were found on the flat surface of the divoted and control tiles. These curves were compared using a log-rank test.

Survival rate in the field

Survival rate in the field refers to the proportion of recruits that survived the deployment on the reef in September. Pearson's χ^2 test was used to compare survival rates of recruits. Several factors were analysed to determine if they influenced recruit survival in the field. Survival rates of recruits inside small and large divots were compared. Furthermore, survival rates were compared between recruits on turf-dominated and green encrusting algae-dominated tiles, caged and non-caged tiles and grazed and non-grazed tiles. Due to a low sample size of recruits on the flat surfaces of divoted tiles (8), Fisher's exact test was used to compare survival rates on flat surface to survival rates in divots and the side of the tile.

4.4 RESULTS

4.4.1 Settlement and laboratory survival experiment

P. damicornis larvae added to containers with divoted tiles showed recruitment preference for small divots ($p < 0.001$ for small divots vs flat, $p = 0.002$ for small divots vs large divots) and preferred large divots over flat surfaces ($p = 0.001$). A mean value of 18.53 ± 2.96 (SE) recruits per 100 cm^2 was found in the small divots, while only 7.56 ± 1.95 (SE) recruits per 100 cm^2 and 1.52 ± 0.47 (SE) recruits per 100 cm^2 were found in the large divots, and on the flat tile surface, respectively.

Divoted tiles had an average recruitment of 6.22 ± 1.08 larvae per 100 cm^2 which was significantly greater than the 1.31 ± 0.41 recruits per 100 cm^2 found on the control tiles ($p < 0.001$). Comparing tiles seeded with the same number of larvae on the same day, divoted tiles showed

significantly higher recruitment rates than control tiles ($t = 4.8$, $df = 11$, $p = 0.001$). The recruitment density on the flat part of the divoted tiles was not significantly different from the recruitment density on the flat tiles (1.42 ± 0.45 (SE) recruits per 100 cm^2, $p = 0.795$).

Active crawling of coral larvae from the flat part of a tile into a divot was observed during the experiment. After 13.5 hours only 13% of the 37 larvae that were placed on the flat part of a divoted tiles were found on the flat part, whereas 64% were found in divots and 21% were swimming.

Survival rates of coral recruits in the laboratory differed significantly between control tiles and divoted tiles ($p = 0.006$). On the control tiles, 11% of the 27 larvae survived while 42% of the 139 larvae recruited to divoted tiles survived. The K-M survival curves did not differ between control and divoted tiles for recruits on flat surfaces (Figure 4.5a, $p = 0.494$). Survival was significantly higher in divots than on flat surfaces (Figure 4.5b, $p = 0.002$) which led to the higher survival rates found on divoted tiles. Overall survival rates in the laboratory did not differ significantly between recruits in small and large divots (Pearson's χ^2, $df = 1$, $N = 116$, $p = 0.392$).

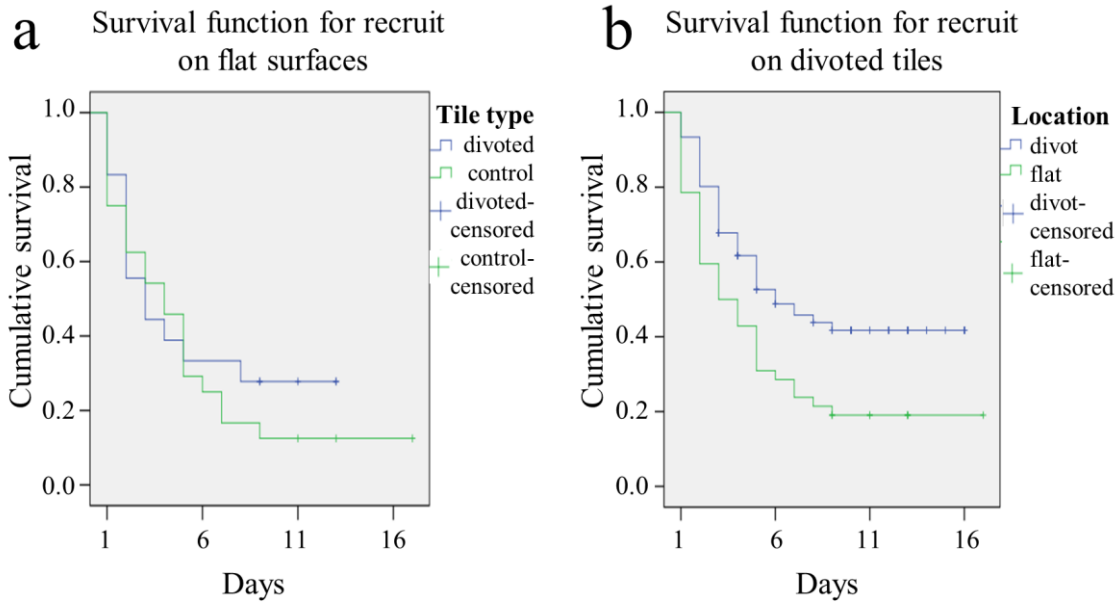

Figure 4.5. Survival of coral recruits up to 17 days after settlement. (a) Estimated Kaplan-Meier (K-M) survival curves for corals that recruited to the flat tile surface of control tiles (*green*) and divoted tiles (*blue*). (b) Estimated K-M survival curves for corals that recruited inside divots (*blue*) and on flat tile surfaces (*green*) of divoted tiles. Coral recruits that survived until the end of the study but less than 17 days, due to them settling later than the first settlers, were included in this analysis as censored data (+ on the graphed lines).

4.4.2 Survival rate in the field

Qualitative visual inspection of the tiles placed in the field revealed that two types of benthic communities established themselves on the tiles (Figure 4.4). Some tiles were covered in thick brown turf algae that retained a lot of sediment. The turf algae seemed to prefer to settle inside the divots and covered the divots completely on some tiles, making them almost invisible. Other tiles were dominated by small green encrusting algal colonies and also had CCA and invertebrates colonise their surface. Green encrusting algae were more common on the flat part of the tile than in the divots. Graze marks were visible on the green encrusting algae if the tiles were uncaged. These marks were more common on the flat part, which could be due to higher grazing on the flat part or lower green encrusting algal cover in the divots. The turf algal assemblage was mostly found on caged tiles while most uncaged tiles had a benthic community dominated by green encrusting algae.

Survival rates of coral spat transferred to the field site were higher on flat surfaces (100%) than on the side of the tile (50%) or in the divots (large 47%, small 66%, $p = 0.006$). Of the measured factors that could influence survival on the tiles (benthic cover of tile, caging, grazing) only grazing showed a significant effect on survival of recruits in divots (Pearson's χ^2 df = 1, N = 54, $p = 0.035$). Survival rates of recruits in divots were higher on grazed tiles (58%) than on non-grazed tiles (29%). Recruits inside divots on caged tiles had a 44% survival rate, 7% lower than on uncaged tiles (Pearson's χ^2 df = 1, N = 54, $p = 0.156$). On turf dominated tiles, 45% of the recruits inside the divots survived, while 49% survived on tiles dominated by green encrusting algae (Pearson's χ^2 df = 1, N = 54, $p = 0.504$).

The overall survival rates (laboratory and field study combined) on the tiles did not differ significantly between divoted and control tiles (Pearson's χ^2 df = 1, N = 166, $p = 0.258$). 29 recruits were found at the end of the study on the divoted tiles (21% overall survival) and 3 were found on the control tiles (12% mortality). No significant difference in overall survival rates was found between flat surface (25%), small divots (14%) and large divots (24%) on the divoted tiles (Pearson's $\chi 2$ df = 1, N = 166, $p = 0.516$).

4.5 DISCUSSION

4.5.1 Settlement

P. damicornis larvae showed a clear preference to settle in small divots shaped like *C. microrhinos* bite marks over large divots shaped like *B. muricatum* bite marks and preferred divots over flat surfaces. More than half of the *P. damicornis* larvae placed on the flat part of the tile moved into divots. These results indicate that *P. damicornis* actively choose to settle in divots rather than on flat surface. Settlement rates to flat surface did not differ between control and divoted tiles, therefore the presence of divots did not lead to less settlement on flat surface but rather to higher settlement overall.

4.5.2 Differences in coral spat survival rates between the laboratory and field study

Survival was higher for recruits inside the divots than on flat surfaces during the laboratory experiment. During the placement in the field however, the opposite was found. It is unclear why survival in the laboratory was higher in divots while survival in the field was higher on the flat surface. One explanation for these results could be the small sample size of the field study. Another explanation could be that factors not present in the laboratory lead to mortality on the reef and that recruits inside divots were more susceptible to them. Both estimated Kaplan-Meier survival curves for recruits in divots and on flat surfaces level off after 9 days, indicating that no coral recruit should die in the laboratory once it reached 10 days of age. Of the coral recruits placed in the field, 70% were 10 days or older. If survival in the field followed the Kaplan-Meier survival curve from the laboratory, none of the recruits on flat surfaces and three recruits in the divots would have died during the field placement. This was true for flat surfaces, however in divots, 33 instead of 3 recruits died. These results indicate that mortality in the field was induced by factors that affect recruits in divots while not affecting recruits on flat surfaces. Recruits that settled on the side of the tiles had similar survival rates to the recruits in the divots, therefore they also seemed to be affected by these factors. Possible factors inducing recruit mortality on the Point Reef in September 2014 include low light levels, high levels of sedimentation and a bleaching event (Bahr et al. 2015). Bleaching would affect recruits found in the divots, on the side and on the flat part of the tile, while sedimentation would likely affect recruits in the divots the strongest, followed by recruits found on the flat part of the tile. Low light levels would affect recruits located on the side of the tiles and likely also recruits inside the divots, especially if these were covered in turf algae, reducing light levels even further. I therefore think that a likely ecological explanation for the differences in

survival rates found between recruits on flat parts of the settlement tiles and recruits inside divots or on the side of the settlement tiles is that these areas differ in the amount of light that coral recruits received. However, the sample size of this experiment was rather low, it is therefore also possible that the trends seen here do not correspond to any ecological patterns.

Within the divots, survival was significantly higher on tiles with grazing marks (58% versus 29%). Grazing marks were found on the flat part of tiles dominated by green encrusting algae. Grazers found near the study location in 2012 and 2013 included *Chlorurus* spp. (0.73 ind. m^{-2}), *Ancanthurus* spp. (0.37 ind. m^{-2}), *Scarus* spp. (0.24 ind. m^{-2}),and *Zebrasoma* spp. (0.06 ind. m^{-2}) (KA Stamoulis, personal communication). Grazers may prevent turf algae from colonizing settlement tiles, however recruits within the divots did not show significant higher survival on tiles without turf algae. I was not able to determine the ecological context of the significant correlation between higher recruit survival in the divots and grazing marks found mainly on the flat part of the tiles. A possible explanation could be that grazing influences the abundance or behaviour of corallivorous invertebrates or other organisms that consume coral recruits. On the other hand, it is also likely that this correlation does not have ecological significance and resulted from the small sample size of the experiment.

4.5.3 Higher recruitment rates did not lead to higher overall survival rates

P. damicornis larvae demonstrated in this experiment that they are capable of active settlement choices, however their choice did not lead to higher overall survival rates in the field. This is surprising because settlement choices as distinct as those reported here are normally established through adaptation reflecting post-settlement growth, survival and reproduction (Young 1990; Raimondi and Morse 2000). In other studies, settlement preferences expressed by coral larvae towards naturally occurring cryptic habitats also did not lead to higher survival rates (Babcock and Mundy 1996; Edmunds et al. 2004; Roth and Knowlton 2009). After 4 months of deployment, a reef study with pocilloporids reported a similar ratio between flat and cryptic habitat as my study (2011). They did not measure initial recruitment patterns and post-settlement mortality, however the similar ratios between their study and mine suggest that the pocilloporid larvae in their study showed a settlement preference for micro crevices but that this did not lead to a higher survival rate. Babcock and Mundy (1996) suggested that the wide distributional range of their study coral species (*Platygyra sinensis* and *Oxyporu lacera*) could be the reason why they

did not see a clear relationship between settlement preference and survival rates. For example, settlement in crevices may be beneficial in parts of the distributional range while it is not elsewhere. Pocilloporids recruit abundantly (Wallace 1985; Harriott and Fisk 1988) and are an important pioneer species colonising reefs after disturbances (Harrison and Wallace 1990), which leads to a wide distributional range. It is therefore likely that survival rates in divots are higher under environmental conditions different from the ones found on the reefs surrounding HIMB and that this led to an adaptive response in settlement choice. This is supported by recruits in divots experiencing higher survival rates during the laboratory experiment. Positive correlations between settlement preference and post-settlement survival rates were also found for other coral species (*Acropora solitaryensis, Echinophyllia apera, Favites pentagona, Platygyra contorta*) (Nozawa 2008, 2010).

My results do not clarify whether the settlement preferences of *P. damicornis* larvae are beneficial to them. They show that the preferred settlement choice can sometimes lead to disadvantages. This has implications for the future survival of *P. damicornis*. The settlement preference of *P. damicornis* is very pronounced. If this settlement preference changes from being advantageous to being disadvantageous for post-settlement survival, then the majority of recruits will experience lower post-settlement survival. As a result, *P. damicornis* recruitment will show a high decrease. Further studies are needed comparing survival rates in the field under different environmental conditions to better determine post-settlement survival rates of recruits in crevices and on flat surfaces and the relative contribution of environmental factors to post-settlement survival.

4.5.4 Positive effect of parrotfish grazing marks on *P. damicornis* recruitment

At the end of the laboratory phase of the experiment the recruitment density inside the divots was higher than outside the divots. I therefore conclude that bite marks of *B. muricatum* and *C. microrhinos* could have a positive effect on *P. damicornis* recruitment. The recruitment success of *P. damicornis* larvae is augmented when bite mark sized divots are present. However, the increase in post-settlement survival found in micro-crevices (Nozawa 2008, 2010) has not been found in the divots of the tiles used in the present study. Therefore, parrotfish bite marks may be too large to provide coral recruits with the survival benefits provided by other cryptic habitat. Field experiments with a larger sample size are needed to draw a clear conclusion on whether parrotfish

bite marks are too large to shelter coral recruits from grazing or if the low survival rate found in the field during this study is due to other factors. My results suggest that herbivores positively influence coral recruitment not only through macroalga removal but also by providing cryptic habitat for larvae to settle in. A healthy herbivore community including *B. muricatum* and *C. microrhinos* therefore increases coral recruitment rates. Furthermore, herbivores positively affect coral cover through macroalgal removal, which increases coral recruitment (Steneck 1997; Mumby et al. 2006a) and helps adult corals compete against macroalgae (Jompa and McCook 2002). Coral reef managers should therefore aspire to increase the populations of large herbivores like *B. muricatum* and *C. microrhinos* on their reefs.

CHAPTER 5

Drivers of net calcium carbonate accretion of early successional benthic communities on a tropical coral reef

5.1 ABSTRACT

Calcification and erosion shape the topographic structure of coral reefs, which is vital for many reef functions and ecosystem services. $CaCO_3$ accretion depends highly on biological processes such as $CaCO_3$ production by calcifiers and erosion by borers and grazers. Palmyra Atoll is located in the central Pacific Ocean and experiences limited impacts from humans and is therefore ideal to study how calcification is affected by natural biophysical forcing factors such as herbivore grazing and hydrodynamic processes. In this chapter I determined the net $CaCO_3$ accretion of early successional benthic communities by measuring the calcification on experimental substrata deployed for 1 year (settlement tiles) and the bioerosion rate on experimental coral pieces (*Fungia* skeletons) deployed for 15 months. These were placed on the fore reefs and on the back reef including two back reef sites with high water flow from the lagoon. To determine bioerosion rates on dead substratum older than 15 months, pieces of coral rock were broken off the reef and analysed for bioerosion. I also investigated how grazing rates, hydrodynamic processes and depth influence $CaCO_3$ accretion rates. $CaCO_3$ accretion varied from 0.27 to 1.36 kg $CaCO_3$ m^{-2} y^{-1} and was negatively correlated with grazing rates and positively correlated with water flow from the southern side of the island. The *Fungia* skeletons (15 months) exhibited very small levels of internal macro bioerosion (0.009 kg $CaCO_3$ m^{-2} y^{-1}). Across all sites, the average $CaCO_3$ budget on recently freed space on the reef was positive. CCA produced 99% of the $CaCO_3$ found on the settlement tiles. The $CaCO_3$ layer deposited by CCA is often grazed upon and likely acts as a protective layer against external bioerosion for the underlying reef rock. CCA is therefore important for sediment production and at the same time cements the reef structure together.

5.2 INTRODUCTION

The topographic complexity of coral reefs is vital for most reef functions and ecosystem services (Done et al. 1996; Graham and Nash 2013). The available habitat for reef-associated species, for example, depends largely on the structure of the reef framework (Alvarez-Filip et al. 2009). This reef framework structure is created and in large part held together by calcifying benthic organisms that deposit calcium carbonate ($CaCO_3$) onto the reef. Erosion weakens the reef framework and slows down net $CaCO_3$ accumulation. $CaCO_3$ budgets quantify the mass of $CaCO_3$ deposited on a reef and take both $CaCO_3$ production and erosion into account. Whether or not a reef platform is rising (positive budget) or sinking (negative budget) depends on the $CaCO_3$ budget of the reef. $CaCO_3$ budgets therefore give important insights on the topographic complexity and the health of coral reefs (Perry et al. 2012; Kennedy et al. 2013).

Reef net growth is a balance between calcification and erosion, including both physical erosion and bioerosion, and varies between a few tens of meters of reef growth and the destruction of tens of meters per thousand years (Macintyre et al. 1977; Smith et al. 1981; Reaka-Kudla et al. 1996). On non-degraded reefs, reef growth and erosion largely balance each other out on an annual basis (MacGeachy and Stearn 1976; Hutchings 1986).

Net $CaCO_3$ budgets exist for only a few reefs (see Kench et al. 2009 and Figure 1.3 for examples). Perry et al. (2008) showed that, at the most fundamental level, $CaCO_3$ budget is mainly influenced by primary $CaCO_3$ producers such as corals, by secondary $CaCO_3$ producers such as calcareous encrusters and by destructors such as bioeroders. These three key biogenic component groups are also most directly impacted by environmental and ecological change. They proposed a ternary approach (Figure 1.3a) toward net $CaCO_3$ budgets, which is well suited to identify the relative importance of these three key functional groups and shows whether or not a reef is accreting or eroding. A shift in the reef's ecological status can impact its $CaCO_3$ production and reef framework development (Eakin 1996; Tomascik 1997; Edinger et al. 2000; Riegl 2001). Coral mass mortality, for example, decreases the $CaCO_3$ production of a reef because secondary $CaCO_3$ producers can often not keep up with bioerosion rates. Exceptions are algal ridges and the reef-flat at Uva Island, Panama (Eakin 1996). To gain a better understanding of the role of $CaCO_3$ accretion in coral reef resilience, $CaCO_3$ budgets on recently freed substratum need to be assessed. This helps

to determine how secondary $CaCO_3$ production outbalances bioerosion and enables predictions of reef growth during the coral recovery phase after major disturbances.

Primary $CaCO_3$ production is negligible on freed space until it contains coral recruits of the age of about one year. Freed benthic space is colonized by early successional benthic organisms consisting of fleshy algae, small coral recruits and non-coral calcifying organisms such as CCA, bryozoans, foraminifera and tubeworms. Non-coral calcifiers often cover a higher percentage of the reef's surface than live corals (Vroom et al. 2006; Vroom 2010) and have calcification rates similar to corals (0.5 - 20 kg of $CaCO_3$ m^{-2} y^{-1} for CCA versus 1.4 and 18 kg of $CaCO_3$ m^{-2} y^{-1} for corals) (reviewed by Harney and Fletcher 2003). The early successional benthic community on Palmyra Atoll was found to deposit 0.73 kg of $CaCO_3$ m^{-2} y^{-1} onto the reefs (Price et al. 2012). Price et al. (2012) found that the percentage cover of calcifying organisms increased as the diel variability in sea water pH increased. However, net calcification rates were similar between sites on Palmyra Atoll, despite differences in diel pH and cover of calcifying organisms. Other factors therefore influence the mass of $CaCO_3$ deposited on this reef by early successional benthic organism.

Palmyra Atoll has a small human population (<20 inhabitants) and therefore minimal exposure to human stressors. Intra-island variations in structure and dynamics of reef communities on Palmyra are likely to be due to natural variations in predation, competition for space, hydrodynamic processes, and natural disturbance events such as storms (Hughes 1989; Rogers 1993; Hughes and Connell 1999; Williams et al. 2013). Calcification rates of CCA species are influenced by herbivore pressure (O'Leary and McClanahan 2010). Intensive grazing by herbivores can give corallines a competitive advantage over other algae (Adey and Macintyre 1973) but it also leads to denuding or excavating of their $CaCO_3$ structure (Steneck 1983a; O'Leary and McClanahan 2010). The thickness of coralline crust, and its contribution to $CaCO_3$ accumulation, can be reduced by herbivore grazing (Steneck et al. 1991). Net $CaCO_3$ production and the abundance of non-coral calcifying organisms are correlated with wave energy (Martindale 1992; Mallela 2007; Pescud 2012). Currents, waves and tidal flushing all transport nutrients and sediments around the reef platform (Mallela 2007). Nutrients and sediments can create turbid conditions, which correlate negatively with net CO_3 production (Mallela 2007). Fabricius and De'ath (2014) for example, found that the percentage cover of CCA decreased as turbid conditions

increased on the reef. On Palmyra Atoll, a man-made Entrance Channel connects the lagoon to the Western Reef Terrace and fore reef. The regular flushing of the lagoon through this channel transports sediment from the lagoon to the reef habitats. Wave strength also differs between sites on Palmyra Atoll. Despite these hydrodynamic processes acting on Palmyra Atoll, their effect on $CaCO_3$ production has not yet been studied. However, the benthic community composition on Palmyra Atoll was found to correlate with sedimentation and changes abruptly from calcifier dominated (corals, CCA) to non-calcifier dominated (turf algae) at a bed shear stress threshold of 18 Nm^{-2} (Williams et al. 2011b; Gove et al. 2015).

Calcifying organisms are more abundant on the reef terrace than on the fore reef, unrelated to variation in diel pH variability (Price et al. 2012). The reef terrace is a shallow protected habitat (<5m) while the fore reef sites chosen were at a depth of 10 meters on the exposed fore reef slope. Bioerosion rates in Jamaica and Mexico vary between reef terrace and fore reef habitats (Perry 1998; Hepburn et al. 2005). Studies on both calcification and bioerosion should therefore incorporate fore reef and reef terrace habitats.

In this study, I investigated $CaCO_3$ deposition and removal by early successional calcifiers and bioeroders on Palmyra Atoll in order to determine the net $CaCO_3$ production on freed space with limited primary $CaCO_3$ production. The first aim of this study was to identify the early successional benthic organisms that deposit $CaCO_3$ onto settlement tiles and then to determine their $CaCO_3$ accretion rates. As a second aim, I investigated if the cover of early successional calcifiers can be used to predict $CaCO_3$ depositional rates. The third aim was to determine if differences in calcification rates are correlated with differences in depth/reef area (fore reef sites were located deeper than back reef sites), herbivore grazing pressure and hydrodynamic processes. My fourth aim was to identify internal bioeroders in dead coral skeletons and to determine the rates at which these organisms erode the coral skeletons. For my fifth aim I compared the secondary $CaCO_3$ production and bioerosion rates to measure the net $CaCO_3$ budget on recently freed benthic space on Palmyra Atoll's coral reefs.

5.3 METHODS

5.3.1 Study site

This study was carried out on Palmyra Atoll (see General Introduction and Chapter 2 for further information about this study area). Hydrodynamic properties vary within Palmyra Atoll. For example, regular flushing of the lagoon onto the reef terrace occurs through a dredged channel (the Entrance Channel Collen et al. 2009) and northern fore reef sites experience higher wave energy (1-3 m wave height) than southern fore reef sites (1-2 m (Williams et al. 2013; Rogers 2015, Chapter 4). Very large storms with waves capable of overtopping atoll islets occur on both sides of the island with high frequency but are likely to be larger and more destructive from the south (Gardner et al. 2014).

I chose ten sites on the reef surrounding Palmyra Atoll identical to the sites used in Chapter 2 and 3(Figure 2.1). Four sites on the fore reef at a depth of 10 meters (FR3, FR5, FR7, FR9), four sites on the Western Reef Terrace at a depth of 3-5 meters (RT1, RT4, RT10, RT13) and two sites adjacent to the dredged Entrance Channel between the lagoons and the reef, also at a depth of 3-5 meters (EC1, EC2). On the fore reef I chose two sites on the southern site of the atoll (FR3, FR5) and two sites on the northern side of the atoll (FR7, FR9). The entrance channel sites (EC1, EC2) and the fore reef site FR3 receive large volumes of water and sediment from the lagoon.

5.3.2 Quantifying calcification

To measure calcification accretion of early successional benthic organisms, 50 settlement tiles were deployed in May/June 2013 at the 10 different sites described above. The settlement tiles were made of clay and measured 10 cm x 10 cm x 1 cm. They were deployed horizontally onto stainless steel stakes (Figure 2.3). Plastic spacers, 1 cm high, were placed between the reef and the tiles to create a cryptic habitat below the tile. Of the 50 tiles deployed, 46 were still in place after one year of deployment.

These settlement tiles were collected in May 2014 after 12 months of deployment and oven dried to a constant mass at 80° C. Subsequently, they were immersed for 24 h in domestic bleach to remove organic matter, rinsed with water and then oven dried a second time at 80° C to a constant mass and weighed (m_1). The settlement tiles were then submerged in 10% hydrochloric acid for 24 h or until all the $CaCO_3$ was dissolved. Then they were rinsed, oven dried a third and

last time at 80° C to a constant mass and reweighed (m_2). The mass of $CaCO_3$ on each settlement tile was determined by the following formula:

$$m_{CaCO_3} = m_1 - m_2 \quad (1)$$

Photographs of the live benthic community on the bottom and the top of all tiles were taken right after they were collected. During this process, the tiles were submerged in temperature controlled seawater (28℃) with air bubbles for oxygen supply to keep the benthic organisms on them alive. The photographs were loaded into the Coral Point Count program CPCe 4.0 (Kohler and Gill 2006) where the benthic cover under 200 stratified random points in a 10 by 10 grid was determined (Method described in detail in Chapter 3). During classification of substratum classes on the tiles, distinctions were made between bare substratum created through grazing and other bare substratum. Dead CCA was further categorized, where possible, into dead due to grazing and dead due to diseases. Parallel lines of dead CCA are produced by grazing fish while diseases cause small round patches of dead CCA (Figure 5.1).

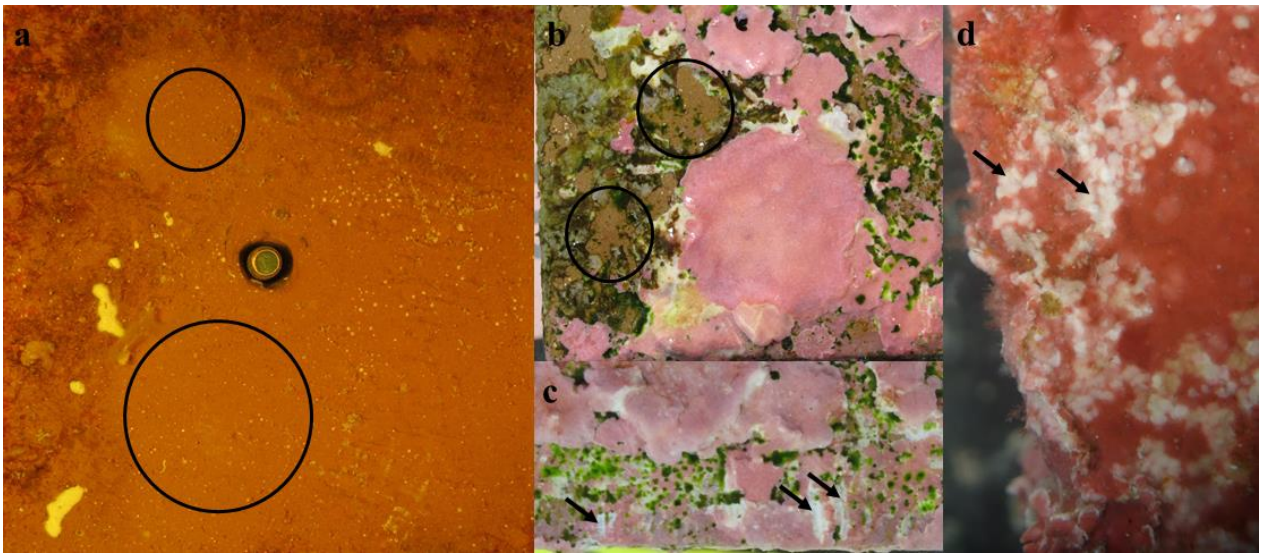

Figure 5.1. Classification system for bare substratum and dead CCA. (a) Bare substratum not created through grazing (inside *black circles*). (b) Bare substratum created through grazing (inside *black circles*). (c) *Black arrows* pointing at dead CCA (white coloration) caused by grazing. (d) *Black arrows* pointing at dead CCA (white coloration) caused by disease.

Calcification rates for six calcifying groups: cryptic CCA (found on the underside of the settlement tile), *Turbicellepora ampla* (bryozoan), *Parasmittina hastingsae* (bryozoan), tubeworms, corals and hydrocorals were determined. These represent the $CaCO_3$ producing organism found on the cryptic side of the settlement tiles. A scalpel was used to collect pieces of these calcifying groups from the cryptic side of settlement tiles deployed for 9 months and 15 months. The pieces were bleached overnight, rinsed in water and dried at 65° C to a constant mass. Then they were weighed (m) and photographed. For cryptic CCA, *T. ampla*, *P. hastingsae* and tubeworms, I loaded the photographs into the image analysis software ImageJ to determine the surface area of the pieces (A). The mean mass per cm^2 (calcification rate: cr) was calculated using Equation 2.

$$cr = \frac{m}{A} \qquad (2)$$

I calculated the mean of these measurements ($\overline{cr_{12,1}}$) as an approximation for the calcification rates after 12 months for each calcifying groups.

Corals and hydrocorals do not have a constant height but grow in different forms, including humps and branches. For this reason, I measured their volume instead of their surface area. This was done by measuring the volume of an entire coral and an entire hydrocoral collected from the settlement tiles using the water displacement method. The density of their $CaCO_3$ skeletons was then calculated by dividing the mass by the volume:

$$D = \frac{m}{V} \qquad (5)$$

As a next step I estimated the mass of $CaCO_3$ deposited on the cryptic side of the tiles using the following formula:

$$m_{CaCO_3\ cryptic} = \sum_{i=CG_1}^{CGn} (\overline{cr_{12,1}} * A_i) + D_C * V_C + D_{HC} * V_{HC} \qquad (6)$$

The surface area (A) of the substrata was obtained from the results of the CPCe analysis described earlier. Calcifying groups (CG) included in the calculation were: cryptic CCA, *T. ampla*,

other bryozoans, and tubeworms. The mass of $CaCO_3$ deposited by corals and hydrocorals was calculated by multiplying the density of corals (D_C) and hydrocorals (D_{HC}) obtained from equation 5 with the volume of corals (V_c) and hydrocorals (V_{HC}) present on the settlement tile. These volumes were estimated from length, width and height measurements on pictures taken of the settlement tiles. The calcification rate of *P. hastingsae* was used as a proxy for the calcification rate of other bryozoans present on the tiles. These otherbryozoan species were not abundant enough to accurately measure their calcification rates, but the thickness of their skeleton was comparable to that of *P. hastingsae*.

The estimated mass of $CaCO_3$ deposited on the cryptic side of the tile was subtracted from the total mass of $CaCO_3$ deposited on the tile to determine how much $CaCO_3$ was deposited on the exposed surface of the tile (Equation 7). Both CCA and vermetids were found on the exposed surface of the tile. Because CCA often overgrew vermetids, sometimes completely, I was not able to distinguish between $CaCO_3$ deposited by exposed CCA and vermetids. On some tiles, part of the exposed surface did not have any or only had very low $CaCO_3$ deposition (blue area, in Figure 5.2). This area was either bare or covered by the brown alga *Lobophora* spp. To be able to compare the calcification rate (cr in kg m^{-2}) of calcifiers (CCA, vermetids) on the exposed surface of the tiles I first calculated the percentage cover of the area which had $CaCO_3$ accretion, hereafter referred to as ACA (Equation 8, red area in Figure 5.2). I then divided the estimated mass of $CaCO_3$ deposited on exposed surfaces by the area which had $CaCO_3$ accretion (Equation 9).

$$m_{CaCO_3\ exposed} = m_{CaCO_3} - m_{CaCO_3\ cryptic} \quad (7)$$

$$\text{Area of exposed side of tile with } CaCO_3 3 \text{ accretion} = 100\ cm^2 - A_{bare} - A_{Lobophora} \quad (8)$$

$$cr_{exposed} = \frac{m_{CaCO_3\ exposed}}{100\ cm^2 - A_{bare} - A_{Lobophora}} \quad (9)$$

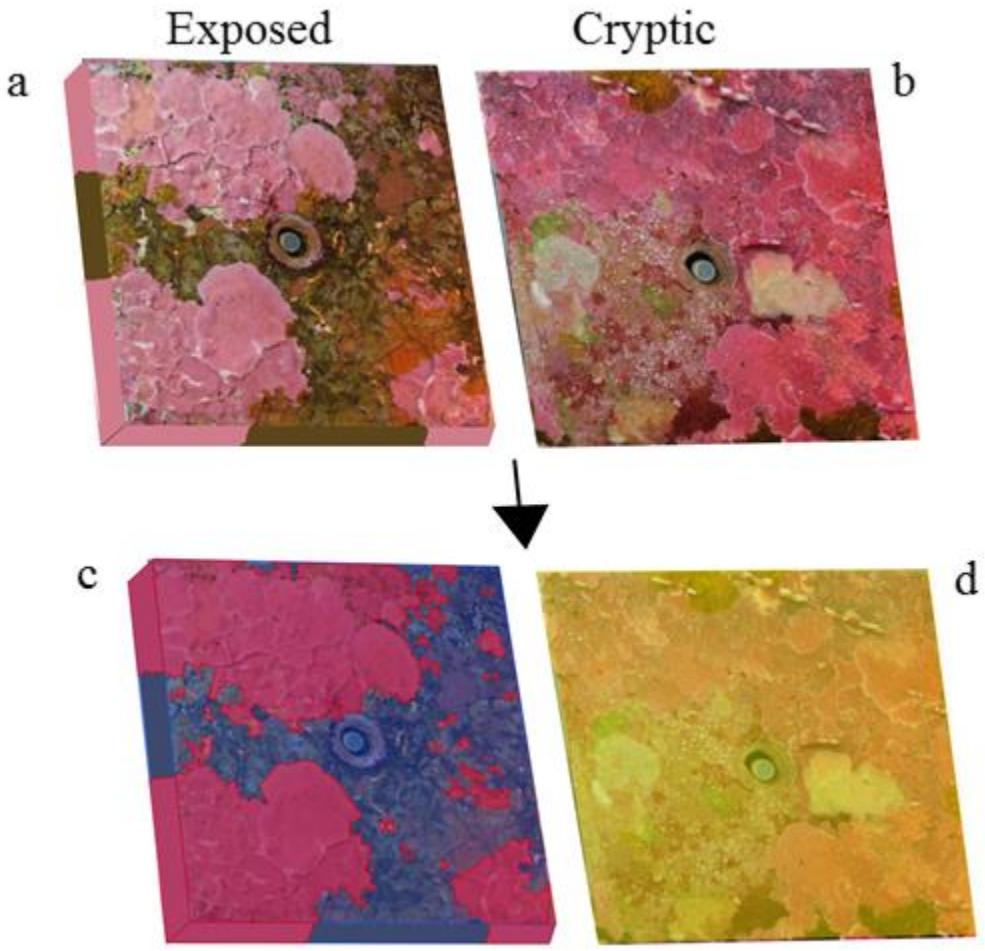

Figure 5.2. Different tile areas used in the calcification study. Benthic cover on the exposed side (a) and cryptic side (b) of a settlement tile deployed on the reef for one year. Three different areas were measured on each tile: cryptic tile area (*yellow area* in (d)), area with $CaCO_3$ accretion (ACA) on the exposed side of the tile (*red area* in (c)), area without $CaCO_3$ accretion on the exposed side of the tile (*blue area* in (c)). I measured the calcification rate (kg m^{-2} y^{-1}) for the entire tile (exposed and cryptic side) and estimated the calcification rates for the cryptic side (*yellow area* in (d)), the exposed side (*blue and red area* in (c)) and the ACA tile (*red area* in (c)).

5.3.3 Quantifying bioerosion

I used *Fungia* corals for the bioerosion study, as they are the most abundant coral genus on the reefs surrounding Palmyra Atoll (Stuart Sandin, Scripps Institute of Oceanography, pers. comm.). All collections were made under the Pacific Remote Islands National Wildlife Refuge Special Use Permit 12533-13014 issued by the U.S. Fish and Wildlife Service.

Live *Fungia paumotensis* were collected from the Penguin Spit reef terrace site at Palmyra Atoll (5° 52' 11.7840" N, 162° 6' 25.1100" W). The *F. paumotensis* were soaked in bleach for 24 h to remove any live tissue. They were then rinsed in fresh water to remove the bleach and examined externally for any signs of borings. An analysis of 10 *F. paumotensis* showed that only the skeletons that showed external signs of boring (e.g., entrance holes for polychaete worms) were likely to contain bore holes internally. I therefore determined that the *F. paumotensis* skeletons used for this study did not show any signs of boring prior to the experiment. The *F. paumotensis skeletons* were cut in half along the transverse plane and its initial mass was measured before it was glued to a PVC plate using Z spar marine epoxy (Figure 5.3). Eighty of these PVC plates were deployed onto stainless steel stakes at the 10 different sites described earlier.

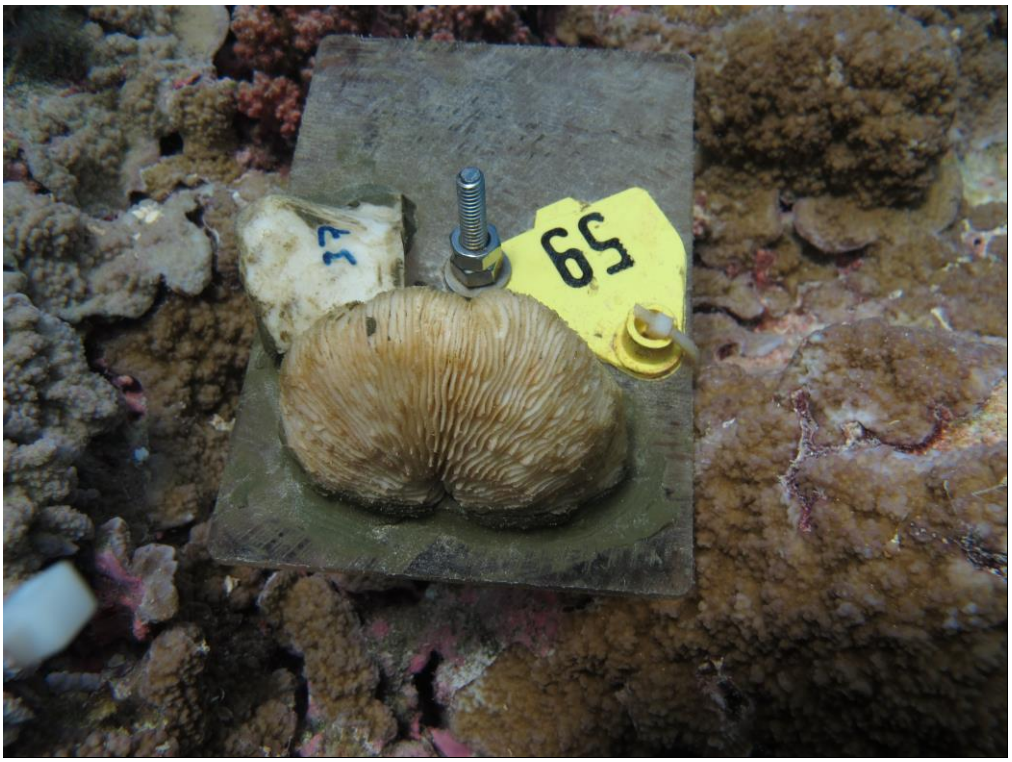

Figure 5.3. Example of a PVC plate with a *Fungia paumontensis* skeleton and a piece of *Tridacna maxima* shell placed on the reef. The *T. maxima* shell pieces were not used for bioerosion measurements as I was not able to distinguish between bioerosion that occurred in the shell before and after deployment.

After 15 months of deployment, 56 of the 80 PVC plates were still in place. These PVC plates were collected and immediately fixed in 4% formaldehyde sea water buffer for 48 h (40 ml formalin (37%), 960 ml filtered sea water and 40 g baking soda) (Preskitt). After being fixed, they were rinsed and air dried for transportation. The pieces of *F. paumotensis* skeleton were removed from the PVC plate and cut into 3 pieces along their frontal plane axis using a slow saw (Figure 5.4).

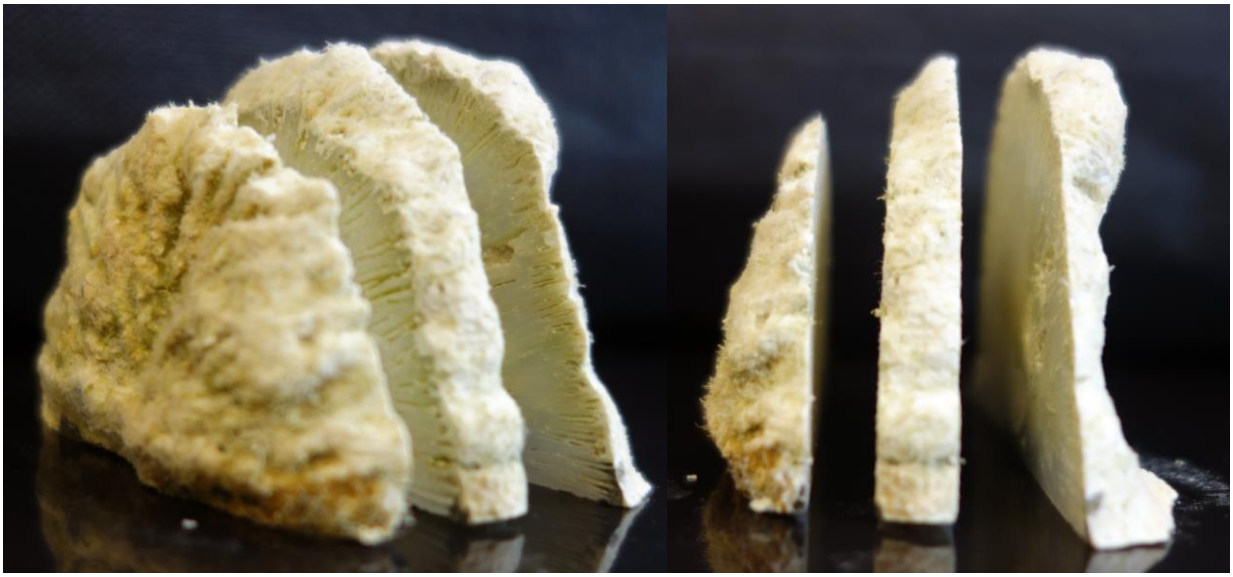

Figure 5.4. Example of the two frontal plane axis cuts made in the *Fungia. paumotensis* skeletons after collection. Pictures are taken of the same *F. paumotensis* piece from different angles.

The exposed surface area that was best preserved (no or less breakage during cut) was photographed for each cut. The total area of the *F. paumotensis* skeleton and the total area of the borings present in the cut surface were measured in ImageJ from the photographs. The percentage of area bored was calculated using the surface area measurements of both cut surfaces. This percentage was used to estimate the volume of $CaCO_3$ that was removed due to borings from the entire *F. paumontensis* pieces. It was assumed that the density of the *F. paumontensis* pieces was uniform within the piece, the estimate percentage of volume removed was therefore converted into an estimated mass of the $CaCO_3$ removed by multiplying it by the initial mass of the *F. paumotensis* piece measured before deployment. The yearly internal bioerosion rate (kg $CaCO_3$ m^{-2} y^{-1}) was calculated by dividing the mass of $CaCO_3$ lost due to bioerosion by the surface area of the *F.*

paumotensis piece. Boring organisms which were exposed through the cutting process were collected and examined under the microscope to determine their taxonomic group.

5.3.4 Net $CaCO_3$ gain/loss

Net $CaCO_3$ accretion rates were determined using two different methods. The first method used the values obtained from the calcification and bioerosion analyses above. Net calcification was calculated by subtracting the mass of $CaCO_3$ (kg $CaCO_3$ m^{-2} y^{-1}) removed through internal bioerosion on the pieces of *F. paumotensis* from the mass of $CaCO_3$ (kg $CaCO_3$ m^{-2} y^{-1}) deposited onto the settlement tiles.

For the second method, pieces of dead coral rock (acroporid, dense and light pocilloporid*s)* were collected by breaking them off the reef. All collections were made under the Pacific Remote Islands National Wildlife Refuge Special Use Permit 12533-13014 issued by the U.S. Fish and Wildlife Service. This had the advantage that some of these pieces were older than 15 months, making it possible to detect bioerosion from taxonomic groups that recruit to dead substratum at a later stage. The disadvantage of this method is that the ages of the pieces are unknown, therefore it was not possible to determine the net annual calcification rate. The pieces of dead coral rock were immediately fixed in 4% formaldehyde sea water buffer for 48 h after collection. After being fixed they were rinsed and air dried for transportation. They were examined for calcifying organisms other than CCA to determine if calcification by these organisms was negligible compared to calcification by CCA. The organisms present were measured to the nearest 0.1 mm using manual callipers. The pieces of coral rock were cut into several pieces using a slow saw. The number of pieces was dependent on the initial size and shape of the piece of dead coral rock. The exposed surface area of the cuts that was best preserved (no or less breakage during cut) was photographed and measured in ImageJ. I measured the total area of the coral skeleton, the area of the coral skeleton that was bioeroded and the area of the $CaCO_3$ accretion by CCA. The perimeter of the dead coral rock was also measured as that determined the available substratum for $CaCO_3$-forming organisms to recruit. Boring organisms which were exposed through the cutting process were collected and examined under the microscope to determine their taxonomic group.

The densities of the three types of coral rock (acroporid, dense and light pocilloporid) were determined by cutting rectangular cuboids from non-bioeroded pieces of coral rock. These pieces were oven dried at 65° C to a constant mass before being weighed. The volume of the rectangular

cuboids was measured using a manual calliper and the density was calculated for each piece. The mean density for each of the three types of coral rocks was calculated. Using these mean densities, I converted the proportional area gains and losses due to $CaCO_3$ accretion and boring into proportional mass gains and losses of $CaCO_3$. For $CaCO_3$ accretion a density of 1'260 kg m^{-3} for CCA (d_{CCA}) was used (Laubier 1962). Net proportional $CaCO_3$ accretion was calculated with the following formula:

$$\text{Net proportional } CaCO_3 \text{ accretion} = \frac{d_{CCA} * a_{CCA} - d_{coral} * a_{bored}}{d_{coral} * a_{coral,initial}} \quad (9)$$

d = density, a = area, $a_{coral, initial}$ = total area of coral rock including bored area

5.3.5 Statistical analysis

Calcification

To determine if the percentage cover of a calcifying group was proportional to the mass of $CaCO_3$ it deposited on the tile, an estimated of the mean calcification rates of the pieces of bryozoans and CCA collected from the cryptic side of the settlement tiles was calculated for different sites and deployment times. The calcification rates on the tiles deployed at different areas of the reef were compared. For CCA, a one way ANOVA was used to determine if mean calcification rates differed between tiles deployed in the Entrance Channel, on the Western Reef Terrace and the fore reef. *T. ampla* and *P. hastingsae* were only found on the fore reef. For this reason, an independent sample t-test was used to determine if the mean calcification rates of *T. ampla* differed between FR5 and FR7, the two sites at which it was found in abundance. *P. hastingsae* was abundant at FR3 and FR5 and these sites were thus used in the independent sample t-test to determine if *P. hastingsae* shows spatial differences in calcification rates. Mean calcification rates of CCA and bryozoans collected on tiles deployed for 9 months and tiles deployed for 15 months were compared using a two sided t-tests. The relationship between the total mass of $CaCO_3$ deposited on the exposed side of the tile and the percentage cover of the main calcifying group (CCA) on that side of the tile was investigated by plotting the $CaCO_3$ deposition against CCA cover. A trend line was fitted to the plot and a regression analysis was performed to determine how well CCA cover explains $CaCO_3$ deposition on the exposed side of the tile.

Total $CaCO_3$ accretion on the tiles was not normally distributed. To determine if $CaCO_3$ accretion differed significantly among the sites an independent sample Kruskal-Wallis test was

performed. I then tested if the calcification rate (kg m^{-2} y^{-1}) for (1) the entire tile, (2) the exposed side of the tile, (2) ACA of the exposed side of the tile and (4) the cryptic side (Figure 5.2) correlated significantly with any of the predictors listed in Table 5.1. These predictors represent biophysical forcing factors such as grazing, physical oceanographic properties and connectivity to the sediment laden lagoon, coral-dominated areas of Palmyra Atoll and fore reef sites with oceanic water. Both analyses were performed in SPSS.

To determine if differences in $CaCO_3$ accretion rates amongst settlement tiles and sites were correlated with differences in depth/reef area (fore reef sites were located deeper than back reef sites) and differences in the above mentioned biophysical forcing factors, a correlation and generalised linear model analysis was performed using the predictors in Table 5.1.

Herbivore grazing removes $CaCO_3$ from the settlement tiles and therefore influences the $CaCO_3$ measurement reported in this study. The mass of $CaCO_3$ lost to grazing was estimated by measuring the area covered in grazing marks on the settlement tiles. CCA crusts can fill up grazing marks within 10 – 30 days if they grow undisturbed, so for this reason grazing marks on corallines is considered a rough indicator of the rate of grazing by excavating herbivores (Steneck 1983b). In this study, I identified grazing marks as (1) bare substratum that was clearly removed by grazers, (2) visible grazing marks on CCA and (3) green encrusting algae which settled inside grazing marks (see Figure 5.1 for examples). The percentage cover of grazing marks on each settlement tile were measured using 200 stratified random points in CPCe (see Chapter 3 for detailed method description). The percentage cover of grazing marks on the settlement tiles was used in the correlation and generalised linear model analysis to approximate the loss of $CaCO_3$ to grazing (Table 5.1).

Hydrodynamic processes influence calcification through the transport of nutrients and sediments (Mallela 2007). A connectivity matrix for 22 sites surrounding Palmyra Atoll was developed using The Coupled-Ocean-Atmosphere-Wave-Sediment Transport (COAWST) program (Warner et al. 2010) (see Chapter 2 for details). This matrix quantifies the water flux to and from these sites. The 22 points used in the water flux model included all four fore reef sites, a site in the middle of the Western Reef Terrace and a site close to the two Entrance Channel sites used in this study. To determine how water flux influences calcification rate I included several different water flux measurements into the correlation and generalised linear model analyses: (1)

water received from the lagoon, (2) water received from coral-dominated sites, (3) water received from fore reef sites, (4) water received from the southern fore reef sites, (5) overall inward water flux and (6) overall outward water flow (Figure 5.5, Table 5.1). Water received from the lagoon is of interest because the lagoon is the major source of sediment on Palmyra Atoll (Williams et al. 2011b). Coral-dominated sites on Palmyra Atoll have high CCA cover (Williams et al. 2013) and fore reef sites have high bryozoan cover in cryptic habitats (Chapter 3). Water received from coral-dominated sites and the fore reef are therefore an indicator of the volume of water received from sites releasing CCA spores and bryozoan larvae. Next to currents, waves and tidal flushing also affect $CaCO_3$ production and the abundance of calcifying organisms (Martindale 1992; Mallela 2007; Pescud 2012). I tested the effect of wave energy and tidal variation on calcification by including north-south and east-west current speeds, wave height, bottom stress, and tidal variation in the correlation and generalised model analyses (Table 5.1).

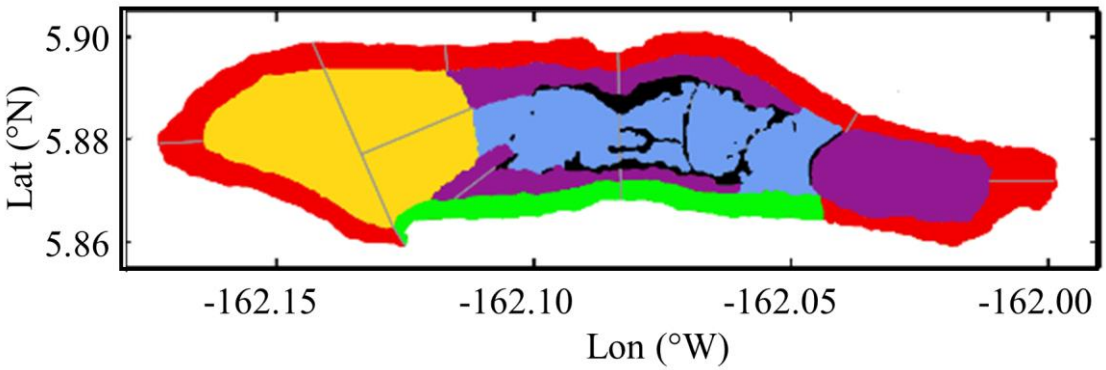

Figure 5.5. The different areas between which water flux was measured. The *black areas* in the centre represent the land mass of Palmyra Atoll. The COAWST model measured water flux between 22 points of origin, which are separated in this diagram by *grey lines*. Some points of origin where grouped together (*same background colour*). *Red and green combined*: Fore reef (9 points or of origin), *green*: Southern fore reef, *blue*: lagoon (4 points of origin), *green, red and yellow combined*: Coral dominated site (substantial part of or entire area has > 50 % coral cover (12 points of origin). Total water influx and out flux were calculated using all areas (*blue*, *green*, *yellow*, *red*, *purple*, 22 points of origin/destination).

Table 5.1. Predictor variables used in correlation and generalised linear model analyses. These predictors were used to determine which factors correlate with changes in calcification rates found on Palmyra Atoll.

Predictor	Category	Sites	Spatial scale of measurement	Indicator includes	Measured in
Grazing rate	Grazing	All	Tile	Bare substratum removed by grazing, grazing marks on CCA, Green encrusting algae	Log transformed percentage cover
E-W velocity	Physical Oceanography	EC1 EC2 FR5 FR7 FR9 RT10 RT4	Site	Average east to west water velocity Sept 2013- June 2014	$m\ s^{-1}$
N-S velocity	Physical Oceanography	EC1 EC2 FR5 FR7 FR9 RT10 RT4	Site	Average north to south water velocity Sept 2013- June 2014	$m\ s^{-1}$
Bottom stress	Physical Oceanography	All	Site	Average estimated bottom stress Sept 2013- June 2014	$m^2\ s^{-2}$

Table 5.1 continued

Predictor	Category	Sites	Spatial scale of measurement	Indicator includes	Measured in
Tidal variation	Physical Oceanography	EC1 EC2 FR5 FR3 FR7 FR9 RT10 RT4	Site	Average variation in water column height above the reef Sept 2013- June 2014	m
Wave height	Physical Oceanography	All	Site	Average wave height Sept 2013- June 2014	m
Depth	Depth/Reef area	All	Site	Average depth the settlement tiles were deployed at	m
Water received from the lagoon	Connectivity	All	Site	Average volume of water received from lagoon from two COAWST model runs	Nr of particles
Water received from coral dominated sites	Connectivity	All	Site	Average volume of water received from sites that have coral cover from two COAWST model runs	Nr of particles
Water received from the fore reef	Connectivity	All	NA	Average volume of water received from fore reef from two COAWST model runs	Nr of particles
Water received from the southern fore reef	Connectivity	All	NA	Average volume of water received from southern fore reef from two COAWST model runs	Nr of particles

Table 5.1 continued

Predictor	Category	Sites	Spatial scale of measurement	Indicator includes	Measured in
Outward water flow	Connectivity	All	NA	Total volume of water leaving the site from two COAWST model runs	Nr of particles
Inward water flux	Connectivity	All	NA	Total volume of water arriving at site from two COAWST model runs	Nr of particles

To better determine which factors influence calcification rates on the settlement tiles, the $CaCO_3$ accretion rates were modelled using generalised linear models. The $CaCO_3$ accretion rates on each entire tile and on the exposed side of the tile followed a gamma distribution. For this reason, a generalised linear model approach with gamma distribution was used to model the $CaCO_3$ deposited per cm^2 on (1) the entire tile, (2) the exposed side of the tile and (3) the ACA of the exposed side of the tile. $CaCO_3$ deposited per cm^2 to the cryptic side was closest to a normal distribution (χ^2= 3.178, df = 3 p = 0.365), so I modelled it using a normal distribution. The predictors in Table 5.1 were used as continuous predictors. The water flux measurements were highly correlated with depth and therefore could not be included in the model. A set of 200 models was generated using the 'best' selection procedure. The model selection criteria were determined using Akaike's information criterion (Akaike 1998). Models within 2 AIC units of the best fitting model are considered to be as good as the best model (Richards 2005) and I therefore included them in my results. This difference is calculated as $\Delta_i = AIC_i - AIC_{min}$. Out of these models I excluded the ones that differed from a higher ranked model solely by the inclusion of additional factors. These models are essentially a more complex version of the former model. As the added complexity did not increase the power of the model, it could be neglected (Burnham and Anderson 2002). All other models were kept, and a set of possible models was created that can explain the relationship between $CaCO_3$ accretion and factors describing the thickness of $CaCO_3$ deposited and biophysical forcing factors between the study sites. Akaike weights were calculated for all models with $\Delta_i < 5$ using the following formula $W_i = \exp\left(-\frac{1}{2}\Delta i\right) / \sum_{j=i}^{R} \exp\left(-\frac{1}{2}\Delta j\right)$. The

Akaike weights were also used to estimate the relative importance of each predictor variable (Symonds and Moussalli 2011). For each predictor, the Akaike weights of all the models within 5 AIC units of the best fitting model that also contained that predictor were summed. The summed Akaike weights for each predictor can be interpreted as the relative importance of that predictor. Predictors that consistently occur in the most likely models have an Akaike weight close to 1 whereas variables that are absent from all models or are only present in poorly fitting models (high AIC values) have an Akaike weight close to 0 (Symonds and Moussalli 2011). The program Statistica was used for this analysis.

The individual predictors were then plotted against the mass of $CaCO_3$ deposited per cm^2 on (1) the entire tile, (2) the exposed side of the tile, (3) the ACA of the exposed side of the tile (4) the cryptic side of the tile. A trend line was fitted to the scatter plot and a regression analysis was performed. This made it possible to determine if the predictor has a positive or negative effect on $CaCO_3$ accretion and how strong this correlation is. This was done in SPSS.

Bioerosion

To determine if internal bioerosion rates varied between sites, the percentages of area bored on the *F. paumotensis* slices were compared using a 1 way ANOVA with a test for location of difference - LSD post hoc test. This was performed in SPSS.

Net CaCO3 gain/loss

Net $CaCO_3$ accretion rates on the dead coral rock pieces were not normally distributed. For this reason, independent sample Kruskal-Wallis tests were performed to determine if (1) net $CaCO_3$ accretion rate, (2) area lost due to boring and (3) area gained through calcification varied amongst acroporid, dense and light pocilloporid coral rock.

5.4 RESULTS

5.4.1 Calcification

$CaCO_3$ accretion on the settlement tiles varied from 0.27 to 1.36 kg $CaCO_3$ m^{-2} y^{-1} with a mean of 0.67 kg $CaCO_3$ m^{-2} y^{-1}. The southern fore reef sites (FR3 and FR5) showed the highest $CaCO_3$ accretion rates (Kruskal-Wallis test statistic = 31.214, N = 46, df = 0, $p < 0.001$, Figure 5.6). They had significantly higher $CaCO_3$ accretion than FR7 (FR3 $p = 0.004$, FR5 $p = 0.022$).

$CaCO_3$ accretion rates at FR3 also differed significantly from RT10 ($p = 0.024$) and RT1 ($p = 0.022$).

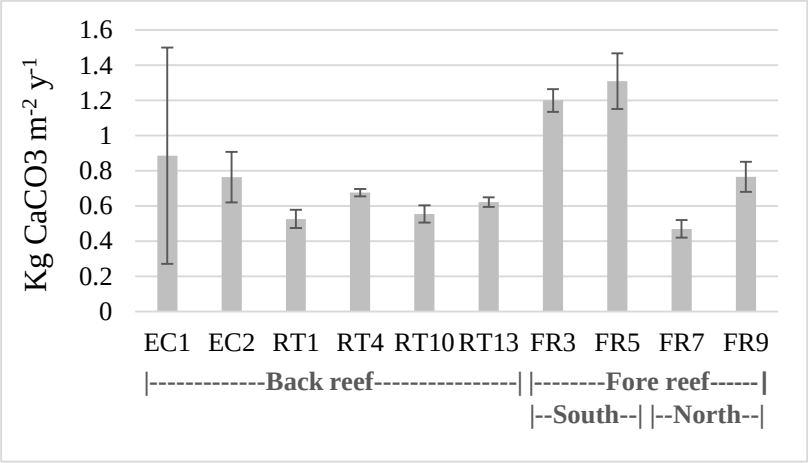

Figure 5.6. $CaCO_3$ production rates by early benthic recruiters. Each bare shows the mean amount of $CaCO_3$ deposited on settlement tiles deployed at the sites for 12 months (5 tiles per site). Error bars = 2SE.

Most of the $CaCO_3$ deposited on the tiles was produced by CCA located on the top and side of the tiles (exposed tile area). Other calcifying organisms found on the tiles were corals, hydrocorals, bryozoans, vermetids and tubeworms. Bryozoans and CCA were the only calcifiers that reached a cover exceeding 2.5% of the tile surface.

The mean mass of $CaCO_3$ produced by *P. hastingsae* found on settlement tiles deployed for 9 and 15 months was 0.019 ± 0.003 kg $CaCO_3$ m^{-2}. Colonies of the bryozoan *T. ampla* (Kirkpatrick 1888) found on settlement tiles deployed for 9 and 15 months deposited a mean of 0.030 ± 0.006 kg $CaCO_3$ m^{-2}. Production of $CaCO_3$ of these two bryozoan species did not differ amongst sites *(T. ampla*, FR5 versus FR7: df = 7, p = 0.973, *P. hastingsae*, FR3 versus FR5: df = 7, p = 0.615) and deployment time (9 and 15 months) (*T. ampla*: df = 8, p = 0.313, *P. hastingsae*: df = 9, p = 0.819). *T. ampla* deposited significantly more kg $CaCO_3$ m^{-2} than *P. hastingsae* (df = 13, p = 0.001).

Cryptic CCA, found on settlement tiles deployed for 9 and 15 months, deposited a mean of 0.028 ± 0.009 kg $CaCO_3$ m^{-2} (N = 21) onto the settlement tiles. The mass of $CaCO_3$ deposited on the cryptic side by CCA was significantly greater on tiles deployed for 15 months than on tiles deployed for 9 months (df = 19, p = 0.012) but did not differ between tiles deployed next to the

Entrance Channel (ECx), on the reef terrace (RTx) or the fore reef (FRx) (df =2, F = 0.353, p = 0.707). CCA on tiles deployed for 9 months deposited a mean of 0.023 ± 0.006 kg $CaCO_3$ m^{-2} (N = 10) while CCA on tiles deployed for 15 months deposited 0.03 ± 0.009 kg $CaCO_3$ m^{-2} (N = 11).

Tubeworm samples were collected from FR3, FR5, FR9 and EC1. Tubeworms found on settlement tiles deployed for 9 and 15 months deposited a mean of 0.007 g ± 0.001 kg $CaCO_3$ m^{-2} (N = 4). One coral recruit and one hydrocoral were collected from the settlement tiles. The skeleton of the coral recruit had a density of 1'520 kg $CaCO_3$ m^{-3}, while the density of the hydrocoral skeleton was 1'800 kg $CaCO_3$ m^{-3}.

An average of 92% of the $CaCO_3$ deposited on the tile was deposited on the exposed side of the tile, which had an average calcification rate of 1.20 ± 0.50 kg $CaCO_3$ m^{-2} y^{-1}. The average mass of the $CaCO_3$ layer (calcification rate) on the exposed side of the tile was 1.38 ± 0.64 kg $CaCO_3$ m^{-2} y^{-1}. Thick layers of CCA as well as vermetids were found on the exposed side of the tile, with CCA often overgrowing vermetids, partially or fully. The mass of $CaCO_3$ deposited onto the exposed side of the settlement tiles increased as CCA cover increased (Figure 5.7).

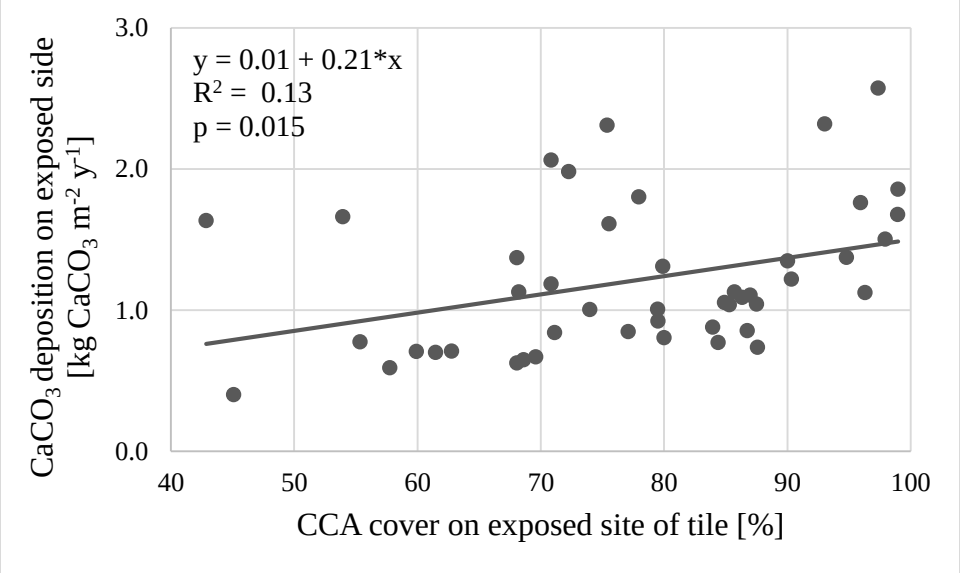

Figure 5.7. Relationship between per cent cover of CCA and $CaCO_3$ deposition on the exposed side of settlement tiles deployed for one year on Palmyra Atoll. *Dots* represents single settlement tiles, the *black line* is a fitted linear trend line. The trend line equation and statistics of the regression analysis are displayed in the right top corner of the graph.

5.4.2 Factors influencing calcification rates

$CaCO_3$ accretion on the settlement tiles correlated negatively with the number of grazing marks on the tiles ($p < 0.001$, $\sum$ Akaike weight = 1, Table 5.2). The $CaCO_3$ accretion on the entire tiles correlated strongly with the log of the grazed area ($R^2 = 0.60$, $p < 0.001$, Figure 5.8). This significant correlation was even higher for the ACA of the exposed side of the tiles ($R^2 = 0.65$, $p < 0.001$, Figure 5.8). No significant correlation was found between the $CaCO_3$ accretion on the cryptic side of the tile and the log of grazed area ($R^2 = 0.01$, $p = 0.433$, Figure 5.8).

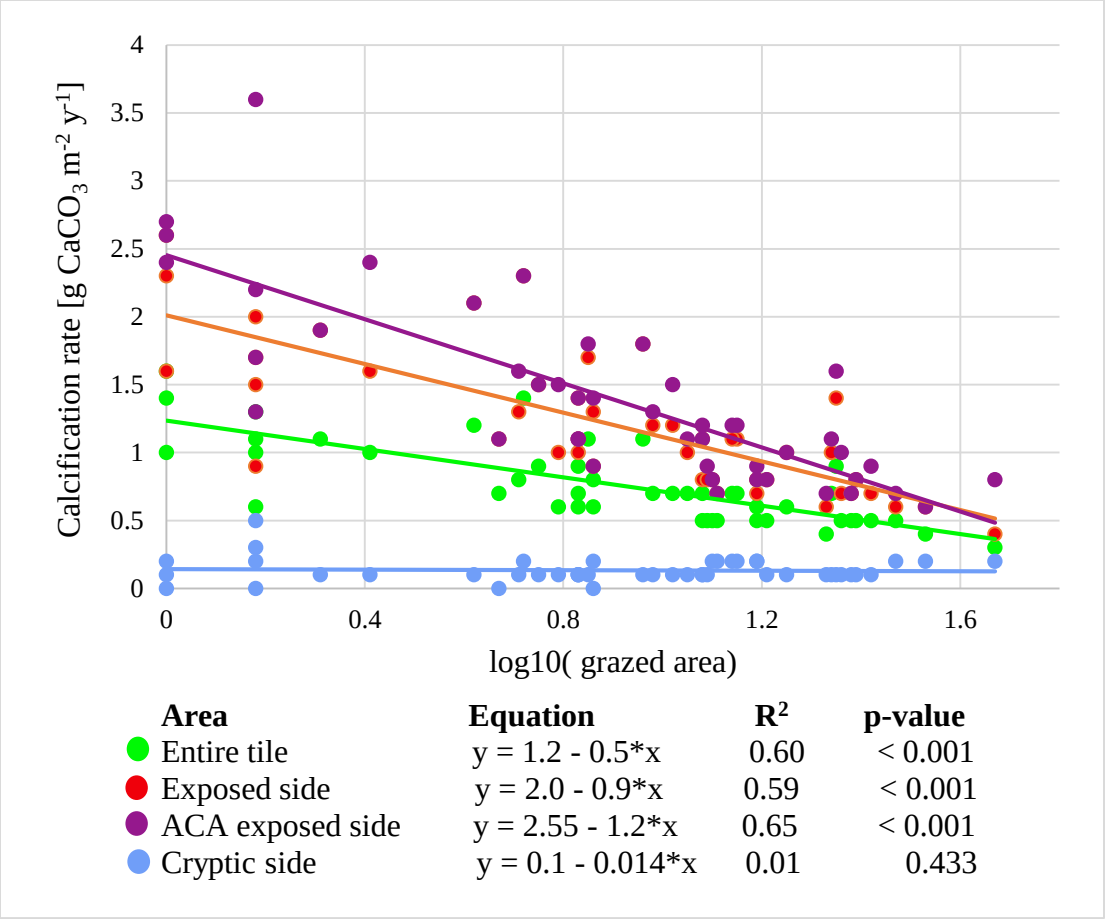

Figure 5.8. Relationships between the amount of herbivore grazing and $CaCO_3$ deposited onto settlement tiles deployed for 1 year on Palmyra Atoll. *Dots* represents single settlement tiles, *lines* are fitted linear trend lines. A key to the different colors used, the trend line equations and statistics of the regression analysis are displayed in the legend below the graph. ACA = Area with $CaCO_3$ accretion on the exposed side of the tile.

$CaCO_3$ accretion on the settlement tiles also correlated negatively with the velocity of currents in the north-south direction ($p = 0.006$, $\sum$ Akaike weight = 0.53, Table 5.2). North-south current velocity correlated strongly with water received from southern fore reef sites (Pearson's correlation coefficient, $r = -0.921$, $p < 0.001$). $CaCO_3$ accretion and water received from southern fore reef sites correlated positively ($R^2 = 0.32$, $p < 0.001$).

$CaCO_3$ deposited onto the ACA of the exposed side of the tiles correlated positively with depth ($p = 0.001$, R^2 wasnot computable due to depth only taking 2 values). Across all sites, depth correlated positively with hydrodynamic processes (wave height ($p < 0.001$), water received from coral dominated sites ($p < 0.001$) and fore reef sites ($p < 0.001$), east-west and north-south current velocity (both $p < 0.001$), inward water flux ($p = 0.020$), tidal variation ($p = 0.031$) and bottom stress ($p < 0.001$)) and negatively with grazing rate ($p = 0.007$).

The significant Pearson's correlation p – values found for $CaCO_3$ accretion on the cryptic side of the tile were higher than the expected p – values for a false discovery rate of 10%. Their significance should therefore be considered with caution. All other significant p values (** and * in Table 5.2) were below the expected p values for a false discovery rate of 10% and no non-significant p values were found that were below the false discovery rate.

5.4.3 Generalised linear models

For $CaCO_3$ accretion on the entire settlement tile, 25 models were within five AIC units of the best fitting model. 44 models were in this range for $CaCO_3$ accretion on the exposed side, 42 models for $CaCO_3$ accretion on the ACA of the exposed side and 41 models for $CaCO_3$ accretion on the cryptic side of the tiles. These sets of models were used to calculate the summed Akaike weight found in Table 5.3. Grazing was included in every single model within five AIC units of the best fitting model for $CaCO_3$ accretion on the entire tile, the exposed side of the tile and the ACA of the exposed side of the tile (Table 5.3). The three models within two AIC units of the best fitting model for the $CaCO_3$ accretion on the entire tile were all found in the set of models within two AIC units of the best fitting model for the $CaCO_3$ accretion on the exposed side of the tile (Table 5.3).

Table 5.2. Factors affecting $CaCO_3$ deposition onto settlement tiles at Palmyra Atoll. This table shows the Pearson's correlation, summed Akaike weight and R^2 values for the relationships between various measurements of $CaCO_3$ deposits (descriptive variables) and the predictors described in Table 5.1. *Red cells* represent significant negative relationships and *green cells* significant positive relationships with a p value < 0.01, a ∑ Akaike weight > 0.50 (if applicable) and a $R^2 > 0.20$.

Predictor		**$CaCO_3$ accretion Entire tile**	**$CaCO_3$ accretion Exposed side**	**$CaCO_3$ accretion ACA of the exposed side**	**$CaCO_3$ accretion cryptic side**
Grazing pressure	Pearson's Correlation	-0.774**	-.768**	-0.808**	0.119
	Sig. (2-tailed)	<0.001	<0.001	<0.001	0.433
	∑ Akaike weight	1	1	1	0.25
	R^2 and direction of effect	0.60 (-)	0.59 (-)	0.65 (-)	0.01 (-)
	N	46	46	46	46
E-W velocity	Pearson's Correlation	-0.315	-0.337	-0.210	0.362*
	Sig. (2-tailed)	0.084	0.064	0.256	0.046
	∑ Akaike weight	0.82	0.72	0.59	0.33
	R^2 and direction of effect	0.01 (-)	0.11 (-)	0.04 (-)	0.13 (+)
	N	31	31	31	31
N-S velocity	Pearson's Correlation	-0.484**	-0.511**	-0.421*	0.427*
	Sig. (2-tailed)	0.006	0.003	0.018	0.017
	∑ Akaike weight	0.53	0.53	0.50	0.30
	R^2 and direction of effect	0.23 (-)	0.26 (-)	0.17 (-)	0.18 (+)
	N	31	31	31	31
Bottom stress	Pearson's Correlation	0.009	0.002	0.090	0.124
	Sig. (2-tailed)	0.951	0.987	0.551	0.412
	∑ Akaike weight	0.71	0.63	0.60	0.30
	R^2 and direction of effect	<0.01 (+)	<0.01 (+)	0.01 (+)	0.02 (+)
	N	46	46	46	46

Table 5.2 continued

Predictor		$CaCO_3$ accretion Entire tile	$CaCO_3$ accretion Exposed side	$CaCO_3$ accretion ACA of the exposed side	$CaCO_3$ accretion cryptic side
Tidal variation	Pearson's Correlation	0.326	0.352*	0.391*	-0.238
	Sig. (2-tailed)	0.052	0.035	0.018	0.162
	∑ Akaike weight	0.22	0.35	0.49	1
	R^2 and direction of effect	0.11 (+)	0.12 (+)	0.15 (+)	0.05 (+)
	N	36	36	36	36
Wave height	Pearson's Correlation	0.140	0.149	0.046	-0.045
	Sig. (2-tailed)	0.354	0.320	0.764	0.766
	∑ Akaike weight	0.66	0.60	0.64	0.36
	R^2 and direction of effect	0.02(+)	0.02(+)	<0.01 (+)	<0.01 (-)
	N	46	46	46	46
Depth	Pearson's Correlation	0.392**	0.372*	0.468**	0.236
	Sig. (2-tailed)	0.007	0.011	0.001	0.114
	∑ Akaike weight	0.53	0.53	0.67	0.35
	R^2 and direction of effect	0.15 (+)	0.14 (+)	0.22 (+)	0.06 (+)
	N	46	46	46	46
Water received from the lagoon	Pearson's Correlation	-0.207	-0.204	-0.218	-0.028
	Sig. (2-tailed)	0.168	0.173	0.145	0.855
	R^2 and direction of effect	0.04 (-)	0.04 (-)	0.05 (-)	<0.01 (-)
	N	46	46	46	46
Water received from coral dominated sites	Pearson's Correlation	-0.121	-0.110	-0.211	-0.082
	Sig. (2-tailed)	0.423	0.469	0.160	0.589
	R^2 and direction of effect	0.01 (-)	0.01 (-)	0.04 (-)	0.01 (-)
	N	46	46	46	46

Table 5.2 continued

Predictor		$CaCO_3$ accretion Entire tile	$CaCO_3$ accretion Exposed side	$CaCO_3$ accretion ACA of the exposed side	$CaCO_3$ accretion cryptic side
Water received from the fore reef	Pearson's Correlation	-0.191	-0.176	-0.241	-0.122
	Sig. (2-tailed)	0.204	0.243	0.106	0.421
	R^2 and direction of effect	0.04 (-)	0.03 (-)	0.06 (-)	0.01 (-)
	N	46	46	46	46
Water received from the southern fore reef	Pearson's Correlation	0.570**	0.594**	0.540**	-0.183
	Sig. (2-tailed)	<0.001	<0.001	<0.001	0.222
	R^2 and direction of effect	0.32 (+)	0.35 (+)	0.29 (+)	<0.01 (-)
	N	46	46	46	46
Outward water flow	Pearson's Correlation	-0.314*	-0.320*	-0.305*	0.040
	Sig. (2-tailed)	0.034	0.030	0.039	0.790
	R^2 and direction of effect	0.1 (-)	0.1 (-)	0.1 (-)	<0.01 (+)
	N	46	46	46	46
Inward water flux	Pearson's Correlation	-0.257	-0.258	-0.241	-0.170
	Sig. (2-tailed)	0.085	0.083	0.106	0.259
	R^2 and direction of effect	0.07 (-)	0.07 (-)	0.1 (-)	<0.01 (+)
	N	46	46	46	46

Table 5.3. Set of models that best predict $CaCO_3$ deposition on settlement tiles deployed for 1 year onto the reef of Palmyra Atoll. This table shows the AIC, the L ratio χ^2 and p values as well as the Aikake weights (w_i) derived from the best fitting models ($\Delta_i < 5$), the number of predictor variables in the model and the names of these variables. These models all have a $\Delta_i < 2$ and differ from a better fitting model by more than just one additional factor. Detailed information on the predictor variables can be found in Table 5.1. B stress = bottom stress, D = depth, EW= E-W velocity, Grazed = grazing rate, NS = N-S velocity, Tidal = Tidal variation, WH = wave height, D.

Area for which $CaCO_3$ deposition (kg m^{-2}) was modelled	AIC	L ratio χ^2	p	wi	No. of variables	Predictors
Entire tile	166.32	44.97	< 0.001	0.16	4	Grazed, EW, B stress, WH
	167.56	47.73	< 0.001	0.08	5	Grazed, EW, NS, D, WH
	167.60	45.69	< 0.001	0.08	5	Grazed, EW, NS, B stress, D
Exposed side	166.71	45.71	< 0.001	0.09	4	Grazed, EW, B stress, WH
	167.13	47.30	< 0.001	0.07	5	Grazed, EW, NS, D, WH
	167.57	46.86	< 0.001	0.06	5	Grazed, EW, NS, B stress, D
	167.72	44.70	< 0.001	0.05	4	Grazed, EW, B stress, D
	168.29	40.14	< 0.001	0.04	2	Grazed, NS
ACA exposed side	-135.98	47.09	< 0.001	0.07	5	Grazed, EW, NS, D, WH
	-135.96	47.08	< 0.001	0.07	5	Grazed, Tidal, EW, B stress, WH
	-135.75	44.86	< 0.001	0.06	4	Grazed, EW, B stress, D
	-135.47	42.58	< 0.001	0.05	3	Grazed, D, WH
	-134.32	43.43	< 0.001	0.03	4	Grazed, NS, B stress, WH
	-134.29	43.40	< 0.001	0.03	4	Grazed, EW, B stress, WH
	-134.24	43.35	< 0.001	0.03	4	Grazed, NS, B stress, D
Cryptic side	43.94	14.17	< 0.001	0.07	2	Tidal, WH
	44.14	13.96	< 0.001	0.07	2	Tidal, EW
	44.16	13.94	< 0.001	0.07	2	Tidal, D
	44.81	13.29	< 0.001	0.05	2	Tidal, B stress
	44.98	13.12	< 0.001	0.04	2	Tidal, NS

5.4.4 Bioerosion

A mean of 0.15% of the *F. paumotensis* skeleton was bioeroded by internal bioeroders after 15 months (N = 56), resulting in a mean bioerosion rate of 0.009 kg $CaCO_3$ m^{-2} y^{-1}. Internal bioerosion varied amongst sites (1 way ANOVA, SS = 0.276, df = 9, F = 2.253, p = 0.035). The LSD post hoc test revealed significant differences, which are shown in Figure 5.9.

Internal bioeroders found inside the *F. paumotensis* pieces were the bioeroding sipunculids and polychaetes. Bioeroding sponges (Clionaidae) and bivalves (*Lithophaga*) were also present in the

coral rock pieces collected from the reef. Grazing marks from herbivorous fishes were found on the outside of the *F. paumotensis* pieces. It appears as if the grazers consumed parts of the *F. paumotensis* pieces because some pieces had dents that resemble bite marks. I was not able to measure the volume or mass of *F. paumotensis* skeleton removed by grazers.

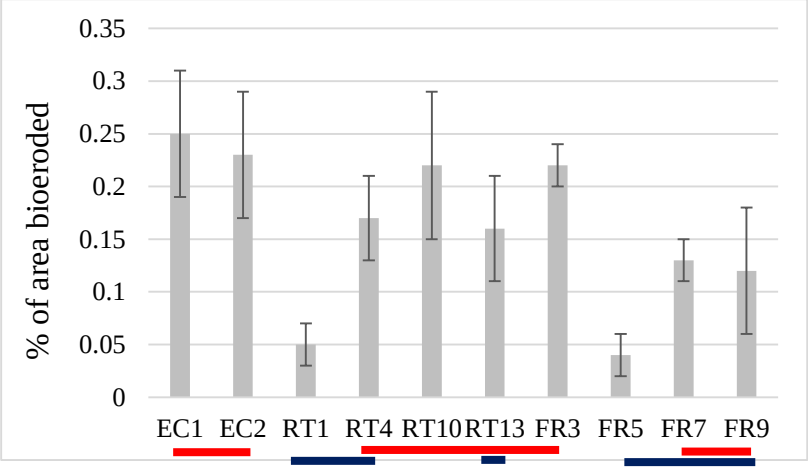

Figure 5.9. Mean per cent internally eroded volume of *Fungia* skeletons after 15 months of deployment on the reef. The *red bars* are drawn under sites that are significantly different from RT1 and FR5 (LSD post-hoc test, $p > 0.05$) while the *blue bars* are drawn under sites that are significantly different from EC1, EC2, FR3 and RT10 (LSD post-hoc test, $p > 0.05$). Error bars = 2SE.

5.4.5 Net $CaCO_3$ gain/loss

The net calcification rate at the ten sites varied from 0.03 to 1.36 kg $CaCO_3$ m^{-2} y^{-1}. These values were calculated by subtracting the mass of $CaCO_3$ removed yearly through internal bioerosion on the pieces of *F. paumotensis* from the mass of $CaCO_3$ deposited yearly on the settlement tiles.

Pieces of coral rock were collected from the same sites as the settlement plates and *F. paumotensis* pieces were deployed. Two additional pieces were collected at North Barren (NB) which is a shallow reef site located to the east of the atoll (see Figure 2.1 for location). The pieces of reef rock had an average net calcification gain of 7% of the mass of the piece of reef rock (Figure 5.10). CCA was the most abundant calcifier on the pieces of reef rock. Coral recruits, vermetids and small colonies of bryozoans were also found on some coral rock pieces. The maximum size (estimated volume) of the coral recruits, vermetids and bryozoans was 75 mm^3. Eighteen coral

rock pieces decreased in mass, indicating that bioerosion removed more $CaCO_3$ than was deposited onto the reef rock by CCA. The other 34 pieces increased in mass, resulting in a net gain of $CaCO_3$. No significant difference was found between net calcification rates amongst pieces of *Acropora*, and dense and light pocilloporid pieces ($p = 0.093$). The proportion of bored rock was also not significantly different amongst these three rock types ($p = 0.676$). The proportion of volume that was gained due to $CaCO_3$ deposition of CCA was significantly greater for the pieces of pocilloporid than for the pieces of *Acropora* (overall $p = 0.002$, dense pocilloporid $p = 0.009$, light pocilloporid $p = 0.001$). Between 0 and 54% (mean = 9%) of the volume of the pieces of reef rock was bored. The $CaCO_3$ deposited onto the pieces of reef rock were equivalent to from 0 to 49% (mean = 15%) of the initial reef rock volume.

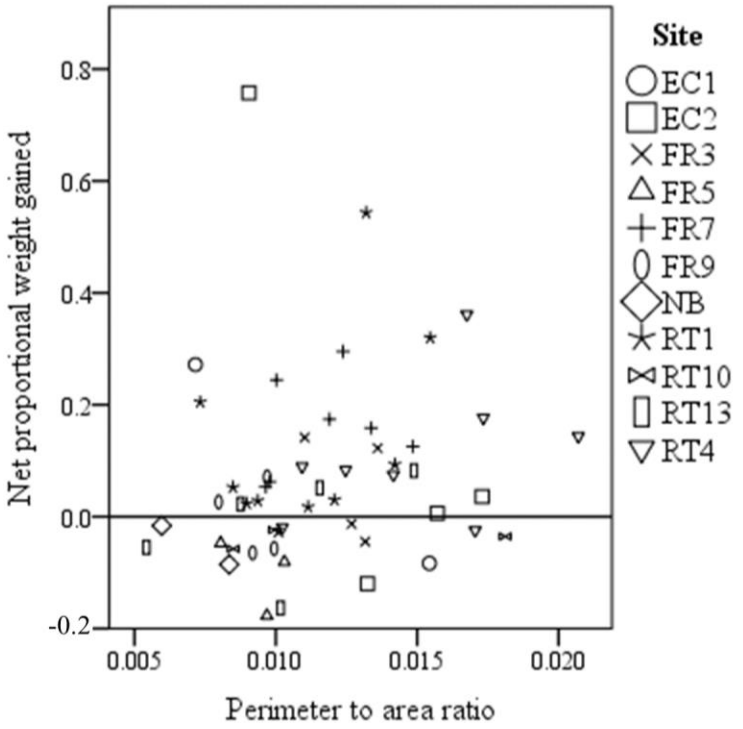

Figure 5.10. Net proportional $CaCO_3$ mass gained/lost on pieces of coral rock after the death of the coral that produced them. Each point on the graph represents a coral rock piece, the symbol indicates which site the piece was collected from (see legend on the left side of the graph). Increase or decrease in mass for each coral rock pieces was measured in proportion to their initial weight. Points located below the line at y = 0 decreased in mass while points located above the line increased in mass. The x-axis shows the perimeter to area ratio of the coral rock pieces (perimeter divided by area).

5.5 DISCUSSION

In this study, I investigated $CaCO_3$ deposition and removal by early successional calcifiers and bioeroders on Palmyra Atoll. $CaCO_3$ is deposited on settlement tiles by CCA, bryozoans, vermetids, tubeworms, corals and hydrocorals. 93% of the $CaCO_3$ deposited on the tiles was produced by CCA located on the top and side of the tiles. On the cryptic side of the tile, $CaCO_3$ accumulation was proportional to percentage cover of calcifier groups, while this was not the case on the exposed side. $CaCO_3$ accretion on the settlement tiles correlated strongly and negatively with herbivore grazing rate, positively with volume of water received from southern fore reef sites, and negatively with north-south current velocity. Only a mean volume of 0.15% of the *F. paumotensis* skeletons was eroded by internal bioeroders after 15 months. The bioeroders present in the *F. paumotensis* skeletons were sipunculids and polychaetes. Bioeroding sponges (Clinoidae)

and bivalves were found in the coral rock pieces collected from the reef. Calcifiers deposited a mean of 0.67 kg $CaCO_3$ m^{-2} y^{-1}on the settlement tiles, while internal bioeroders eroded a mean of 0.009 kg $CaCO_3$ m^{-2} y^{-1}. This leads to an overall increase in $CaCO_3$ on the reef. Some of the coral rock pieces collected from the reef had a negative $CaCO_3$ budget. However, overall the coral rock pieces showed a net $CaCO_3$ weight gain of 7%.

5.5.1 Calcification

$CaCO_3$ accretion varied from 0.27 to 1.36 kg $CaCO_3$ m^{-2} y^{-1} and was similar to the mean $CaCO_3$ accretion rates reported on settlement tiles in Tobago, the Great Barrier Reef, the northern Line Islands and Barbados (Stearn et al. 1977; Price et al. 2012; Mallela 2013; Browne et al. 2013). CCA produced 99% of the $CaCO_3$ accretion on the tiles (exposed and cryptic side). It deposited a thick layer of $CaCO_3$ on the exposed side of the settlement tiles. This layer was 5 to 7 times thicker than the $CaCO_3$ deposited by CCA and bryozoans on the cryptic side of the tile.

Table 5.4. $CaCO_3$ accretion rate measurements on settlement tiles from different locations around the world. Rates are given as the full range of values observed in the study (Full range), the range of site averages reported by the study (Range of site averages), the average reported by the study (Average).

Location	**$CaCO_3$ accretion rate (kg $CaCO_3$ m^{-2} y^{-1})**	**Study**
Palmyra Atoll	0.27 - 1.36 (Full range)	This study
Palmyra Atoll	0.66 - 0.72 (Range of site averages)	Price et al., 2012
Tobago	0.35 - 1.50 (Full range)	Mallela, 2013
Great Barrier Reef	0.1 - 1.1 (Full range)	Browne et al., 2013
Barbados	0.17 - 2.38 (Full range)	Stearn et al., 1977
Japan	0.72 - 1.90 (Full range)	Matsuda, 1989
Azores	0.0 - 0.9 (Full range)	Wisshak et al., 2010
Jamaica	0.2 (Average)	Mallela and Perry, 2006

Biophysical forcing factors affecting calcification

$CaCO_3$ accretion on the settlement tiles correlated negatively with the area covered by herbivore grazing marks. Some species of grazers remove $CaCO_3$ (Steneck 1983a; O'Leary and McClanahan 2010) and therefore diminish the thickness of the $CaCO_3$ layer as well as injuring the CCA colonies (Steneck and Paine 1986; Steneck et al. 1991). Grazing marks from herbivorous fish were found near the edge of the tiles while marks from gastropod grazing were common on the entire exposed area of the tile. The majority of grazing marks removed the complete layer of

benthic substratum, with the result that the bare substratum below the CCA/fleshy algae became visible again. On Palmyra Atoll, herbivore grazing on the reef benthos reduces CCA cover at least temporarily, while on many other reefs, CCA cover increases with grazing pressure due to macroalgal and turf algae removal (Steneck 1983a, 1986; Littler and Littler 2007). O'Leary and McClanahan (2010) proposed that under high grazing pressure of fish and urchins the negative effect of CCA excavation and denudation by grazers outweighs the often stated positive effect of removal of their space competitors. When macroalgae and turf algae are abundant, an increase in herbivore grazing leads to an increase in CCA cover and with it an increase in calcification due to removal of their space competitors (Steneck 1983a, 1986; Littler and Littler 2007). However, under high grazing pressure as seen at Palmyra Atoll, macroalgae and turf algae are rare (Hamilton et al. 2014), and increase in herbivore grazing therefore leads to higher grazing pressure on CCA and with it a decrease in CCA cover due to excavation and denudation (O'Leary and McClanahan 2010). An increase of herbivore abundance therefore does not always increase the ecosystem services a reef provides. However, bioerosion of $CaCO_3$ by herbivore grazers depends largely on the composition of the herbivore functional group: while urchins, gastropods and parrotfish are major $CaCO_3$ eroders, damselfish mainly crop fleshy algae and protect their territory from other herbivores and therefore reef erosion (Kiene 1988; Eakin 1996). An increase in grazing urchins, gastropods and parrotfish abundance therefore likely lead to negative effects on $CaCO_3$ accretion once a threshold is reached, while an increase in damselfish abundance may never have negative implications for the $CaCO_3$ budget.

The variation in $CaCO_3$ accretion between settlement tiles decreased as they become more heavily grazed (Figure 5.8). The calcification rates of intact CCA colonies with no grazing marks are very likely influenced by biophysical forcing factors other than grazing, for example wave energy (Martindale 1992; Mallela 2007; Pescud 2012), turbidity (Mallela 2007; Fabricius and De'ath 2014) or diel pH levels (Price et al. 2012). For this reason, the correlation between $CaCO_3$ deposition and grazing is weaker for settlement tiles with a low proportion of grazing marks. When grazing pressure is high, most CCA colonies are injured and for many this injury affects the entire thickness of their crust. This means that both the meristem and the perithallus are wounded. Vertical growth ceases until the intercalary meristem is regenerated (Steneck et al. 1991). This leads to lower calcification rates, and with it reduced responses to other biophysical forcing factors. Furthermore, regular grazing will destroy the $CaCO_3$ layer deposited onto the settlement tiles. It

therefore also destroys the evidence of influences other biophysical forcing factors had on $CaCO_3$ accretion. The effects of other biophysical forcing factors on $CaCO_3$ are therefore very likely reduced by grazing when grazing pressure is high.

Of the hydrodynamic processes examined in this study, only the volume of water received from southern fore reef sites and currents moving from north to south correlated with calcification rates. Furthermore, there was no correlation with wave height or bottom stress as found in other studies (Martindale 1992; Mallela 2007; Pescud 2012). However, Gove et al. (2015) found the CCA cover on Palmyra Atoll declines sharply at a mean bed shear stress threshold of 18 Nm^{-2} giving way to a turf dominated benthic environment. It is therefore very likely that calcification rates decrease with wave height and bottom stress on Palmyra Atoll but that that the range examined in this study was not sufficient to document this change.

Calcification rates were highest on the southern fore reef sites. Furthermore, the amount of water received from the southern fore reef correlated positively with calcification rates found at other sites. The tiles on the southern fore reef had low amounts of grazing marks on them, which likely lead to high overall calcification rates. However, these calcification rates were still higher than on other tiles with similar grazing pressure. One possible explanations why the southern fore reef sites have higher calcification rates is that they are often sheltered from wave-driven flow. Generally strong waves from the north drive flow from the north to the south across the Atoll, but sometimes wave direction and flow is reversed (Rogers 2015: Chapter 6). The southern fore reef sites are therefore often sheltered from the wave-driven flow from the north (Gove et al. 2015). This is unlikely caused by the lower wave height or bottom stress associated with a decrease in in the strength of the north-south current, as I have not found a correlation between these predictors and $CaCO_3$ accretion. It is therefore not clear which aspect of being sheltered from north driven flow leads to an increase in $CaCO_3$ accretion on the southern fore reef sites. The high productivity of CCA at the southern fore reef sites likely spills over to other sites that are well connectivity to the southern fore reef sites, for example through the dispersal of spores. Further more detailed studies are needed to test this hypothesis.

$CaCO_3$ accretion increases with depth on Palmyra Atoll. The deeper sites (fore reef) should therefore have higher $CaCO_3$ accretion than the shallower sites (back reef). However, $CaCO_3$ accretion rates on the northern fore reef sites were within the range found on the back reef. It is

therefore likely that the positive correlation between $CaCO_3$ accretion and depth is a result of high $CaCO_3$ accretion rates on the southern fore reef sites rather than deeper sites in general having a higher $CaCO_3$ accretion rates than shallower sites.

Estimating $CaCO_3$ accretion rates from percentage cover data of calcifiers

The thickness of the $CaCO_3$ layer deposited by cryptic CCA and bryozoans did not vary significantly between different areas on the reef. The percentage cover of these taxonomic groups was therefore used to estimate the mass of $CaCO_3$ deposited on the cryptic side of the tiles. The mass of $CaCO_3$ found on the exposed side of the tile, on the other hand, only correlated weakly with the percentage cover of CCA, which was the main calcifier present on that side of the tiles. Calcification rates at Palmyra Atoll are similar between sites despite them having different percentage covers of calcifying organisms (Price et al. 2012). My results support the work of Mallela (2007) who states that cover of an encrusting species may not be proportional to its calcification rate. Calcification rates measured by visually estimating the cover of encrusters should be interpreted with caution. Measuring actual $CaCO_3$ accretion in kg of $CaCO_3$ m^{-2} y^{-1} as done in this study gives more exact measurement of net $CaCO_3$ accretion rates than those determined from visual inspection (percentage cover) alone.

Bioerosion

Rates of internal bioerosion of the *F. paumotensis* skeleton pieces were low. Polychaetes and sipunculids were the only bioeroders found inside the *F. paumotensis* skeletons. They are generally the first bioeroders that colonised a substratum, indicating that the succession of the boring community is not yet completed (Chazottes et al. 1995; Edinger 2001). The bioerosion rate found inside the *F. paumotensis* skeletons at Palmyra Atoll was comparable to the rate of bioerosion attributed to polychaetes and sipunculids in bioerosion blocks made out of dead *Porites* that were deployed for one to two years on the Great Barrier Reef, in the Galapagos and on La Reunion (Kiene and Hutchings 1994; Chazottes et al. 1995; Reaka-Kudla et al. 1996; Peyrot - Clausaude et al. 1999; Tribollet et al. 2002; Osorno et al. 2005). The internal bioerosion of the pieces of coral rock collected from the reef at Palmyra was, on average, over 50 times higher than the bioerosion rates of the *F. paumotensis* skeletons at Palmyra. Large worm bore holes, extensive boring by sponges and a few mollusc shells were found inside some of these coral rock pieces. This bioeroding community is well established, indicating that the pieces of coral rock had been

dead for at least 2-3 years (Chazottes et al. 1995; Edinger 2001). I found similar bioerosion rates inside pieces of dead Acropora, and dense and light pocilloporids. These findings should be interpreted with caution as I do not know if the coral pieces I selected differed in their average age after death. It could therefore be possible that bioerosion works faster in different skeletal types but the trend was not discernible in my samples.

High internal bioerosion rates on very shallow back reef sites compared to deeper fore reef were reported in Discovery Bay, Jamaica and Mexico sites (Perry 1998; Hepburn et al. 2005). Differences in bioerosion rates between sites on Palmyra Atoll were not due to their location on the back or the fore reef. Sites with significantly higher bioerosion rates were found both on the fore reef and the back reef and the same was true for sites with significantly lower bioerosion rates. The three sites which had significantly high bioerosion rates received a large volume of water from the lagoon. The lagoon water is often more turbid than the water arriving from the open ocean. Large number of boring worms has often been reported at turbid water sites, including sediment-rich lagoons and river outflows (Risk et al. 1995; Macdonald and Perry 2003; Hepburn et al. 2005). Furthermore, Perry (1998) found that in Discovery Bay the rate of bioerosion attributable to worms was similar between the back reef and the shallow fore reef. The presence of boring worms (polychaetes and sipunculids) is therefore more closely linked to turbidity than to a specific reef area. Only polychaetes and sipunculids eroded the *F. paumotensis* pieces in this study. It is therefore likely that differences in bioerosion were due to differences in volume of water received from the more turbid lagoon rather than bioerosion differing between back reef and fore reef sites.

5.5.2 Net $CaCO_3$ gain/loss

Primary $CaCO_3$ production by coral recruits made up 0.03% of the total $CaCO_3$ production on the settlement tiles while the other 99.97% was produced by secondary calcifiers, mainly CCA. Internal erosion removed 0.009 kg of $CaCO_3$ m^{-2} y^{-1} from the *Fungia paumotensis* skeletons deployed on the reef. I was not able to reliably quantify bioerosion due to grazing on *F. paumotensis* skeletons. However, $CaCO_3$ accretion on the settlement tiles was strongly correlated with the area of the tile covered in grazing marks. According to the trend line of the correlation between $CaCO_3$ accretion and area with grazing marks on the tiles, grazers removed between 0 and 0.8 kg $CaCO_3$ m^{-2} y^{-1} from the settlement tiles. My findings are therefore in line with Chazottes et al. (1995) who found that grazers are responsible for a large proportion of the total bioerosion

on reefs located on Central Pacific atolls (Chazottes et al. 1995). A ternary diagram of the $CaCO_3$ budget (Figure 5.11) show that in the first year after space becomes available, it accumulates 0.27 - 1.37 kg $CaCO_3$ m^{-2} due to $CaCO_3$ production by CCA and bioerosion (mainly grazers) ((1) in Figure 5.11). I collected coral rock pieces to determine if internal bioerosion rates increased as dead coral skeleton becomes older than the 15 months old *F. paumotensis* pieces. The reef rock pieces gained an average of 7% of their mass, this indicates that the overall $CaCO_3$ budget remains positive in the absence of new coral recruitment even a few years after space is freed up. However, the variation in volume of skeleton bored and volume of $CaCO_3$ deposited onto the skeleton was large: between 0 and 54% (Mean = 9%) of the coral skeleton was bored and additional $CaCO_3$ deposition made up between 0 to 49% (Mean = 15%) of the reef rocks initial volume. I therefore concluded that the $CaCO_3$ budget found on freed space will become more variable and move closer towards stasis after the initial year ((2a) in Figure 5.11). However, this prediction is in absence of coral recruitment. If a coral successfully recruited onto the free space, the $CaCO_3$ budget will also slowly move towards an increased proportion of primary $CaCO_3$ production ((2b) in Figure 5.11). Under this scenario, the ratio between bioerosion and secondary primary production will likely stay the same, scenario (2b) therefore represents an upward shift from scenario (2a). This upwards shift results in high net $CaCO_3$ accretion similar to reefs with high rates of primary production or algal ridges (Perry et al. 2008, Figure 1.3).

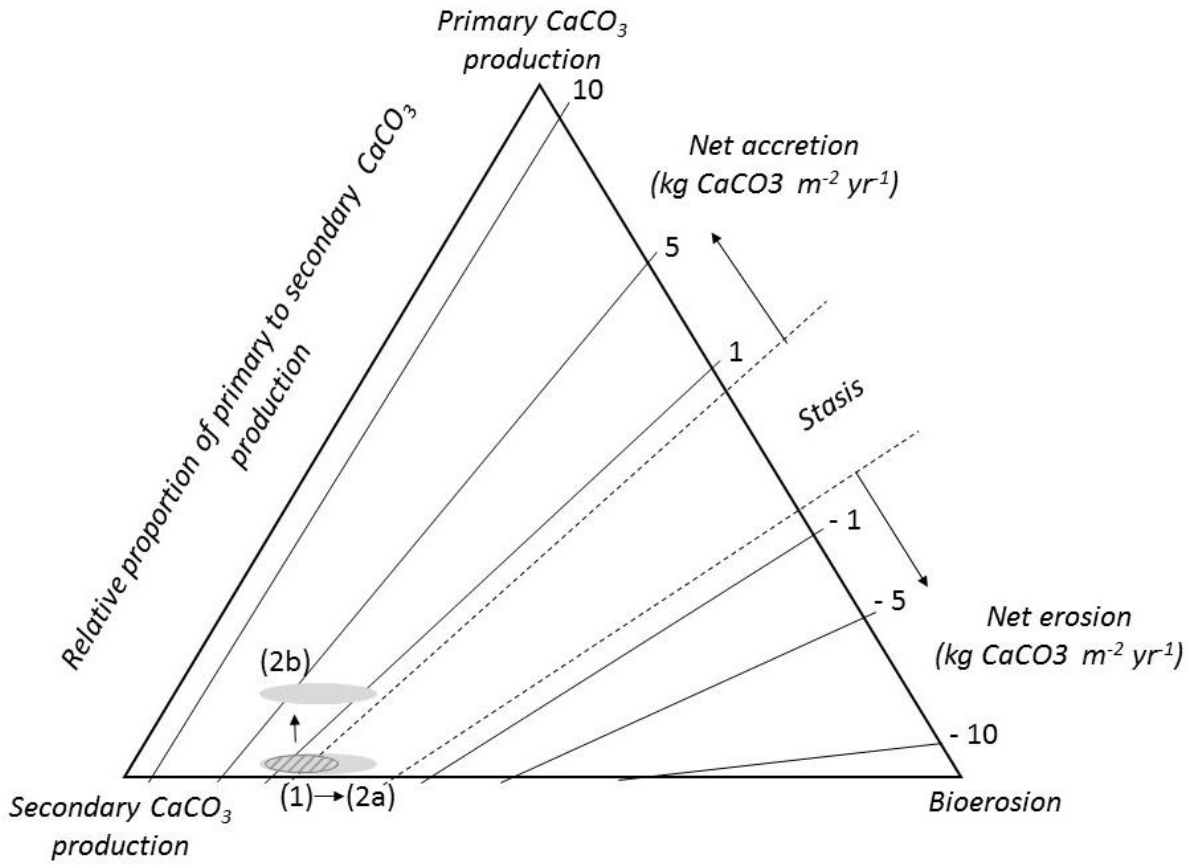

Figure 5.11. Net $CaCO_3$ budget of recently freed reef space on the reef surrounding Palmyra Atoll. (1) (*striped oval*) shows the $CaCO_3$ budget of freed reef space one year after it became available on the reef. (2) (*grey ovals*) shows the future trajectory if (2a) coral recruitment is absent or (2b) one or more corals successfully recruited to the free space. Ternary diagram approach adapted from Perry et al. (2008) and explained in Figure 1.3.

I identified herbivorous fishes and gastropods as main external bioeroders of $CaCO_3$ produced by CCA. Parts of the *F. paumotensis* skeletons were also externally eroded, so it is likely that on Palmyra Atoll, herbivores not only erode a large proportion of the $CaCO_3$ deposited by CCA but also large parts of dead coral skeletons. However, the pieces of dead coral rock I examined did not show large grazing scars produced by external bioerosion. This may be due to the presence of thick CCA crusts on many of these pieces. Grazing intensity of urchins has been found to decrease with an increase of CCA cover (Chazottes et al. 2002); the same could apply to herbivorous fishes and gastropods. The thick CCA crusts found on the pieces of coral rock could therefore prevent high rates of grazing on coral rock by (1) being a less attractive food source for

grazers and/or (2) acting as a protective layer that is consumed by grazers instead of the coral rock. Even though macroalgae and turf algae are preferred over CCA by grazers on Palmyra Atoll, they are rare and grazed upon on a daily basis (Hamilton et al. 2014). When macroalgae and turf algae are rare, grazers are not very selective on what they graze upon (Birkeland et al. 1985) and may also graze on CCA. It is therefore not very plausible that CCA prevents grazing on its underlying coral rock on Palmyra Atoll simply by being a less attractive food source. It is more likely that CCA prevents external bioerosion on the underlying reef rock mainly by acting as a protective layer. The abundant thick layers of CCA found on Palmyra Atolls reefs therefore have several functions: (1) they produce a large part of the $CaCO_3$ ingested by herbivore grazers and are therefore important for sediment production, (2) they cement the reef structure together (Adey 1998), and (3) they likely act as a protective layer against external bioerosion for the underlying reef rock.

5.5.3 Conclusion

This study provides important insight into the $CaCO_3$ accretion rate of recently freed space on Palmyra Atoll. The ratio between secondary $CaCO_3$ production and bioerosion is in favour of production on Palmyra Atoll and $CaCO_3$ accretion reaches a level close to productive algal ridges (Perry et al. 2008). A positive ratio between secondary $CaCO_3$ production and bioerosion has so far only been documented for the reef flat at Uva Island and for ungrazed algal ridges (Eakin 1996; Perry et al. 2008). Palmyra Atoll therefore possesses an unusual combination of high secondary $CaCO_3$ production and low bioerosion rates, despite intensive grazing on CCA (average of 11% of tile area covered in grazing marks). However, many fossils and extant reefs are composed primarily of $CaCO_3$ produced by secondary calcifiers (Vroom 2010). A coring study conducted in 1904 on Funafuti Atoll (Tuvalu) revealed that most of the $CaCO_3$ was produced by CCA, followed by *Halimeda* spp., foraminifera and lastly, coral (Finckh 1904). It is therefore likely that high secondary $CaCO_3$ production was the norm on many (non-degraded) reefs in the past. In the event of coral mass mortality, the reefs on Palmyra Atoll will likely continue to grow for several years even in the absence of coral recruitment. The reef's topography will likely be preserved by CCA depositing $CaCO_3$ on top of dead coral skeletons, cementing their structure and protecting them from grazers.

The net $CaCO_3$ budget calculated here can be combined with coral growth data obtained from the 3D benthic models of the photomosaics created by my collaborators at Scripps Institute of Oceanography to determine net $CaCO_3$ budgets (including primary production) for each of the study sites. Once the net total $CaCO_3$ budgets are developed, future net total $CaCO_3$ budgets can be predicted. For example, my results for $CaCO_3$ accretion on recently freed space could be used together with the current net total $CaCO_3$ budget to predict how the net total $CaCO_3$ budget on Palmyra Atoll changes after a mass coral mortality event. These predictions can also provide important insight about how resilience affects $CaCO_3$ accretion. The changes in coral cover experienced during disturbances on other reefs (Figure 1.3b, c) can be modelled for Palmyra Atoll and the outcomes in net total $CaCO_3$ accretion can be compared. This would determine if $CaCO_3$ accretion after a disturbance differs between the resilient reefs of Palmyra Atoll and these other more degraded reefs.

CHAPTER 6

General Discussion

The aim of this thesis was to contribute to a better understanding of coral recruitment, calcification and bioerosion on a pristine coral reef and to determine how biophysical forcing factors affect these three processes. Benthic community composition on pristine coral reefs is closely linked to biophysical forcing factors (Williams et al. 2015), however only a few studies have investigated coral recruitment, calcification and bioerosion on pristine coral reefs (e.g. Pari et al. 1998; Roth and Knowlton 2009; McCauley et al. 2010; Price 2010) with all but one study being conducted at Palmyra Atoll. The overall objective of this thesis was to increase the understanding of how biophysical forcing factors influence benthic recruitment and $CaCO_3$ accretion at Palmyra Atoll. I found that local ocean currents are one of the factors that influence coral recruitment, calcification and bioerosion rates. Most pocilloporids likely recruit close to their parents, while my results suggest that the origin of poritid larvae is from distant locations. Pocilloporid recruitment rates were also significantly correlated with the successional stage of the benthic community on the settlement tiles, especially the cover of bare substratum and bryozoa. Bare substratum covered in biofilm and CCA were preferred as settlement substrata by coral recruits, however both pocilloporids and poritids settled on a wide range of benthic substrata. Furthermore, *Pocillopora damicornis* larvae showed a significant settlement preference for divots shaped like parrotfish bites over a flat settlement surface. Coral recruits were good competitors against encrusting algae but were often outcompeted by filamentous and upright algae. Settlement tiles were almost entirely colonised by benthic organisms within three to twelve months of deployment. Colonisation was generally faster on the back reef than on the fore reef. Bryozoa were almost entirely absent on the shallower back reef sites but abundant at fore reef sites (FR3, FR5 and FR7), especially on tiles deployed for 9 months. The $CaCO_3$ budget of recently created bare space on the reef was positive after one year and negatively correlated with herbivore grazing pressure on the benthic community. Past one year after the death of a coral colony, bioerosion rates within pieces of coral (internal bioerosion) increased but overall bioerosion rates (internal and external) rarely exceeded $CaCO_3$ deposition by CCA.

6.1 LIMITATIONS

This section provides an overview of the limitations associated with the research conducted and how these limitations were addressed or could be addressed in the future.

The coral recruitment and calcification rates reported here were obtained from settlement tiles placed close to intact benthic communities on Palmyra Atoll. They are therefore well suited to predict how small patches of bare substratum are colonised within the intact benthic community, for example when a single coral colony dies. It is likely that coral recruitment and calcification rates will differ profoundly from what I found here if bare substratum becomes available on a large scale. The absence of local adult coral colonies will likely influence coral recruitment patterns (Harriott and Fisk 1988; Connell et al. 1997; Vermeij 2005; Gilmour et al. 2013; Salinas-de-León et al. 2013; Chong-Seng et al. 2014; Kayal et al. 2015). In 2014, large bare patches of reef were created on Palmyra Atoll, by the removal of a ship wreck and clearance of an area previously completely covered in corallimorph (Work et al. 2008; Kelly et al. 2012). The Smith lab at Scripps is measuring benthic recruitment to these areas. Once their study is completed, we will be able to compare the benthic successional pattern reported here for small patches of bare substratum (10 x 10 cm) against those for larger areas (10s of m^2).

A net $CaCO_3$ accretion budget measures the final balance of calcification and bioerosion processes. Internal and external erosion of dead coral skeletons can be determined with accuracy because the skeleton itself does not accrete $CaCO_3$ in the period surveyed (e.g. Chazottes et al. 1995). $CaCO_3$ production by CCA and erosion, however, is more difficult to measure since both happen simultaneously (Smith 1973). Most measurements of $CaCO_3$ production by CCA, including $CaCO_3$ accretion rates on settlement tiles reported in Chapter Five, therefore implicitly include ambient erosion by fish and invertebrates (Kennedy et al. 2013) and reveal the net outcome of $CaCO_3$ production by CCA and its erosion (Perry et al. 2008). However, a reef with high production of $CaCO_3$ by CCA and high erosion of this $CaCO_3$ may have the same net outcome of $CaCO_3$ accretion as a reef with low $CaCO_3$ production by CCA and low erosion of the former. Flow respirometry is a method often used to estimate coral reef community metabolism including net community calcification (NCC) measurements (Langdon et al. 2010), which provides insight into how much $CaCO_3$ is produced by the benthic community (mainly corals and CCA) at a given time. In the above stated example, flow respirometry may be able to estimate $CaCO_3$ production by CCA

and with it the mass of CCA-derived $CaCO_3$ that was eroded and can therefore provide information on the processes that led to the net $CaCO_3$ budgets measured on deployed artificial substratum. NCC was measured on the Western Reef Terrace and in the Entrance Channel area at Palmyra Atoll in 2012 using Lagrangian drifts (Koweek et al. 2014). Koweek et al. (2014) found that NCC on Palmyra Atoll varies on a diel cycle with a high amplitude only recorded before at Ningaloo Reef in Western Australia (Falter et al. 2012). Furthermore, at Palmyra Atoll, the ratio between net community calcification and net community production (NCC:NCP) varied with the ecological community composition (cover of hard corals, CCA, *Halimeda* spp., and macroalgae) (Koweek et al. 2014). The NCC:NCP ratio reflects the balance between carbon being incorporated into inorganic (e.g. $CaCO_3$) and organic carbon production. This suggests that the mass of $CaCO_3$ deposited per cm^2 by each of the different taxonomic groups investigated by Koweek et al. (2014) is similar among sites within the back reef of Palmyra Atoll. CCA was one of the taxonomic groups they investigated, so it is likely that $CaCO_3$ production by CCA does not vary within back reef sites which supports my finding that differences in $CaCO_3$ accretion found amongst settlement tiles are largely caused by variation in grazing pressure.

The settlement preference experiment with divots shaped like parrotfish bites (Chapter Four) was performed in a water table with a single coral species (*P. damicornis*). This has limitations because organisms do not always react the same way in the laboratory as in the field. Furthermore, as only a single species was used in this experiment, I can not draw any conclusions about settlement preferences of other coral species. Within the Reefs Tomorrow Initiative (RTI) programme, a group from Stanford University investigated recruitment rates to settlement tiles with divots shaped like parrotfish bites. They surveyed the tiles in the field after two weeks and under the microscope after one year. Their results suggest that recruitment rates in the field are similar to the trends I found in the water tables (Fiorenza Micheli, personal communication).

6.2 IMPLICATIONS FOR CORAL REEF MONITORING AND CONSERVATION

Coral recruitment, calcification and bioerosion rates were significantly higher at some sites within Palmyra Atoll than others (Figure 6.1). I did not however, find a clear difference between back reef and fore reef habitats, as described by Roth and Knowlton (2009) for coral recruitment. Overall, the fore reef and back reef sites were very similar in terms of pocilloporid recruitment: 30% of the tiles deployed on the fore reef and 31.3% of the tiles deployed on the back reef

supported pocilloporid recruits and recruitment numbers were 0 - 7 and 0 – 8 per tile, respectively, at sites other than FR9 and the Entrance Channel (Figure 6.1a). FR9 and the Entrance Channel sites differed significantly from this Palmyra-wide pattern. Not only were more tiles colonised by pocilloporids at these sites (72.5% at FR9 and 53.8% at the Entrance Channel), the maximum number of pocilloporid recruits was also higher, with 30% of the tiles at FR9 supporting between 8 and 29 pocilloporid recruits and 11% of the tiles at the Entrance Channel supporting between 10 and 37 pocilloporid recruits. FR9 and the Entrance Channel had higher adult pocilloporid cover than the other sites at Palmyra Atoll. Pocilloporid recruitment therefore correlated with adult pocilloporid cover as outlined in Chapter two and found elsewhere (Harriott and Fisk 1988; Penin et al. 2010; Penin and Adjeroud 2013; Chong-Seng et al. 2014; Kayal et al. 2015). This has important implications for coral reef conservation as it shows that pocilloporids recruit locally and may not be capable of recovering from a disturbance if a large area of local pocilloporid cover is lost.

Pocilloporid recruitment was not the only factor in which sites differed significantly from other sites in their reef area (back reef, fore reef). On both the back reef and the fore reef I identified sites (FR9, RT1) that differed significantly from the others in the composition of the early successional benthic community found in cryptic habitats (Chapter Three). The slower recruitment of benthic organisms to bare substratum and lower bryozoan cover at FR9 compared to other fore reef sites likely increased pocilloporid recruitment at this site (Chapter Two). $CaCO_3$ accretion was greatest on the southern fore reef (Figure 6.1b, Figure 6.2). This was to a large extent due to low grazing pressure compared to other sites (Figure 6.2). These three examples of benthic properties being significantly different at certain sites of Palmyra Atoll emphasize the need to monitor sites that reflect the diversity of the study area (Rogers et al. 1994) and to investigate each site individually before grouping them together by habitat type or other factor.

Within-site variation for all three processes measured and reported in this thesis (recruitment, calcification and bioerosion) was highest at the two Entrance Channel sites (Figure 6.1a, b, c). However, this area has previously been found to have lowest coral species biodiversity and the highest evenness (spread between taxa) on the back reef (Williams et al. 2008b). Variability in the benthic state (e.g. coral cover and composition) therefore does not always overlap with variability in benthic processes such as recruitment, calcification and bioerosion. This highlights the

importance of measuring benthic processes such as recruitment, calcification and bioerosion next to benthic state monitoring in order to obtain a fuller picture of reef health (McClanahan et al. 2012; Perry et al. 2012; Kennedy et al. 2013; Mumby et al. 2014).

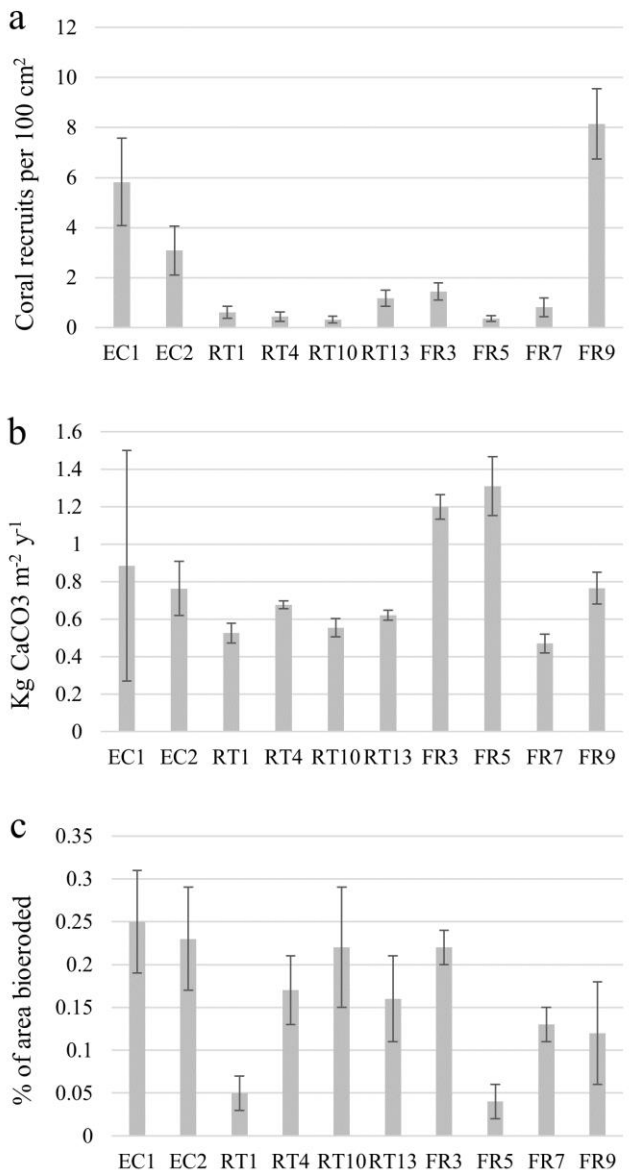

Figure 6.1. a) Mean number of coral recruitment found on settlement tiles at each site (including all deployment durations: 3, 9, 12, 15 months). (b) mean community calcification rate on settlement tiles deployed for 1 year at each site. (c) Mean percentage of volume of *Fungia paumontensis* skeletons that was bioeroded after 15 months of deployment at each site. Error bars = 2SE.

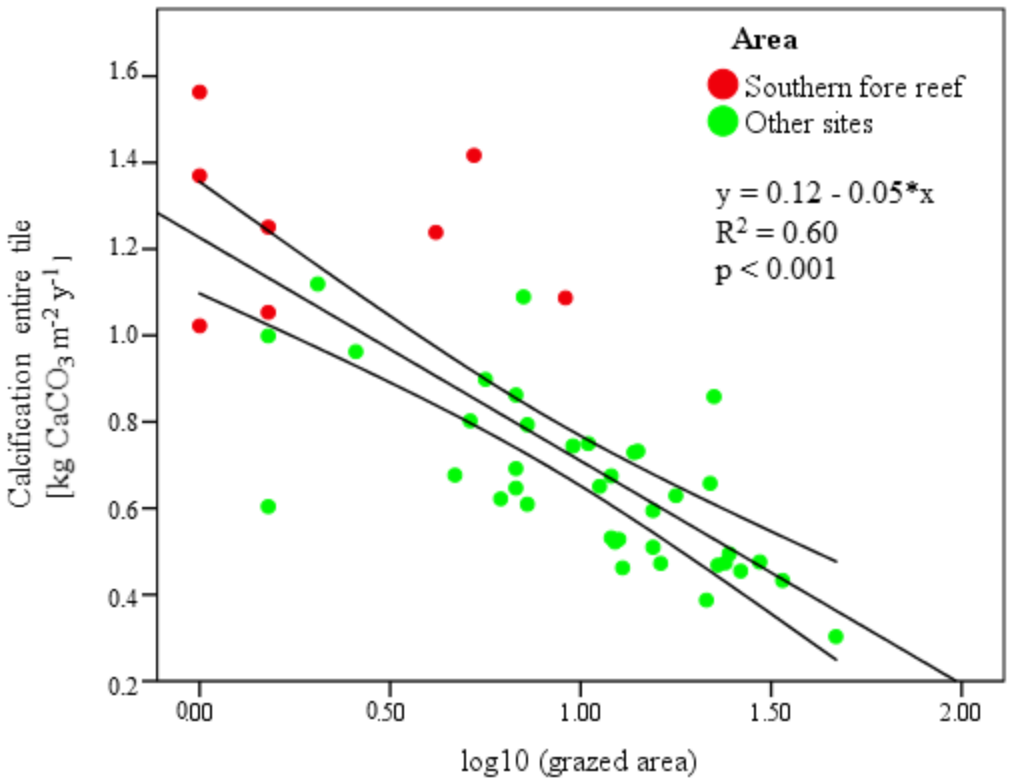

Figure 6.2. Relationship between herbivore grazing and $CaCO_3$ deposition onto the settlement tiles deployed for 1 year Palmyra Atoll. *Dots* represent single settlement tiles, the *straight line* in the middle is the fitted linear trend line. The equation of the trend line and regression statistics are displayed in the top left corner of the graph. The *two lines enclosing the trend line* show the 95% confidence interval of the mean. Tiles were grouped into southern fore reef sites (*red*) and other sites (*green*).

6.3 KEY GROUPS OF ORGANISMS SHAPING THE BENTHIC COMMUNITY

6.3.1 Herbivores

Herbivores are key reef-associated species that have a large impact on the benthic community composition of coral reefs (Steneck 1997; Mumby et al. 2006a). Jouffray et al. (2015) found that in Hawai'i (Main Hawaiian Islands and Northwestern Hawaiian Islands) macroalgal cover decreases as herbivore abundance increases. However, the dominant herbivore functional group influences which regime will be present: grazers create a turf-dominated regime and scrapers a calcifier-dominated (coral and CCA) regime (Jouffray et al. 2015). In this thesis, I have

reported that CCA is abundant on the reefs surrounding Palmyra Atoll despite it being frequently injured by scraping herbivores (Chapter Five). These injuries lead to a decrease in CCA cover on the exposed side of the settlement tiles as seen in Figure 6.3, where grazing (increase in cover of green encrusting algae and biofilm) affects CCA cover almost as much as turf algae cover. According to the findings of Jouffray et al. (2015) and the high abundance of CCA at Palmyra Atoll, CCA benefits from the high abundance of scraping herbivores, despite them having a negative effect on $CaCO_3$ accretion and cover of CCA. Herbivore grazers likely have a large effect on the benthic community at Palmyra Atoll (Sandin et al. 2008; McCauley et al. 2010; Hamilton et al. 2014; McCauley et al. 2014) as the benthic community at Palmyra Atoll is dominated by calcifiers (Smith et al. 2016), despite water nutrient levels on Palmyra Atoll exceeding the threshold for outbreaks of macroalgal blooms (Sandin et al. 2008). I furthermore found that the scraping steephead and bumphead parrotfish both produce grazing marks in reef substratum that are preferred for settlement over flat surface by *P. damicornis* larvae. An increase in grazing marks from scraping herbivores therefore affects the reef by resulting in (1) a decrease in turf and CCA cover and to a lesser extent *Lobophora* spp. cover, (2) a decrease in $CaCO_3$ accretion by CCA, (3) an increase in sediment production and (4) an increase in coral settlement.

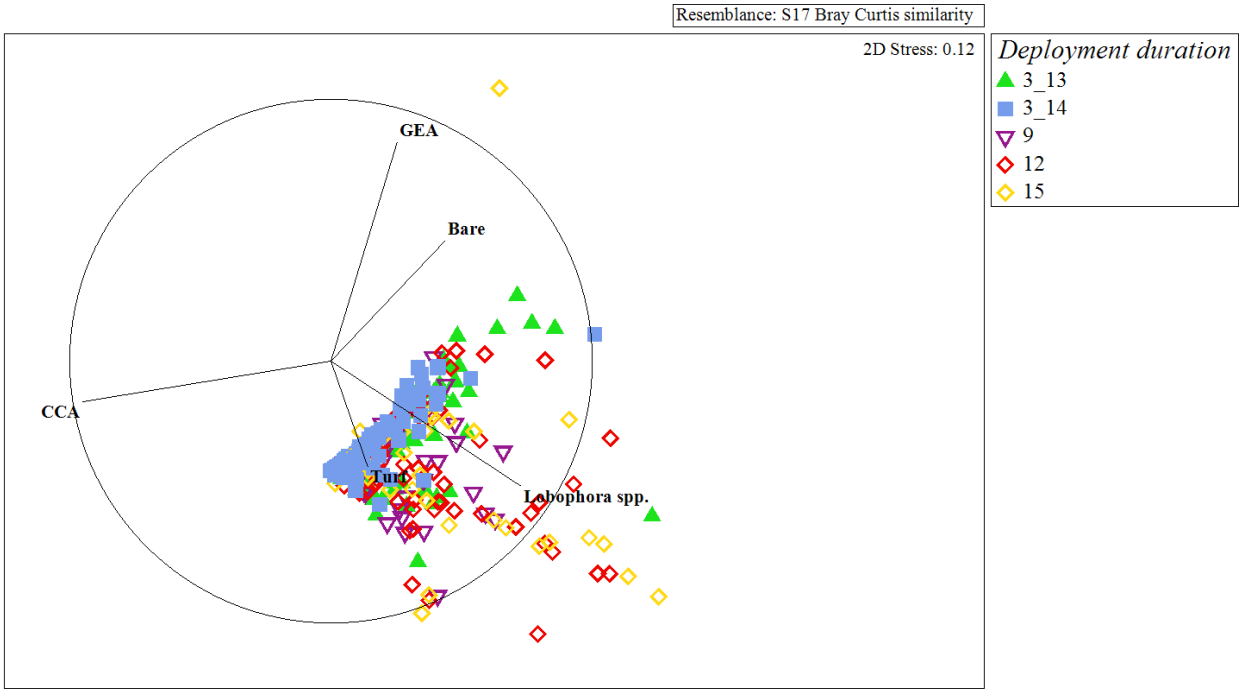

Figure 6.3. Benthic community composition on the exposed side of settlement tiles deployed for 3, 9, 12 and 15 months at Palmyra Atoll. The vectors in this MDS plot show Pearson's correlations with a value > 0.3. Each symbol represents a single tile. Tiles are grouped according to their deployment duration: 3_13: 3 months in 2013, 3_14: 3 months in 2014, 9: 9 months, 12: 12 months and 15: 15 months. The chosen resemblance measure and 2D stress value of the MDS analysis can be found on the top right corner of the MDS plot.

6.3.2 Diversity of herbivorous species

Herbivorous species on coral reefs are often classified into functional groups because they differ in their impact on the coral reef benthos. Functional groups are either based on foraging range, e.g. 1-100 cm^2, 0.5-1 m^2 or up to 0.5 ha (Carpenter 1986), or on feeding methods: scrapers/excavators, grazers/detritivores, and algal browsers (Cheal et al. 2010). Foraging ranges give insight into how frequently a patch of benthos is grazed (frequent for small ranges), while feeding methods describe the outcome for the benthos, from being completely cleared and excavated to being cropped.

Bumphead and steephead parrotfish differ in their feeding method as bumphead parrotfish are able to graze on live corals. In Chapter Four, I found that *P. damicornis* larvae prefers settling in grazing marks shaped like steephead parrotfish bite marks compared to larger divots shaped like bumphead parrotfish bite marks. Steephead parrotfish therefore likely have a higher positive

impact on coral recruitment than bumphead parrotfish. This may be an adaptation by pocilloporids to (1) the presence of bumphead parrotfish, as this fish species was found to negatively affect adult pocilloporid colonies (McCauley et al. 2014) or (2) grazing marks located on live coral and the associated risk of being overgrown by the coral repairing its injury. My results and those reported by McCauley et al. (2014) on bumphead parrotfish on Palmyra Atoll therefore imply that while both bumphead and steephead parrotfish positively affect coral cover through increased coral settlement, overall steephead parrotfish have a stronger positive influence on coral cover and diversity.

The grazing marks found on the exposed side of the settlement tiles were caused by herbivores with different foraging ranges. Grazing scars from large and medium sized fish were only observed on the edges of the tiles, possibly due to factors associated with tile set up prevented herbivorous fish from grazing the other areas of the tile. However, this may also be due to the tiles being mainly covered in CCA, which is not intensely grazed upon by herbivorous fish at Palmyra Atoll (Hamilton et al. 2014). Many of the grazing scars found on the settlement tiles were from grazing gastropods, which therefore are likely the main external bioeroder of $CaCO_3$ on Palmyra Atoll. These gastropods are classified as micro-herbivores, which have restricted mobility and small foraging ranges (1 - 100 cm^2) and graze individual patches of algae more frequently than herbivores with a larger foraging range (Carpenter 1986). A single grazing gastropod could therefore bioerode a large mass of $CaCO_3$ from a settlement tile. The high variability in cover of grazing marks (0-81%) could be caused by some settlement tiles being occupied by one or more gastropods creating many grazing marks, while other tiles were only sporadically grazed by herbivorous fish. I did not find any gastropods on the settlement tiles during analysis in the lab and could therefore not test this hypothesis. The presence of gastropods on the settlement tile could be affected by whether or not the tile was placed inside a damselfish territory. Damselfish protect their territory from other grazers including scarids and gastropods (Sammarco et al. 1986; Kiene 1988) and their feeding method causes only minor damage to the underlying CCA. It is therefore possible that the variation in grazing intensity found on the settlement tiles is caused by interactions between damselfish and gastropod grazers. Further studies are needed to test this hypothesis.

6.3.3 Turf algae

Despite turf algae being omnipresent on coral reefs, they are often ignored or lumped into categories such as “dead coral” or “rubble” during benthic surveys (Smith et al. 2016). Until recently turf algae have been thought to be an early successional stage of macroalgae which makes “turf-dominated” a unstable transitional state of coral reefs (Diaz-Pulido and McCook 2002; Ceccarelli et al. 2011). However, experimental studies and field observations from Hawai’i and Palmyra suggest that “turf-dominated“ could be its own stable regime (McCook et al. 2001; Knowlton 2004; Bellwood and Fulton 2008; Jouffray et al. 2015; Gove et al. 2015). Turf algae were low in abundance at the Palmyra study sites, but their cover is likely heavily affected by herbivore grazers. Parrotfish and surgeonfish prefer turf algae as a food source (Hamilton et al. 2014) and turf algal cover increases on Palmyra Atoll when large grazers are excluded (McCauley et al. 2010). Grazing by parrotfish, surgeonfish and possibly other herbivores is therefore likely to be responsible for the low mean turf algal cover of 2.35% ± 0.31 SE on the exposed side of the settlement tiles. Grazing fish cannot access turf algae on the cryptic side of the settlement tiles; however, turf algal cover was also low on that tile side (3.28% ± 0.33 SE). To test if turf algae expand their cover from the exposed side of the tile over the edge to the cryptic side, as observed for *Lobophora* spp., I plotted the turf algal cover on the cryptic side of the settlement tile against the turf algal cover on the exposed side of the same tile (Figure 6.4). However, they do not correlate with each other, which implies that the turf algal cover on the ungrazed, cryptic side of the settlement tile is not influenced by herbivore grazing on turf algae, not even indirectly through the turf algae abundance on the exposed side of the tile. The cryptic and exposed side of the tiles represents different niches and likely host different turf algae assemblages as these can vary significantly on a spatial scale of centimetres (Harris et al. 2015). I found that turf algae affect coral recruitment negatively through overgrowth competition (Chapter Three). Because coral recruits were found to mainly recruit to the cryptic side of the tiles, grazing by herbivorous fish on turf algae most probably has only a small effect on recruitment rates.

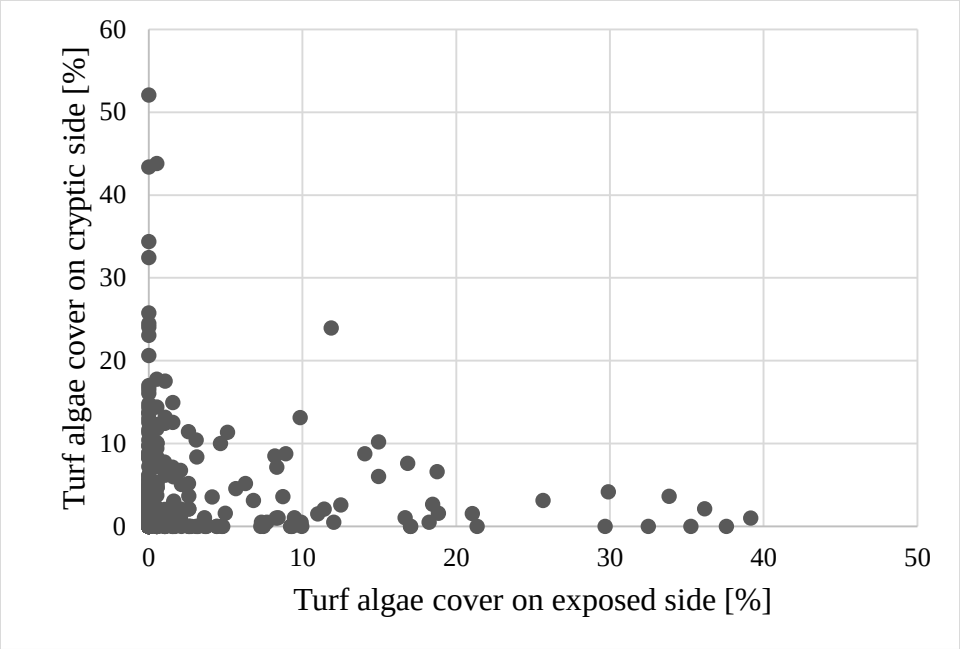

Figure 6.4. Relationship between percentage turf algal cover on the exposed and cryptic sides of the settlement tiles. *Dots* represent single settlement tiles deployed at Palmyra Atoll for either 3, 9, 12, or 15 months.

6.3.4 CCA

CCA plays an important role on coral reefs because it produces $CaCO_3$, cements the reef structure together (Adey 1998) and induces metamorphosis in a diverse range of coral genera (Morse et al. 1988, 1996; Heyward and Negri 1999; Baird and Hughes 2000; Baird and Morse 2004; Harrington et al. 2004; Golbuu and Richmond 2007; Ritson-Williams et al. 2010, 2014). I observed that CCA deposits 4 to 6 times more $CaCO_3$ per cm^2 on the exposed than on the cryptic side of the tiles. CCA cover on the exposed side is therefore vital for the positive $CaCO_3$ accretion reported in Chapter Five. However, metamorphosis of coral larvae is induced by CCA species that recruit to cryptic habitats (Harrington et al. 2004; Ritson-Williams et al. 2010). Post-settlement survival of coral recruits on these CCA species is enhanced because they slough less frequently than other CCA species (Harrington et al. 2004; Ritson-Williams et al. 2010) and are poor competitors against coral recruits (Chapter Three). The thick CCA crusts found on the exposed side of the tiles, on the other hand, often overgrew large vermetids (tube-dwelling gastropods, 1 cm (L) x 1 cm (W) x 0.5 cm (H)), indicating that CCA species located on the exposed side of the tiles are capable of overgrowing large obstacles. These CCA species may therefore also be capable

of outcompeting and overgrowing much smaller coral recruits. Coral recruitment, and with it coral cover, therefore profits from a high CCA cover in cryptic environments. While the ecological reef health (high coral cover) and geomorphic reef health (high $CaCO_3$ accretion) both benefit from a high CCA cover, they do so in different ways. This finding is a good example of how geomorphic condition and ecological condition of a coral reef often differ from each other (Kleypas et al. 2001; Perry et al. 2008).

6.4 CORAL REEF RESILIENCE AND RECOVERY

6.4.1 Possible mechanisms leading to recovery from disturbances on Palmyra Atoll

The only recorded large scale disturbance on Palmyra Atoll, was a mass bleaching event in 1998, which created a coral dead zone of about 6.5 km long on the Western Reef Terrace. The area recovered from this disturbance but changed from being dominated by branching *Acropora* spp. to an assemblage of *Pocillopora*, *Montipora*, *Pavona*, *Stylophora* and *Porites* spp. (Williams et al. 2008b, 2010). My PhD thesis focused on two factors that influence the recovery aspect of resilience: coral recruitment and net $CaCO_3$ budgets on recently freed space. It is important to mention that the process and rate of recovery depends largely on the type (acute or chronic) and intensity of the disturbance (Connell et al. 1997; Graham et al. 2011). The findings of my thesis show how the coral reef of Palmyra Atoll recovers from small disturbances at the scale of a single coral colony. In the following section, I will formulate general predictions for recovery from larger disturbances based on the comparison of coral recruitment rates and net $CaCO_3$ budgets over the natural range of benthic community composition and biophysical forcing factors present on Palmyra. The differences amongst sites make it possible to determine how coral recruitment rates and the net $CaCO_3$ budget are affected by changes in local adult coral cover, grazing pressure and the succession of benthic cover.

$CaCO_3$-producing organisms (CCA, bryozoans, corals, hydrocorals, tubeworms) colonise the majority of recently created bare substratum on Palmyra Atoll. This leads to high secondary $CaCO_3$ production (especially by CCA), which supports both reef accretion and sediment production by herbivore grazers. Even though net $CaCO_3$ production on recently freed space varied amongst sites at Palmyra Atoll depending on the mass of $CaCO_3$ removed by herbivore grazers, I concluded that net $CaCO_3$ production is positive in the first year after primary $CaCO_3$ producers (corals) are lost. The largest decrease in mass of $CaCO_3$ of the coral rock pieces collected from the

reef structure was 20%. Overall, these pieces had a mean 7% $CaCO_3$ mass gain as a consequence of CCA deposition of $CaCO_3$ being higher than the loss due to internal bioerosion. The reefs of Palmyra Atoll are therefore likely to accrete $CaCO_3$ and maintain their topographic complexity while recovering from a disturbance.

Coral recruitment rates were highly variable both within and between sites. I found between 0 and 44 coral recruits on the settlement tiles. Large parts of the variation in presence and abundance of pocilloporids recruits (77.6% of all recruits) are predictable while predictions for poritids recruitment rates are more challenging (Chapter Two). For example, my results suggest that if the local adult pocilloporid cover decreases due to a disturbance, then pocilloporid recruitment rates will likely decrease as these are positively correlated (Chapter Two). Pocilloporid recruitment rates at FR9 with pocilloporid cover of 12.0% was 6.73 ± 1.26 recruits per 100 cm^2 (mean ± SE) while the pocilloporids at FR7 (2.8% cover) were unable to produce enough coral larvae for successful localised pocilloporid recruitment. This indicates that even if suitable substratum for settlement and post-settlement survival is abundant (as on the twenty tiles deployed at FR7 for three months: mean 36% ± 3.7 (SE) biofilm and 24% ± 2.0 (SE) CCA cover), pocilloporids are unable to recruit to it. Insufficient larval availability therefore likely caused the recruitment failure of pocilloporids at FR7. Recruitment failure, despite the abundance of suitable settlement substratum, has also been documented for the Caribbean and Guam (Colgan 1987; Hughes and Tanner 2000).

Pocilloporid recruitment rates are also dependent on the reef substratum available. In Chapter Two, I reported that pocilloporid recruitment rates decreased with age of the settlement tiles, likely due to them being positively correlated with percentage cover of bare substratum. On Palmyra Atoll, reef substratum is therefore most suitable for pocilloporid settlement and post-settlement survival shortly after it is freed up by a disturbance, which can lead to elevated pocilloporid recruitment rates after disturbances that did not influence pocilloporid larval supply. However, many disturbances lead to large decreases in coral larval production (Birkeland 2015b, 2015a) which dampens coral recruitment for 2-3 years post disturbance (Colgan 1987; Brown 1990; Arthur et al. 2006; Sheppard et al. 2008; Halford and Caley 2009; Gilmour et al. 2013). In these cases, the available bare substratum covered in biofilm is not rapidly colonised by corals due to a lack of coral larval supply. By the time enough coral larvae are produced, the reef substratum

is already recolonised by other benthic organisms. Fortunately, coral larvae are also able to successfully recruit to reef substratum colonized by CCA. I even found that coral larvae change their settlement preference from bare substratum covered in biofilm to CCA once biofilm becomes rare (Chapter Three). Successful recruitment after disturbances therefore profit from a high CCA cover. The dependency of coral recruitment on the presence of either bare substratum or CCA has been demonstrated in a 30 year study at Heron Island, Great Barrier Reef where recruitment rates correlated positively with the combined abundance of bare substratum and CCA (Connell et al. 1997). It is therefore important that bare substratum is colonised by CCA rather than macroalgae to ensure that suitable settlement substratum continues to be available. On Scott's Reef, an isolated reef system in north Western Australia, coral larval supply was reduced by 94% for 6 years after a disturbance (Gilmour et al. 2013). Scott's reef had a high herbivorous fish density which even increased after the disturbance, which prevented turf and macroalgal to dominate the reef substrate once coral larval production re-established. This example shows how important a healthy herbivore population is for reef recovery. In this thesis I have found that a large population of parrotfish, especially steephead parrotfish, will likely also increase recruitment rates of corals via the creation of bite marks. My findings therefore add additional new evidence to the importance of CCA and parrotfish grazing for coral reef recovery (Mumby et al. 2006a; Hughes et al. 2007)

6.4.2 Possible causes of the regime shift observed at Palmyra Atoll

On most Pacific atolls and some Caribbean reefs, algal ridges can be found in habitats with high wave conditions. Corals and the macroalgae *Halimeda* spp. struggle to survive in these habitats and active grazing on corallines is limited (Adey 1978, 1998). Frameworks of CCA are often extensive on these algal ridges (Adey 1998; Perry et al. 2008). However, on Palmyra Atoll, regime shifts from calcifying (i.e. CCA) to non-calcifying regimes (i.e. turf algae) have been observed on algal ridges (Gove et al. 2015). Gove et al. (2015) identified that CCA-dominated algal ridges become turf-dominated once a bed shear stress threshold of 18 N m^{-2} is reached. After super-typhoon Bopha damaged the eastern reefs of Palau immensely, the foliose red macroalga *Liagora* sp. rapidly colonised reefs with moderate wave exposure, whereas reefs with low wave exposure remained *Liagora*-free (Roff et al. 2015). This example shows that Palmyra Atoll is not the only place where a regime shift associated with wave energy has been reported. Gove et al. (2015) attributed the regime shift on Palmyra Atoll to either competitive exclusion or repeated disturbance continually resetting the benthic community to an earlier successional state. While turf

algae are often reported to rapidly colonise bare substratum (Halford and Caley 2009; Fong and Paul 2011), I did not find this trend at the sites I surveyed at Palmyra Atoll. Turf algal cover on the cryptic side of the settlement tiles was low at each of the successional stages (3, 9, 12, and 15 months) and showed little variation over time. Furthermore, a MDS plot of benthic cover on the exposed side of the settlement tiles (Figure 6.4) shows that turf algal cover is generally lowest at tiles deployed for 3 months compared to longer deployment durations. My results therefore imply that it is unlikely that the regime shifts observed by Gove et al. (2015) were caused solely by the benthic community being continually reset to an earlier successional state. Their other explanation for the sudden change from a CCA-dominated regime to a turf algal-dominated regime is competitive exclusion (Gove et al. 2015). The competitive exclusion principle states that complete competitors cannot coexist (Hardin 1960). The occurrence of calcifying regimes, turf regimes and macroalgal/sand regimes can be strongly predicted using biomass of herbivores (Jouffray et al. 2015). Turf algae are the preferred food source of parrotfish and surgeonfish on Palmyra and every cm^2 of turf algae is cropped ~6 times a day on the reef terrace and 1.3 times a day on the fore reef (Hamilton et al. 2014). However, increased wave energy affects the grazing rates, foraging patterns (Foster 1987) and swimming performance of herbivorous fish (Fulton et al. 2005). It is therefore likely that the increase in turf algal abundance reported by Gove et al. (2015) is due to decreased herbivore grazing. The exclusion of large herbivores for 4 months on the northern fore reef led to a significant increase in turf algae; CCA cover, however, did not decrease (McCauley et al. 2010). This indicates that at least at a temporal scale of 4 months, absence of grazing does not lead to complete competitive exclusion of CCA by turf algae. It is, however, probable that increased wave energy either decreases the competitive strength of CCA or regularly resets the benthic community to an earlier successional stage, which then cannot be recolonised by CCA due to the lack of grazing. To test this, areas of the algal ridge on Palmyra need to be cleared to observe the benthic succession on these ridges.

6.4.3 Topographic complexity as an indicator of reef resilience

The physical three-dimensional structure of the reef ecosystem and its topographic complexity provides a habitat for reef-associated species and is important for ecosystem services such as tourism and shore line protection (Done et al. 1996; Alvarez-Filip et al. 2009; Graham and Nash 2013). Topographic complexity has therefore potential to be used as an indicator of reef resilience (Mumby et al. 2014). However, topographic complexity is still understudied and further

research is needed to determine how topographic complexity affects coral reef resilience and if it is suited to be used as an indicator of resilience (McClanahan et al. 2012). A recent resilience model included topographic complexity and determined that marine protected areas are only effective to sustain the ecosystem services provided by a reef if the reef has a high structural complexity (Rogers et al. 2015a). Positive relationships between topographic complexity and coral cover and the ability of the coral reef to recover from disturbance have all been reported, whereas macroalgal and turf algal cover correlate negatively with reef topographic complexity (Colgan 1987; Guzman and Cortés 2007; Graham and Nash 2013). In Chapter Five, I reported that CCA cover is also vital to maintain the topographic complexity of a coral reef. I observed that CCA deposits a large mass of $CaCO_3$ onto the reef structure. Pieces of coral rock collected from the reef framework were often covered in a thick layer of $CaCO_3$ produced by CCA (up to 49% of the initial volume of the coral rock). This layer can act as a protective 'shield' from external bioerosion to the underlying coral skeleton. Furthermore, CCA cements the coral reef framework together (Adey 1998), and it therefore strengthens the outside of these coral rock pieces, which enabled pieces with up to 54% internal bioerosion to withstand physical erosion. Cover and calcification rate of CCA are therefore important indicators of a reef's ability to retain its topographic complexity and should be considered as indicators for reef resilience.

6.4.4 Reefs Tomorrow Initiative (RTI)

One main difference between resilient and non-resilient reefs is that resilient reefs recover quickly from major disturbances that create a lot of bare substratum all at once (Graham et al. 2011; Birkeland 2015a). It is therefore important to have a clear appreciation of what happens to bare substratum on resilient reefs in order to understand how the recovery side of resilience works. Collectively, my results contribute to the understanding of the fate of bare substratum on the reefs of Palmyra Atoll. They therefore contribute to the Reefs Tomorrow Initiative (RTI) programme by shedding light on reef recovery and the biophysical forcing factors that influence it.

The data and the results of this PhD thesis were shared with my collaborators within RTI, providing them with a detailed understanding of how bare substratum is colonised by benthic organisms. I investigated coral recruitment in detail, determining how different biophysical forcing factors (local coral cover, currents, local benthic cover) affected recruitment rates. This analysis was performed using a water flux model and coral cover data produced by collaborators at RTI.

My results from Chapter Two therefore linked local coral cover and currents to coral recruitment. Coral recruitment influences coral cover, so the insights gained here about coral recruitment can be used to explain differences in coral cover found on Palmyra Atoll. Chapter Three contains a detailed description of interactions between corals under the age of fifteen months and other benthic organisms, including settlement preferences and competitive strength. These values can be directly used to model early successional benthic communities and therefore predict settlement rates and post-settlement mortality in coral recruits under different benthic community compositions. Coral recruits often interact differently with benthic organisms other than adult corals (Birrell et al. 2008; Barott et al. 2012), so my findings complement the data on adult corals and their interactions with other benthic organisms collected from the photomosaics. Chapter Four dealt with settlement preference and early post-settlement mortality of *P. damicornis* regarding divots shaped like parrotfish bite marks. The results of that Chapter form the link between the study of parrotfish home ranges, grazing rates and diet preference and the study investigating long term (>1 year) recruitment rates onto settlement tiles with divots shaped like parrotfish bite marks. My study was able to provide estimates of initial settlement rates into these grazing marks enabling my collaborators working on the long term recruitment study with divoted tiles at Palmyra Atoll (Stanford University RTI group) to form conclusions regarding settlement preference and post-settlement survival rates. Lastly, I also determined the $CaCO_3$ budget on recently dead or cleared reef rock, by measuring calcification and bioerosion rates. This was the first investigation of bioerosion at Palmyra Atoll and therefore provides important input into the RTI model concerning stability of the reef formation after a major disturbance. Furthermore, it gives a general indication of the mass of $CaCO_3$ that is reworked by external and internal bioeroders, which both produce $CaCO_3$ sediment for island accretion.

The results of this PhD research therefore helped RTI to determine how a suite of biophysical forcing factors affect ecological outcomes. The empirical research of Phase II of RTI will focus on experimental manipulations and expands the geographic scope of data collection. My research identified interesting questions for experimental manipulations: Is $CaCO_3$ accretion by CCA higher in damselfish territories? Does the benthic succession on high wave energy areas differ from the benthic succession reported in this thesis for the fore and back reef? The geographical expansion of data collection will be important to determine if the relationships found in this thesis and within RTI are typical for Pacific atolls, uninhabited Pacific atolls or unique to Palmyra Atoll.

6.4.5 Applying knowledge of reef resilience from Palmyra Atoll to other locations

Williams et al. (2015) found that natural biophysical drivers such as mean sea surface temperature, wave energy and mean chlorophyll-*a* concentration are well suited to explain differences between hard coral, CCA and macroalgal cover amongst uninhabited islands in the Pacific. These natural biophysical relationships were not present on populated islands in the Pacific. Human impacts on these reefs therefore lead to a decoupling of these biophysical relationships. This has implications for how the insights gained into reef resilience on uninhabited Palmyra Atoll can be extrapolated to other inhabited sites. Because biophysical drivers affect the reef benthos in similar ways on uninhabited islands in the Pacific, it is likely that the implications found for resilience at Palmyra Atoll also apply to other uninhabited islands within the Pacific (e.g. the 39 uninhabited islands studied by Smith et al. (2016)). However, the biophysical models built for uninhabited Pacific islands have a low explanatory power on inhabited Pacific islands (Williams et al. 2015). I therefore want to emphasise that a high level of caution should be taken when extrapolating implications for reef resilience at Palmyra Atoll to inhabited islands within the Pacific. The biophysical drivers examined in this thesis differed partially from the biophysical drivers examined by Williams et al. (2015). The two main biophysical drivers examined in this thesis, herbivore grazing and current movement, were not included in Williams et al.'s (2015) study. It is therefore uncertain if biophysical relationships found in this thesis hold true for other uninhabited islands and/or are decoupled for reef systems of inhabited islands.

In my thesis, two observations were made that support observations from Caribbean reefs. Habitat availability was identified as a limiting factor for coral recruitment while larval supply acted both as a limiting and a regulating factor. Similar conclusions were reported in the Florida Keys and the British Virgin Islands came to the same conclusion (Carlon 2001; Vermeij 2005). Recruitment rates to the reefs of Palmyra Atolls are therefore limited and regulated in a similar way to less pristine reefs in the Caribbean. While this is a rather broad observation that involves multiple processes, I also found similarities on a more detailed process level. Coral recruits on Palmyra Atoll and in Belize change their settlement preference for biofilm from preference to avoidance when biofilm becomes scarce (~10-20% cover) (Arnold and Steneck 2011). Coral recruits instead showed an augmented preference for settlement onto other benthic substrata such as CCA, *Peyssonnelia* spp. and invertebrate crusts. Palmyra Atoll differs from the Florida Keys, the British Virgin Islands and Belize in almost every way imaginable: biogeographical region, reef

system, connectivity, benthic composition, composition of grazers, level of degradation and level of anthropogenic stress. The detected similarities however, show that processes found on pristine reefs can also be found on degraded reefs, even in other regions of the world. The identification of such similarities is important for several reasons. Firstly, they provide more insight on fundamental processes on coral reefs. For example, the combined interpretation of the change in settlement preference reported in this thesis and by Arnold and Steneck (2011) shows that both changes occurred as biofilm cover became scarce, providing an hypothesis to be tested by future studies. Secondly, it shows that degraded and healthy reefs can function in similar ways, creating hope that degraded reefs may be able to recover. Lastly, once such a similarity is identified, the healthier reef can act as a baseline for the more degraded reef.

6.4.6 Are Caribbean reef models useful to determine resilience in the Indo-Pacific?

Most coral reef resilience studies have focussed on the Caribbean, which leads to the question of whether the findings from these studies can be used to describe resilience elsewhere, for example, in the Indo-Pacific. Roff and Mumby (2012) concluded that while the thresholds of coral cover and grazing proposed by Mumby et al. (2007) may only be applicable to Caribbean reefs, the prevailing reef management paradigms are also applicable to Indo-Pacific reefs: minimise pollution and loss of grazers (Roff and Mumby 2012).

In this thesis, I found that one of these paradigms for resilience, "more herbivore grazing = higher resilience," is not always true. At Palmyra Atoll, out of the three taxonomic groups (CCA, turf algae and *Lobophora* spp.) the cover of the macroalgae *Lobophora* spp. decreased the least in cover as grazing pressure increased (Figure 6.4). While herbivore grazing is certainly important on Palmyra because it reduces turf algal cover (McCauley et al. 2010), it is one of the few locations where an increase in grazing leads to a decrease in CCA cover and secondary $CaCO_3$ production (Chapter 4). An increase in grazing at locations like Palmyra Atoll with very high grazing pressure, therefore leads to a decrease in resilience and does not follow the paradigm "more herbivore grazing = higher resilience" (O'Leary and McClanahan 2010).

Furthermore, resilience studies from the Caribbean focus on the regime shift between coral and macroalgal-dominated reefs (Mumby et al. 2007; Anthony et al. 2011). However, in the Pacific, a third possible stable state has been found: the turf algal-dominated state, which in Hawai'i is more common than the macroalgal-dominated state (Jouffray et al. 2015; Gove et al.

2015). Pacific reefs therefore do not show a correlation between coral and macroalgal cover and their resilience potential would be better measured in cover of reef builders (coral and CCA) versus cover of fleshy algae (turf algae, macroalgae) (Smith et al. 2016).

While Pacific reefs differ from Caribbean reefs in the role turf algae plays for their benthic composition (stable versus transient state), uninhabited Pacific reefs differ from inhabited reefs in the role biophysical forcing factors play in shaping the reefs. I therefore argue that resilience models constructed for Caribbean reefs cannot fully predict resilience in Pacific reefs and that within the Pacific, two different kind of resilience models need to be constructed, one for inhabited coral reefs and one for uninhabited reefs.

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Appendix I

This study was conducted as an additional project at the Division of Aquatic Resources (DAR) nursery on Sand Island, Oahu. The results were presented at the 23rd annual Hawaiian Conservation Conference which took place between August 3rd and 7th 2014 in Hilo, Hawai'i. The setup of the nursery tanks prevented a suitable test to determine the causes of growth rate differences between tanks as many of the tanks had more than one unique abiotic or biotic factor. Nonetheless, my results show that *Pocillopora damicornis* larvae can be successfully reared in water tanks and survive and grow in the field in absence of disturbances such as coral bleaching. I therefore included the findings of this study in this Appendix.

Exploring the possibility of rearing Pocillopora damicornis coral spat in coral nursery tanks

A1.1. ABSTRACT

Coral reef managers and scientists are exploring the possibility of counteracting coral cover declines by employing different reef restoration strategies. *Pocillopora damicornis* fragments at the DAR coral nursery have been found to produce larvae that settle on the nursery tank walls. The aim of this study was to determine if the *P. damicornis* spat on the tank walls could be used for reef restoration. Spat were removed from the nursery tank and glued onto terracotta tiles and pieces of coral rubble. These were placed on the reef in front of the nursery (field) and in six different nursery tanks (lab) for six months and monitored during this deployment. A bleaching event during the first month of the field placement lead to 71% mortality of spat placed in the field. The spat in the tanks only had 5% mortality during the same period. After the bleaching event, mortality rates were comparable between spat placed in the field and the laboratory. Spat placed in the field experienced shrinkage of their surface area during the first month of deployment, which was more prevalent for bleached spat. A significant difference in growth rates of spat between the nursery tanks was also observed. This may be the result of abiotic and biotic differences between the tanks. My study showed that *P. damicornis* spat produced as a by-product at a coral nursery are suited

for reef restoration. However, transplantations should be avoided during the warmest months or if bleaching is predicted as coral bleaching can induce high mortality of coral spat placed in the field it is recommended.

A1.2. INTRODUCTION

The ongoing rapid rate of coral reef degradation calls for an integration of 'active' measures in coral reef management. One proposed 'active' measure is reef restoration, which can restore lost coral cover, while conservation often just reduces the rate of degradation (Coelho and Manfrino 2007; Rinkevich 2008). Restoration ecology, which is widely used in terrestrial ecology (Rinkevich 2008), is expected to become the dominant discipline in environmental science in the 21st century (Hobbs and Harris 2001).

Larvae from *Pocillopora damicornis* fragments in nursery tanks have been observed to settle on the walls of the tanks at a coral nursery on Sand Island, Oahu, Hawai'i. This nursery's current focus is on growing *P. damicornis* fragments for reef restoration. In this study I investigated if the nursery could also use the large number of small *P. damicornis* spat found on the tank walls for reef restoration. To test this, different size classes of coral spat were transplanted onto terracotta tiles and pieces of coral rubble. These were placed in different nursery tanks as well as on the reef next to the nursery. This enabled me to determine if spat transplantation to other tanks and to the reef can be achieved by measuring the respective mortality and growth rates of the spat. For the nursery tank placement I also noted the different abiotic and biotic set up of the tanks in order to determine possible factors that influenced mortality and growth rates. A bleaching event (Bahr et al. 2015) affected the spat placed on the reef, which made it possible to measure mortality and growth rates during a bleaching event and after.

A1.3. METHODS

A1.3.1. Research site

This experiment was conducted at the Department for Aquatic Resources' Coral Restoration Nursery on Sand Island, Oahu, Hawai'i (DAR nursery 21° 18' 15.3073" N 157° 52' 14.6136" W). This nursery produces *P. damicornis* fragments for coral reef restoration and has fragments and colonies growing in most of their tanks (all except tank three in this study). The *P. damicornis* fragments were sourced from the reef in front of the nursery from where the unfiltered

water in the tanks is also drawn. The experiment was conducted in six nursery tanks (lab) as well as on the reef in front of the nursery (field).

A1.3.2. Abiotic and biotic factors in nursery tanks

The abiotic and biotic set up of the nursery tanks were assessed on the 26th of July, 2014 (Table A1.1).

Table A1.1. Abiotic and biotic set up of the nursery tanks. First column lists the different abiotic and biotic factors present in the tanks. The second column shows what unit or scale the factor was measured in, the third column what code it was given and the forth column shows what type of factor it is. The last column shows the values for this factor in each tank. Zeros represent absence of a factor or organism.

Abiotic and biotic factors	**Units**	**Code**	**Type**	**Tank**					
				1	2	3	4	5	6
Volume	m^3	Vol	abiotic	9.80	1.61	0.66	1.29	10.00	8.30
Time since last time tank was emptied and completely cleaned	0 = most recent, 3 = least recent	Age	abiotic	3	1	1	0	0	2
Shading	0 = shaded, 1 = non shaded	S	abiotic	0	1	1	1	1	1
Bubbles	2 = strong, 1 = weak, 0 = none	B	abiotic	2	1	1	0	0	1
Flow	2 = strong, 1 = weak	F	abiotic	1	2	2	1	1	2
Pocillopora damicornis	1 = presence, 0 = absence	PDAM	biotic	1	1	0	1	0	1
***P. damicornis* recruits**	1 = presence, 0 = absence	Rec	biotic	1	0	0	0	0	1
Other corals	1 = presence, 0 = absence	COR	biotic	1	1	0	1	0	0
Black snails	3 = abundant, 2 = common, 1 = rare, 0 = absence	BS	biotic	2	0	0	1	0	3
Aiptatia pulchella	3 = abundant, 1 = rare, 0 = absence	APUL	biotic	1	3	3	1	0	3
Tripneustes gratilla	Nr of organisms	TGRA	biotic	10	4	3	3	0	7

Table A1.1 continued

Predictor	Units	Code	Type	Tank					
				1	**2**	**3**	**4**	**5**	**6**
Acanthurus triostegus	Nr of organisms	ATRI	Biol.	1	1	0	0	1	2
Unique biological set up Tank 2[2]	1 = presence, 0 = absence	Bio T2	Biol.	0	1	0	0	0	0
Unique biological set up Tank 3[3]	1 = presence, 0 = absence	Bio T3	Biol.	0	0	1	0	0	0
Unique biological set up Tank 4[4]	1 = presence, 0 = absence	Bio T4	Biol.	0	0	0	1	0	0
Unique biological set up Tank 5[5]	1 = presence, 0 = absence	Bio T5	Biol.	0	0	0	0	1	0
Unique biological set up Tank 6[6]	1 = presence, 0 = absence	Bio T6	Biol.	0	0	0	0	0	1

[2]*Thalassoma duperrey*, blue surgeonfish [3]bigger snails [4]small non-black snails, tunicates, shrimp [5]*Stylocheilus striatus* black and white striped damselfish, flatworm, box sponge, unidentified fish [6]Bivalves

A1.3.3. Experimental set up

Spat were collected from the walls of nursery tank with a spatula one and held in an aquarium for up to 3 hours as they were transferred to arrays as fast as possible after collection. The water in the aquarium was changed regularly during this time period to keep water conditions uniform. Three spat of different sizes (small/non branching 0.02 - 0.34 cm^2, mean = 0.2 cm^2, medium/small branches 0.18 - 1.32 cm^2, mean = 0.5 cm^2, large/several branches 0.45 - 2.29 cm^2, mean = 1.1 cm^2) were glued with superglue onto either a terracotta tile or a piece of coral rubble with no benthic growth on it. This took a few seconds per spat and the spat were submerged in sea water right after attachment once the super glue was dry. These sizes represent the whole size spectrum of spat that colonised the tank wall at that time. The terracotta tile and piece of rubble represent two important settlement substrata for recruitment studies and allow me to test for differences in mortality and growth between them. One terracotta tile and one piece of rubble were cable tied to a piece of plastic mesh with mesh size 1 cm^2. This set up with a total of six spat is referred to as an array (Figure A1.1). A string was pulled through the plastic mesh in order to hang the arrays along the walls of the nursery tanks or tie them to bricks for placement on the reef. Three arrays were placed in each of the six nursery tanks and twelve arrays were placed on a small reef next to the nursery at a depth of 2 meters. Both lab and field arrays were placed vertically. Spat

placed in tanks were collected on the 29th of July, 2014, and placed in their tanks on the same day. Spat placed on the reef were collected on the 12th of August, 2014, and placed in a nursery tank for a week before being deployed on the reef. Conditioning of the spat was not necessary as the water in the tanks is drawn from the reef on which they were deployed. Pictures of tiles and pieces of rubble were taken before deployment, in September 2014, November 2014 (tanks only) and January 2015. This enabled me to follow each individual spat over time.

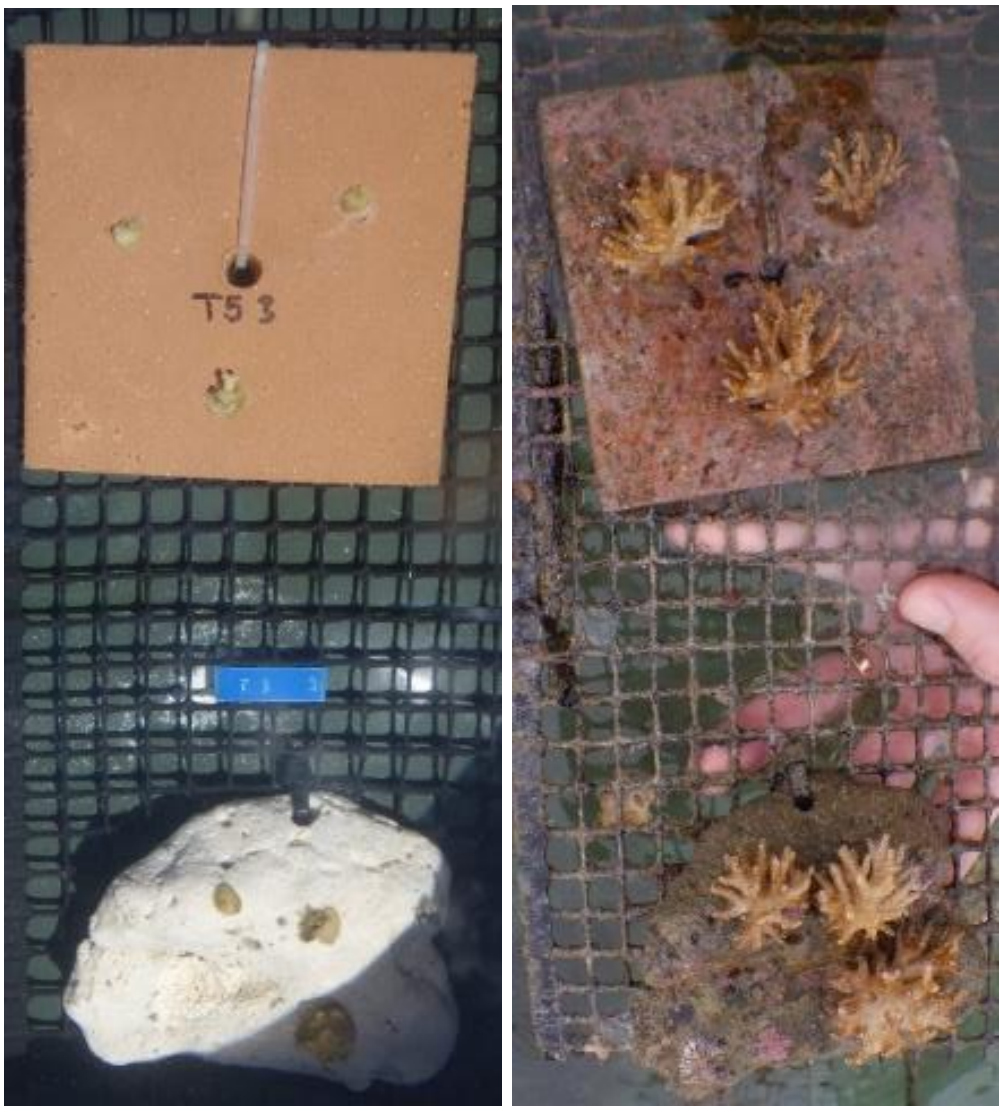

Figure A1.1. Pictures of an array which is made up of a terracotta tile and a piece of coral rubble. Each tile and piece of coral rubble contains three coral spat: a small, a medium and a large sized one. The picture on the left shows the array before deployment and the picture on the right shows the same array after 163 days of deployment in a water tank at the coral nursery.

A1.3.4. Mortality

A visual census of the coral spat using the pictures taken of the arrays was used to determine spat mortality. Spat mortality was assumed when a spat was missing completely or when no live tissue was apparent. Pearson's χ^2 test was used for comparing the mortality between spat placed in the tanks and on the reef for (1) the whole time period of the experiment and (2) before and after the 30th of September, 2014. Spat placed on the reef experienced coral bleaching before the 30th of September, 2014, so I wanted to test if the bleaching affected survival in the field. Furthermore, the mortality before and after the 30th of September was also compared separately for spat placed in the tanks and on the reef. Mortality rates between spat on terracotta tiles and pieces of coral rubble and between different spat size classes were analysed for spat placed in the tanks and on the reef separately using Pearson's χ^2 test. The mortality counts in all of the individual tanks had an expected count of less than five; for this reason, the Fisher's Exact test was used to determine if mortality differed between tanks. SPSS was used for the statistical analysis.

A1.3.5. Growth rates

The area covered by each spat was measured in ImageJ 1.48v (Rasband 1997). The pictures taken of the arrays at different sampling intervals were loaded into ImageJ. The size of the mesh the pieces of rubble and tiles were cable tied to was used as a unit of measurement (1 cm^2). For each picture, five lengths of different mesh squares were measured (in pixels) and their average was used to determine the pixel to centimetre conversion rate for that picture. In each image, each spat was hand traced in the program and the area was measured and recorded.

The growth rate was then calculated by subtracting the size of the spat at time t from the size of the spat at time t+1. This resulted in a growth rate measured in cm^2. To compare growth rate between different sized spat, I was interested in how much the spat area changed in proportion to the size of the spat at the beginning. Furthermore, to compare growth rate between different time intervals, daily changes in area were calculated, as the time intervals between sampling were of different lengths. The proportional daily growth rate (PDG rate) was calculated using the following formula:

$$\text{Proportional daily growth rate} = \left(\frac{\text{Size of coral spat at t} + 1}{\text{Size of coral spat at t}}\right)^{\left(\frac{1}{\text{days}}\right)} - 1$$

The PDG rates were normally distributed and had a homogeneous variance. A repeated measures ANOVA with Tukey's HSD *post hoc* test was used to determine if the PDG rate varied between (1) spat on tiles and on rubble pieces, (2) different spat sizes, (3) different tanks and the reef deployment and (4) different time intervals. An Independent-Sample t-test was used to determine if PDG rates differed between bleached and non-bleached spat.

A1.4. RESULTS

A1.4.1. Mortality rates

The overall mortality rate of spat placed on the reef was greater than of the spat in the nursery tanks (75% versus 15% mortality, Pearson's χ^2 (df = 1, N = 180), $p < 0.001$, Figure A1.2). For the spat placed in the tanks, no difference in mortality was found between different sizes (Pearson's χ^2 (df = 2 N = 72), $p = 0.211$) or between spat on terracotta tiles and pieces of coral rubble (Pearson's χ^2 (df = 1, N = 72) $p = 0.586$). The same was true for spat placed on the reef (Size: Pearson's χ^2 (df = 2, N = 108,) $p = 0.179$, Tile versus rubble: Pearson's χ^2 (df = 1, N = 108), $p = 0.299$). Overall coral mortality did not differ among the six tanks (Fisher's exact test $p = 0.239$).

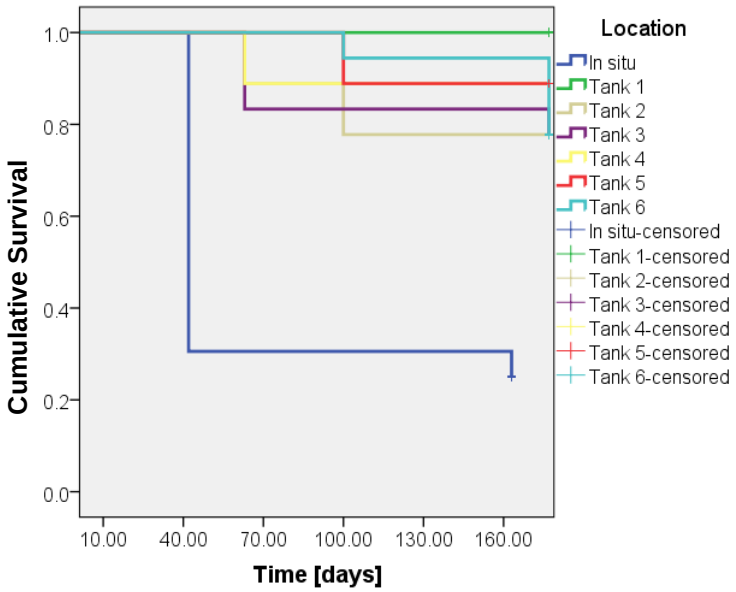

Figure A1.2. Spat survival rates in each tank and on the reef. The Kaplan-Meier curves (*coloured lines*) show the percentage of coral spats that survived after 63, 100 and 177 days in the tanks and after 42 and 163 days on the reef. *Plus signs* at the end of each line represent coral spats that survived until the end of the experiment (censored data). Three arrays were placed in each tank (a total of 18 spat per tank). Twelve arrays (a total of 72 spat) were placed on the reef.

Despite being placed in the tanks earlier and having a longer first sampling interval, the spat in the tanks had a significantly lower mortality rate during their first sampling interval than the spat placed on the reef. The spat that were placed on the reef had a 71 % mortality rate between deployment and the 30th of September, 2014 (42 days of deployment) versus the 5 % mortality rate of the spat placed in tanks until then (63 days of deployment, Pearson's χ^2 (df = 1, N = 167), $p < 0.001$). In the second sampling interval, mortality of spat on the reef (14%) and in the tanks (12%) did not differ (Pearson's χ^2 (1, N = 124), $p = 0.486$). The mortality of spat placed on the reef during the first 42 days of deployment (71%) was significantly greater than the mortality rate in the second sampling interval (14%, Pearson's χ^2 (df = 1, N = 93) $p > 0.001$). The mortality rate in the nursery tanks increased from 5% to 12% between the first and the second sampling interval, however this was not significant (Pearson's χ^2 (df = 1, N = 198) $p = 0.088$).

A1.4.2. Growth rate

Spat grew an average of 0.015 ± 0.0011 (SE) times their current size per day. No significant difference was found in the proportional daily growth rate (PDG rate) between spat on terracotta tiles (0.009 ± 0.001 (SE)) and spat on coral rubble pieces (0.008 ± 0.001 (SE), df = 1, F = 2.353, p = 0.131). Small spat had a greater growth rate in proportion to their size than medium and large sized spat (small: 0.011 ± 0.001 (SE), medium: 0.009 ± 0.001 (SE), large: 0.006 ± 0.001 (SE), df = 2, F = 8.716, p = 0.001, S vs M: p = 0.030, S vs L: p = 0.001). Spat placed on the reef grew significantly more slowly than spat in the tanks (Figure A1.3, df = 6, F = 15.167, $p < 0.001$, reef vs each tank individually: $p < 0.001$ for all). There was a significant difference in growth between sampling intervals (df = 1, F = 30.538, $p < 0.001$) and growth between sampling intervals and lab and field placement (df = 1, F = 25.426, $p < 0.001$). Before the first sampling, spat placed on the reef decreased by 0.010 ± 0.002 times their current size per day, while spat placed in the tanks increased by 0.010 ± 0.002 times their current size per day. After the first sampling, spat on the reef grew 0.007 ± 0.001 times their current size per day and spat placed in tanks grew 0.011 ± 0.001 times their current size per day. No significant difference in growth rates between sampling intervals was found for spat placed in tanks (df = 1, F = 0.475, p = 0.493) while growth rates were significantly greater in the second sampling period (df =1, F = 34.586, $p < 0.001$). Growth rates varied significantly between the different tanks (df = 5, F = 4.369, $p < 0.001$), with tank 1 showing a lower growth rate than tank 5 (p = 0.011) and tank 3 (p = 0.007).

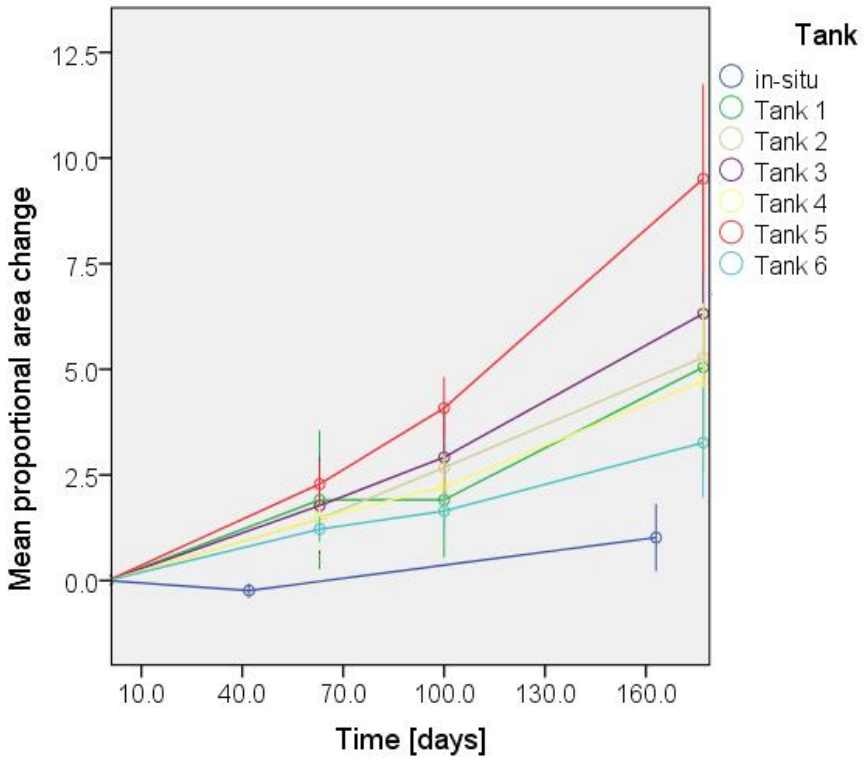

Figure A1.3. Mean proportional area change of spat over time. The area change was calculated as a proportion of the initial size of the coral spat. *Circles* show when the area of the coral spats where measured. *Lines* were drawn to connect the *circles*; their slope indicate how fast the coral spat area increased/decreased. The error bars represent 95% confidence intervals.

A1.4.3. Growth rates of bleached and non-bleached spat

Ten of the nineteen spat placed on the reef were completely white due to bleaching when they were photographed on the 30th of September 2014.Three of these bleached spat died between September and January, while none of the unbleached spat in the field died in that time interval. The skeletons of two of the dead spat were found on the tiles and had larger areas than in September, indicating that they died between October and January.

The area of most spat placed on the reef decreased in their first month of deployment (September sampling). Many of them lost their branches or a portion of the colony. The area of the spat that had been bleached decreased by an mean of 42% ± 9.6 (SE), while the non-bleached spat only had an mean 7 % ± 11.2 (SE) area decrease (t = -2.364, df = 17 p = 0.030). Both bleached and non-bleached corals grew between October and January. Non-bleached corals grew to 2.8 ±

0.63 (SE) times their September size in this time interval while bleached corals grew an average of 1.4 ± 0.33 (SE) times their September size. These growth rates did not differ significantly from each other (t = -1.822, df = 16, p = 0.087).

Between October and January, the spat on the reef grew wider bases and started to grow multiple small non-branched stumps. This led to a different morphology compared to the spats in the tanks which concentrated their growth on branching (Figure A1.4).

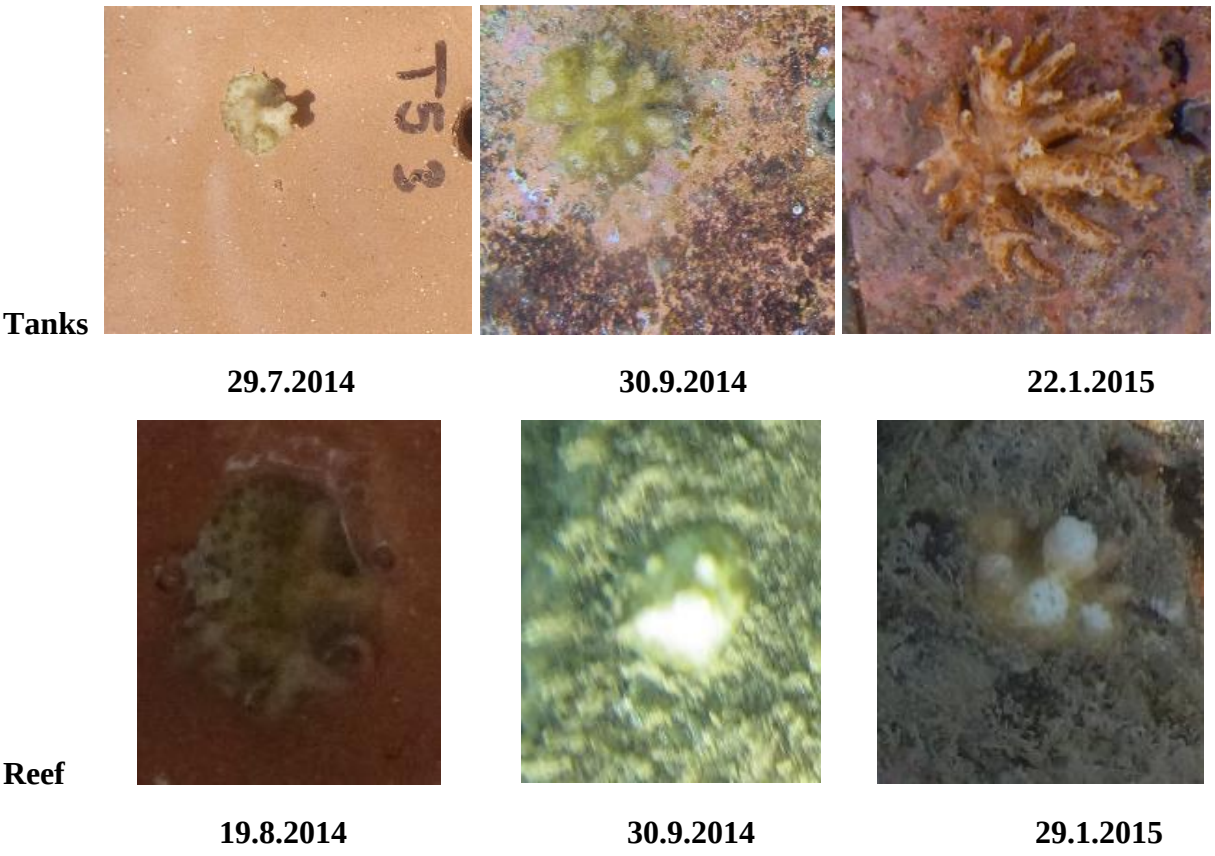

Figure A1.4. Examples of growth morphologies of spat in the tanks and on the reef. Time series pictures taken of two coral spat, one growing in a nursery tank (*top row*) and the other on the reef (*bottom row*). The development of extensive branches can be seen in the pictures taken of the spat in the tank. The decrease in area during the first sampling interval is visible in the picture series for the spat on the reef, as are the stump-like branches it developed during the second sampling interval.

A1.5. DISCUSSION

A1.5.1. Ex situ coral spat rearing

This experiment showed that rearing of *P. damicornis* spat in coral nursery tanks resulted in high survival and growth rates of spat. This is therefore a suitable technique to produce spat that are large enough to be transplanted to restoration sites.

A1.5.2. Transplantation to reef habitat

During the first month of the reef placement, 75 % of the coral spat decreased in size, mainly as a result of the loss of branches. This has also been observed for other *P. damicornis* and *A. millepora* spat (Raymundo and Maypa 2004; Guest et al. 2013). Both these studies found shrinkage to be more prevalent in larger spat. In my work, after the initial loss in area, spat placed on the reef grew as fast as spat in the tanks. However, they grew differently compared to spat in the tanks, growing a wider base while spat in tanks grew more branches.

A1.5.3. Effects of bleaching on coral spat survival

The spat that were placed on the reef struggled to survive during a bleaching event but showed high survival rates otherwise. No bleaching response of spat in tanks was observed, despite them receiving the same water as the spat on the reef. Recent studies show that low water flow can lead to the breakdown of the coral-microalgal symbiosis (Nakamura et al. 2003). It is therefore likely that the water flow in the tanks or the dissolved oxygen associated with it helped to prevent coral bleaching. Other studies have also reported elevated mortality rates in coral spat and fragments due to bleaching. Guest et al. (2013), for example, found that mortality rates of 50 cm^2 large *Acropora millepora* spat placed in the field spiked during a bleaching event while survival rates at a sheltered nursery site not affected by bleaching was almost 100%. Bleaching also led to increased mortality rates of transplanted coral fragments of seven different coral species in the Philippines. Corals transplanted a year and two years before the bleaching event were similarly affected. Of all the disturbances experienced during their study in the Philippines (heavy precipitation, one typhoon and two super typhoons), Shaish et al. (2010) noted that bleaching had the highest negative effect on coral fragments. Therefore, the possibility of occurrence of bleaching events and other disturbances has to be taken into account during coral reef restoration planning, for example by avoiding coral transplantations during the warmest months of the years (Fisk and Edwards 2010).

A1.5.4. Abiotic and biotic factors influencing growth rates

My experiment showed that coral spat growth rates did not only differ between the field and laboratory treatment but also differed between the tanks. Seven fish and invertebrate species were only found in Tank 5, in which spat growth rate was significantly higher than in other tanks. I was therefore not able to determine which biotic factor present in Tank 5 led to higher coral growth rates.

A1.5.5. Overall conclusion

In this study I assessed the mortality and growth of coral spat that originated from larvae released by *P. damicornis* fragments in an land-based coral nursery. I aimed to determine if spat transplantation to nursery tanks and reef habitats can be achieved and measured the success of spat as a function of mortality and growth rates. This study shows that coral spat reared naturally in nursery tanks are well suited to be used for coral restoration. Survival rates of the coral spat were high in nursery tanks and on the reef with the exception of low survival on the reef during a bleaching event. Transplantation of coral spat to reef habitats should therefore be well planned with a focus on avoiding transplantation during the warmest months. Harvest and relocation of coral spat was not time consuming in this study and could be done using the same technique (removal by chisel and attachment with super glue) in the future. Passive (as a bi-product) or active *P. damicornis* spat rearing can therefore increase a nurseries capacity to produce corals suited for reef restoration. Further studies are needed to determine under which conditions *P. damicornis* are capable of producing coral larvae and if the larval yield can be increased by changing conditions in the tanks.

Appendix II

Table A2.1. List of top 31 ecological factors examined by McClanahan et al. (2012). *Values in bold* indicate the top 10 values in each column; the 11 *ecological factor names in bold* indicate the feasible (feasibility > 5) ecological factors which ranked among the top ten factors for perceived importance or empirical evidence of resilience (Table from McClanahan et al. (2012)).

	Perceived importance (0 to 10)			Scientific evidence (−5 to +5)			Feasibility (0 to 10)
Ecological factor	**Resilience**	**Resistance**	**Recovery**	**Resilience**	**Resistance**	**Recovery**	
(1) Resistant coral species	**15.57**	**8.70**	**6.87**	**7.15**	**4.07**	**3.07**	**8.04**
(2) Temperature variability	**13.96**	**8.14**	5.82	**6.14**	**3.64**	2.50	**7.71**
Stress-resistant symbionts	**13.39**	**7.75**	5.64	**5.36**	**3.36**	2.00	3.19
(3)Nutrients(pollution)	**13.25**	**6.04**	**7.21**	**5.59**	**2.44**	**3.15**	5.63
(4) Sedimentation	**12.63**	**5.59**	**7.04**	**4.78**	**2.20**	**2.58**	6.73
(5) Coral diversity	**12.43**	**6.04**	6.39	4.11	**2.04**	2.07	**7.07**
(6) Herbivore biomass	**11.75**	4.29	**7.46**	**4.96**	1.64	**3.32**	**7.44**
(7) Physical human impacts	**11.67**	4.89	6.78	**4.81**	**1.96**	**2.85**	6.38
(8) Coral disease	**11.59**	**6.06**	5.54	3.81	**2.31**	1.50	6.43
Tidal mixing	**11.58**	**6.46**	5.13	4.41	**2.50**	1.91	4.83
(9) Macroalgae	11.46	3.89	**7.57**	**4.70**	1.33	**3.37**	**8.48**
(10) Recruitment	11.43	3.46	**7.96**	**4.89**	1.04	**3.86**	6.67
(11) Fishing pressure	11.39	4.32	7.07	**4.43**	1.46	**2.96**	**7.04**
Herbivore diversity	11.00	4.36	6.64	4.00	1.54	2.46	**7.33**
Habitat complexity	10.64	**5.08**	5.56	2.81	1.29	1.52	6.04
Connectivity	10.61	3.04	**7.57**	3.13	0.61	2.52	2.70
Mature colonies	10.39	4.21	6.18	2.81	1.07	1.74	**7.07**
Light (stress)	10.27	**6.31**	3.96	3.15	**2.31**	0.84	6.04
Coral size class distribution	10.08	4.81	5.27	2.58	1.19	1.38	6.88
Substrate suitability	10.00	2.39	**7.61**	2.93	0.36	**2.57**	6.52
Upwelling	9.83	5.04	4.78	2.63	1.46	1.17	4.71
Coral growth rate	9.79	2.71	**7.07**	1.79	−0.46	2.26	4.37
Proximity of other coastal habitats	9.67	4.04	5.63	3.39	1.36	2.04	**7.14**
Hard coral cover	9.50	3.71	5.79	3.14	0.88	2.27	**8.82**
Rapidly growing species	9.36	2.64	**6.71**	2.14	−0.64	**2.79**	6.89
Topographic complexity	9.19	4.74	4.44	2.26	1.22	1.04	6.19
Physical impacts	9.16	4.04	5.12	3.24	1.31	1.93	6.82
Wind mixing	8.00	4.00	4.00	2.71	1.52	1.19	4.45
Crustose coralline algae	7.81	2.54	5.27	0.35	0.00	0.35	6.62
Bioerosion rate	7.54	3.29	4.25	2.07	0.82	1.25	4.57
Exotics and invasives	7.00	3.04	3.96	2.42	0.92	1.50	5.00

Summary of the scaled perceived importance, scientific evidence, and feasibility of measurement for the top 31 factors. Perceived importance and feasibility are based on responses from 28 coral reef experts. Scientific evidence is based on a review of the journal literature with a distinct objective scale based on the level of evidence (see SI methods). Resilience scores are the sum of resistance and recovery scores. Values in bold indicate the top 10 values in each column; the 11 ecological factor names in bold indicate the feasible (feasibility>5) ecological factors which ranked among the top ten factors for perceived importance or empirical evidence of resilience.

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Appendix III

Table A3.1. The predictors that were tested in the correlation analysis and used the model building. The dark grey boxes represent sites and time periods for which data is available for the predictors. White boxes represent missing data. The last column shows the unit in which the predictor was measured in.

Predictor	**EC**		**RT**				**FR**				**Unit**
	1	**2**	**1**	**4**	**10**	**13**	**3**	**5**	**7**	**9**	
Time											
Collection date											**Month field trip was conducted in**
Deployment duration											**Number of months deployed after last analysis**
Succession stage of benthic community											**Total number of months deployed**
Proxies for suitable substratum for settlement and post settlement survival											
CCA cover											**Percentage cover**
Biofilm cover											**Percentage cover**
Peyssonnelia spp. cover											**Percentage cover**
Bryozoan cover											**Percentage cover**
Proxies for local larval supply											
Adult hard coral cover											**Percentage cover**
Adult Pocilloporid cover											Percentage cover
Adult Poritid cover											Percentage cover
Proxies for distant larval supply											
Inward water flux											Nr of particles
Water received from coral-dominated sites											Nr of particles
Water received from lagoon											Nr of particles
Water received from Western Reef Terrace											Nr of particles
Water received from fore reef											Nr of particles
Proxy for retention											
Outward water flow											Nr of particles

Table A3.1 continued

Predictor		EC		RT				FR				Unit
		1	2	1	4	10	13	3	5	7	9	
Environmental factors												
Temperature	May 2013-Sept 2013	■	■	■	■	■	■	■	■	■	■	°C
	Sept 2013-May 2014	■	■	■	■	■	■	■	■	■	■	
	May 2014-Sept 2014	■	■	■	■		■	■	■	■	■	
E-W velocity, N-S velocity & Standard deviation of the above	May 2013-Sept 2013				■	■		■		■	■	$m\ s^{-1}$
	Sept 2013-May 2014	■	■		■	■			■	■	■	
	May 2014-Sept 2014	■	■							■	■	
Bottom stress	May 2013-Sept 2013	■	■	■	■	■	■	■	■	■	■	$m^2\ s^{-2}$
	Sept 2013-May 2014	■	■	■	■	■	■	■	■	■	■	
	May 2014-Sept 2014	■	■									
Tidal variation	May 2013-Sept 2013				■	■	■	■	■	■	■	m
	Sept 2013-May 2014	■	■		■	■		■	■	■	■	
	May 2014-Sept 2014	■	■						■	■		

Appendix IV

This appendix shows the results of the CPCe trial using 16, 32, 48, 64, 80, 96, 128, 160, 192, 208 and 256 stratified points on 10 settlement tiles to determine the number of stratified points needed for an accurate percentage cover results. The benthic cover determined with CPCe using 208 and 256 points differed between 0 and 4% for benthic organisms that covered more than 60% of one side of the tile (Figure A4.1a), between 7 and 12% for benthic organisms that covered between 40 to 60% of one side of the tile (Figure A4.1b), between 3 and 22% for benthic organisms that covered between 8 and 20% of one side of the tile (Figure A4.1c), between 10 and 170% for benthic organisms that covered between 1 and 8% of one side of the tile (no graph as n = 16). Comparing actual cover for substrata covering 25, 10, 3.8, 3.4, 2.3 and 1.6% of the settlement tile with estimated cover from the CPCe trials showed that estimated percentage cover generally becomes closer to actual cover as more points are used in the analysis (Figure A4.1d,e,f). Estimated percentage cover for substrata covering 25 and 10% of the tile were close to actual cover when 128 or more points were used (Figure A4.1d). The reliability of the percentage cover data did not change much between estimates calculated with 160, 208 and 256 CPCe points. I therefore decided to use 200 CPCe points per tile side to obtain reliable percentage cover data for benthic substratum on the tiles. The results of this trial also showed that the proportional error in the benthic cover data decreases as the benthic cover of a substratum increases.

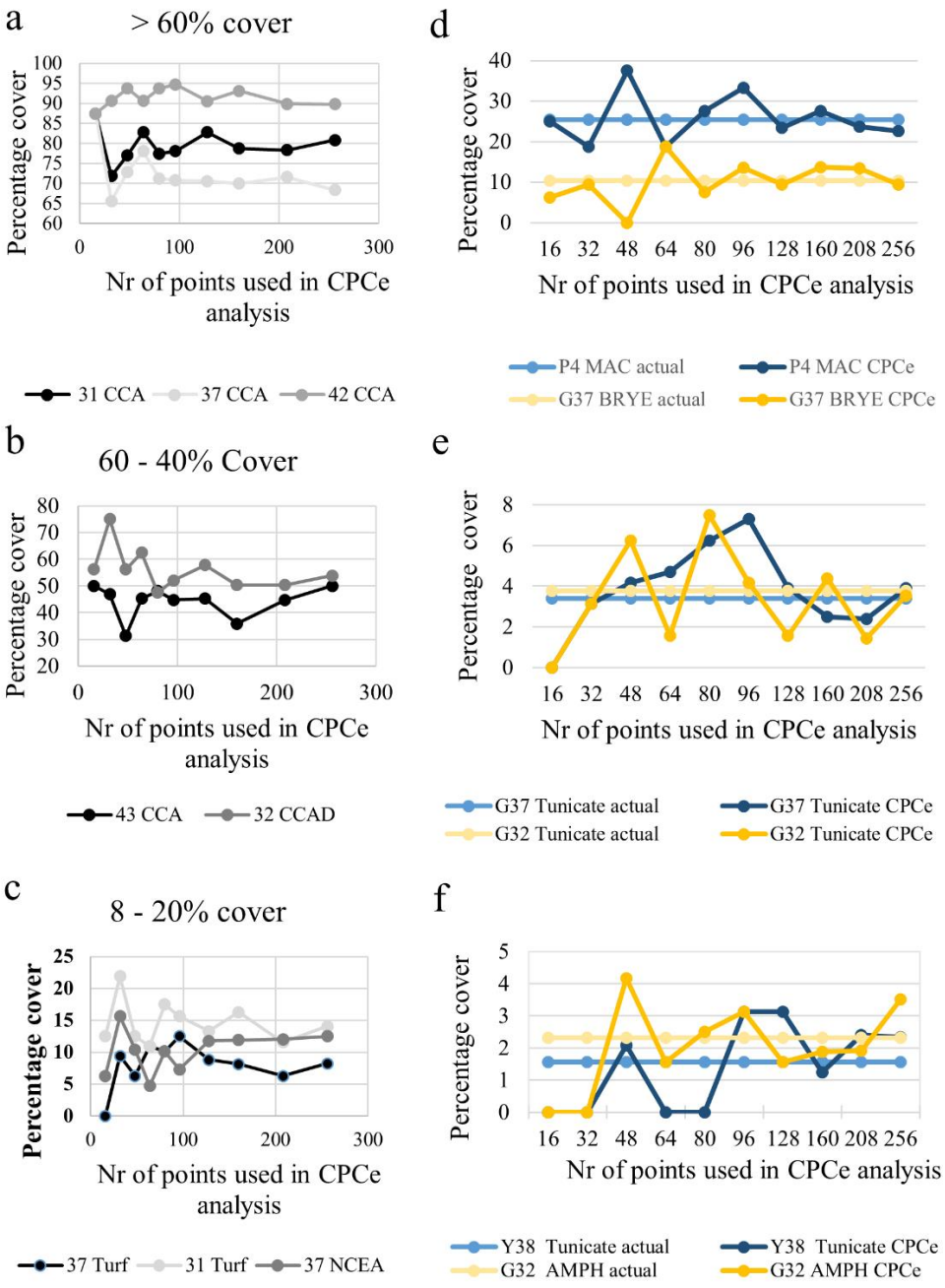

Figure A4.1. Results of CPC trial. (a) – (c) estimated percentage cover calculated with CPCe using between 16 and 256 stratified random point. (a) substrata which are abundant (>60% cover) on the settlement tile, (b) substrata which were common (60-40% cover) on the settlement tile, (c) substrata with low cover (8-20% cover) on the settlement tile. (d) - (f) estimated percentage cover calculated with CPCe using between 16 and 256 stratified random point (*bold colours*) and the actual cover of the substratum on the settlement tile (*light colours*). (d) substrata with low cover (10-30 % cover) on the settlement tile, (e) substrata with very low cover (3-4% cover) on the settlement tiles, (f) rare substrata (1-3% cover) on the settlement tiles. AMPH = amphipod tubes. BRYO = bryozoans, CCA = crustose coralline algae, CCAD = dead crustose coralline algae, NCEA = non-crustose encrusting algae, MAC = macroalgae.

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