Impact of the local environmental variability on the patterns of coral recruitment on Indo-Pacific reefs

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Abstract

Coral reefs are threatened by a range of human activities at both local and global scales. The result of these impacts has resulted in a worldwide decline in the coral reef ecosystems. Corals are the principle reef builders and the maintenance of their populations is fundamental for healthy reef ecosystems. Local environmental factors are critically important in shaping coral populations, particularly at the post-settlement phase, when young coral colonies are most vulnerable to disturbances. In this context, understanding the environmental factors that drive coral recruitment and affect coral survivorship in the early life history stages is vital to effectively manage coral reefs.

In this thesis I began by investigating the effect of abiotic and biological factors on coral recruitment and juvenile coral life history stages using settlement panels deployed in the Wakatobi Marine National Park (SE Sulawesi, Indonesia). My objectives were to assess the spatio-temporal variability in coral recruitment rates and juvenile abundance. I used a modelling approach to identify the environmental factors that affected the distribution and abundance patterns of corals. Then, I focused on the main environmental factors, identified from previously published research, affecting coral recruitment. I conducted a caging experiment to assess the impact of fish predation on coral juveniles. Finally, I analysed the development of the benthic community and the interactions between corals and benthic organisms in the first two years of colonisation of artificial bare surfaces.

I found high spatial and temporal variability in recruitment rates over seven years of data, values were lower than on other Indo-Pacific reefs and ranged from 9.6 (±8.21 SE) to 317.19 (±12.76 SE) rec. m^{-2}; while juvenile abundance ranged from 4.2 (±1.49 SE) to 33 (±6.36 SE) juv. m^{-2}. The local characteristics of the sites, such as coral cover, influenced the distribution of coral colonies in early life history stages; furthermore differences in coral density between the two life history stages (juvenile and recruits) were consistent over time. However, no single or combination of factors adequately explained abundance patterns for either recruits or juveniles. Fish predation did not appear to be the main cause of coral post-settlement mortality in the Wakatobi and it affected only 10.8% of the coral juveniles in the experiment. In contrast, 58.51% of the coral juveniles were found to be overgrown by algae and other invertebrates, however only turf and green encrusting algae affected coral survivorship. Coral colony abundance and the number of interactions with other benthic organisms, especially crustose

coralline algae (CCA) and sponges, increased over time on panels and they were different between the front and back side of the panels, which was attributed to differences in light and predation regimes. Coral recruitment was higher on older benthic communities, although none of the known coral recruitment promoters, such as CCA, or competitors, such as turf algae, were correlated with coral abundance.

My results show that changes in coral populations between the recruit and juvenile stages are likely driven by small-scale processes. The site characteristics determine the final patterns, which vary over time following temporal fluctuations in environmental factors. The effect of the interactions between algae and sponges with coral recruits and their influence on juvenile survivorship suggests these organisms having a role in coral recruitment success and highlight their importance as a focus for reef management. Furthermore, the use of long term studies allowed a better understanding of the high variability present in coral recruitment and the trends of the recruitment process, which are useful information for conservative purposes.

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Contributions

All fieldwork, analyses and writing were carried out by the author with the following exceptions:

Chapter 2

Project design: Author with guidance from Assoc Prof James Bell

Data collection: Author with exception of the environmental data sourced from studies performed by Dr Abigail Powell

Analysis: Author

Writing and editing: Author with editing by Assoc Prof James Bell

Chapter 3

Project design: Author with guidance from Assoc Prof James Bell

Data collection: Author with exception for the coral recruitment data collected in 2008 and 2009 sourced from separate studies performed by Dr Pelayo Salinas de León and 2014 data collected by the monitoring team of Opwall

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Writing and editing: Author with editing by Assoc Prof James Bell

Chapter 4

Project design: Author with guidance from Assoc Prof James Bell

Data collection: Author

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Writing and editing: Author with editing by Assoc Prof James Bell

Chapter 5

Project design: Author with guidance from Assoc Prof James Bell

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Analysis: Author

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Chapter 1 Introduction

Coral reefs are characterised by biodiversity patterns that are the result of the interaction of different physical and biological factors that determine the distribution patterns of individual species (Connell 1997). However, coral reefs are under threat; global scale effects such as climate change and ocean acidification have already resulted in the loss of key species, reducing overall biodiversity (Hoegh-Guldberg *et al.* 2007; IPCC 2007). These impacts will likely change reef structure and composition in the future (Hughes 1994; Marshall & Baird 2000; Pandolfi *et al.* 2003; Bellwood *et al.* 2004; Feary *et al.* 2007; Norström *et al.* 2009; De'ath *et al.* 2012). Furthermore, these global stressors combined with local scale impacts from tourism, overfishing, mineral extraction, and the release of nutrients and sediment from the land, are significantly impacting tropical marine systems (Hughes 1994; Jackson 1997; Nyström *et al.* 2000; Dulvy *et al.* 2003; Hughes *et al.* 2003; Halpern *et al.* 2008). It has been estimated that more than 60% of coral reefs are threatened by local activities while 75% of reefs worldwide have already been impacted by a combination of local factors and temperature stress (Burke *et al.* 2012) and this is going to increase to 90% by 2030 (Burke *et al.* 2012).

The degradation of coral reefs results in a loss of coral cover and overall biodiversity (Gardner *et al.* 2003; Bruno & Selig 2007). Such deterioration causes damage to all reef species and also effects humans, who often depend on the marine resources provided by reefs (Dulvy *et al.* 2003; Munday 2004). In fact, coral reefs provide an important livelihood for local communities through the trade and export of marine products, such as food and aquarium species, and they also have an important role in the tourism industry (e.g. recreational diving and cruises) (Edwards & Gomez 2007; Hoegh-Guldberg *et al.* 2009). Many studies have tried to estimate the economic value of coral reefs by looking at fisheries productivity, tourism, coastal development and all the services derived from the reef and it is estimated they are worth over a hundred billion dollars annually (Burke *et al.* 2012). Such valuations are important for promoting better management (Cesar 2000) and influencing political decisions to prevent further declines in coral reef quality (Burke *et al.* 2012). However, new polices are needed in many regions to protect reefs from further degradation, particularly to improve water quality and control nutrient inputs (De'ath *et al.* 2012). To make these interventions effective, more information is required about the processes that drive the distribution patterns of coral reef species, and particularly the factors that influence the recruitment and survivorship in the first

stages post-settlement of scleractinian coral living in shallow water, especially of the coral families more commonly found in coral early life history stages, such as Pocilloporidae, Poritidae, Acroporidae, Faviidae and Agariciidae. This information is important to understand coral population ecology and for the management of coral reefs (Sponaugle *et al.* 2002). Little is currently known about the biological and physical factors that regulate the distribution patterns of coral and how these patterns change through time. Understanding the processes that are responsible for the generation of population structure is fundamental for the design of marine reserve networks (Palumbi 2003; McLeod *et al.* 2010).

1.1 Coral connectivity and regulation of larval dispersal

Connectivity is defined as the degree of linkage between different populations (Saenz-Agudelo *et al.* 2011). From an evolutionary perspective, connectivity can be defined as the degree to which gene flow affects the evolutionary processes within populations (genetic connectivity) (Waples & Gaggiotti 2006). From an ecological perspective, demographically connected populations are those in which population growth rates are affected by dispersal (Lowe & Allendorf 2010; Saenz-Agudelo *et al.* 2011). In marine ecosystems, populations are connected by the exchange of larvae or the migration of adults, which maintains their abundance and genetic variability (Cowen & Sponaugle 2009; Ritson-Williams *et al.* 2009a). For most benthic marine organisms, larval dispersal is the most important process whereby larvae travel from a source population to their final destination. However, connectivity is a broad term and includes all the processes from reproduction to the settlement phase. It is fundamental to keep populations 'healthy' and larval dispersal has a primary role in preventing local extinction (Cowen *et al.* 2007; Pineda *et al.* 2007). It is considered to be the life history stage that permits the expansion of populations and is essential for population maintenance (Strathmann *et al.* 2002; Cowen & Sponaugle 2009). For coral populations exposed to different environmental threats, and where local ecological factors have a negative influence on larval availability, an external supply of larvae is vital to maintain coral communities.

Although marine populations were traditionally thought to be well connected by the long distance dispersal of planktonic larvae (Heck & McCoy 1978; Cowen *et al.* 2000), and for this reason marine populations have historically been considered as 'open populations' (Roberts 1997), there are multiple barriers to dispersal both over short and long distances (Almany *et al.* 2007; Jones 1997). Cowen (2000) suggested that populations can be classified as **'**open' or 'closed', where in 'close' system new individuals are provided through self-recruitment with

no exchange of larvae and genetic material with other populations (Hixon *et al.* 2002). However, recently Christie (2010) suggested that the levels of connection are more complex because of the continuous interaction between larval retention and exchange, the influence of different environmental factors, and the different life history strategies of marine species (Bak & Engel 1979; Adjeroud *et al.* 2007a).

The different life histories and reproduction strategies used by marine species are connected to the distance of larval transport and therefore gene flow (Hellberg 1996), and to the duration of their pelagic phase before they settle or metamorphose (Cowen & Sponaugle 2009). The length of the larval stage varies for each species; it can last from less than an hour (Carlon & Olson 1993) to several years (Steneck *et al.* 2009). It might be expected that larvae with a long planktonic period have the potential for long distance dispersal using oceanic currents (Bohonak 1999; Shanks *et al.* 2003), and can therefore maintain connectivity between geographically isolated populations. For example, in the Hawaiian Archipelago, Grigg (1981) estimated the larval duration of *Acropora* sp. to be 91 days, which is quite long compared to most coral species, and he suggested that those larvae could reach Johnson Atoll, 720 km from the parental reef (Harrison *et al.* 1984), thereby maintaining connectivity across the Hawaiian archipelago. This hypothesis was confirmed in a genetic study on *Porites lobata* in the same area conducted by Polato *et al.* (2010) showed that the longer the larval stage the further larvae were dispersed. In contrast, in a study of *Acropora tenuis* and *Seriatopora hystix*, larvae disperse less than 20 km from the source reef. This distance is in the lower part of the range of the model developed by Cowen (2006), which was based on the typical larval dispersal distance using biophysical data taken in the Caribbean region (Underwood *et al.* 2009).

There are some disadvantages to a long pelagic larval duration (PLD) as a result of environmental and biological interactions which vary in time and space (Nyström *et al.* 2000; Largier 2003). Physical variables such as hydrodynamic process, water currents (Roberts 1997), larval behaviour (Koehl *et al.* 2007), temperature, salinity, reproduction strategy (Hohenlohe 2004), latitude and acoustics (Vermeij *et al.* 2010b) regulate larval dispersal. Different research methods have been used to better understand the importance of these barriers. Direct methods include observational studies, which might involve tagging individuals when it is possible and mapping the larvae routes (see Hedgecock *et al.* 2003; Jones *et al.* 2005; Hellberg 2007). Indirect methods include genetic surveys, biogeographic analysis and models based on the physical, biophysical and larval properties (Nathan *et al.* 2003). The application of these methods allows the effective dispersal distance to be estimated. For

example, research conducted at Ryukyus Island in southern Japan using population genetic analysis on the spawning coral species *Acropora tenuis* found connections between two reefs 150 km apart, and it was possible to identify which reef was the larval source, which helped in the recovery of one of the two reefs after a bleaching event (Nishikawa *et al.* 2003). The use of molecular analyses has also shown the existence of genetic connectivity between populations of the same species up to 500 km distance (Nishikawa *et al.* 2003).

Research conducted using mark and recapture techniques on the reef fish *Pomacentrus amboinensis* has shown that the 15–60% of the larvae remain close to the original reef (Jones *et al.* 1999, 2005). This finding supports the suggestion that the interaction of environmental factors and larval behaviour can result in larvae being retained close to their natal population and promoting the self-recruitment (Jones *et al.* 1999; Swearer *et al.* 1999; Almany *et al.* 2007; Kinlan & Gaines 2007). As a consequence, if self-seeding is the main source of larvae, the whole recruitment process depends completely on local environmental factors, such as sedimentation, predation, eddies (Leis 2000; Andutta *et al.* 2012), tides, waves and surface water movements (Largier 2003), available substrate, spatial competition, light, water turbidity, chemical gradients and depth (Baird & Hughes 1997; Dunstan & Johnson 1998; Hughes *et al.* 1999a; Glassom *et al.* 2004). A combination of these factors will therefore influence population dynamics. Factors, such as currents, temperature and spawning period, change seasonally and may have a different effect on the recruitment rate at different times of the year. Ultimately, the final distribution patterns and population demography of marine organisms are influenced by a combination of all these different physical and biological factors that can modify the structure of the communities at different spatial-temporal scales (Jackson 1992; Karlson & Hurd 1993).

1.2 Coral recruitment

In scleractinian corals, the main reef builders, reproduction and recruitment are the most important factors for controlling the growth of populations, driving the maintenance of reef health, resilience to disturbance, and the recovery of degraded reefs (Babcock & Mundy 1996; Caley *et al.* 1996; Mora & Sale 2002; Warner & Cowen 2002; Fox 2004). Recruitment is the process of adding new individuals to a population (Caley *et al.* 1996); it includes the settlement of coral larvae and the deposition of the skeleton and can last up to 4 months (Wallace 1985a). Recruitment is critical for the maintenance of populations of sessile marine organisms (Connolly & Roughgarden 1999; Roughgarden 1988) and is fundamental for the reproduction,

variability and health of corals (Gaines & Bertness 1992; Caley *et al.* 1996).

The distribution pattern of coral larvae on reefs is driven by different environmental factors which are likely to have different influences and importance on the settlement and post-settlement survivorship of coral recruits (Maida *et al.* 1994; Mundy & Babcock 1998a).

1.2.1 Factors influencing the settlement of corals

Regardless of the dispersal potential of coral larvae, most coral reefs are self-seeding (Harriott & Fisk 1988; Sammarco & Andrews 1988). A positive correlation has been found between coral cover, larvae production and juvenile abundance by a number of authors (Sammarco & Andrews 1988; Harriott 1992; Johnson 1992; Harriott & Banks 1995; Chiappone & Sullivan 1996; Underwood *et al.* 2007, 2009). As a consequence, populations are not likely to be dependent on distant sources for the availability of coral larvae (Kinlan & Gaines 2007; Jones *et al.* 2009). However, impacted coral reefs that rely solely on self-seeding are likely to be at high risk as distant larval sources are unable to accelerate the recovery time (Bellwood *et al.* 2004; Fox 2004). Understanding the dependence of a coral reef on self-recruitment is critically important for conservation and restoration projects and knowledge of the larvae population source is fundamental for developing effective management plans. However, the choice made by larvae about where to settle on the reef is also determined by the combination of larvae behaviour and environmental preferences; coral larvae are able to distinguish between different environments (Ritson-Williams *et al.* 2009b).

According to Fisk and Harriott (1990), the primary driver of coral recruitment rate is the availability of suitable settlement surfaces that are free from sedimentation and grazing pressure and have sufficient exposure to light. Sedimentation has an important role in both the settlement and post-settlement process (Hodgson 1990). An earlier laboratory recruitment experiment with surfaces differently affected by sedimentation showed how even a small increase in sedimentation rate can produce a significant change in the larval settlement patterns (Babcock & Davies 1991). Coral larval settlement rate is higher where grazers, such as sea urchins, fish, gastropods, and starfish, feed on reef surfaces as they clear it of filamentous and non-coralline algae that are usually effective competitors for the available space with the coral recruits (Brock 1979; Dart 1972). In addition, light intensity determines the depth range at which coral larvae will settle (Erftemeijer 2012; Mundy & Babcock 1998). As a consequence, recruits show different distribution patterns across reefs and even between sites on the same reef. These patterns can be observed by looking at both the abundance of recruits and the

taxonomic composition of the settlers. The combination of the overall environmental factors explains in part the spatial variation of coral recruits. Recently the importance of crustose coralline algae (CCA) has been recognised as another important factor in determining the final coral cover and composition (Golbuu & Richmond 2007; Buenau *et al.* 2011, 2012). Depending on the species, CCA can have an inhibitive or facilitating effect on coral larvae settlement.

There is considerable temporal variation in the abundance of coral recruits (Wallace 1985b; Dunstan & Johnson 1998; Ho & Dai 2014). While seasonal variability has been connected to different reproduction behaviours, such as spawning season (Fox 2004), annual variation has been explained in a number of different ways, such as fluctuations in environmental factors (e.g. effects of El Niño Southern Oscillation; ENSO) or events connected to these factors (e.g. *Acanthaster placi* outbreaks) (Wallace 1985b; De'ath *et al.* 2012). The identification of annual variation in recruitment patterns in scleractinian corals is important in order to understand the overall trend and the scales at which such trends operate.

Many research on coral recruitment used artificial surfaces, particularly settlement panels deployed on the reef, with several studies showing that they have similar recruitment rates as the natural reef (Mundy 2000; Salinas De León *et al.* 2011). A major advantage of panels is that they can be taken out of the water for microscopic examination, facilitating estimation of recruitment rates and taxonomic identification through the skeleton calcium that coral larvae release in the first hours after settlement (Babcock *et al.* 2003). At this stage of recruitment process, most recruits present only a single polyp or a few, sometimes slightly elevated on the panel, according to the morphology of the adult coral species. The coral families Pocilloporidae, Acroporidae, Poritidae, Faviidae and Agariciidae already presents the characteristics of the family at the single polyp stage, while other families develop later. Pocilloporidae is a branching coral with polyp diameter up to 1.0mm and usually; Acroporidae can be branching, tabular or bushy as an adult species. Poritidae can be flat, massive or branching, with polyps. Faviidae can be massive, branching, encrusting, it has big polyps, while Agariciidae has poorly defined walls and its polyps seems interconnected, forming massive adult corals.

The deployment of panels in specific positions, with the front side exposed to predation and sedimentation, and the back side less affected by these factors, has shown that coral larvae, despite the lack of light, generally prefer to settle on the back side of the panels in cryptic

locations, which are more protected (Wallace 1985a; Mundy 2000; Babcock *et al.* 2003; Salinas De León *et al.* 2012a). These kinds of studies have been carried out in different environmental conditions allowing the factors that influence coral recruitment and determine the distributional pattern to be determined.

1.2.2 Mortality during the post-settlement phase

The post-settlement phase begins when the coral recruits metamorphose and fix permanently to the substratum. Some authors define this phase more precisely, like Vermeji (2008), who extends in the post-settlement stage to the point at which each coral recruit has at least two polyps separated by a wall and with a developed skeleton. The post-settlement stage is a very delicate phase for coral recruits (Edmunds 2007), and involves high mortality. This early post-settlement mortality shapes adult coral populations (Penin *et al.* 2011).

In this early stage of their life history, coral recruits are particularly vulnerable to environmental factors that affect their survivorship and growth to the adult phase. In recent years, *in situ* observations and laboratory experiments have been conducted to understand the tolerance and limits of coral recruits to predation (Baria *et al.* 2010; Penin *et al.* 2011), sedimentation (Birrell *et al.* 2005; Granja Fernandez & Lopez 2008), spatial competition (e.g. algae overgrowth, CCA) (Jackson & Buss 1975; Benzoni *et al.* 2011) and light (Anthony & Connolly 2004). These studies have provided a better understanding of the role of environmental factors have on the final distribution pattern of corals and have shown the importance of these factors in the different life history stages of corals (Figure 1.1). These factors have a stronger influence on the survivorship of settlers due to the limited energy available for recruits to resist to stress, such as competitive interactions with other organisms.

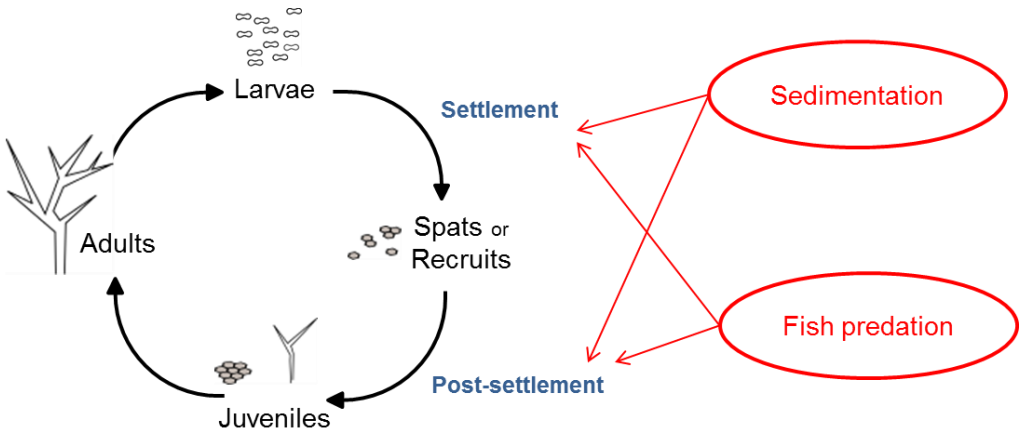


Figure 1.1 Diagrammatic representation of recruitment process and the factors that influence this process at different life stages. Black arrows: transformation from coral larvae to juvenile and adult colonies; red arrows: factors that influence different phases of recruitment that will be considered in this study. Adults: coral colony able to reproduce; Larvae: early free-swimming life history stage; Spat/recruits: recently settled and metamorphosed corals smaller than 10 mm; Juveniles: multi-polyps units with total length between 10 and 50 mm

Predation is one of the most important factors influencing the survivorship of small coral colonies (Penin *et al.* 2010, 2011). Grazers keep the reef clear of algae, but while they feed on algae positioned near settlers they can accidentally damage the polyps. A laboratory experiment conducted with *Pocillopora damicornis* and blenny fish (Blennidae) showed how single polyps are damaged the most by blennies; in contrast colonies composed of 6–8 polyps have a higher resilience to predation (Christiansen *et al.* 2008). This result confirmed previous studies that suggested that the small size of recruits makes them more vulnerable to predation than bigger colonies (Zilberberg & Edmunds 2001; Golbuu & Richmond 2007).

Juvenile growth rate also affects the time it takes for coral community to change; as juveniles reach the adult phase, they contribute to population dynamics through reproduction. Knowledge of coral growth rates is important for estimating the time required by the reef to recover from disturbances (Bellwood *et al.* 2004). Research in the Virgin Islands, where the growth of juvenile corals has declined in recent years, has shown that recruits whose post-settlement phase lasted longer than the average time for individuals of the same species had a reduced survival probability (Edmunds 2007). Furthermore, recruits that do not grow above 3 mm in their first two or three months, against an average growth rate of 10–34 mm y^{-1}, have only a 20% chance of survival (Rylaarsdam 1983). This means that an understanding of any factors that decrease juvenile growth and increase mortality rate in the post-settlement phase is important in measuring recruitment.

Survival rate can be influenced by the direct and indirect effects of many factors. For example, a positive correlation has been found between anthropogenic pressure and sedimentation rate; human activities in coastal environments and river catchments generally increase the amount of suspended sediment in the water. Finer sediment grains contribute to water turbidity, with sediments settling on the reef covering the polyps and reducing light further; this last effect can suffocate corals and reduce growth rate (Richmond 1993). Sediment also contains microbes whose metabolism leads to anoxia in the areas of the coral in contact with the bacteria as a consequence of sulphur reduction process (Erftemeijer *et al.* 2012; Weber *et al.* 2012). The sediment tolerance of corals is species-specific, and it is likely to vary across seasons and locations (Erftemeijer *et al.* 2012). Over longer periods, high sedimentation induces stress, decreasing the recovery potential (Nyström *et al.* 2000) and coral density and causing changes in coral community composition (Rogers 1990; Dubinsky & Stambler 1996; Gilmour 1999; Gilmour *et al.* 2006).

The estimation of post-settlement mortality requires an initial understanding of the overall coral recruitment rates, established by a preliminary assessment of the abundance of recruits and juveniles (Penin *et al.* 2010). The comparison of these densities with adult colony density can give an estimation of the mortality rate at different stages of the coral lifecycle, and potentially identify those stages being most affected by human impacts. In order to explain the main drivers of the mortality process, many experiments examined the different ecological factors that might be responsible for juvenile mortality in the post-settlement phase (Christiansen *et al.* 2008; Penin *et al.* 2010, 2011), but their interaction and the limit of resilience compared to coral recruits are still unknown.

1.3 Coral reefs in the Wakatobi Marine National Park

Indonesia is at the centre of the Coral Triangle region, which is famous for its high biodiversity and richness (Barber 2009). The Wakatobi Marine National Park (WMNP) in South Sulawesi, covering 1.39 million hectares, is the second largest marine park in Indonesia and UNESCO nominated it as a World Biosphere Reserve in July 2012. The Wakatobi MNP is a coral reef system (see Figure 1.2) in the Banda Sea eco-region, which is an area crossed by complex water currents and with high reef diversity (McMellor & Smith 2010). Four main islands and smaller atolls compose the Wakatobi MNP; they are characterised by different coral cover and composition and vary in their topography (e.g. reef flat depth and distance from the coast) and ecological factors that affect each reef, such as optical depth and sedimentation rate (Hennige

et al. 2008). Previous research has recorded a continued decline in the abundance of coral in the park and found that anthropogenic disturbances resulting from the discharging of waste water, fishing activities and exploitation of the local marine area (e.g. use of coral as a building material) impact the marine environment surrounding human settlements (Crabbe & Smith 2005; Cullen 2007; Haapkylä 2007).

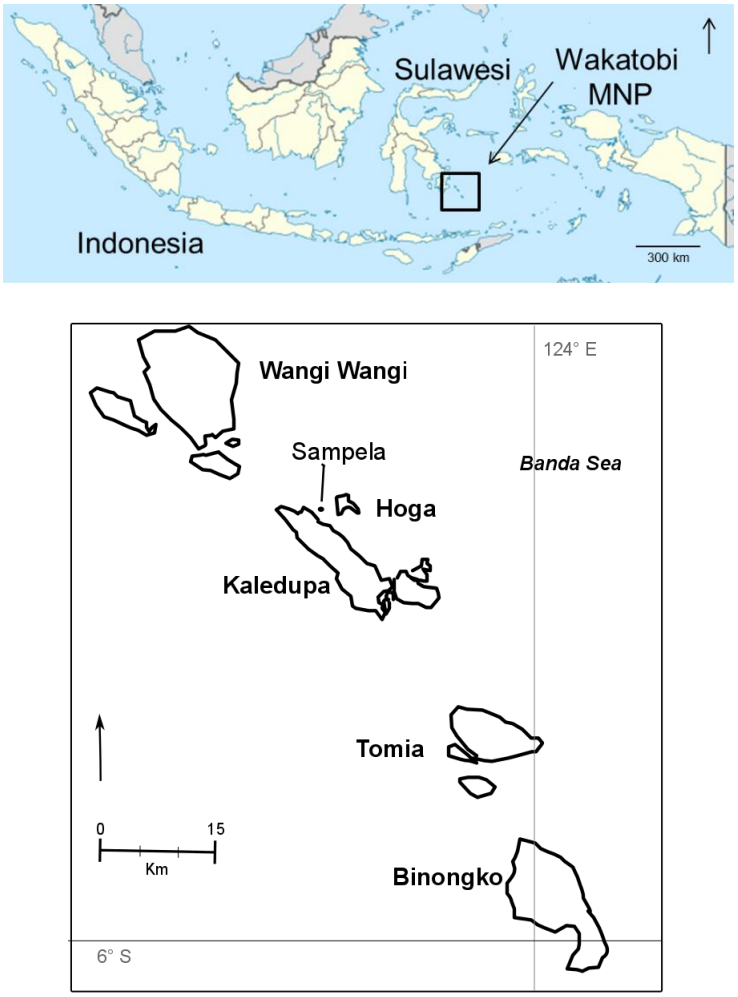


Figure 1.2 On the top: map of Indonesia. On the bottom: map of the Wakatobi Marine National Park (Indonesia)

Particularly, the reef on the North East of Kaledupa Island is highly impacted in correspondence to a Bajau (sea gypsies) settlement of about 2,000 people located on the reef flat and seagrass area (Figure 1.3). Bajau are a traditionally nomad population that usually move on houseboats between Malaysia, Philippines and Indonesia. The livelihood and food of Bajau population depend completely on resources coming from the ocean and Bajau are

specialized in exploiting the reef using artisanal coral mining, fishing blasting and other activities (Cullen 2007). In contrary to the nomad life, where Bajau exploit a marine area and then leave it to use a new one, giving time to the reef to recover, the permanent village of Sampela modified not only the landscape, but the overall reef close to the village.

The activities of the Bajau population are recognised as one of the major problem for the conservation of marine resources in the Wakatobi (Cullen 2007). For instance, coral rock is used to build the basement of the hut on stills on the reef flat (Figure 1.3). The reef next to Sampela present high levels of degradation, with high sedimentation rate and water turbidity. Sampela reef lost the 80% of its coral cover between 2002 and 2011 (Curtis-Quick 2013). Despite the entitlement as marine national park, the low control and poor management of the Wakatobi allowed the practise of destroying human activities(McMellor 2007).

Figure 1.3 The Bajau settlement of Sampela, on the reef flat of Kaledupa Island in the Wakatobi Marine National Park. Huts are built on stilt on a basement composed by coral rock. Coral mining for building purposes is highly practised all around the area of Sampela,

Salinas De León *et al.* (2011, 2012a) conducted several studies in the Wakatobi MNP looking at coral recruitment rate using two sites characterised by different coral cover and ecological factors: one with relatively high coral cover (Hoga) and another impacted by disturbance, with low coral cover and experiencing high sedimentation (Sampela). Seasonal and annual surveys of coral recruitment have been conducted by using settlement panels made of terracotta, based on a modification of the method used by Mundy (2000). A preliminary study in the Wakatobi MNP showed that recruitment rate on panels is comparable to natural reef (Salinas De León *et al.* 2011) and that there is variation in coral abundance and species composition across different reefs and seasons. In accordance with the research conducted by Nzali *et al.* (1998), these authors also hypothesised that a relationship existed between coral cover and recruitment rate,

which suggests that most of the available larvae settle in close proximity to their parents, maintaining the local coral population**.** Furthermore, as in earlier studies (Baggett & Bright 1985; Carleton & Sammarco 1987; Harriott & Fisk 1987; Mundy 2000) higher recruit abundance was recorded on the back surfaces of the panels compared to the front. The front sides of the panels were likely more exposed to environmental factors, especially in Sampela where the front sides collected a thick layer of sediments that may inhibit settlement (Salinas De León *et al.* 2012a). Importantly, the presence of this heavy sedimentation, along with differences in grazer abundance between the sites, meant it was not possible to separate the effects of coral cover, sedimentation and grazing on recruitment rate. Finally, post-settlement mortality rates have also been estimated by measuring the abundance of coral juveniles at Sampela and Hoga, and there were clear differences in the final abundance, pattern and families composition of corals. Spatial and temporal variation in recruitment rate suggests that environmental factors are very important in driving the recruitment process and that habitat differences might explain differences in post-settlement mortality rate across different sites rather than larval availability (Salinas De León *et al.* 2012a).

Based on these studies in the Wakatobi MNP, three main factors have been recognised as having primary importance in determining coral recruitment patterns: adult coral colony abundance, sedimentation, and predation. Chronic sedimentation seems to have a high impact in Sampela, while suspended sediments affect recruit survival by reducing the amount of light reaching coral polyps. Different predation rates could also explain differences in recruitment rates, especially because there are different fish abundances and species present on the two reefs (Salinas De León *et al.* 2012a), but since most of the recruits settled on the back side of the panel, the effect of fish predation is not easily studied (Salinas De León *et al.* 2012a). To date there have been no studies considering the interaction between these two factors. Since the possibility of the reefs recovering from degradation is strictly correlated to the success of the recruitment process of hard corals, additional research is required to understand how these factors affect the ecology of scleractinian coral populations and drive coral post-settlement mortality.

1.4 Goals and thesis structure

The main goal of this research was to investigate the ecological factors that drive the settlement and post-settlement survival in scleractinian corals at local scales in the Wakatobi MNP. I investigated how these factors influence the distribution pattern of coral settlers on reefs with different physical and biological conditions. Specifically, I conducted surveys and manipulative experiments to assess the factors influencing corals at different life history stages.

Initially I explored the spatial and temporal variability in coral recruitment across sites characterised by different environmental factors. Chapter 2 describes the large-scale recruitment study modelling the biological and physical factors that correlate with the recruitment rates of reef corals. I used nine sites located on two reef systems characterised by different environmental factors (e.g. coral cover, sedimentation rate).

Specific objectives included:

1. To characterize the study sites through the collection of data on physical and biological factors (e.g. coral cover, sedimentation, predation, and water flow).
2. To survey the distribution patterns of scleractinian coral recruits and juveniles.
3. To determine any relationships between environmental factors on coral recruit and juvenile density and diversity using a modelling approach.

Chapter 3 describes an investigation into the temporal variation in abundance and assemblage composition of different coral life history stages in order to identify temporal trends in coral recruitment.

Specific objectives included:

1. To determine coral recruitment rates across nine sites characterised by different environmental conditions over two consecutive years.
2. To determine coral recruitment rates and juvenile abundance over a seven-year period at two reef systems of different environmental qualities.

The second part of this thesis explores the role of specific environmental factors on coral recruitment distribution pattern. In Chapter 4 I assessed the impact of fish predation on coral recruit and juvenile survival by conducting a manipulative experiment (fish exclusion by caging).

Specific objectives included:

1. To examine the impact of fish grazing activity on coral recruit and juvenile abundance by assessing the overall full and partial mortality rate in coral populations.
2. To assess any correlation between coral colony size and mortality rate in order to detect coral colony sizes that have a higher probability of being accidentally removed from the surface or damaged.
3. To investigate effect of overgrowing on variation in coral size and variation in photosynthetic efficiency of coral recruit and juvenile mortality.

In Chapter 5 I investigated the first stages of the benthic community development over two years and the effect of spatial competition on coral recruit and juvenile abundance, and assemblage composition.

Specific objectives included:

1. To determine any associations between the main benthic families and coral colonies after one and two years of benthic community development.
2. To assess the interactions between benthic organisms and coral colonies, and to investigate the outcome of the interactions in order to detect relationships between benthic groups and coral recruits.

The overall outcomes of this research are discussed in the final chapter in the context of the high dynamism present in the coral recruitment process and the implications for coral reef management.

Chapter 2 Spatial variability in patterns of coral recruitment in the Wakatobi Marine National Park, Indonesia

2.1 Abstract

Coral recruitment is an important process for reef maintenance and is driven by a suite of abiotic and biological factors. These factors also strongly influence corals at different life history stages and determine the final patterns of coral abundance and diversity. The impact of local variables on recruitment processes has previously been shown across sites characterised by different environmental conditions. However, there is little understanding of the effect of disturbance on the abundance patterns of different coral life history stages. I therefore investigated the influence of environmental variables on coral distribution patterns by analysing the abundance of recruits (less than 1 year old) settled on artificial panels and juveniles (<40 mm) on natural reef across nine sites characterised by different abiotic and biological factors in the Wakatobi Marine National Park (South-East Sulawesi, Indonesia). Significant spatial variation was found in recruit abundance between sites and orientation (top or bottom) of settlement panels, but not among depths. No single variable that were measured adequately explained the variability and distribution patterns of the coral recruits. High post-settlement mortality occurred between the recruit and juvenile stages with a large decrease in overall density, which changed from 112.97 (±11.16 SE) recruits m^{-2} to 9.63 (±0.24 SE) juveniles m^{-2}. There was significant spatial variation in juvenile abundance across sites and depths (PERMANOVA; df=8, $P<0.05$). None of the variable or combinations of variables explained the patterns of juvenile abundance. There was a shift in the coral assemblage structure between different life history stages, suggesting differential mortality patterns between different coral families. Despite the lack of correlation between coral abundance patterns and the variables I measured, the orientation of the recruits and the variation in family distribution patterns between life history stages suggests that there might be a variable that was not included in this study that strongly influences these patterns, such as light availability. Elucidating the factors responsible for the patterns observed will help local managers to promote specific interventions at local scales in order to improve coral reef management.

2.2 Introduction

Coral recruitment is fundamental for maintaining healthy coral populations and promoting reef restoration after disturbance (Dulvy *et al.* 2003; Munday 2004). In recent decades surveys conducted on coral reefs worldwide have highlighted high levels of spatial variability in coral recruitment patterns (Hughes & Connell 1999; Adjeroud *et al.* 2007a; Penin & Adjeroud 2013) at different scales: oceanic, regional (Soong *et al.* 2003), and local (O'Leary & Potts 2011).

The dispersal of coral larvae can connect reefs at different scales, depending on the reproductive strategy of the species being considered (broadcasting versus brooding of larvae), the duration of spawning season (Underwood *et al.* 2009), larval abundance (Potts *et al.* 1985), larvae navigation (Edmunds 2000b; Pineda *et al.* 2007), and pelagic larval duration (Graham *et al.* 2008). Sammarco & Andrews (1989) found that recruitment is likely to be mostly a local scale phenomenon. Despite the long larvae dispersal potential for most coral species, most larvae appear to settle close to their natal reef, meaning that the recruit composition should be similar to the adult population. However, this correlation has only been found in a few studies as local environmental factors affect the abundance and distribution patterns of corals (Chiappone & Sullivan 1996; Nzali *et al.* 1998; Vermeij & Sandin 2008; Salinas De León *et al.* 2012a).

Coral larvae have preferences for specific settlement sites (Hughes *et al.* 1999a). They can follow chemical (Miller & Mundy 2003) and physical cues, such as the light intensity optimal for growth (Fisk & Harriott 1993), low turbidity (Browne *et al.* 2012) and water flow (Goldenheim & Edmunds 2011), which can affect their physiology and growth rates. A primary condition required for settlement is the availability of surfaces free from sedimentation (Hodgson 1990; Gilmour 1999; Edmunds *et al.* 2014a), however exposed surfaces are more accessible to grazers and coral predators, and as a consequence some larvae prefer to settle in cryptic environments (Wallace 1985a; Mundy 2000; Adjeroud *et al.* 2007b) that offer more protection from predation and are less impacted by sedimentation (Penin *et al.* 2010; Edmunds *et al.* 2014b). Edmunds *et al.* (2014a) reported that in the presence of an equal distribution of refuges on exposed and more sheltered positions, larvae preferred the more exposed sites, which had higher light availability.

Earlier research reported a decrease in coral abundance rates in young coral populations during the recruitment process, where high differential mortality rates affect the coral colonies of various life history stages (Babcock *et al.* 1986; Wilson & Harrison 2005; Penin *et al.* 2010).

Overall the mortality rate has been inversely correlated with the age of the colonies and this rate appears to be different among coral taxa, causing variation in the patterns of coral family composition (Nozawa *et al.* 2013; Penin & Adjeroud 2013).

A number of studies have compared the abundance and assemblage structure of coral various life history changes (recruits, juveniles and adults) at sites with different environmental conditions (Wilson & Harrison 2005; Penin *et al.* 2010), and have highlighted a relationship between abiotic and biological variables and the survival of coral life history stages. It is likely that different factors affect coral survival at different life history stages. These correlations between coral survival and local ecological factors have been assessed using a combination of observations, surveys and manipulative experiments (Edmunds 2000a; Fox 2004; Linares *et al.* 2012; Trapon *et al.* 2013a).

Penin *et al.* (2010b) found that coral recruit mortality was associated with local fish abundance, while predation rate by corallivorous fish was negatively correlated with the size of coral colonies (Christiansen *et al.* 2008). Christiansen *et al.* (2008) found a positive correlation between the size of coral recruit and the possibility of being eaten by fish; single polyp recruits were more susceptible to grazers and predators than colonies composed of a few polyps (Vermeij & Sandin 2008) because multi-polyp colonies are better able to deal with partial predation (Edmunds 2007). There are a number of other environmental factors and interactions that have been correlated to colony size or life history stages. For example, spatial competitors are likely to have increasing importance to the growth of the coral colony (Babcock & Mundy 1996). As the colony increases in size, more space is required, especially for encrusting and massive species, and their relationship with the other benthic organisms present on the reef will influence survival, direction and growth rate of corals (Box & Mumby 2007; Sandin & McNamara 2012). Algae, and marine invertebrates such as sponges, soft corals ascidians and molluscs, also cover reefs and are strong competitors for space, and can overgrow and suffocate the coral recruits (Lenihan *et al.* 2011).

Recently, reef ecologists have begun investigating the interacting impacts of multiple disturbances on coral recruits and juveniles (Hixon 2011; Lenihan *et al.* 2011; Erftemeijer *et al.* 2012; Ban *et al.* 2014). Experimental studies conducted to assess the impact of sedimentation and predation on coral juveniles (Baria *et al.* 2010; Penin *et al.* 2011; Davies *et al.* 2013; Trapon *et al.* 2013c) have found differences in responses depending on the size of colony or the coral taxa (Penin *et al.* 2011). Composition, intensity and interactions between

local co-existing disturbances differently affect the recruit and juvenile populations. These disturbances affect not only the abundance, but also the coral assemblage composition (Benayahu & Loya 1984; Erftemeijer *et al.* 2012; Ban *et al.* 2014) and it is likely that the importance of individual variables varies at each life history stage (Penin *et al.* 2007). These previous studies suggest that local factors influence the success of the coral recruitment process and determine spatial variability at small localised scales. However, there is still a lack of information on the role and importance of the ecological variables that affect reefs at small scales.

This research was conducted in the Wakatobi Marine National Park (WMNP) in South Sulawesi, Indonesia, which is situated in the middle of the Coral Triangle, an area well known for its high diversity and richness in coral species. The WMNP supports reefs of different qualities, which, despite the short distance between them, have high variability in coral distribution and abundance patterns. A previous coral recruitment study by Salinas De León *et al.* (2012a) in this region found spatial variability in the abundance of recruits between two reefs characterised by different environmental factors. The positive association between coral cover and recruitment rate suggested that the reefs were mostly self-seeding and that recruitment occurred at the local scale. A high mortality was also reported in the post-settlement phase along with a shift in dominance from the Pocilloporidae family at the recruit stage to the Faviidae family in the juvenile stage (Salinas De León *et al.* 2011, 2012a). Sedimentation and predation were suggested as the main drivers of the overall recruitment process. However, because this study was conducted only at a limited number of sites and included only two reef systems chosen for their different reef qualities, it is unknown whether the same patterns would be observed across a varying environmental conditions.

The aims of this study were to measure the spatial variability and patterns of coral recruitment to artificial panels and quantify juvenile abundance across sites and depths characterised by different coral coverage and environmental conditions; and to model the factors explaining the spatial variability found in the recruit and juvenile coral populations.

2.3 Methods

2.3.1 Study site

The Wakatobi Marine National Park, covering 1.39 million hectares, is the second largest marine park in Indonesia and UNESCO nominated it as a World Biosphere Reserve in July

2012. The WMNP is a coral reef system (see Figure 2.1) in the Banda Sea eco-region, which is an area crossed by complex water currents with high reef-associated diversity (McMellor & Smith 2010). Four main islands and a number of smaller atolls are found in the WMNP; sites in this area are characterised by different coral cover and composition and vary in their topography (e.g. reef flat depth and distance from the coast) and the ecological factors that affect each reef, such as optical depth and sedimentation rate (Hennige *et al.* 2008) (see Table 2.1).

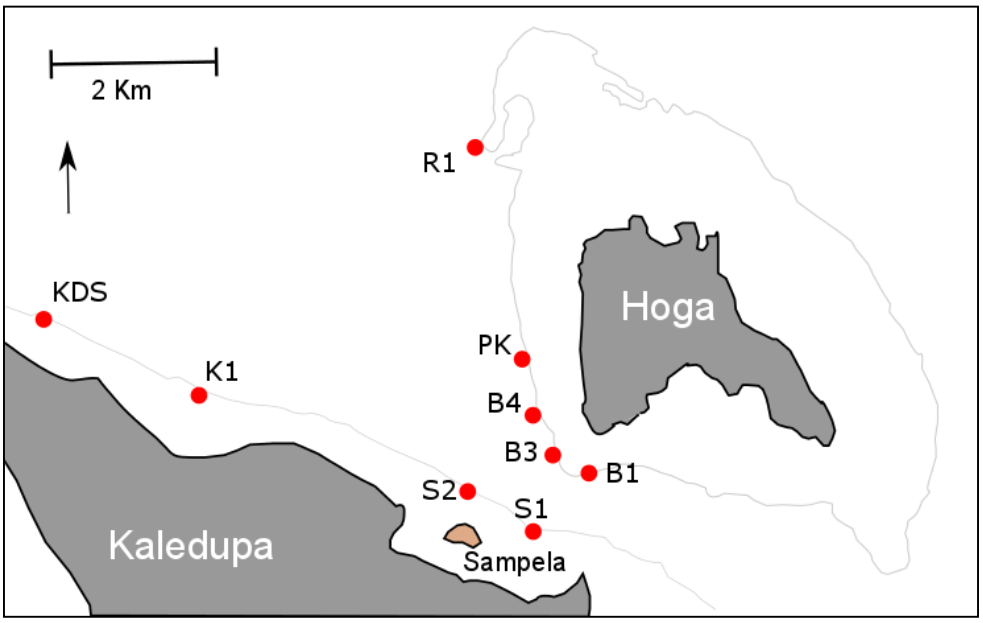


Figure 2.1 Map of the sites used in this study in the Wakatobi MNP, Indonesia (B1= Buoy 1; B3= Buoy 3; B4= Buoy 4; PK= Pak Kasim's; R1= Ridge 1; S1= Sampela 1; S2= Sampela 2; K1= Kaledupa 1; KDS= Kaledupa Double Spur). Light grey line outlines the coral reef boarders.

The nine sites included in this study were selected based on their variability in ecological characteristics and are located on two separate reef systems, Hoga and Kaledupa. The distance between any two study sites ranged from 250 m to approximately 5 km.

Table 2.1 Summary of the main characteristics of the study sites in the Wakatobi MNP, Indonesia (Powell 2013)

Site	Topography	Coral cover	Main abiotic characteristics	Main biological characteristics
Buoy 1 5° 28' 48.22"S 123° 45' 35.01"E	Southern site on Hoga reef, slope up to 30 m, sandy bottom.	Coral cover ~20-30%	Low sedimentation, low flow and moderate turbidity.	Average fish abundance.
Buoy 3 5° 28' 29.57"S 123° 45' 29.40"E	Positioned about 150 m from the shore, steep slope up to 30 m, sandy bottom. Presents caves and hangovers. High diving activity.	Coral cover ~23-32 % mostly Pocilloporidae, Poritidae and Acroporidae spp. (93%)	Average sedimentation.	High crustose coralline algae cover.
Buoy 4 5° 28' 20.42"S 123° 45' 26.48"E	About 250 m north of B3, 30 m depth, sandy bottom. It present caves and hangovers, and areas covered by coral rubble.	High coral cover ~45%,	Average sedimentation	High sponge abundance and low algae
Pak Kasim's 5° 28' 1.30"S 123° 45' 20.49"E	About 400 m north of B4, wall up to 50 m depth, about 100m from the buoy it turns to gentle sandy slope. Sandy bottom and rubble patches.	High coral cover ~55%, Poritidae dominance.	Low sedimentation and moderate turbidity.	Low sponge abundance, low algae, average fish
Ridge 1 5° 27' 10.76"S 123° 45' 8.82"E	Northern site on Hoga island, wall up to 50 m depth.	Coral cover ~26-33%, mostly foliose and massive species; Acroporidae, Poritidae and Gorgonians.	Low turbidity, low sedimentation, and high flow	High soft coral coverage, average sponge and average fish abundance.
Sampela 1 5° 29' 4.47"S 123° 45' 13.78"E	Southern site on Kaledupa island. Gentle sandy bottom, rarely reaches 16 m. Sandy bottom. Close to Bajau village (sea gypsy) and fish fences.	Coral cover ~5-17%, mostly massive species, the most common are Poritidae and Faviidae 60%	High sedimentation, turbidity, and flow.	High soft coral, sponge and algae abundance.
Sampela 2 5° 28' 59.76"S 123° 44' 54.75"E	Similar to Sampela 1, gentle sandy slope, large coral rubble patches.	Low coral cover 7%, coral assemblage similar to similar to Sampela 1.	High sedimentation and turbidity.	High soft coral, sponge and algae coverage. Low fish abundance.
Kaledupa 1 5° 28' 19.18"S 123° 43' 32.64"E	About 300 m from the shore and mangrove forest, presence of fish fences. Slope up to 50 m, sandy bottom.	Coral cover ~6-16%, Poritidae dominance, Acroporidae common. Gorgonians on the slope.	Low flow and average sedimentation.	High soft coral and sponge, high fish abundance.
Kaledupa Double Spur 5° 27' 56.16"S 123° 42' 14.29"E	Northern site on Kaledupa island, steep wall. Flat covered by coral rubble due to recent fish bombing.	Coral cover ~20-30%. Gorgonians on the slope.	Low sedimentation and average flow.	Moderate soft coral coverage low sponge, high CCA. High fish abundance.

2.3.2 Environmental factors

Data for environmental variables identified as influencing coral recruitment patterns in previous studies were collected between 2011 and 2013; abiotic and biological variables were measured between June–August 2011 by Powell *et al.* (2014) and data on fish abundance were collected as part of the ongoing monitoring program at the research station on Hoga Island between June–August 2013 (Operation Wallacea, unpublished data). The abiotic variables measured were: steepness of the reef slope, temperature, sedimentation, turbidity, water flow and depth, and the biological variables were: abundance of hard coral, soft coral, sponge, corallivorous fish, crustose coralline algae (CCA), non-coralline algae, and chlorophyll-α. For full details of how these data were collected see Table 2.2 from Powell *et al.* (2014).

Three variables, turbidity, temperature, and chlorophyll-α, were recorded by deploying a data logger set (RBR XR-420) on each reef slope at about 10 m for 24 hours at three different time periods, leaving at least 5 m between the deployment sites. Sediment traps were deployed on the reef and were collected after 3 days. Traps were brought to the laboratory where sediments were filtered using filter papers, dried at 100°C in an oven for at least 24 hours, separated into different size fractions, and then weighed (see English *et al.* 1997). Reef angle was measured on site using a protractor mounted on a spirit level and the inclination of the reef was measured by rotating the protractor from the horizontal position at 0°, verified by a spirit level, until it reached a parallel position to the reef. The gradient of the inclination was then read on the protractor. Water flow was measured by deploying a current meter (Valeport Model 106) for 24 hours at three different time periods.

Benthic composition was measured using 1 x 1 m^2 quadrats on the reef slope at approximately 10 m. The photographs of the quadrats were then analysed by Coral Point Count (Kohler & Gill 2006) using 100 random points distributed on the quadrat area. The main benthic categories identified were: sponges, hard coral, soft coral, crustose coralline algae, other non-coralline algae, rock, rubble, sand, and others.

Table 2.2 Ecological factors measured at each study site in the Wakatobi MNP (Indonesia). Data source: Powell *et al.* 2014.

Variables	Units	Sites								
		Buoy 1	Buoy 3	Buoy 4	Pak Kasim's	Ridge 1	Sampela 1	Sampela 2	Kaledupa 1	Kaledupa Double Spur
Angle per site	°	58.33 (+25.43)	64.17 (+14.63)	78 (+5.66)	66.67 (+19.92)	65 (+21.68)	46.67 (+31.09)	50 (+16)	52.67 (-20.7)	62.83 (+33.86)
Temperature	°C	27.37 (±0.21)	27.91 (±0.04)	27.82 (±0.37)	28.06 (±0.13)	27.66 (±0.13)	27.73 (±0.12)	27.67 (±0.32)	28.12 (±0.18)	27.92 (±0.21)
Turbidity	Standard turbidity units	1.45 (±0.69)	0.72 (±0.74)	0.76 (±0.63)	0.93 (±1.06)	0.19 (±0.33)	3.88 (±4.58)	2.92 (±0.98)	0.26 (±0.17)	0.78 (±0.38)
Chlorophyll-a	µg/l	0.25 (±0.13)	0.33 (±0.08)	0.26 (±0.14)	0.14 (±0.06)	0.33 (±0.08)	0.39 (±0.1)	0.39 (±0.12)	0.42 (±0.19)	0.26 (±0.08)
Sediment	g dry weight/day	0.162 (±0.029	0.235 (±0.202)	0.168 (±0.099	0.122 (±0.065)	0.112 (±0.022)	0.357 (±0.168)	0.322 (±0.051)	0.124 (±0.019)	0.109 (±0.047)
Flow	m/s	0.002 (±0.0084)	0.02 (±0.024)	0.018 (±0.023)	0.028 (±0.033)	0.04 (±0.046)	0.063 (±0.044)	0.056 (±0.038)	0.014 (±0.02)	0.038 (±0.041)
Hard Coral	% Cover	23.36 (±11.26)	31.45 (±16.74)	45.59 (±15.18	57.05 (±13.83)	35.7 (±13.62)	11.11 (±7)	7.73 (±5.43)	4.63 (±3.77)	27.49 (±14.86)
Soft Coral	% Cover	4.96 (±3.03)	1.38 (±1.79)	3.88 (±5.76)	11.11 (±3.9)	17.34 (±16.96)	6.39 (±5.44)	2.23 (±2.7)	22.13 (±10.15)	13.08 (±8.39)
Sponge	Abundance	48.67 (± 8.08)	65.33 (±7.32)	101 (±7.32)	48 (±5.7)	77.50 (±11.57)	103.67 (±25.97)	64.17 (±16.43)	51.17 (±6.09)	47 (±4.45)
CCA	% Cover	20.81 (±11.21)	27.34 (±24)	22.32 (±15.82)	15.12 (±6.72)	12.23 (±10.66)	14.38 (±15.53)	14.12 (±7.79)	12.15 (±6.79)	27.43 (±11.75)
Non-coralline algae	% Cover	4.18 (±2.44)	4.16 (±2.44)	2.37 (±2.44)	2.27 (±1.75)	6.86 (±5.02)	6.8 (±6.8)	1.12 (±4.83)	2.73 (±1.8)	2.97 (±2.44)
Corallivorous fish	Number/125 m^2	81.67 (±2.05)	81.67 (±2.05)	81.67 (±2.05)	121.17 (±3.5)	139 (±4.3)	55.17 (±1.05)	55.17 (±1.05)	157.83 (±4.8)	158.67 (±4.71)

Fish surveys were conducted by deploying a 50 m transect tape at 6 and 12 m depth. After leaving the tape for 5 minutes to allow the fish to acclimate (Fowler 1987), all fish within the transect area of 50 m length, 5 m wide and 5 m high, were recorded. Three replicate transects were conducted at each site and depth at times randomly chosen between 7 am and 4 pm. Due to logistic constraints it was not possible to carry out all the measurements at the same time at each site.

2.3.3 Coral recruitment survey

Artificial panels are widely used to study coral recruitment (e.g. Harriott & Fisk 1988; Tomascik *et al.* 1996; Dunstan & Johnson 1998; Fox 2004; Glassom *et al.* 2004; Adjeroud *et al.* 2007a; Green & Edmunds 2011). A previous study in the same locality as the present one tested various coral recruitment methodologies using artificial settlement plates (see Salinas De León *et al.* 2011). This previous study demonstrated that settlement rates to the back of terracotta tiles show no significant difference compared to those on natural substrata, and the authors have therefore suggested the tile settlement rates are a suitable surrogate for natural recruitment rates. Settlement panels can be deployed on the reef in an optimal position and orientation, and can also be easily removed for inspection.

My survey was conducted using terracotta tiles (20 × 10 × 0.7 cm) sourced locally. The tiles were deployed between July–August 2012 and collected in June–July 2013. Between 6 and 8 panels were deployed at each site, for a total of 120 panels at least 2 m from each other. A gap of about 2 cm was left between the panels and the reef to facilitate the recruitment (Harriott & Fisk 1987). Seventy-two panels were deployed at 6 m at 9 sites and 48 panels at 12 m across seven sites. Panels could not be placed at 12 m at the Sampela sites as the sites extends out to 11 m. Tiles were attached directly to the reef using a modified method described by Mundy (2000) and used by Salinas De León *et al.* (2011) (see Figure 2.2).

Panels were retrieved and taken in seawater to the laboratory to be labelled and analysed by examining while still fresh each tile under a dissecting microscope. The tiles were then left in a chlorine solution for 24 h to dissolve the organic material present on the surface (after Salinas De León *et al.* 2011). After the tiles were rinse in freshwater and air-drying, they were analysed again using a microscope to identify the skeleton of the coral recruits.

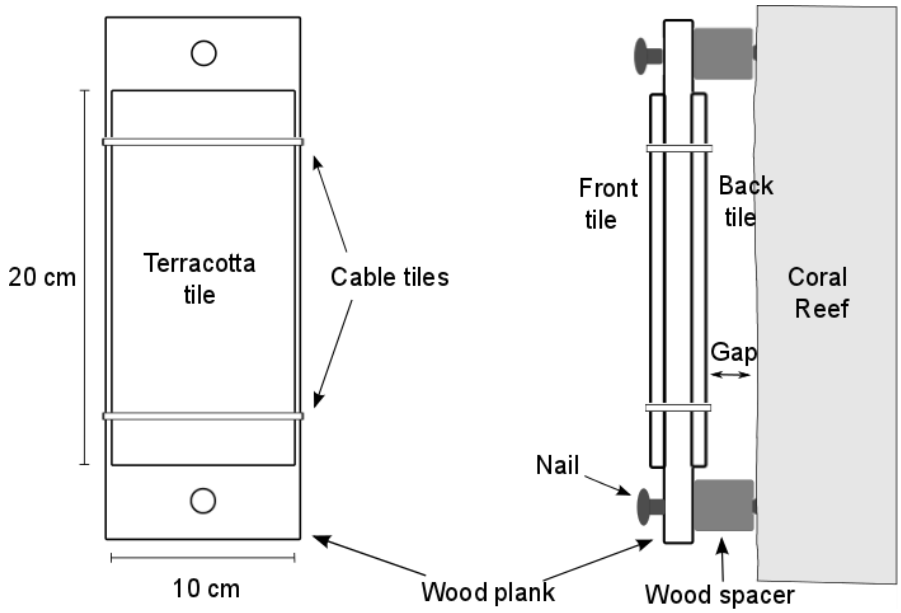


Figure 2.2 Scheme of the settlement panel and method of attachment to the reef. These panels were developed by Salinas De León and they have been used to monitor the recruitment rate in the Wakatobi MNP previously (From Salinas De León *et al.* (2011)

Recruits were identified to family level and wherever possible to genus level. Acroporidae, Pocilloporidae and Poritidae are all easy to identify in their early life history stage and have been described by English *et al.* (1997), Baird & Babcock (2000) and Babcock *et al.* 2003 (Figure 2.3). The remaining recruits that were either damaged or not identifiable were categorised as 'Others'. Recruit density was standardised as number of recruits per square meter (rec. m^{-2}).

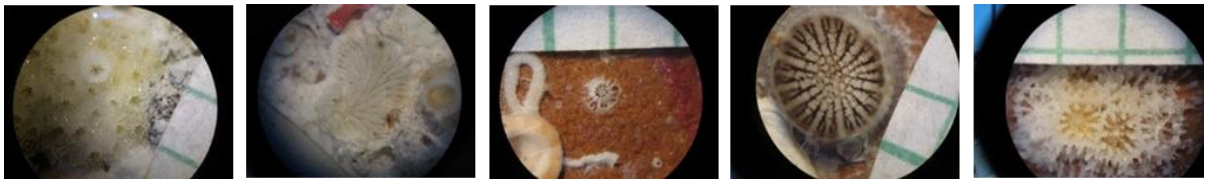


Figure 2.3 Coral recruits of different coral families observed with a dissecting microscope during the analysis of the settlement panels. Panels were bleached to remove the organic material and expose the skeleton of the recruit. The size of the polyp were estimated by positioning a piece of graph paper next to the coral recruit. Graph paper used in the digital images shows one line per two millimeters

2.3.4 Juvenile surveys

In this study juvenile colonies were those measuring <40 mm in diameter that were attached to the reef substratum and did not display the fractured surface characteristic of asexual recruits (see Edmunds 2000a). I used the same method as described by Salinas De León *et al.* (2011) to estimate juvenile abundance. The survey was conducted between June and August 2013.

Juvenile abundance was assessed at each site using 20 quadrats (0.5 × 0.5 m) along a 50 m transect at 6 and 12 m depths. At the two Sampela sites the survey was conducted only at 6 m. Juveniles were photographed underwater and identified to genus level. Juvenile density was standardised to abundance per square meter (juv. m^{-2}).

2.3.5 Data analysis

Coral recruit and juvenile data were analysed within the software package PRIMER v.6 (Plymouth Marine Laboratory, UK). Recruitment data were root-squared transformed to normalise the data and analysed with Jaccard resemblances. This metric considers the presence or absence of the category and is used to deal with datasets containing a large number of zeros. Individual panels were considered as replicates within the sites. Juvenile abundance data were root-squared transformed and the similarity matrix was calculated using the zero-adjusted Bray-Curtis coefficient (Clarke *et al.* 2006). Bray-Curtis is commonly used for biological data and works with non-metric similarities (Anderson & Willis 2003). Constrained canonical analysis of principal coordinates (CAP) was used to examine differences in ecological variables between the sites relative to differences in community structure. Differences across sites were ascertained with 9999 random permutations on the Bray-Curtis matrix and the result was plotted in a two-dimensional plot. The correlation between the environmental factors and the CAP axes was measured by Spearman's rank correlation and visualised in multivariate space with vectors. The length of each vector represents the importance of the specific variable in differentiating the sites, while the direction shows a positive or negative correlation. The circle shows the threshold for a correlation of 1.

A non-parametric permutational multivariate analysis of variance (PERMANOVA) based on the resemblance matrix using 9999 random permutations was used to analyse the spatial variability in recruitment and juvenile abundance across all sites. This method was used because of its flexibility, as no assumptions need to be made about the data distribution and it can be used with small sample sizes (Anderson 2001). Two fixed factors were used: site (nine levels) and depth (two levels).

Diversity indices were used to examine the diversity present at each site based on the number of the genera present and the abundance of each genus. Juvenile diversity differences between sites and depth were measured with three different diversity indices: the Shannon-Wiener Index (H'), richness with Margalef Index (d), and evenness with Pilou's Index (J'). Multidimensional scaling (MDS) was used to explore any differences in coral assemblages between sites.

Distance-based multiple linear regression (DistLM) allows any correlation between multivariate data and single and combinations of predictor variables, such as environmental factors (Mc Ardle & Anderson 2001), to be identified. Predictors can be categorical or continuous and data normality is not a requirement. The variables I used were first analysed with a Draftsman Plot to identify any correlations. Sedimentation and turbidity were found to be highly correlated and therefore turbidity was excluded from the analysis. The remaining factors were normalised by ranking. I chose to conduct the analysis with the *Best* procedure, which identifies the best fitted model for *n*-variables, using the AIC_c criterion selection. AIC_c is a modification of Akaike's (1973) coefficient AIC that considers all the possible permutations and gives the most parsimonious model for each number of predictor variables; lower AIC values correspond to a best fit model, however this criterion is penalised when considering a high number of variables (Symonds & Moussalli 2011). The AIC_c formula is modified from the AIC formula by the addition of a correction factor that adjusts it in order to be more efficient in all cases when the number of samples is small compared to the number of predictor variables, such as in the present study.

The DistLM test output gives the best-fitted and the overall best model with the best R^2 and lowest AIC_c. Results of the DistLM*best* analysis were visualised on a two-dimensional plot using a Distance-based redundancy analysis (dbRDA), where the axes are correlated to the fitted values. Spearman's rank correlation was used to explore the relationships between the samples and the principal coordinate axes.

2.4 Results

2.4.1 Site differentiation

The results of the CAP showed differences in the ecological characteristics between the sites. The factors that were different between sites were coral cover, site steepness, chlorophyll-α concentration, and sedimentation rate. The sites can be grouped based on similarities in their ecological characteristics: Ridge 1, Kaledupa Double Spur, Buoy 1 and Pak Kasim's are characterized by high hard and soft coral abundance, fish abundance, and algal abundance; Sampela 1 by high abundance of soft corals, algae and high current flow; Kaledupa and

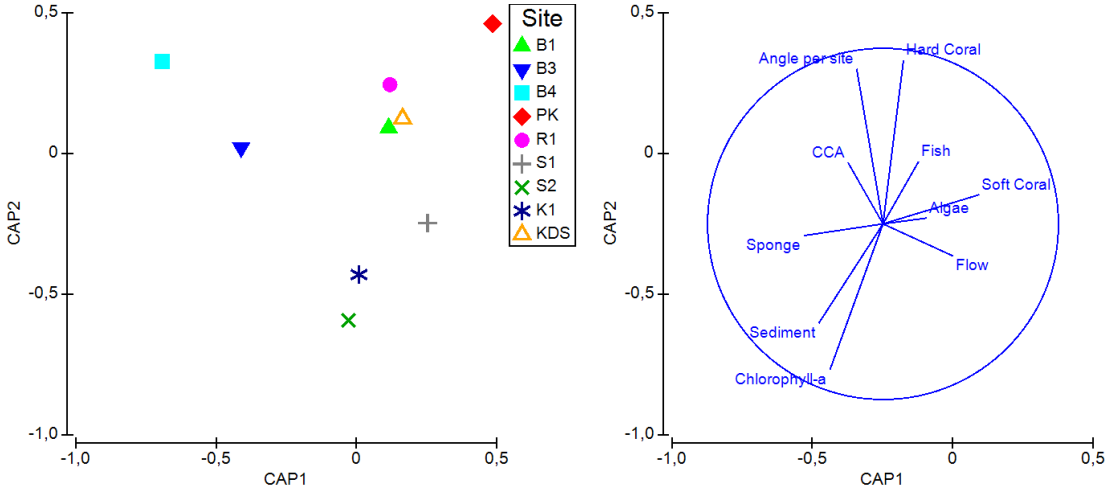


Figure 2.4 Results of the Canonical Analysis of Principal coordinates (CAP) showing the differences in physical and biological characteristics between sites in the Wakatobi MNP. The differences between sites and the correlation with the environmental factors are shown separately. Axes are the combination of the principle components that give them more variations. The spread of the samples shows the direction of the higher variance existent between the samples. In the graph on the right hand, the direction and the length of the vectors represent their correlation to the samples. Only factors correlated to the sample with Spearman's r>0.2 are shown in the graph. Algae category pooled data of all the algal groups investigated.

Sampela 2 by high current flow and high levels of chlorophyll-α; and Buoy 3 and Buoy 4 by high CCA abundance and steeper slopes (see Figure 2.4).

2.4.2 Coral recruit surveys

A total of 118 out of 120 panels were retrieved; 70 at 6 m and 48 deployed at 12 m; the two missing panels were lost from B1 and PK. The total number of recruits across all sites was 317; 181 at 6 m and 136 at 12 m. The number of recruits found on a single panel ranged from 0 (at least one tile without recruits was found at each site) to 19 (found at B1) at 6 m, and from 0 (tiles without any recruits were found at all sites) to 23 (at R1) at 12 m.

The overall mean number of recruits across all sites with data from 6 and 12 m pooled was 112.97 (±11.16 SE) rec. m^{-2}; the maximum mean was 200 (±51.89 SE) rec. m^{-2} at B1 and the minimum was 12.50 (±4.23 SE) rec. m^{-2} at S1. At 6 m the overall mean recruit abundance on tiles was 64.08 (±9.69 SE) rec. m^{-2}. The mean recruit abundance ranged from 135.71 (± 70.26 SE) rec. m^{-2} found at B1 to 6.25 (±4.23 SE) rec. m^{-2} recorded at S1. At 12 m the mean recruit abundance was 70.78 (±13.05 SE) rec. m^{-2}. Only at two sites, B4 and K1, recruits abundance was higher at 12 m than at 6m. The values ranged from 110.71 (±48.84 SE) rec. m^{-2} at PK to 39.29 (±45.83 SE) rec. m^{-2} at R1 (Figure 2.5). Overall, 64.15% of the recruits found had settled on the back side of the panels.

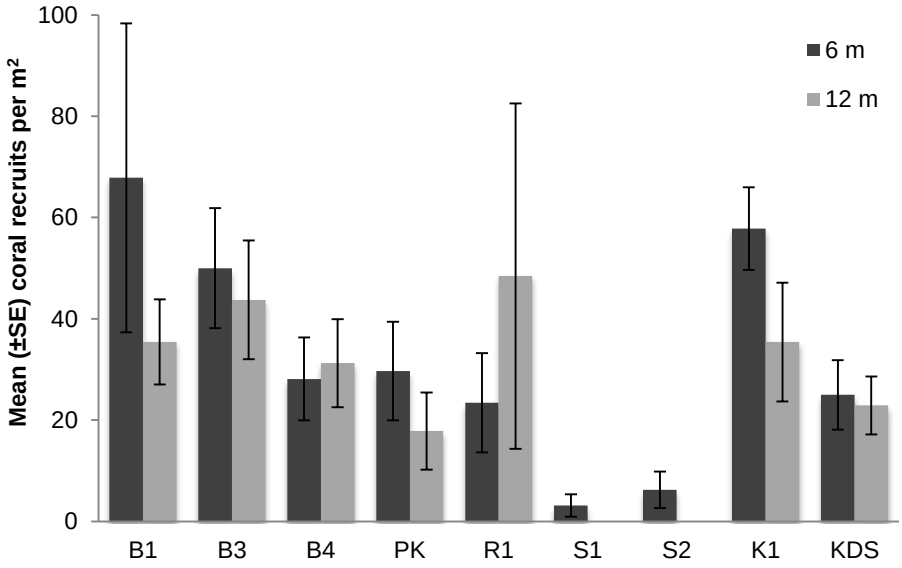


Figure 2.5 Mean (± Standard Error) number of recruits per m^2 found on settlement panels deployed at 6 m and 12 m from July-August 2012 to June-July 2013 at nine study sites in the Wakatobi MNP

The overall recruit abundance was significantly different across sites (PERMANOVA, df=8, P=0.02), but not between depths. When looking at the assemblage composition, no significant differences in coral recruitment were found across sites (PERMANOVA, df=8, P>0.05) or between depths (PERMANOVA, df=7 P>0.05). Significant differences were found in the composition of the recruit families between the front and the back sides of the tiles, but not across depths (Table 2.3).

Table 2.3 Result of the PERMANOVA analysis for the spatial distribution of coral recruits between sites, depths and sides of the settlement panels deployed at 6m for one year

Factor	df	SS	MS	Pseudo-F	P
Overall abundance					
Site	8	15176	1897	4.9123	**0.0216**
Side	1	1004.2	1004.2	2.9647	0.1145
Depth (Site)	7	2680.9	383	0.9721	0.4546
Site*Side	8	6001.5	750.2	2.2201	0.1440
Depth (Site)*Side	7	2353.7	336.2	0.8534	0.5444
Recruit assemblage					
Site	8	23813	2976.6	1.0887	0.3963
Side	1	15042	15042	13.1650	**0.0005**
Depth (Site)	7	13133	1876.1	1.6602	0.1145
Site*Side	8	15097	1887.1	1.6643	0.1108
Depth (Site)*Side	7	7910.1	1130	0.8891	0.6146

Of the total recruits, 73.6% could be identified to family level and were from five main families: Acroporidae, Pocilloporidae, Poritidae, Agariciidae and Faviidae (see Table 2.4). The differences in the distribution of coral families between sites are shown in Figure 2.6; no obvious patterns were found in the distribution of the coral recruits between sites and depths.

Table 2.4 Percentage of total coral recruits from different families across all sites and at two depths (6 m and 12 m), and percentage of orientation preference of overall coral recruits.

Coral families	Overall	6 m	12 m	Orientation	
				Back side	Front side
Acroporidae	8.50	8.8	8.1	44.4	55.6
Agariciidae	4.71	5.5	3.7	70.4	29.6
Faviidae	15.72	11.5	21.3	42.6	57.4
Pocilloporidae	25.47	29.7	19.9	33.3	66.7
Poritidae	19.18	19.8	18.4	0.0	100.0
Others	26.42	24.7	28.6	16.7	83.3

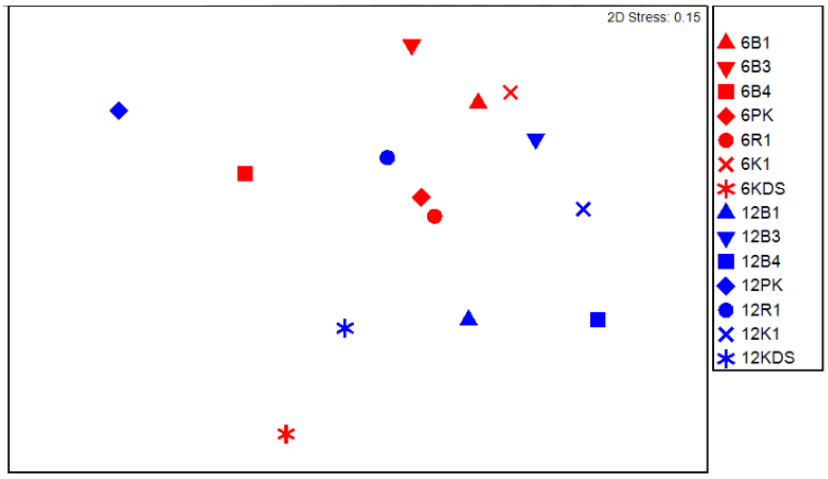


Figure 2.6 Unconstrained non-metric multidimensional scaling (nMDS) showing the differences in the distribution of coral recruit families across 9 sites and two depths in the Wakatobi MNP. The legend describes the depth at which the panels were deployed (6 or 12 m) followed by the site. The distance between the points reproduces the distances on the Bray-Curtis matrix on a bidimensional plot, while the stress value estimate how well the configuration fit to the observed distance matrix, where 0.15 is an acceptable value.

Pocilloporidae was the most common family in the overall recruit assemblage and it was also the most abundant at both depths. In addition, recruits belonging to the Pocilloporidae were more common on the upper side of the panels across all sites and depths, while Faviidae recruits were never located on front sides.

DistLM*best* analysis explored the correlations between the coral pattern and the ecological factors distruibution across sites. The result of this analysis provided only weak evidence to support the predictor variables being responsible for the overall variability in recruit distribution as they each explained only a small amount of the variability (DistLM*best*, AICc= 1439.6, R^2=0.11). The best model explaining the spatial distribution for the overall abundance of recruits across sites included just one predictor variable, which was flow. An additional DistLM*best* analysis was performed, where settlement on the front and back side of the panels was analysed separately. This was conducted in order to find which ecological factors most affected the larvae in choosing the orientation. The best model only explained 8% of the variation in the coral recruits on the front side of the panels across all sites and depths. The variables responsible were flow (4.2%), CCA (1.5%) and soft coral (1.3%) (AICc=785.17, R^2=0.08). However, the predictor variables identified in the best model as significant for the back side of the tiles were flow (5.5%) and chlorophyll-α (0.8%), which together explained only 7.43% of the variation in recruit distribution (AICc=821.16, R^2=0.07) (Table 2.5).

Table 2.5 Summary table of the result of the DistLM*best* analysis for coral recruits. Each recruit pattern was explained by a different combination of variables, however they all explain just a small amount of the overall variability. The table show the AICc value, where ower values show a better fit of the data to the model; the percentage of the overall variability explained by the predictors and the contribute of each predictor; pseudo-F and P are the results of the PERMANOVA test.

Response	AICc	% Total variation explained	Predictors	% Variability explained by each predictor	Pseudo-F	P
Overall coral recruit abundance	1439.60	11	Flow	11	30.37	0.1136
Total recruits abundance on the front sides	785.17	8	Flow	4	52619	**0.0026**
			CCA	1.5	19.08	0.1392
Total recruits abundance on the back sides	820.83	7	Flow	6	68.25	**0.0009**
			Chlorophyll-α	1	10.02	0.3950

2.4.3 Coral juvenile surveys

A total of 806 juveniles were recorded across all sites and depths: 451 at 6 m and 355 at 12 m (see Figure 2.6). The overall mean juvenile abundance was 9.63 (±0.24 SE) juv. m^{-2} across all sites and depths, and this value ranged from 4.20 (± SE) juv. m^{-2} at S1 to 16.40 (± SE) juv.m^{-2} at K1.

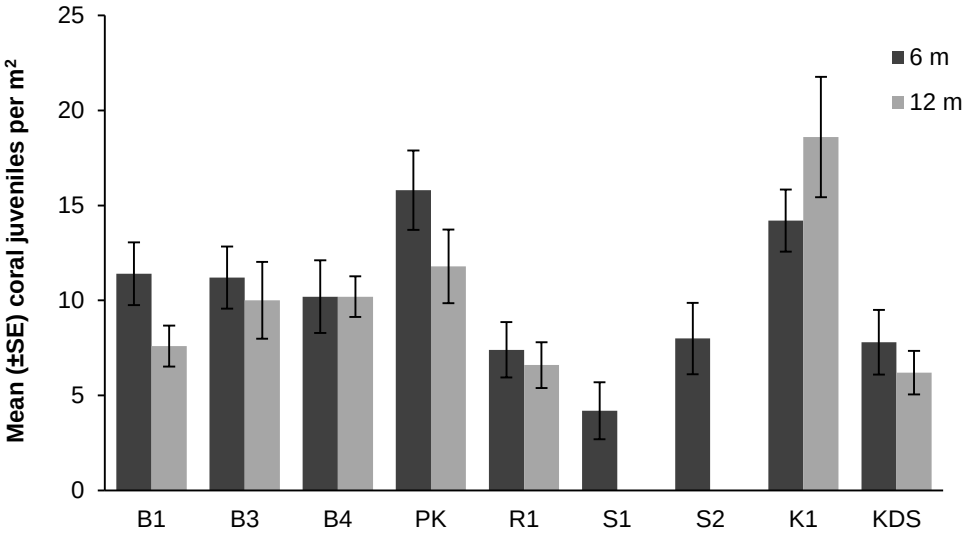


Figure 2.7 Mean (± Standard Error) coral juvenile abundance per m^2 at each site using 20 quadrats of 0.5 m^2 deployed along a 50 m transect deployed at 6 and 12 m at nine sites in the Wakatobi MNP

There was significant variation in the abundance of coral juveniles across sites (PERMANOVA, df=8, P=0.0015) and depths (df=7, P=0.01) (Table 2.6).

Table 2.6 Result of the PERMANOVA analysis of the spatial variation in coral juvenile abundance between nine sites and depths (6 and 12 m).

Factor	df	SS	MS	Pseudo-F	P
Site	8	7235.8	904.5	1.8867	**0.0061**
Depth	1	2173.9	2174	4.5346	**0.0088**

A total of 49 genera from 15 families were found; one family was found at only three sites at 12 m, two families were present at eight sites and six families were recorded at all the sites (see Table 2.7).

The total number of juvenile families recorded across locations ranged from 7, found at Sampela 1 at 6 m, to 12, found at Kaledupa 1 at both depths. The five most common families represented 71.22% of all the juveniles recorded: Agariciidae 20.84% (2.02 m^{-2} across sites), Faviidae 19.85% (1.96 m^{-2}), Poritidae 13.77% (1.3 m^{-2}), Pocilloporidae 12.16% (1.17 m^{-2}) and Acroporidae 4.59% (0.44 m^{-2}) (see Figure 2.7).

Table 2.7 Diversity of juvenile corals at the nine study sites in the Wakatobi MNP. The table report the overall values by site and in the row below the values separated by depth. S= species number; N= total abundance, H'= Shannon-Wiener; d= Margalef index; J'= Pilou's evenness. Data were not collected at 12 m at Sampela 1 (S1) and Sampela 2 (S2) for 12 m

Sites	Families		Genera		Abundance		H'		d		J'	
	Overall		Overall		Overall		Overall		Overall		Overall	
	6 m	12 m	6 m	12 m	6 m	12 m	6 m	12 m	6 m	12 m	6 m	12 m
B1	11		26		95		2.78		5.49		0.85	
	9	10	20	17	57	38	2.60	2.59	4.70	4.40	0.87	0.91
B3	10		25		106		2.85		5.15		0.88	
	9	9	18	19	56	50	2.66	2.67	4.22	4.60	0.92	0.91
B4	11		24		102		2.83		4.97		0.89	
	9	10	18	20	51	51	2.65	2.73	4.32	4.83	0.92	0.91
PK	11		26		138		2.70		5.07		0.83	
	10	9	18	18	79	59	2.54	2.49	3.89	4.17	0.88	0.86
R1	12		20		70		2.67		4.47		0.89	
	11	11	16	13	37	33	2.53	2.30	4.15	3.43	0.91	0.90
S1	7		11		21		2.28		3.28		0.95	
	7	-	11	-	21	-	2.28	-	3.28	-	0.95	-
S2	11		18		40		2.67		4.61		0.92	
	11	-	18	-	40	-	2.67	-	4.61	-	0.92	-
K1	13		28		164		2.84		5.29		0.85	
	12	12	20	25	71	93	2.70	2.70	4.46	5.29	0.90	0.84
KDS	11		19		70		2.45		4.24		0.83	
	9	9	12	12	39	31	2.22	2.21	3.00	3.20	0.89	0.89

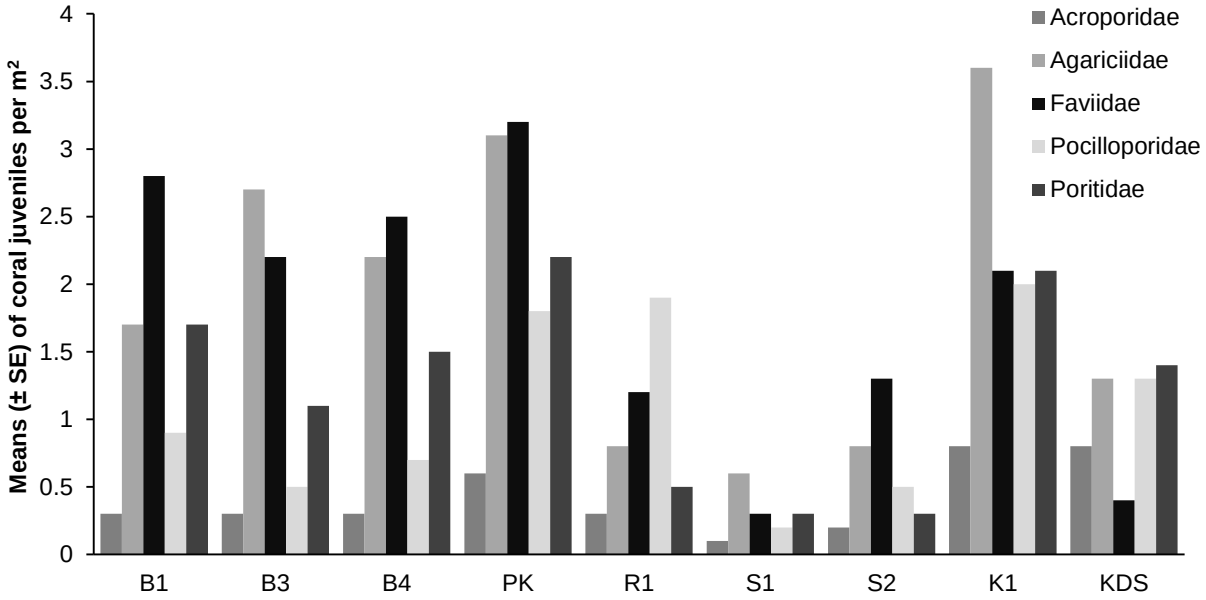


Figure 2.8 Mean (± Standard Error) abundance of coral juvenile families per m^2 at nine sites in the Wakatobi MNP. Data from 6 and 12 m depths were pooled

Table 2.8 Result of the PERMANOVA analysis comparing the assemblage composition of coral juvenile families across nine sites and two depths, 6 and 12 m (nested in site)

Families	Site					Depth				
	df	SS	MS	Pseudo-F	P	df	SS	MS	Pseudo-F	P
Acroporidae	6	1082.7	180.45	12.8310	0.0082	7	98.5	14.06	0.1247	0.9965
Pocilloporidae	6	3435.7	572.61	4.3399	0.0393	7	923.6	131.94	0.5524	0.7936
Poritidae	6	2996.5	499.42	1.4636	0.3248	7	2388.6	341.23	1.3242	0.2372
Agariciidae	6	7263.2	1210.5	1.6944	0.2411	7	5001.1	714.45	2.4519	**0.0172**
Faviidae	6	7217.4	1202.9	1.9791	0.1937	7	4254.5	607.79	2.1543	**0.0348**

Few families showed significant spatial variability across sites or among depths (see Table 2.8). Differences in the juvenile coral assemblage were found among depths (see Figure 2.9); the sites at 6 m were characterised by a higher abundance of all the main coral families, while sites at 12 m.

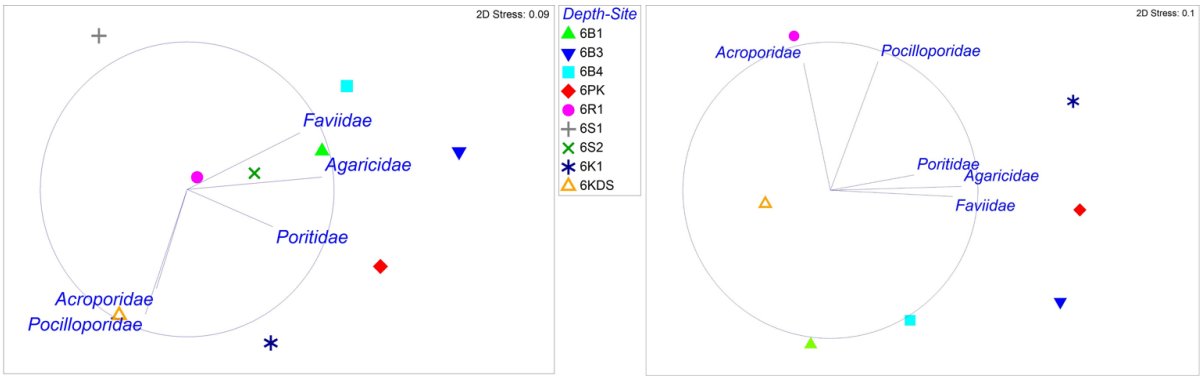


Figure 2.9 Multidimensional scaling (MDS) plot exploring the difference in the distribution of juveniles of the five main families (Pocilloporidae, Acroporidae, Poritidae, Faviidae, and Agariciidae) at 6 m (left hand graph) and 12 m (right handgraph) across sites at the Wakatobi MNP

The result of the DistLM*best* analysis showed that five predictor variables were responsible for the distribution of coral juveniles across sites, but they only explained 6.5% of the spatial variability (see Figure 2.9). These predictors were water flow rate (1.94%), temperature (1.65%), soft coral abundance (1.57%), algal abundance (1.54%) and CCA abundance (1.54). Three more variables were found to have a weak significant correlation with the juvenile variability, although they were not included in the best model; they were corallivorous fish abundance (1.54%), sediment rate (1.50%) and sponge abundance (1.25%).

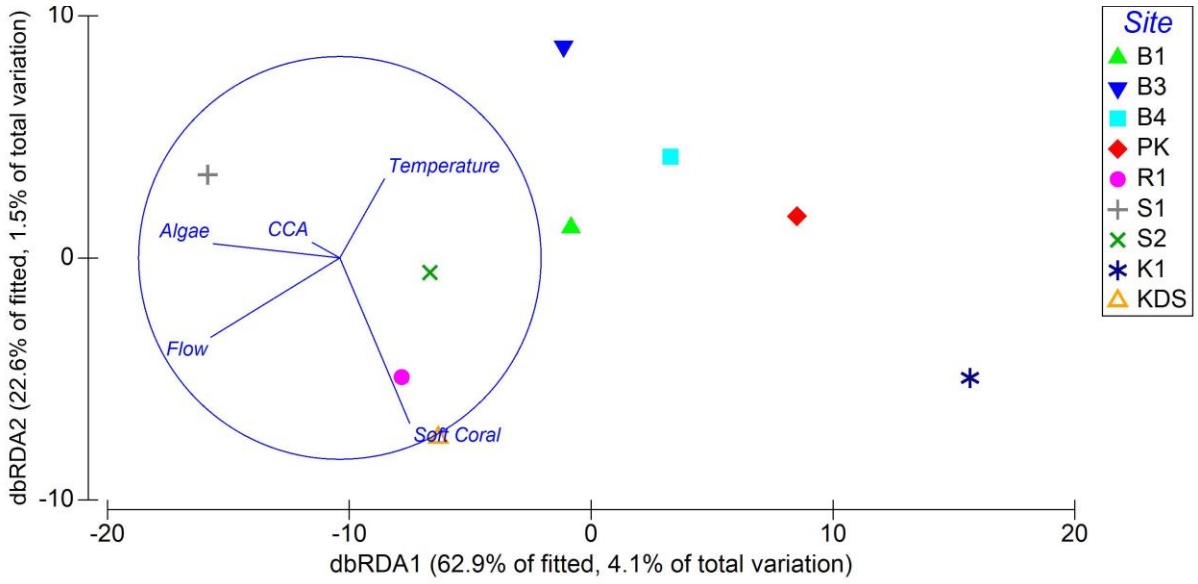


Figure 2.10 Distance-based redundancy analysis (dbRDA) plot visualising the fitted model for coral juvenile abundance pattern with the lowest AICc

Table 2.9 Summary of the result of the DistLM*best* analysis at family level for coral juveniles. Each coral family pattern was explained by a different combination of variables. For every group of coral juvenile family or single families, listed in the 'Response' column, is showed the model that fit better with low AICc value and the percentage of juvenile distribution explained by the model. Predictor column lists the factors included in the best model and their contribution to the overall model

Response	AICc	% Total variation explained	Predictors	% variability explained by each predictor	Pseudo-F	P
Main coral juvenile families abundance			Temperature			0.0032
			Sedimentation			0.0049
			Quadrat angle			
			Fish			
Acroporidae	1488.8	2.5	Fish	2.5	8.18	0.0038
Agariciidae	1833.9	7.1	Temperature	3.3	10.73	0.0012
			Algae	3.2	10.50	0.0001
			Flow	2.7	7.36	0.0077
Faviidae	1023.8	8.4	Flow	3.6	11.83	0.0002
			Soft coral	0.4	149.19	0.2238
			CCA	0.2	1.55	0.2146
			Fish	0.1	2.86	0.0875
Pocilloporidae	1733.4	4.7	Soft coral	4.7	15.86	0.0002
Poritidae	1763.0	3.6	Flow	2.5	8.14	0.0046
			Temperature	0.1	2.98	0.0850

The results of the DistLM*best* analysis for the five main families and the factors explaining their distribution are shown in Table 2.9. The best model for each analysis includes many variables, but never explains more than the 8% of the spatial variability across sites.

2.5 Discussion

In this chapter I explored the spatial variability in coral early life history stages and the factors that explained these patterns in the Wakatobi MNP. The population dynamics of young corals are very important in maintaining reef health (Babcock & Mundy 1996; Ritson-Williams *et al.* 2009a). Physical and biological factors are thought to drive the recruitment process at local scales and, especially in the post-settlement phase, these factors influence the abundance and patterns of coral recruits and juveniles, which subsequently shapes the adult population (Miller & Weil 2000; van Woesik & Jordán-Garza 2011). However, few studies have examined the interaction of multiple factors at different stages of coral recruitment (but see Raimondi & Morse 2000; Davies *et al.* 2013; Trapon *et al.* 2013a). I found significant variability in recruit abundance across sites, but not between depths, and there was a preference for settling on the back side of the panels; however, no single predictor variables I measured adequately explained the distribution and abundance of coral recruits. Coral juvenile abundance and assemblage composition were significantly different across sites and depths, and a shift in assemblage composition occurred between the two life history stages. However, once again the interaction of several variables only explained a small amount of the variability.

My results showed small-scale variability in coral recruit abundance between sites with different habitat characteristics but were unable to identify any factor or combination of factors that explain the variability. The results suggest that other factors not considered here may explain the variability and should be examined in the future, such as nutrients availability. The identification of the main factors influencing coral recruitment will be important in planning future specific management actions at each site in order to increase the recruitment rate, especially in sites with low adult coral abundance.

2.5.1 Role of ecological factors in coral recruitment

The overall coral recruitment rate was 67.5 (± 7.79) rec. m^{-2}, which is lower than rates reported at other sites in the Indo-Pacific area (Dunstan & Johnson 1998; Reyes & Yap 2001; Quinn & Kojis 2008; Green & Edmunds 2011; Penin & Adjeroud 2013; Ho & Dai 2014); the mean recruit abundance at each site varied widely and the spatial variability was significant across

sites. Despite this there was no significant difference in recruit abundance among depths, but at Kaledupa recruits were slightly more abundant at 6 m than in deeper waters, which is consistent with earlier studies where recruit abundance has been negatively correlated with depth (e.g. Quinn & Kojis 2008; Ho & Dai 2014).

The recruit families identified were found at most of the sites, although the taxonomic composition was highly variable; Pocilloporidae was the most abundant family at all the sites. This family is also dominant in other areas of the Coral Triangle, such as in Komodo (Fox 2004) and in the Philippines (Reyes & Yap 2001), but not in Bunaken (Schmidt-Roach *et al.* 2008).

It was not possible to identify a dominant factor or a combination of factors that explained the variability found across sites by modelling the overall recruit abundance; none of the twelve variables analysed were included in the best model and each individual variable explained only a very small proportion of the recruit variability. In comparison to Salinas De León *et al.* (2012a) study, I did not observe the correlation between coral coverage, sedimentation rate, predation and recruitment rate found by, but I also found that overall sites characterised by high coral cover also had high recruitment rates.

The absence of a correlation between coral cover and recruitment rate has also been found in other studies in the Pacific area and it has been proposed that other processes regulate recruitment (Quinn & Kojis 2003; Fox 2004; Penin & Adjeroud 2013), for example mortality in the early days following settlement. High mortality occurs within the first 24 hours after coral recruit settlement. Martinez & Abelson (2013) found that approximately 44% of coral recruits do not survive the first day and only the 8–13% of the corals survive the first three months after settlement, however these values are influenced by local factors and different processes (Wilson & Harrison 2005). Most recent investigations on recruitment have examined populations that have already been affected by local disturbances, which may explain the lack of correlation between coral cover and recruitment rate.

Recruitment in the Wakatobi occurs throughout the whole year, although the main spawning peak is thought to be between November and March, during the wet season (Salinas De León *et al.* 2012a). It is likely that if I had collected the settlement panels immediately after the peak season I would have found higher recruitment rates and potentially a correlation with the coral cover. Salinas De León *et al.* (2012a) suggested that sedimentation and predation explained the distribution and orientation of the recruits in the Wakatobi; the authors only found a few

recruits on the front side of their panels, which were covered by turf algae and sediment and easily accessed by grazers and predators. In my study I found 36% of recruits on the front side of the panels; in addition two families showed a consistent preference with respect to orientation: Pocilloporidae settled mostly on the front side of the panels, Faviidae was only found on the back side; the other families had a preference for the back side. The higher abundance of recruits found on the exposed surface of the panels might be explained by a decline in predator abundance since the study by Salinas De León *et al.* (2012a) carried out between 2007 and 2009. This is supported by a recent study on fish populations in the Wakatobi conducted by Curtis-Quick (2013), who reported a decline of fish abundance at all my study sites between 2001 and 2012.

To date only a few studies have reported recruits settling on the front, or upper, side of panels (e.g. Nakamura & Sakai 2009), and usually recruit abundance is too low to be considered relevant (e.g. Harriott & Fisk 1988; Kuo & Soong 2010; Salinas De León *et al.* 2012a). However, some studies have found patterns consistent with my study; for example Fox (2004) reported differences in preference for orientation in different families. In her study Acroporidae preferred to settle mostly on upper surfaces while Pocilloporidae was mostly found in the gap between panels and the reef. Recently, Ho & Dai (2014) found that 53% of the recruits settled on the top (front) side of the panels and this preference was negatively correlated with depth. They suggested that the driver of recruit distribution was likely to be light availability, which has also been proposed in similar studies (Rogers *et al.* 1984; Babcock & Mundy 1996; Adjeroud *et al.* 2007a). However in my study, turbidity, strictly connected to light availability, was not identified by the DistLM*best* as a potential predictor of coral pattern variability, suggesting that light might have a small or none role.

The presence of other benthic organisms is likely to influence recruit distribution. In my survey, the back side of the panels were covered by benthic organisms such as ascidians, bryozoans, sponges, molluscs and CCA. Some of these organisms, like CCA, have been previously found to increase the recruitment rate (Raimondi & Morse 2000; Price 2010), while others are competitors for space and can grow faster than the recruits (Birkeland 1977; Birrell *et al.* 2005; Vermeij 2005; Box & Mumby 2007; Benzoni *et al.* 2011). On the back side of the panels I observed recruits overgrown by CCA and sponges, similar to previous studies (e.g. Wilson & Harrison 2005; Vermeij 2006). When recruit skeletons were found completely covered by other organisms, it was not possible to assess if the recruits had died before or after being overgrown as the skeleton was only detected after bleaching the panels for examination. An additional

study is recommended to identify the causes of death of these corals in order to assess the effects of the individual disturbances on the recruit population.

In general, considering the overall disturbance present at each site, an explanation for the correlations between physical and biological variables and recruit distribution found by Salinas De León *et al.* (2011, 2012b), but not observed in my study, could be that the two reef systems used in the previous study represented two very different habitats; one reef had been heavily affected by disturbance while the other was moderately healthy. In my study I included more reefs across a broader environmental gradient.

In conclusion, I found that recruit abundance was variable across sites, but not depth, and that the ecological variables considered in this study did not explain very much of the variation in coral recruit abundance between sites. The orientation of the recruits suggests that future studies should include other variables in the analysis, such as nutrients availability (Weber *et al.* 2006; Risk 2014).

2.5.2 Coral juvenile abundance patterns across sites and depths

The overall density of juveniles across sites was among the lower values previously found in the Indo-Pacific (Roth & Knowlton 2009; Salinas De León *et al.* 2012a) and it was variable both with respect to abundance and in family assemblage composition across sites and depths. The juvenile population diversity was high at most of the sites. Low diversity was found at Sampela 1, however, the 21 juveniles found at this site belonged to 11 different genera, suggesting that despite the low coral abundance, diversity was still moderate in the area.

As expected, the density of juveniles was much lower than the density of recruits; it changed from 112.97 (±11.16 SE) m^{-2} to 9.63 (±0.24 SE) m^{-2}, presumably as a result of mortality (Penin *et al.* 2010; Salinas De León *et al.* 2012a). However, this decline will be an underestimate as the colonies counted in the juvenile surveys will have settled in different years and they do not represent the survival of a unique year of recruitment, as juveniles probably included colonies up to 2–4 years old, depending on the growth rate of each species (Schmidt-Roach *et al.* 2008). I found some evidence for differential mortality based on the variation in taxa assemblage composition, the dominant family being Pocilloporidae at the recruit stage with Agariciidae and Faviidae more common at the juvenile stage. Similar changes in coral assemblages in early life history stages have also been reported from Moorea (Penin *et al.* 2010) and Fiji (Quinn & Kojis 2008). This shift can be explained by the characteristics of the Pocilloporidae family. This family has long-lived larvae and a high settlement rate, which is then followed by high

mortality in the post-settlement phase. Other families are likely to produce fewer larvae and grow slower, but seem to be more resistant to disturbance.

When modelling the overall juvenile abundance, the interaction of different variables again explained only a small portion of the variation in the dataset, and no variable was found to be particularly important. A similar result was found when I analysed the five main families individually, where more predictor variables explained the variation in pattern. However, these variables differed for each family and the total amount of variability explained was always lower than 6.5%, with most of the variability being unexplained. The absence of a higher correlation between the juvenile variability and the factors analysed might be due to the variable measurements. Data on the ecological factors, as described in the methods section, were collected over a limited time period and these values do not consider temporal variation, such as seasonal fluctuations (likely to affect temperature and sedimentation), and inter-annual variation. For example, during the wet season, after heavy rains sedimentation on the reef tends to increase as sediments are transported from inland to the reef. Moreover, measurements were taken just at one intermediate depth between the two depths used in this study for coral surveys, so the final data analysis was conducted by compiling the data from two different depths at the same sites. However, in order to even out some of this variability, the environmental variables were measured at different days and times.

In conclusion, I found that there was significant variation in the abundance pattern of corals at early life histories across sites, but it was not possible to find an overall model that explained the variation in density and the shift in taxonomic composition. Light availability was not included in this study and it is likely is not important in determining the coral recruitment pattern, although based on previous research it could have a role in recruit distribution (Mundy & Babcock 1998b; Ho & Dai 2014). Furthermore, to better analyse the relationship between young coral abundance patterns and local environmental factors, more measurements of the variables should be conducted throughout the year to assess their variation.

Chapter 3 Temporal variability in coral recruitment in the Wakatobi Marine National Park, Indonesia

3.1 Abstract

Temporal variation in physical and biological factors, such as temperature and predation, can have strong effects on the abundance of shallow water coral fauna. Scleractinian corals have a primary functional role on coral reef and any variation in coral cover might influence recruitment rates, which are an important driver of population maintenance, for some coral species. Understanding temporal variation in coral recruitment patterns is important for effectively managing coral reefs. The main goal of the study described in this chapter was to investigate temporal variation in coral recruitment rates over a two-year period in the Wakatobi Marine National Park (Indonesia) at 1) sites with different environmental characteristics; and 2) two reef systems with different environmental conditions (Hoga and Sampela) over a seven year period, pooling data from previous study by Salinas De León *et al.* (2012a) in order to detect any temporal patterns in recruitment rates. In addition, surveys on juvenile corals were conducted at the same sites in order to assess any variation in assemblage composition between the recruit and juvenile stages. There was no significant temporal variation in coral recruitment patterns between sites with different environmental characteristics ($df=1$, $P>0.05$), however spatial variation was evident ($df=1$, $P=0.003$) and differences in assemblage composition between sites was consistent between years in the two-year study across many sites ($df=1$, $P=0.007$). In the seven-year dataset at the two reefs, temporal and spatial variation in recruitment rate and assemblage composition was found ($df=8$, $P<0.005$). The annual variation in recruitment rates between the two reefs was not consistent; Hoga had higher recruitment rates than Sampela in all the years of the study. Temporal and spatial variability was found in juvenile abundance between reefs ($df=3$, $P<0.05$, and $df=1$, $P<0.05$) and there was a shift in assemblage composition over the course of the study. These results represent useful information to reef management in order to foreseen and prevent abnormal changes in the coral population, and allow the identification of the areas more important for coral recruitment.

3.2 Introduction

In recent decades climate change, ocean acidification, and localised anthropogenic activities, such as fishing, industrial development and tourism, have affected marine ecosystems

worldwide (Hoegh-Guldberg *et al.* 2007). These activities produce ecosystem changes that can lead to the degradation of habitats and loss of diversity. Changes in ecosystems can affect not only local human communities, whose livelihoods are often based on marine resources, but also the global economy (Burke *et al.* 2012). For these reasons, it is important to understand changes that are occurring in the marine environment by monitoring key species and investigating the factors that affect their survivorship in order to conserve threatened ecosystems (Bellwood *et al.* 2004; Hoegh-Guldberg *et al.* 2007).

Environmental variation in marine ecosystems can cause changes in the abundance and composition of communities (van Woesik & Jordán-Garza 2011). While some of these effects can be detected immediately, such as mortality, others are more subtle, especially when reproduction is disturbed. The consequences of disturbance can manifest months or even years later, depending on the reproductive frequency and growth rate of the organisms affected. Corals are one such taxa whose reproduction strongly depends on environmental conditions (Ritson-Williams *et al.* 2009a).

Corals are one of the main reef-building organisms in tropical marine ecosystems, and therefore any changes in population structure or survivorship will have an impact on the overall reef ecosystem (Bruno & Selig 2007). Understanding inter-annual variation in coral populations is important for preventing reef degradation and managing reefs effectively. Coral recruitment has been recognised as a key process for coral reef maintenance, as the supply of new recruits maintains coral populations. However, as coral reproduction is strongly influenced by environmental variability there can be considerable temporal variability in recruitment patterns and subsequently coral assemblage structure (Ritson-Williams *et al.* 2009a).

Previous studies that have investigated temporal variation in coral recruitment have examined variation in density and assemblage composition between reefs of different typologies (e.g. fore-reef, back-reef, lagoon) and over different temporal scales (Fisk & Harriott 1990; Dunstan & Johnson 1998; Soong *et al.* 2003; Glassom *et al.* 2004). Considerable inter-annual variation was observed for coral recruitment, ranging from little to no variation to recruitment rates varying up to five times higher or lower between consecutive years. The variability in recruitment occurring between years and areas was characterised by different environmental conditions (e.g. Dunstan & Johnson 1998; Edmunds 2000b; Soong *et al.* 2003; Glassom *et al.* 2004; Adjeroud *et al.* 2007a; Green & Edmunds 2011).

Coral gamete production, which is correlated with the reproductive mode of the corals (brooding or spawning) is subjected to strong seasonality (Edmunds 2000a; Ho & Dai 2014). One previous study found that recruitment patterns were consistent across years for brooding species and more variable for broadcast spawners, depending on the time of spawning, larval dispersal, and larval duration (Dunstan & Johnson 1998). Peak gamete release into the water usually occurs during the summer, when the warmer water temperature triggers reproduction and promotes higher gamete production; however, fecundity and recruitment rate are not linearly correlated (Hughes *et al.* 1999a, 2000; Edmunds 2000a).

Several environmental factors have been associated with temporal variation in coral recruitment rates, and particularly for specific coral families, including temperature (Edmunds *et al.* 2010; Green & Edmunds 2011; Ho & Dai 2014), water motion (Fisk & Harriott 1990; Edmunds *et al.* 2010; Green & Edmunds 2011), light availability (Ho & Dai 2014), and competition with other benthic organisms, such as bryozoans, oysters, serpulids (Dunstan & Johnson 1998; Glassom *et al.* 2004), turf algae and macroalgae (Edmunds 2000a). There is spatio-temporal variability at a range of spatial scales, from local to regional (Adjeroud *et al.* 2007a). In addition, recruitment rates vary at the same scale as environmental gradients (Adjeroud *et al.* 2007a; Green & Edmunds 2011).

Most of the studies on temporal variation in coral recruitment have been based on data collected over two to four years. These studies found temporal variation in recruitment rates, but they did not cover a period of time sufficient to detect any recurrent patterns. For this reason, gather and compare results from different studies conduct in the same area in different times allow to investigate fluctuation and trends of coral recruitment. The importance of understanding how coral recruitment rate varies in time and how this variability affects reef maintenance is of primary important for coral reef management, however little is known about it. Therefore it is important to conduct longer-term surveys to allow fluctuations in coral recruitment rates to be detected and to further understand natural patterns of variability.

This study investigated temporal variability in coral recruit and juvenile abundance in order to assess any differences in variation between corals of different life histories and sizes. Understanding patterns of inter-annual variation in recruitment and survival of juvenile corals is important for understanding and managing coral reefs effectively. My study was conducted in the Wakatobi Marine National Park (WMNP; South Sulawesi, Indonesia. Coral reefs in this region are characterised by a range of different environmental conditions and have experienced

different degrees of degradation. Over the last decade the overall coral cover in the Wakatobi has declined by 31.05±1.59%, and in some areas, coral cover has decreased by up to 83% of initial cover (Curtis-Quick 2013).

Salinas De León *et al.* (2012a) measured temporal variation in coral recruitment in the Wakatobi between 2007 and 2009. Their study monitored two reef systems with different coral cover and quality for two consecutive years and found that overall recruitment rates were higher in the second year and that there was seasonality in recruitment rate, which was similar at both reefs, but with lower rates at the more degraded site. In all sampling seasons, the recruitment rates were always higher at the higher-quality reef, suggesting that rates were likely to be correlated with coral cover and with the level of impact by disturbance. Based on Salinas De León *et al.* (2012a), if coral cover is correlated with coral recruitment rates then decreases in coral cover, such as the coral decline that occurred in the Wakatobi between 2002 and 2011, should result in reduced coral recruitment. However, these authors found recruitment rates between 2007 and 2009 were twofold higher in the second year of the study. These outcomes highlight our poor understanding of the temporal variability in recruitment rates and the effects of the environmental conditions on coral recruitment.

In this study I conducted surveys to investigate the temporal variation in coral recruitment rate and assemblage composition 1) across a range of sites with different environmental conditions over two consecutive years (see Chapter 2); and 2) between two reef systems representing reefs of different qualities over a seven-year period. For the second survey I also collected data on the abundance and assemblage composition of coral juveniles in order to assess any temporal variability at different coral life stages.

3.3 Methods

3.3.1 Study site

This study was conducted in the Wakatobi MNP (see Chapter 2 for further site details), which lies between the Indian and the Pacific oceans. Species from both oceans co-exist, resulting in particularly high biodiversity. The Indo-Pacific region is characterised by the wet season, which occurs from October to March, with an average water temperature in the Wakatobi of 28.9 °C, and the dry season, from April to September, with an average temperature of 27.2 °C (Crabbe & Smith 2005).

The nine sites used in this survey were located in the middle of the Wakatobi Archipelago, on two different reef systems, Hoga and Kaledupa (see Chapter 2 for a map of the sampling sites). The sites are located along the Hoga and Kaledupa Islands. The minimum distance between sites on the same reef was 200 m, while the furthest distance between sites was 5 km. Sites to the south of Kaledupa, including Sampela 1 and 2, are degraded and have been overexploited by human activities (particularly coral mining and overfishing). Overall, the sites are characterised by differences in exposure to waves and currents, topology, substratum composition, benthic community composition, rugosity and sedimentation rates (see Chapter 2 for full details).

3.3.2 Recruit and juvenile surveys

The data used for this study were collected from three different sources. Data from 2011–2013 were collected by myself; data from 2007–2008 were collected by Salinas De León (published in Salinas De León *et al.* 2011, 2012a) and data from 2014 are part of the ongoing monitoring program (Operation Wallacea, unpublished data) (Table 3.1).

Temporal variation was analysed a) between the nine sites experiencing different environmental variables across two years and b) between two reef systems with two replicate sites each: Hoga (replicate sites are Buoy 3 and Buoy 4) and Sampela (Sampela 1 and Sampela 2) over a seven-year period.

Table 3.1 Coral recruit and juvenile data collection by year and number of sites surveyed in the Wakatobi MNP. Data from 2008 and 2009 were collected by Salinas De León *et al.* (2011, 2012a); data from 2014 were collected by Operation Wallacea.

	2008	**2009**	**…**	**2011**	**2012**	**2013**	**2014**
Coral recruits							
9 sites (Short-term)					This study	This study	Operation Wallacea (6 sites)
Hoga and Sampela (Long-term)	Salinas De León et al. 2011	Salinas De León et al. 2012					
Coral juveniles							
Hoga and Sampela		Salinas De León et al. 2012		This study	This study	This study	

Settlement panels were used as the sampling unit in the data analysis. In the short-term (2012–2013) survey, the data were also compared between the sites while for the long-term survey (data collected between 2008 and 2014) the data were analysed at reef system level with two replicate sites per reef.

Recruit and juvenile surveys followed the same data collection methodology described in Chapter 2. Settlement panels were used to collect recruit data and were deployed at 6 m depth in July–August each year the study was conducted and collected in June–July of the following year. Juvenile data were collected using 20 × 0.25 m^2 quadrats placed haphazardly along a 50 m transect at 6 m depth. All the coral colonies less than 40 mm in length were considered juveniles (after Bak & Engel 1979; Edmunds 2000a) and identified to family or genus where possible. The main recruit and juvenile families identified were Acroporidae, Pocilloporidae and Poritidae; Agariciidae and Faviidae were identified only at juvenile level. All the other colonies were grouped in an 'Other' category.

3.3.3 Data analysis

Temporal variability in recruitment and juvenile abundance and assemblage composition data were analysed in the PRIMER v.6 (Plymouth Marine Laboratory, UK) environment. Data were first normalized and transformed by square root, then analysed with a PERMANOVA based on a Bray-Curtis dissimilarity matrix. For the long-term survey, three factors were used: year (random), reef (fixed), and site nested in reef. For the short-term survey only two factors were used: year (random) and site (fixed); reef was not considered a relevant factor for this analysis as the nine sites were considered independent from each other due to the differences in their environmental characteristics.

Multidimensional Scaling (MDS) was used on the Bray-Curtis dissimilarity matrix to investigate the differences in the coral recruit assemblage across years at each site. Variability in coral population assemblage composition was investigated by comparing the relative percentage of the main coral families at each reef system for each year.

3.4 Results

3.4.1 Short-term recruitment survey: Temporal variability in coral recruitment over two years

Overall, 127 recruits were recorded at 6 m depth in 2012 and 181 in 2013, while the overall mean values were 45.44 (± 12.23 SE) rec. m^{-2} and 64.08 (±9.69 SE) rec. m^{-2}, respectively. Values ranged from 78.12 (± 27.75 SE) rec. m^{-2} found at B3 to 21.83 (±6.9 SE) rec. m^{-2} at S2 in 2012 and 135.71 (± 30.50 SE) rec. m^{-2} found at B1 and 6.25 (±2.20 SE) rec. m^{-2} at S1 in 2013 (Figure 3.1). When analysing the recruit abundance at each site individually, there was

no significant temporal variability between the two years (PERMANOVA, df=1, P>0.05). However, significant spatial variability was found in overall recruit abundance (PERMANOVA, df=1, P=0.0023) and assemblage composition (PERMANOVA, df=1, P=0.0001) across sites in both years (Table 3.2).

Table 3.2 Result of the PERMANOVA analysis for the spatial distribution of coral recruits between two years (2012 and 2013) and nine sites in the Wakatobi MNP

Factor	df	SS	MS	Pseudo-F	P
Recruit abundance					
Year	1	371.9	371.9	1.1308	0.2940
Site	8	15192	1899.1	8.7364	**0.0023**
Year*Site	8	1739	217.4	0.6610	0.7488
Recruit assemblage					
Year	1	419.8	419.8	0.4435	0.6909
Site	8	24155	3019.3	3.4859	**0.0001**
Year*Site	8	7572.8	946.6	1.0929	0.3689

The pattern of recruitment rates across sites was not consistent between years. In 2012 the highest recruitment rate was found at Buoy 3, followed by Buoy 4 and Kaledupa 1, while in 2013 the highest values were recorded at Buoy 1 followed by Buoy 3 and Kaledupa 1. The sites at Sampela had the lowest recruitment rates in both years. Pak Kasim's, Ridge 1 and Kaledupa Double Spur had similar recruitment rates over time (Figure 3.1). However, the variation in recruitment rates at the same site between different years was variable; one site (Buoy 1) recorded an increase in rates between 2012 and 2013, while at all the other the rates decreased.

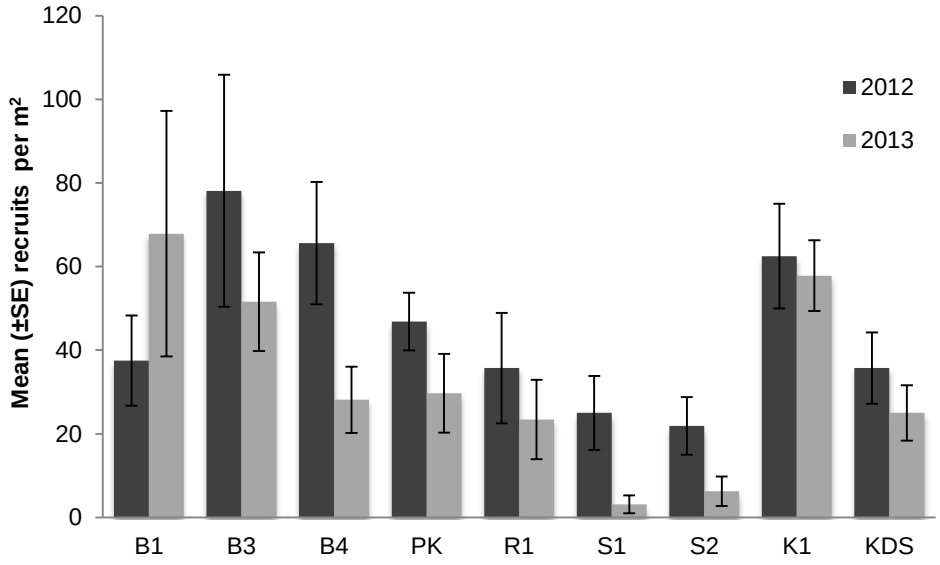


Figure 3.1 Mean (± Standard Error) recruitment rates per m^2 recorded on settlement panels deployed for 12 months in 2012 and 2013 in the Wakatobi MNP (Indonesia) across nine sites (see Figure 1 in Chapter 2 for the information about the abbreviations used in the legend)

The MDS plot showed no clear difference in coral recruit assemblage composition sites across years, and assemblage composition remained similar at each site over the two-year period (Figure 3.2).

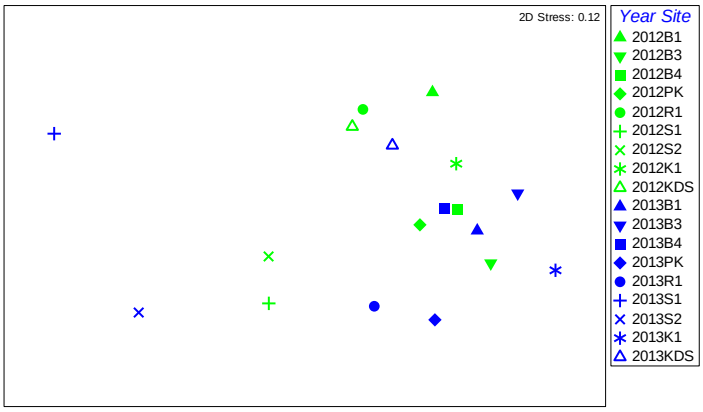


Figure 3.2 Multidimensional Scaling (MDS) plot to examine any differences in the assemblage composition of the main coral recruit families at each of the nine sites in two years. The legend describes the year of data collection (2012 or 2013) followed by the site. The distance between the points reproduces the distances on the Bray-Curtis matrix on a bidimensional plot, while the stress value estimate how well the configuration fit to the observed distance matrix, where 0.12 is an acceptable value.

The recruit assemblage composition was variable between the nine sites, although it is important to note that 39.4% of the recruits in 2012 and the 41.8% in 2013 were not identifiable. Despite these values are higher than those found in other coral recruitment studies, difficulties in coral recruit identification are common and due to the little development of corals in this early life history stage. Pocilloporidae was most abundant in both years (37% and 29.7%), followed by Poritidae (16.5% and 19.8%) and Acroporidae (7.1% and 8.8%).

In 2012, Pocilloporidae was the most common family at most of the sites, it was second to Poritidae only at Sampela. In 2013 Poritidae was as common as Pocilloporidae. Acroporidae had a low settlement rate in 2012 and was not found Pak Kasim's, and Sampela 1 and 2, while in 2013 it was not found at Buoy 4, but was recorded at Pak Kasim's (Figure 3.3).

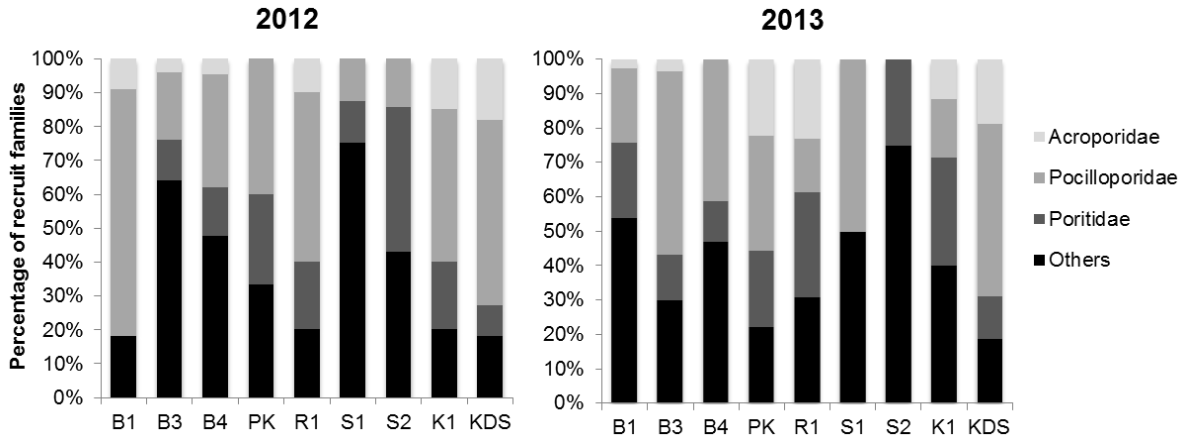


Figure 3.3 Percentage of coral recruits from different families recorded in 2012 and 2013 on settlement plates deployed for 12 months at 6 m depth at nine sites in the Wakatobi MNP (Indonesia)

At the sites where the overall coral recruitment was limited to only a few recruits, it was difficult to investigate the overall recruit population composition. For example, Sampela 1 and Sampela 2 had a total of 8 and 7 recruits in 2012 and 2 and 5 in 2013, respectively, but most of the recruits were unidentifiable, making it difficult to draw conclusions about the recruit assemblage composition at these sites. When analysing the temporal variability at each site, I found no significant differences in abundance or assemblage composition between 2012 and 2013, and recruitment rates appeared stable between these two years (Figure 3.4).

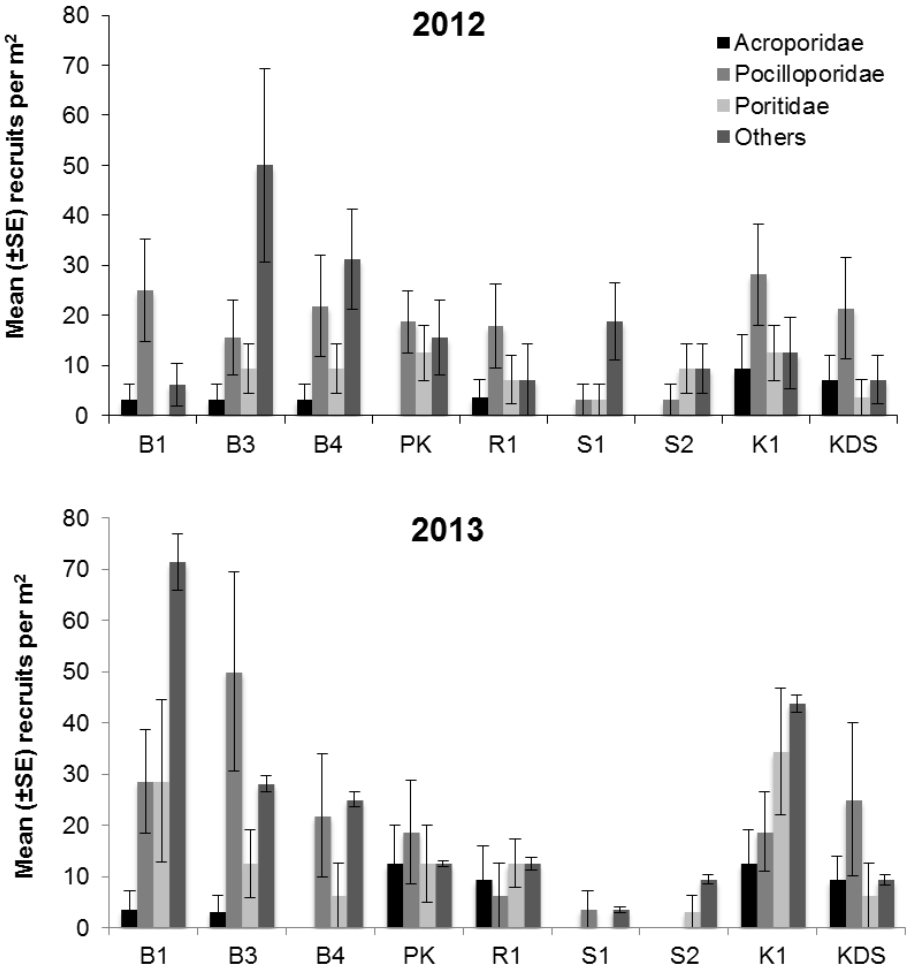


Figure 3.4 Mean (± Standard Error) number of coral recruits per m^2 for the most common coral families recorded in 2012 and 2013 at nine sites in the Wakatobi MNP

3.4.2 Long-term survey on coral recruitment among two reef systems over seven years

Overall, 580 recruits were found in the surveys over 7 years. The lowest value was 58 recorded in 2013 (44.69 ±9.68 SE rec. m^{-2}) and the highest was 268 (209.38 ±101.56 SE rec. m^{-2}) in 2009. The mean recruitment rates ranged from 71.9 (±28.47 SE) rec. m^{-2} to 317.19 (±12.76 SE) rec. m^{-2} for Hoga and 9.6 (±8.21 SE) rec. m^{-2} and 101.6 (±13.27 SE) rec. m^{-2} for Sampela. Sampela had lower recruitment rates in all the years compared to Hoga, with the 2014 rates at Hoga being more than three time higher than at Sampela (Figure 3.5).

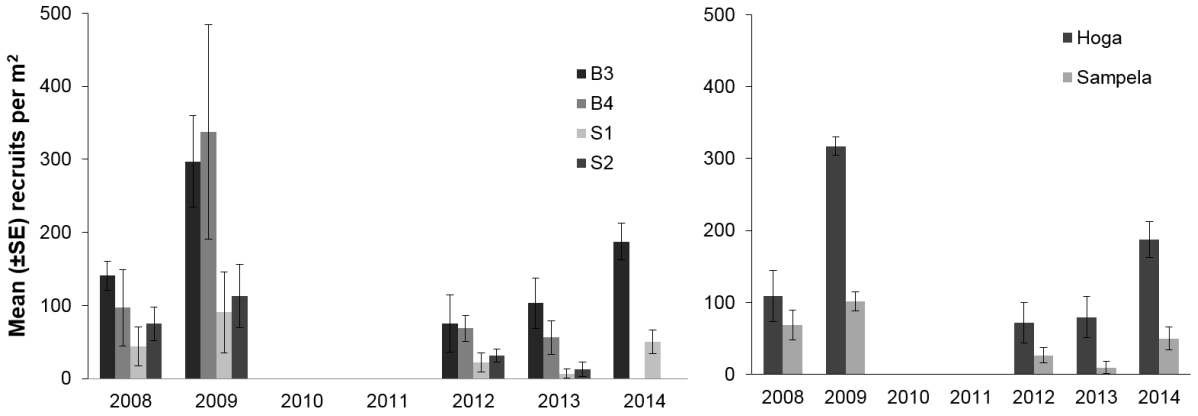


Figure 3.5 Mean (± Standard Error) number of coral recruits per m^2 recorded a) at the two reef systems (Hoga and Sampela) with two replicate sites each and b) overall mean at each reef system (Hoga: B3 and B4; and Sampela: S1 and S2) between 2008 and 2014. In 2010 and 2011 no data were collected, while in 2014 data were collected only at one site per reef

Overall, Pocilloporidae recruits were recorded in the greatest numbers at both reef systems, followed by Poritidae and Acroporidae recruits. At Hoga the 'Other' category included a minimum of 33% of the overall recruits found in 2012 and a maximum of 55% in 2013, while at Sampela it included more than the 60% of the overall recruits found in all years. As the overall recruitment was low at Sampela, it is difficult to draw conclusions about the recruit assemblage composition (Figure 3.6). Variation in recruitment rates in any particular year at Hoga did not correspond to a similar variation in rates at Sampela.

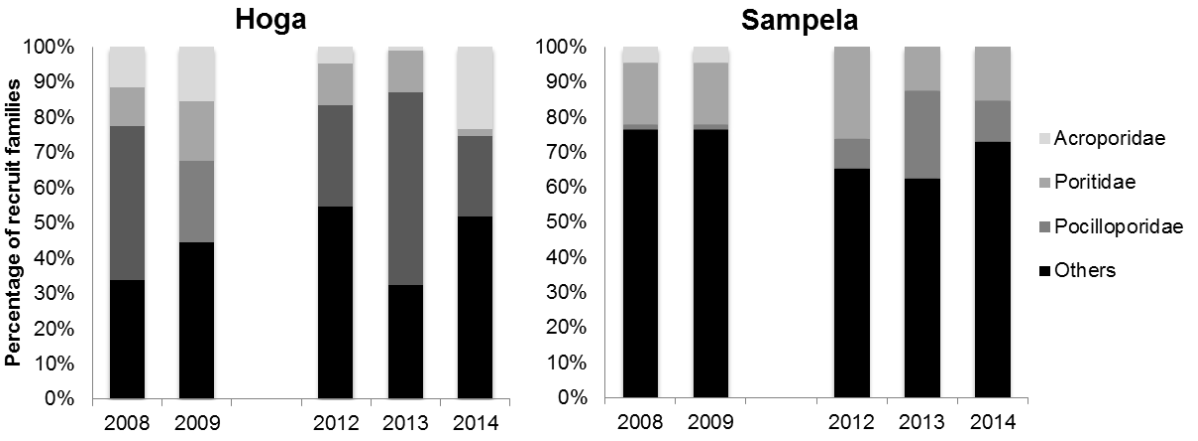


Figure 3.6 Percentage of the assemblage comprised of the main coral recruit families identified at two reef systems (Hoga and Sampela) between 2008 and 2014 in the Wakatobi MNP. In 2010 and 2011 no data were collected

Spatial and temporal variation were present in coral recruitment between the two reefs (PERMANOVA, df=4, P=0.0044; df=1, P=0.0247). Furthermore, there was an interaction between site and year for the coral recruit assemblage composition data (PERMANOVA, df=8,

P=0.0151) and there were high levels of variability in the abundance of the main families across sites over the seven-year period (Table 3.3). Generally, the individual family abundances were always higher at Hoga than at Sampela, except for Poritidae in 2014: however, in that year only one replicate site per reef system was surveyed.

Table 3.3 Result to the PERMANOVA analysis for the spatial distribution of coral recruits between five years, two reefs (Hoga and Sampela) with four replicate sites (Buoy 3 and Buoy4 at Hoga reef and Sampela 1 ans Sampela 2 at Sampela reef) in the Wakatobi MNP

Factor	df	SS	MS	Pseudo-F	P
Year	4	22937	5734.2	4.0527	**0.0044**
Reef	1	6519.4	6519.4	7.3832	**0.0247**
Site (Reef)	3	2226.2	742.1	0.6041	0.7562
Year*Reef	4	5221	1305.2	0.9225	0.5479
Year*Site (Reef)	8	11323	1415.4	1.9278	**0.0151**

Pocilloporidae was the dominant family every year except 2009, when Poritidae and Acroporidae were more abundant. Poritidae recruits usually had relatively low abundance at both reefs, while Acroporidae was highly variable across years. In 2012 and 2013 Acroporidae abundance was very low at Hoga and it was not found at all at Sampela between 2012 and 2014 (Figure 3.7).

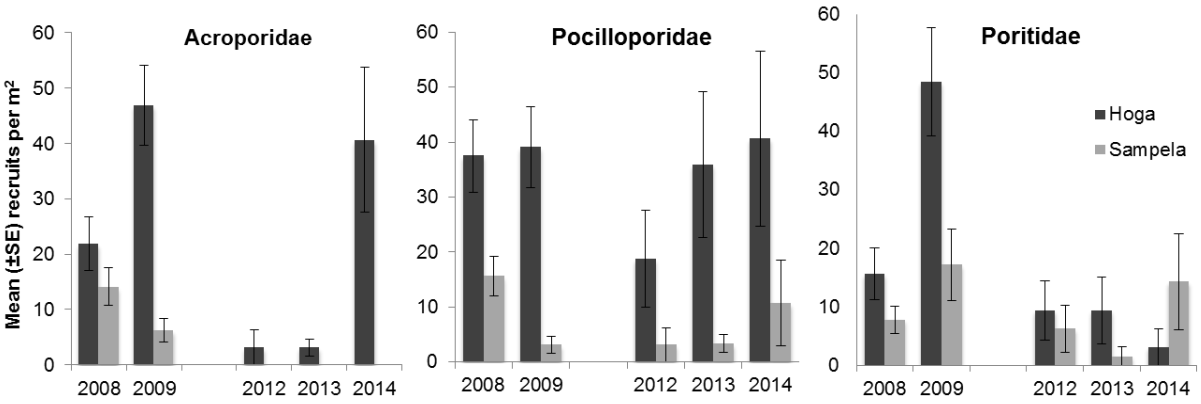


Figure 3.7 Mean (± Standard Error) number of coral recruits for each of the three main families, Pocilloporidae, Poritidae and Acroporidae, per m^2 recorded between 2008 and 2014 at two reef systems: Hoga and Sampela

High temporal variability in coral recruitment rates was present in Acroporidae (PERMANOVA, df=4, P=0.0126) and Poritidae (PERMANOVA, df=4, P=0.0471), while Pocilloporidae presented only a weak temporal variability when there was an interaction

between year and site (PERMANOVA, df=8, P=0.05), variability across reefs was also significant (PERMANOVA, df=1, P=0.0462) (Table 3.4).

Table 3.4 Result of the PERMANOVA analysis for the spatial distribution of coral recruit families (Acroporidae, Pocilloporidae and Poritidae) between years, reefs, and replicate sites.

Factor	df	SS	MS	Pseudo-F	P
Acroporidae					
Year	4	7377	1844.2	6.4719	**0.0126**
Reef	1	652.96	652.96	2.738	0.1161
Site (Reef)	3	454.93	151.64	0.6491	0.774
Year*Reef	4	3986.3	996.58	3.4972	**0.0452**
Year*Site (Reef)	8	2280.6	285.07	2.0784	**0.0389**
Pocilloporidae					
Year	4	932.53	233.13	0.4870	0.7421
Reef	1	1220.8	1220.8	5.3631	**0.0462**
Site (Reef)	3	593.93	197.98	0.4978	0.6423
Year*Reef	4	372.44	93.11	0.1945	0.9328
Year*Site (Reef)	8	3830.8	478.85	1.9495	**0.05**
Poritidae					
Year	4	2436.6	609.14	3.8971	**0.0471**
Reef	1	89.52	89.52	0.4375	0.641
Site (Reef)	3	246.95	82.32	0.4836	0.6884
Year*Reef	4	1923.3	480.83	3.0762	**0.0558**
Year*Site (Reef)	8	1250.2	156.28	0.7961	0.6092

3.4.3 Temporal variation in coral juvenile abundance and assemblage composition

During the four surveys 938 coral juveniles were recorded at the two reef systems: 248 (24.8 ±3.45 SE rec. m^{-2}) in 2009, 255 (12.75 ±1.69 SE rec. m^{-2}) in 2011, 267 (14.51 ±1.67 SE rec. m^{-2}) in 2012 and 168 (8.4 ±1.23 SE rec. m^{-2}) in 2013. In 2013 lower values were recorded on both reefs (10.7 ±6.1 SE rec. m^{-2} at Hoga and 6.1 ±1.22 SE rec. m^{-2} at Sampela), while in 2009 higher values were recorded at both reefs (31.8 ±3.99 SE rec. m^{-2} at Hoga and 17.8 ±2.9 SE rec. m^{-2}).

Significant variability in the abundance and assemblage composition was found for coral juveniles between years (PERMANOVA, df=3, P<0.05) and reef systems (PERMANOVA, df=1, P<0.05), but not between replicate sites (PERMANOVA, df=2, P>0.05) (Table 3.5);

there was no significant difference between Buoy 3 and Buoy 4 on the Hoga reef and Sampela 1 and Sampela 2 on the Sampela reef (Figure 3.8).

Table 3.5 Result of the PERMANOVA analysis for the spatial distribution of coral juveniles between years, reefs, and replicate sites

Factor	df	SS	MS	Pseudo-F	P
Year	3	25965	8654.9	11.976	0.0024
Reef	1	16125	16125	10.444	0.0114
Site (Reef)	2	808.6	904.3	1.21	0.3876
Year*Reef	3	254.3	751.44	10.398	0.4412
Year*Site(Reef)	6	333.5	722.24	0.644	0.8479

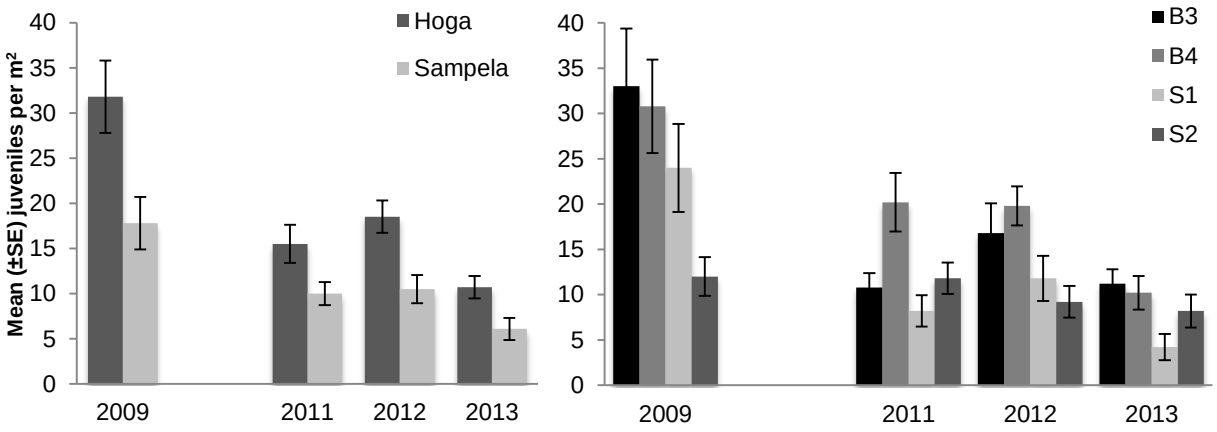


Figure 3.8 Mean (± Standard Error) number of coral juveniles per m^2 recorded across five years at Hoga and Sampela reef systems. Data were not collected in 2010

Table 3.6 Mean (± Standard Error) number of coral juveniles per m^2 recorded at each site with data pooled for each reef system. In the grey column the percentage of the variation in juvenile abundance is compared to the previous juveniles survey. The last column on the right shows the total variation in juvenile abundance between 2009 and 2013

	2009	2011		2012		2013		Overall
Buoy 3	33 (±6.36)	10.8 (±1.58)	-67.3	16.8 (±3.29)	15.5	11.2 (±1.63)	-33.3	-66.1
Buoy 4	30.8 (±5.16)	20.2 (±3.24)	-34.4	19.8 (±2.14)	-1.9	10.2 (±1.91)	-48.5	-66.9
Sampela 1	24 (±4.86)	8.2 (±1.73)	-65.8	11.8 (±2.49)	43.9	4.2 (±1.49)	-64.4	-82.5
Sampela 2	12 (±2.15)	11.8 (±1.73)	-1.7	9.2 (±1.75)	-22	8.2 (±1.88)	-10.9	-31.7
Hoga	31.9 (±3.99)	15.5 (±2.11)	-51.4	18.3 (±1.79)	18.1	10.7 (±1.24)	-41.5	-66.5
Sampela	18 (±2.91)	10 (±1.27)	-44.4	10.5 (±1.55)	5	6.2 (±1.22)	-40.9	-65.6

The relative abundance of the five main juvenile families represented 86.62% of the overall 443 juveniles found in 2009, 77.42% of the 255 in 2011, 69.75% of the 267 in 2012 and 70.1% of the 168 in 2013. There was an overall decline in the total abundance of coral juveniles and in the abundance of individual families over time (Table 3.6).

Analysing the abundance of the five main families separately, I found that Poritidae and Faviidae varied across years and between reefs, Agariciidae varied only across reefs and Acroporidae varied only across years, while Pocilloporidae did not show any significant variation across years or reef systems (Figure 3.9).

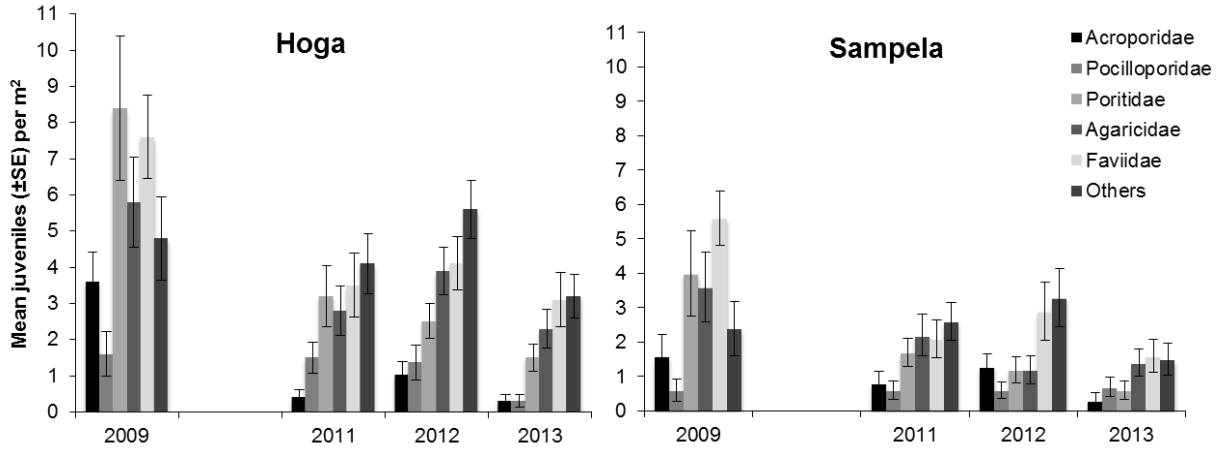


Figure 3.9 Mean (± Standard Error) number of coral juveniles per m^2 belonging to the five main families per m^2 recorded at a) Hoga and b) Sampela reef systems between 2009 and 2013

3.5 Discussion

The short term survey found little temporal variability in coral recruit abundance across nine sites that are characterised by different environmental conditions, with recruitment rates being similar at each site over the two years of the survey. However, spatial variability was found at both years, even though the pattern of coral recruitment rate was not consistent, suggesting that local environmental characteristics were affecting the recruitment process. For the long-term survey, significant temporal and spatial variability in overall recruitment rate was found over the seven years and among the reef systems. Recruit assemblage composition changed between reefs and across years and this variation was consistent. Temporal variability in juvenile abundance and assemblage composition was recorded across years and between reefs. The five main coral juvenile families varied independently over the study period. These results demonstrate that the survival from recruit to juvenile varied over time and across reefs. I also

found that recruit and juvenile patterns of abundance and assemblage composition varied independently between these two life history stages, sites, and coral families.

3.5.1 Absence of trends in temporal variability in coral recruitment abundance and assemblage

For the short-term survey conducted at nine sites experiencing different environmental conditions, differences in the recruitment rates between the sites were consistent over the two years of sampling, despite 43% more recruits being recorded in the second year. The recruitment rates at each site showed high levels of variation because of the high variability at the panel level. In contrast, in the long-term survey, recruitment rates fluctuated considerably at both reef systems over the study period. For example, in 2013 the recruitment rate at Hoga was slightly higher than in 2012, while at Sampela the rate was one-third lower. This is consistent with other studies where high variability in recruitment rates across consecutive years has been reported with up to fivefold increases in some cases (see Wallace 1985a; Gleason 1996; Glassom *et al.* 2004; Adjeroud *et al.* 2007a; Nakamura & Sakai 2009). Although overall the variation in recruit abundance on the Hoga reef did correlate with those at Sampela, these rates did not show any obvious upward or downward trend.

There were differences in the abundance of the individual recruit families over time. Pocilloporidae recruits did not show any significant variation in abundance across years, consistent with a previous study that found that seasonal recruitment rates were consistent throughout the year (Salinas De León *et al.* 2012a). The absence of temporal variation in Pocilloporidae recruit abundance was also found at Ryukyu Archipelago in South Japan, where only spatial variation was present and the distribution of recruits was related to reproductive mode. As most of the Pocilloporidae corals are brooding species, the larvae settle only a short distance from the adult colonies and are affected by mortality in the water column due to the short time the larvae spend in the water (Nakamura & Sakai 2009). However, these studies contrast with the results found in the Red Sea (Glassom *et al.* 2004), at Moorea (Adjeroud *et al.* 2007a), and on the Great Barrier Reef (Dunstan & Johnson 1998), where temporal and spatial variation in recruit abundance has been reported and correlated with the reproductive mode of the local Pocilloporidae colonies, suggesting that the local species composition determines the scale of variability.

Acroporidae and Poritidae recruits showed wide temporal variability in abundance across years in this study, but other studies have found low or no variability (Green & Edmunds 2011). High

levels of temporal variability in abundance of Acroporidae recruits was found on the Great Barrier Reef (Dunstan & Johnson 1998), in the Red Sea (Glassom *et al.* 2004), and in Japan (Nakamura & Sakai 2009), however in my study there was variation in settlement rates across years. Years of low recruitment rate were followed with random years of higher recruitment rates, maintaining the population and reef diversity; this is likely to be due to the coral reproductive mode (Warner & Chesson 1985; Harriott & Banks 1995; Adjeroud *et al.* 2007a; Irizarry-Soto & Weil 2009). However, in my study reproductive mode was not included as a factor in the analysis, and so could not be investigated as the main reason for the variation in recruitment rates.

Irizarry-Soto & Weil (2009) found that reproductive success was more favourable for some coral taxa in some years while in other years other (non-coral) taxa were more successful. Furthermore, the success was independent of the reproduction mode adopted by the coral taxa. Therefore, significant temporal variability in recruitment rates was found whenever a successful year was included in a multi-year study. As a consequence variability was not present when only years of non-favourable conditions were analysed (low larval availability, high mortality or other post-settlement events), with low and consistent rates among consecutive unsuccessful years. It is possible that long-term surveys on recruitment rate can detect patterns wherever a sequence of successful and not-successful years is included.

The decline in coral cover, recorded since 2002 in the Wakatobi (Curtis-Quick 2013) could not be compared to the data on coral recruitment rates collected between 2008 and 2014, because of the lack of coral recruitment data before 2008 and in 2010 and 2011. As a consequence, it was no possible to assess the existence of the correlation between coral cover and recruitment rate suggested by Salinas De León *et al.* (2012a). While coral cover has been decreasing in the last decade, recruitment rates were highly variable between years. For example, the rates recorded in 2009 were double those in 2008. However, the lack of information on recruitment rates for some years in the long-term survey may mask some patterns.

3.5.2 Temporal variability in the juvenile population

The analysis of the juvenile data over a five year-period showed a decline in the abundance and change in assemblage composition. In particular, the relative proportions of the main families were variable and a shift occurred in dominance, from the Poritidae family, which was the most common in 2009, to the Faviidae family from 2011 onward.

The abundance of juvenile families varied across both years and reefs. At the family level, a large decrease in density occurred between the recruit and the juvenile stages. Taxa such as Pocilloporidae usually have a high colonisation rate followed by high mortality, which seems to be independent of initial density (Edmunds 2000a; Irizarry-Soto & Weil 2009). A previous study in the Caribbean found that juvenile survivorship was not correlated with the reproductive mode of corals (Edmunds 2000a; Irizarry-Soto & Weil 2009) and the authors suggested that juvenile taxa responded differently to the local environmental conditions present at recruitment time. However, in my study juveniles were identified only to family level or to genus, and therefore it was not possible to analyse the survivorship of taxa based on reproductive mode.

Because of the missing data on juvenile abundance in 2010, it was not possible to determine if the decrease in juvenile density recorded between 2009 and 2011 was progressive, or if data recorded in 2009 represented a year of exceptionally high survivorship, or if a major disturbance occurred and affected the juvenile abundance. However, the decline in abundance was different for each coral family: Pocilloporidae was least affected and its abundance remained consistent at the same time Acroporidae abundance declined.

In my study, the dominant families at the juvenile stage, Agariciidae, Acroporidae and Faviidae, had low densities at the recruit stage, indicating that they have high survivorship. Acroporidae had a low recruitment and survival rate in the Wakatobi, however in other studies this family showed different levels of resistance to mortality, from very high to marginal. Because of the small number of colonies found in this study, it was not possible to gain a better understanding of its survival (Dunstan & Johnson 1998; Glassom *et al.* 2004). Poritidae and Faviidae were variable across years and reefs, and both had low settlement rates, however Faviidae became a dominant family at the juvenile stage. Pocilloporidae had high mortality after high recruitment, but then it did not show further temporal or spatial variation, as populations seemed to have been less affected by post-settlement events.

3.5.3 Impact of thermal anomalies on coral recruitment in the Wakatobi

A decline in both recruit and juvenile abundance occurred between 2009 and 2012, where recruitment rates decreased by more than one-third at all sites. At Hoga in 2011 the juvenile population was less than half than 2009, while at Sampela the decrease was less pronounced and at both reefs a shift in juvenile assemblage composition occurred.

Between 2009 and 2011 one of the strongest ENSO event of the last 50 years was recorded in the West Pacific and South East Asia and it affected many marine organisms, causing coral bleaching and fish mortality (Tan & Heron 2011; Feng *et al.* 2013). The average Sea Surface Temperature (SST) in the Pacific area increased in 2011, peaking in February–March, when a rise of more than 2°C was recorded in Western Australia (Pearce *et al.* 2011) At the same time SST rose an average of 1.6°C in the Indo-Pacific area (5°N–5°S, 120–170°W) (Feng *et al.* 2013).

As a consequence of the increase in water temperature, about 50% of the coral bleached in West Malaysia (Tan & Heron 2011), while at Moorea the rise of water temperature that preceded the bleaching event was likely to have promoted larval production with a subsequent rise in recruitment rates (Adjeroud *et al.* 2007a).

In 2010 a particularly severe thermal anomaly was recorded in the Wakatobi where an increase of about 2°C water temperature was reported (Smith 2012, unpublished data; Curtis-Quick 2013). This temperature anomaly was followed by a bleaching event in the following year and the recruitment rates recorded were significantly lower. This unusual variation in temperature might explain the high recruitment rates found in my study in 2009, where larvae production might have been triggered by the increase of water temperature followed by the decline in both coral reproduction and survival of young coral colonies in the Park.

Unfortunately, the lack of data on recruitment rates for 2010 and 2011 prevented me from assessing any correlation between recruitment rates and these thermal anomalies. Furthermore, in the juvenile survey, a decrease in juvenile abundance was observed between 2009 and 2011.

3.6 Conclusion

The research reported in this chapter highlights the importance of annual monitoring of coral recruitment over a period of time and the need to include a sufficient number of sites to represent the overall variability in environmental conditions present in the area. The comparison of data from different years allows temporal variation in recruitment rate to be detected. Such information may allow predictions to be made for coral recruitment trends and aid with coral reef management. Knowing in advance the more favourable years for coral recruitment can help in planning intervention to reduce the disturbances resulting from more predictable stressors.

Despite it not being possible to control factors such as thermal anomalies, other causes of disturbances that might influence coral recruitment rate can be monitored. Specific rules to

regulate activities such as fishing and sediment dredging can help to control predation and sedimentation rates, which also affect the recruitment process. Appropriate interventions would be particularly important in years when the coral recruitment rates are expected to be low due to uncontrollable factors (e.g. climatic conditions). Active reef management is particularly important in areas where recruitment rates are usually low or where reef rehabilitation is required.

In the future more specific studies should be conducted in order to better understand how predictable factors, such as predation and sedimentation, affect mortality in young coral populations.

Chapter 4 Importance of fish grazing to coral juvenile mortality

4.1 Abstract

Fish grazing has been identified as an important impact responsible for coral recruit (corals recently settled) mortality in the early post-settlement phase and the size of the colony was correlated to the possibility to be affected by grazing activity. Grazers also regulate the growth of algae, which are competing with young coral colonies for available space. This chapter describes an investigation into the role of fish grazing in coral juvenile (< 2 years old) mortality and colony growth. I conducted a fish exclusion experiment using settlement panels with coral colonies settled *in situ* in the Wakatobi Marine National Park (Indonesia) and I measured variations in photosynthetic efficiency (Fv/Fm) of coral juveniles in order to assess physiological stress correlated to grazing activity. Only 3.49% of the juveniles were estimated to have died as result of grazing activity and colony size was not correlated with mortality rate. There was variation in coral colony size; this was influenced by the size of the colony at the beginning of the experiment but was independent of the caging treatment. Colonies increased or reduced in size over the experiment across all treatments, but the relationship between the magnitude of the change in colony size and initial size of the coral colony remained unclear. The lack of algal consumption by fish might have induced differential changes in size and decrease in photosynthetic efficiency that influenced the survival of colonies. Overall, grazing seems unlikely to have been the main cause of juvenile mortality in this experiment. During the experiment, 28.38% of coral juveniles have been overgrown by other benthic organisms, mostly algae. Overgrowth was consistent between treatments and did not caused mortality to coral juveniles, although a significant decrease of 44% and 22.2% in Fv/Fm values was measured in all the juvenile colonies overgrown by green and turf algae respectively. It is important to consider that the coral sample size used in my study was small and unevenly distributed between treatments. Further studies could investigate better the role of grazers in algae regulation, the interaction between benthic organisms, especially algae, and coral juvenile, and the threshold of overgrown juvenile survivorship in the post-settlement stages.

4.2 Introduction

In recent years there has been increasing interest in coral reef restoration following their decline worldwide (review by Bruno & Selig 2007; Burke *et al.* 2012; De'ath *et al.* 2012). The

disturbances that threaten coral reefs include changes in climatic conditions and ocean acidification (Manzello 2010; Doropoulos *et al.* 2012a), and more local environmental impacts, such as increases in sedimentation as a result of changes in land use (Rogers 1990; Field *et al.* 2000; Erftemeijer *et al.* 2012) and direct human disturbances, such as coral mining (Crabbe *et al.* 2004; Halpern *et al.* 2008). Several studies have focused on the early life history stages of corals in order to better understand the ecological processes that drive coral recruitment and enhance its success (for example see review by Ritson-Williams *et al.* 2009a; and work by Rylaarsdam 1983 and van Woesik & Jordán-Garza 2011).

Predation is thought to play an important role in controlling coral colony distribution; for example, corallivore activity can determine the final patterns of species abundance for coral recruits and juveniles (Gleason 1996; Penin *et al.* 2011; Davies *et al.* 2013). Coral early life history stages are more vulnerable to stress than adult colonies; the small size and the limited energy available to react to disturbances make them easy prey, and weak competitors for space and resources (Hughes & Jackson 1985; Hughes 1994; Zilberberg & Edmunds 2001; Doropoulos *et al.* 2012b). Therefore young corals are more sensitive to environmental variation, such as fluctuations in water temperature, irradiance and sedimentation rates (Rylaarsdam 1983; Vermeij 2005; Box & Mumby 2007), than adult corals. In addition, it is likely that the causes of mortality in young corals vary with age and size (Cooper *et al.* 2014).

Previous research has suggested that in the first months after settlement coral recruit mortality is mostly caused by biological factors (Miller & Hay 1998; Wilson & Harrison 2005; Penin *et al.* 2011). Young corals that are affected by disturbance can suffer minor to major damage; visible signs of stress in corals include colony bleaching, decreased growth rate and a reduction in size. The consequences of stressors on corals vary according to their intensity; corals can usually recover when the impact is small and for a short time, but more intense disturbance could lead to partial or complete death of the colony (Connell 1997a; Baker *et al.* 2008; Penin *et al.* 2011; Johns *et al.* 2014), where partial mortality refers to the death of only a portion of coral colony polyps.

Different disturbances play important roles in determining the survivorship rate of coral colonies in the post-settlement stage, when mortality rates can exceed 50% just two days after settlement (Miller & Hay 1998). Several studies have highlighted the impact of grazing fish on coral recruits (Lewis 1986; Gleason 1996; Nozawa 2008; Baria *et al.* 2010; Penin *et al.* 2011; Trapon *et al.* 2013c); while grazers feed on algae, especially on turf algae and crustose coralline

algae (CCA), coral settlers can be accidentally removed from the substrate or inadvertently experience damage (Box & Mumby 2007; Hoey & Bellwood 2008).

Fish grazers sometimes actively avoid small colonies, although the threshold of the colony size that was resistant to grazing activity was variable by geographical location and fish species present on the reef (Birkeland 1977; Gleason 1996; Christiansen *et al.* 2008). For example, the fish families Acanthuridae and Scaridae, which exert a strong mortality pressure on young corals, were found to actively avoid small coral recruits in the Caribbean (Birkeland 1977), while the same two families caused high mortality in the coral recruit population in Moorea (Gleason 1996), although the overall feeding habit at fish family levels is influenced by fish species composition. In contrast, another study in the Caribbean found grazers feeding indiscriminately on juveniles regardless of their size (Bak & Engel 1979).

A recent laboratory experiment to investigate the relationship between grazing and coral colony size suggested that accidental grazing was more frequent at coral early life history stages and it was found to negatively correlate with colony size (Christiansen *et al.* 2008). In that study, conducted in controlled conditions, blennies (family Blennidae) damaged only small colonies because older corals had a higher resilience, however blennies are likely to be more selective than big grazers (Christiansen *et al.* 2008). Single grazing events, such as a small fish bite, compromise the survival of entire juvenile coral colonies (Christiansen *et al.* 2008). Most of the scars typically found on corals are the result of parrotfish (family Scaridae) grazing, which are considered the main responsible for damages to corals (Miller & Hay 1998; Penin *et al.* 2010; Trapon *et al.* 2013c). Parrotfish grazing activity include scrape and excavate, removing pieces on substrate with the algae and leaving evident scars; this activity promotes the accidental removal of coral recruit recently settled (Hoey & Bellwood 2008). However, other grazers, including surgeonfish (family Acanthuridae), triggerfish (family Balistidae), rabbitfish (family Signatidae), and corallivores, including butterflyfish (family Chaetodontidae), starfish (e.g. *Achantaster planci*), echinoids and molluscs (e.g. *Drupella*), feed on coral (Sammarco 1985; Penin *et al.* 2011; Davies *et al.* 2013). Surgeonfish and rabbitfish usually feed on the upper layer of the algae leaving intact the lower portion and the substratum (Trapon *et al.* 2013c). In addition, grazers also control algal growth, potentially reducing the level of competition between algae and coral (Miller & Hay 1998; Box & Mumby 2007; Hughes *et al.* 2007; Baria *et al.* 2010; Davies *et al.* 2013).

Algal abundance correlates with coral survivorship at all coral life history stages (McCook *et al.* 2001). Although some algae, such as CCA, promote coral recruitment at the settlement stage, other algae species compete for space with corals at all coral life history stages (River & Edmunds 2001; Harrington *et al.* 2004; Haas *et al.* 2010). Macroalgae and turf algae can shade and overgrow young coral colonies, affecting coral growth rate by causing reductions in colony size, suffocation, and it may also induce mortality (Birrell *et al.* 2005; Vermeij 2006; Ferrari *et al.* 2012). Considering the strong impact of algae on coral, algal regulation provided by grazers plays an important role, particularly in early coral life history stages (Box & Mumby 2007; Brandl *et al.* 2013; Trapon *et al.* 2013c; Cooper *et al.* 2014). However, algal abundance also increases sediments on coral reefs; for example, turf algae trap sediments that then smother coral recruits and reduce the space available for coral expansion (Birrell *et al.* 2005). Moreover, it has also been shown that sedimentation rate has a negative correlation with grazer abundance, where grazing activity was affected by the sediment layer present on the reef (Goatley & Bellwood 2012). In summary, there is a strong correlation between coral recruit survivorship, grazers activity, and algae abundance.

The interaction between multiple factors increases the range of responses of coral colonies to these disturbances, from physiological stress to colony mortality, where the effects of these interactions are not just additive, but also synergistic (Ban *et al.* 2014). Therefore it is difficult to discriminate the effects of different disturbances, and this represents a major challenge in the study of post-settlement processes. Grazing has been identified as one of the main stressors at early coral life history stages and more studies need to focus on its association with other factors, such as algal abundance, in order to better understand how they are correlated (Gleason 1996; Box & Mumby 2007; Venera-Ponton *et al.* 2011; Trapon *et al.* 2013c).

The importance of grazers as algae regulators has increased in the last few decades, principally because phase shifts from coral to algal dominated reefs have been observed in different geographical regions (Lirman 2001; Hughes *et al.* 2007; Ledlie *et al.* 2007; Bruno *et al.* 2009; Norström *et al.* 2009). In the Caribbean, a decline in grazers, due to overfishing and a die-off of the dominant bioeroder *Diadema*, caused the loss of coral cover and an increase of algae abundance in the early 1980s (Hughes 1984). This has not only affected coral recruitment but also the potential for reefs to recover (Adam *et al.* 2015).

Previous research has used manipulative experiments to investigate the impact of fish grazers on coral recruits (for example Miller & Hay 1998; Baria *et al.* 2010; Trapon *et al.* 2013c).

These studies focused mostly on recently settled coral colonies under controlled conditions in laboratories on clear tiles, where spatial competition was not present. However, the effect of grazing on older coral colonies, such as juveniles, settled *in situ* on more complex surfaces, more similar to real reef environments, has not been previously examined.

In this chapter, 1) I investigated the impact of fish grazing on coral juveniles by carrying out a fish exclusion study (caging treatment) similar to those used to investigate the effect of predation on coral recruit survivorship. My objectives were to: a) assess the overall full and partial mortality (damaged colonies) rate in the juvenile coral population due to grazers; b) to assess if initial size of coral juveniles influences the outcome of the interaction with grazers, in order to detect correlations between coral size and probability of accidental removal of juveniles from the surface or colony damage; c) to examine variations in coral colony size and determine whether treatment or the initial size had a role in this variation, and d) to assess stress due to fish grazing activity on coral juveniles by measuring variation in the photosynthetic efficiency (Fv/Fm).

Then, 2) I investigated the impact of spatial competition between coral juveniles and benthic organisms, focusing on algae, in different grazing regimes. My objectives were: a) to assess the predominant benthic groups overgrowing juvenile coral colonies in different fish grazing regime; and b) to determine sign of stress in overgrown coral juveniles by measuring variation in photosynthetic efficiency (Fv/Fm).

4.3 Methods

This study was conducted between June 2011- August 2013 in the Wakatobi Marine National Park (South Sulawesi, Indonesia). Thirty settlement panels, constructed following the modified method of Mundy (2000) (described in Chapter 2), were deployed in August 2011 on the reef at Buoy 4 at 6 m (see map in Chapter 2). Panels were left submerged for 22 months to allow settlement of coral larvae and development of coral juveniles.

In June 2013, settlement panels were then collected and taken to the laboratory in seawater. Juveniles were counted and wherever possible identified to family level; those not identifiable were pooled into an 'Others' group. For this experiment I only used coral juveniles on the back side of the panels, which were protected from grazing because of their cryptic position. The back side is usually preferred by coral larvae for settlement, so I expected to find a higher abundance of colonies than on the front side of the panels (see data on coral recruitment rate in

Chapters 2 and 3). Coral juveniles with two or more polyps or a primary polyp with a robust skeleton raised from the surface, as opposed to flat recruits, were included in the study (see Figure 4.1).

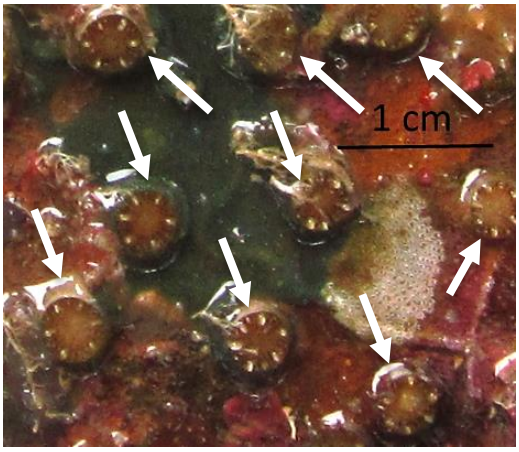


Figure 4.1 Primary polyps (indicated by white arrows) settled on settlement panel used for the fish exclusion experiment. The circular walls (corallites) with the septa of the polyps are visible in the image.

Environmental disturbances and interactions with other organisms cause stress to coral colonies which can display as decrease of coral colony size or a decline in the photosynthetic efficiency (Fv/Fm). The effects of these disturbances can be detected by assessing changes in the size of the coral settlers and variations in photosynthetic efficiency values (Philipp & Fabricius 2003) measured by an Imaging PAM (I-PAM). Despite the great potential of using the I-PAM in the field of coral physiology, to date only a few publications report its use on coral colonies or fragments (Hill *et al.* 2004; Ralph *et al.* 2005; Cooper & Ulstrup 2009). While more studies have used the I-PAM on coral extracts (Howells *et al.* 2011), none have used it on juvenile corals.

Digital images and measurements of the photosynthetic efficiency of the colonies were taken. Fv/Fm values of the coral juveniles was measured using the MAXI version of the I-PAM (Heinz Walz GmbH, Effeltrich, Germany). The photosynthetic parameters were recorded for the overall tile by placing the tiles, one at a time, in a small tank of seawater in a dark chamber for about 10 minutes to allow acclimation of the photoreceptors before being examined under the I-PAM.

Samples were then placed under the I-PAM camera where the application of pulse amplitude modulated light (PAM) measured different fluorescence parameters on the surface of the tile. A measurement light (ML) captured the minimum fluorescence level (Fo), then, an actinic light (AL) was applied and the maximum fluorescence level (Fm) was recorded. Fv was the difference between Fm and Fo and the ratio of Fv/Fm indicates the photosynthetic efficiency. The following settings were applied to the I-PAM: Measuring Intensity 1, Measuring

Frequency 1, Gain 2, Damping 3, Saturating Intensity 10, Red Gain 205, Fm-Factor 1.030, F-Factor 1.000.

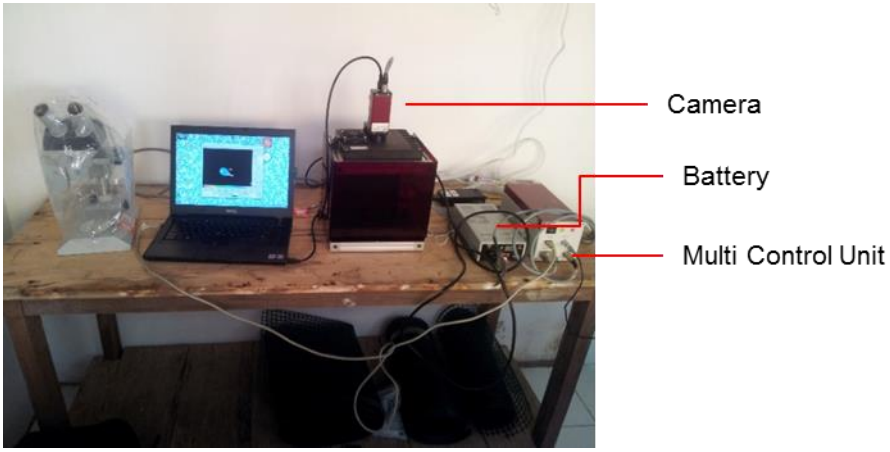


Figure 4.2 Set-up of the I-PAM in the laboratory. The MAXI version of the I-PAM used in my study consisted of: a multi control unit (1) that connects the measuring heads to the camera (2) and is powered by an external battery (3). Measuring heads are positioned on a mounting stand with a bottom plate where the sample is positioned. On the top is the CCD camera. The MCU is also connected to the computer

The segmentation of the frame, analysis and visualisation on a computer screen using the dedicated software ImagingWinGigE V2.45i (see Figure 4.2). Calculation of the photosynthetic values of different areas of the image was performed later using the recorded files. More areas of interest (AOI) were selected on the same image and the software automatically measured the average values of the different fluorescence parameters for each of the selected areas. Comparison of the values between different AOI allowed the detection of differences in fluorescence on the surface. Three different areas (AOI) of each coral juvenile was selected for the measurement of Fv/Fm and a mean was calculated (see Figure 4.3).

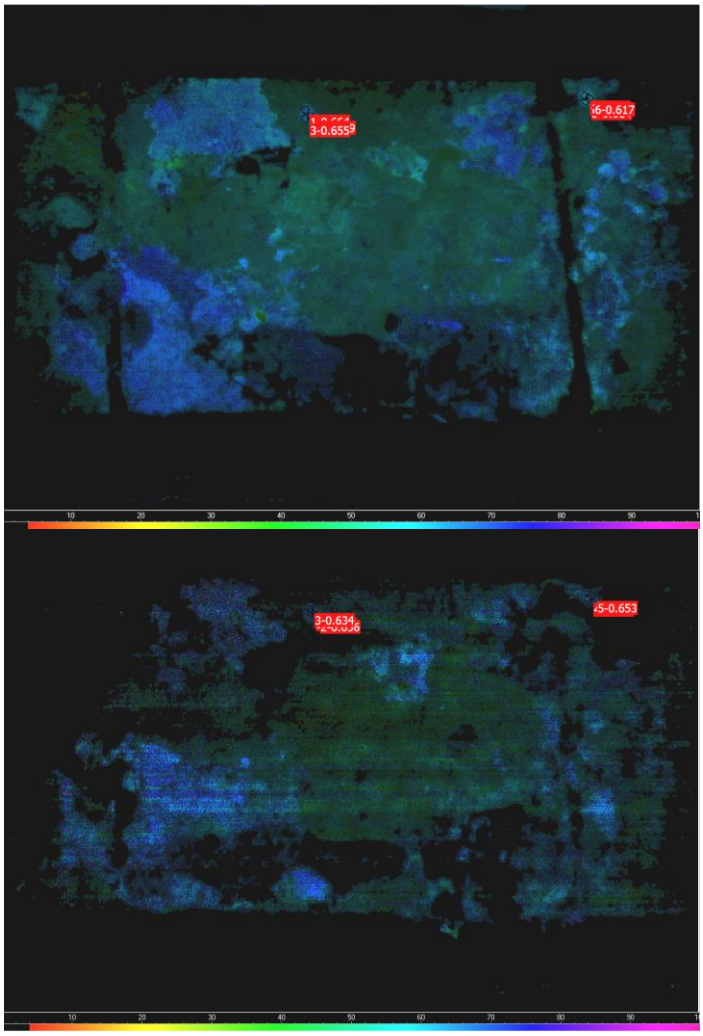


Figure 4.3 The output of the I-PAM analysis. The images were taken of the same tile before (top) and after (bottom) the manipulative experiment. In both digital image the surface of the tile is visible, while the coloration corresponds to the Fv/Fm values for each point of the image (below each digital image is reported the scale bar with the corresponding Fv/Fm values). The red labels indicate the mean Fv/Fm values of three different measurements taken for each of the two coral juveniles present on the tile

The panels were then deployed back on reef at 6 m; fifteen panels at each of the two adjacent replicate sites, Buoy 3 and Buoy 4. Panels at each site were randomly assigned to each of three treatments, which consisted of: 1) complete fish exclusion by full cage to protect the panels from grazing; 2) half-cage in order to test for any cage effect; and 3) control, which had no cages. Cages were built using a PVC net with 15 mm mesh, and were fixed with nails and cable tiles to the reef (see Figure 4.4). Caged tiles were not accessible by macro grazers, such as parrotfish, but smaller fish, such as blennies, may still have been able to pass through the mesh and feed on the tiles. Half-cages were used to assess any cage artefact on the experiment; the half-caged panels were accessible by grazers of all the sizes, as the cages had no tops.

1) 2)

Figure 4.4 Photos of the cage treatments used for the fish exclusion experiment; 1) full cage 2) half-cage, built with a PVC mesh. Full cages completely exclude predation by large fish on the tiles, half-cages have the top side open. The settlement panels were first fixed on the reef wall, treatments (cage, half-cages or control) were then applied haphazardly to the panels

The experimental panels were checked weekly and the mesh of cage treatments was cleaned of algae in order to avoid light shading and sedimentation.

I collected the tiles after 6 weeks, in August 2013, and measured juvenile survival, damage, or change in size. Digital images and Fv/Fm measurement were repeated for each tile following the same procedure used at the beginning of the experiment. Tiles were then bleached following the procedure described in Chapter 2. At the end of the study some of the juvenile colonies were dead from sources other than grazing, such as overgrowth; therefore only coral colonies visible during the initial and the final observation times of the tiles in the laboratory were included in the data analysis for the change in colony size.

Digital images were analysed with Coral Point Count with Excel extensions (CPCe v.4.1; Kohler & Gill 2006). The maximum length (with an error of 0.1 mm) and area (measured using the tool lasso in the software) of each coral settler identified were measured from photos taken at the beginning and end of the experiment. At the end of the experiment, colonies were divided in three groups: survivors, complete mortality (missing colonies), and damaged or 'partial mortality' (which included colonies with either bare skeleton and loss of tissue or partial removal of the skeleton). The effective change in area was measured in cm^2 for all the colonies found at the end of the experiment as relative percentage of area loss (the final size was multiplied by 100, the result was then divided by the initial size). Missing colonies were recorded as having a size loss of -100%.

4.3.1 Data analysis

Data analysis was limited by the small number of juveniles found at each of the replicate sites, therefore the data for the two replicate sites were pooled together to provide a more robust analysis.

The effect of the caging treatment on juvenile mortality and change in colony size were analysed within PRIMER v.6 (Plymouth Marine Laboratory, UK). The data were transformed by square root and a resemblance matrix was constructed based on a presence/absence matrix using the Jaccard coefficient, where absence indicated the colonies that had died. The effect of the fish exclusion treatment on juvenile mortality was assessed using PERMANOVA with one fixed factor (treatment) with three levels. The effects of the size of the coral and its interaction with the treatment on juvenile mortality were investigated by adding the initial size as covariate in the PERMANOVA analysis.

The effect of cage treatment on colony mortality was assessed by analysing the data on the change in juvenile size. The variation in size of the juvenile colonies were measured as a percentage, considering the initial size as 100%. The data were transformed by square root and a Bray-Curtis dissimilarity matrix was produced. The change in juvenile size between treatments was assessed using PERMANOVA analysis with one fixed factor (treatment). The effect of the initial size of the juveniles on the change in size was investigated by adding the covariate 'initial size' to the PERMANOVA analysis with a one fixed factor (treatment). The interaction between treatment and colony size was also analysed. Wherever a significant difference between treatments was found, a pair-wise *post hoc* test was carried out in order to examine which treatment was responsible for the differences found.

PERMANOVA analysis was performed in order to assess significant differences in the variation of average Fv/Fm values between treatments. Differences in Fv/Fm values in coral juveniles available to predation were analysed one fixed factor, treatment, with three levels; cage, half-cage and control. Differences in Fv/Fm values in coral juvenile overgrowth were analysed using treatment as fixed factor and overgrowing organisms as a random factor with seven levels.

Turf algae coverage was measured with CPCe, between the digital images taken of each experimental tile before and after the experiment. Variations in coverage were expressed as percentage. I also measured the proportion of coral colonies overgrown by other organisms

during the experiment and identified the main benthic categories overgrowing the coral colonies.

4.4 Results

4.4.1 Distribution pattern of coral juveniles at the start of the experiment

Overall, 229 juveniles were found on the back side of the 30 panels used in the experiment; 77 colonies were on tiles in the cages, 77 on the control tiles, and 75 in the half-caged tiles. Other colonies were found partially covered by other benthic organisms or had not developed a recognisable skeleton, and these were excluded from the analysis. Juveniles appeared to have settled randomly on the tiles; some settled directly on the tile surface while others settled on the top of other benthic organisms, such as bivalves and CCA. Since juveniles were not equally distributed between replicate sites and treatments, data were pooled together from the two sites.

Colony number found on individual tiles ranged from 0-64. No colonies were recorded on 6 tiles (4 of the control tiles and two of the caged tiles). A total of 64 juveniles colonies were found on a single tile in the control treatment. These juvenile colonies belonged primarly to Family Faviidae and were likely have settled at different times during the experiment due to the range of sizes recorded. The other families identified were Acroporidae, Agariciidae, Pocilloporidae, Poritidae and Dendrophylliidae.

4.4.2 Mortality of juveniles and importance of colony size

Four juveniles were missing at the end of the experiment: two in the cage treatment and two in the control. Damaged coral juveniles (considered as partial mortality of the colony) due to predation was rare across all the treatments: two colonies in the cage treatment, one in the control, and one in the half-cage lost tissue and part of the skeleton. Partial mortality with tissue loss from the skeleton that remained bare was never found (Table 4.1).

Overall mortality, both full and partial, was therefore low, only 3.49% of coral juvenile colonies, and not significantly different between treatments (PERMANOVA, df=2, P=0.11) (Table 4.2).

Table 4.1 Summary of the total number of coral juveniles present in each treatment (cage, half-cage and control) at the beginning of the experiment and the abundance of the colonies affected by mortality: full (missing coral colonies), partial (tissue loss sometimes followed by skeleton loss) and overall mortality

	Total juveniles at the beginning of the experiment	Mortality		
		Full	Partial	Overall
Cage	77	2 (2.6%)	1 (1.3%)	3 (3.9%)
Half cage	75	0	2 (2.7%)	2 (2.7%)
Control	77	2 (2.6%)	1 (1.3%)	3 (5.8%)

Table 4.2 Result of the PERMANOVA analysis assessing differences in coral juvenile mortality between three treatments (cage, half-cage and control) in a fish exclusion experiment. Experiment was conducted at 6 m depth for 6 weeks in the Wakatobi MNP

Factor	df	SS	MS	Pseudo-F	P
Treatment	2	436.0	218.50	1.96	0.11
Residual	82	9093.4	110.90		
Total	84	9529.4			

Overall, the mean size of juveniles was variable between treatments as a consequence of the different time of settlement and variable growth rate between coral families. In the cage treatment the size of the colonies varied considerably, while in the other two treatments the juveniles were more similar to each other in size (Figure 4.5).

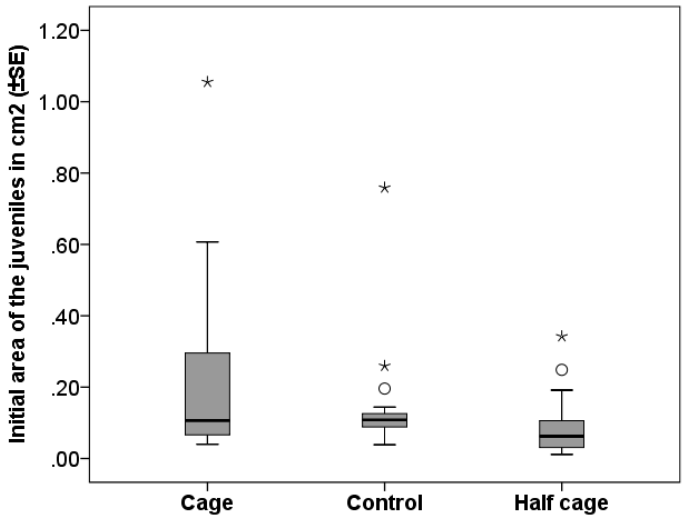


Figure 4.5 Coral juvenile area measured in June 2013, at the beginning of the experiment, in cm^2 (±SE) of coral juveniles in the three treatments (cage, half-cage and control) used in the experiment. Circles and stars indicate minor and major outlier values, respectively

Treatment did not affected mortality rate (PERMANOVA, df=2, P=0.0535) and overall the size of the colonies was not a significant factor for the coral mortality (PERMANOVA, df=1, P=0.2135). The interaction between colony size and treatment was not significant in determining differences in mortality (PERMANOVA, df=2, P=0.6769) (Table 4.3).

Table 4.3 Result of the PERMANOVA analysis assessing the effect of size on the differences in mortality between treatments. Colony size was used as covariate and treatment as the main factor

Factor	df	SS	MS	Pseudo-F	P
Colony size	1	105.27	105.27	0.9529	0.2135
Treatment	2	662.95	331.47	3.0007	0.0535
Colony size x Treatment	2	34.46	17.23	0.1559	0.6769
Residual	81	8761.20	108.16		
Total	84	9529.40			

4.4.3 Effect of fish exclusion treatment on variation in coral colony size

Variation in coral juvenile size was different between treatments, only in the half cage treatment coral juveniles increase their size of an average of 36.86% (± 10.552 SE). In the cage and control treatments I recorded a decrease in coral juvenile size of -8.96 (± 16.77 SE) and -2.31 (±4.64 SE) respectively (Figure 4.6).

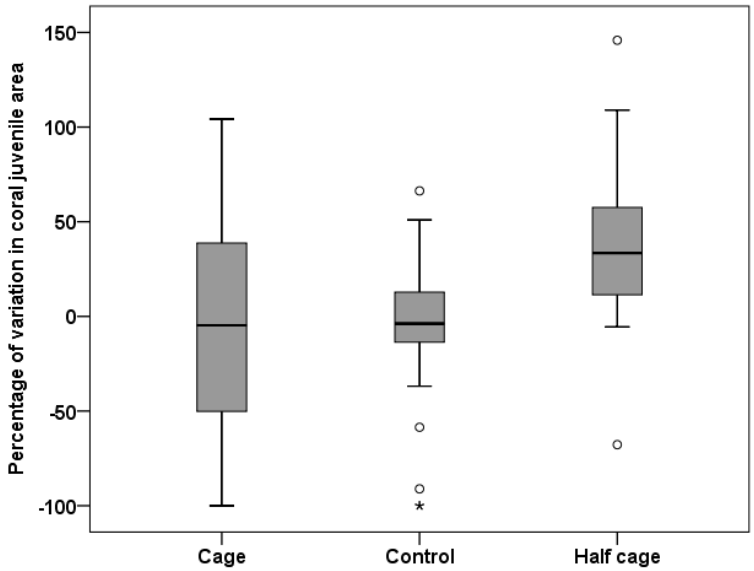


Figure 4.6 Variation in size of coral juvenile colonies showed by treatment (cage, half-cage and control). The average variation by treatment correspond to the black line in the box plots, while the bars show the range of the fluctuation. Circles and stars represents outlier values. Circles and stars indicate minor and major outlier values, respectively

Overall, the variation in the area of coral juveniles that occurred during the experiment in all the treatments was not significant (PERMANOVA, df=2, P=0.0551) (Table 4.4).

Table 4.4 Result of the PERMANOVA analysis assessing the differences in the variation in area in coral juvenile colonies divided in three treatments (cage, control and half cage) between the beginning and the end of a fish exclusion experiment. Treatments were applied to settlement panels deployed on the reef at 6 m depth for 6 weeks in the Wakatobi MNP

Factor	df	SS	MS	Pseudo-F	P
Treatment	2	627.2	313.62	2.7407	0.0551
Residual	74	8468	114.43		
Total	76	9095.3			

When the initial size of the juveniles was included as covariate in the analysis, treatment was found to be statistically significant for differences in the change in size between treatments (PERMANOVA, df=1, P=0.0472) showing that initial size influence the variation of colony size. Overall the initial size of the colony was found to influence relative change in size. Smaller coral colonies increased in size faster than bigger colonies. However, the interaction between colony size and treatment was not statistically significant; change in size was random between treatments (Table 4.5).

Table 4.5 Result of the PERMANOVA analysis detecting the effect of the initial size of juvenile colonies on the change in size for three different treatment groups (cage, control and half cage) in a fish exclusion experiment

Factor	df	SS	MS	Pseudo-F	P
Colony size	1	3297.20	3297.20	46.5160	**0.0001**
Treatment	2	402.24	201.12	2.8327	**0.0472**
Colony size * Treatment	2	363.03	181.51	0.0972	0.0972
Residual	71	5032.80	70.88		
Total	76	9095.30			

The pair-wise test showed that the control and half-cage treatments were the two groups most different from each other with respect to the change in colony size (Table 4.6).

Table 4.6 Pair-wise *post hoc* comparison to detect the treatments responsible for the differences found with the PERMANOVA analysis that detected the effect of the initial size of juvenile colonies on the change in size for three different treatment groups (cage, control and half cage)

Groups	t	P
Cage, Control	1.5568	0.1149
Cage, Half cage	0.2207	0.9693
Control, Half cage	2.3465	0.0164

Effect of treatment on variation in Fv/Fm in coral juveniles not affected by grazers

Measurements of the variation in photosynthetic efficiency of coral juveniles were conducted on only 42 of the 84 (50%) colonies: 57.1% of the colonies (*n*=8) in the cage group, 57.9% (n=23) in half-cage treatments, and 44.2% (*n*=11) in the control group.

The largest difference in Fv/Fm values compared to the other treatments occurred in the control; variation in the half-cage treatment was evident, but it did not vary significantly from the others (Table 4.7 and Figure 4.7). Significant variability was found in the variation of average Fv/Fm values between treatments, especially between coral juveniles located in the cage and control group, showing that treatment had an effect on coral juveniles (Table 4.8 and 4.9).

Table 4.7 Variation in photosynthetic efficiency (Fv/Fm) values occurred in coral juveniles located in three treatments (cage, half-cage and control) during a fish exclusion experiment. Coral juveniles were placed on settlement panels deployed at 6 m depth on the reef, treatments were applied to the panels haphazardly and the experiment pasted 6 weeks

N.	Treatment	Start mean	End mean	Δ	Variation (%)
1	Cage	0.430	0.444	**0.014**	**3.18**
2	Cage	0.661	0.632	- 0.029	- 4.34
3	Cage	0.656	0.638	- 0.018	- 2.69
4	Cage	0.648	0.688	**0.039**	**6.07**
5	Cage	0.605	0.634	**0.029**	**4.74**
6	Cage	0.627	0.513	- 0.114	- 18.17
7	Cage	0.560	0.638	**0.077**	**13.80**
8	Cage	0.623	0.589	- 0.034	- 5.51
9	Control	0.647	0.473	- 0.174	- 26.88
10	Control	0.683	0.489	- 0.193	- 28.32
11	Control	0.608	0.449	- 0.159	- 26.19
12	Control	0.637	0.459	- 0.178	- 27.94
13	Control	0.614	0.448	- 0.166	- 26.98
14	Control	0.664	0.578	- 0.086	- 12.90
15	Control	0.594	0.421	- 0.173	- 29.12
16	Control	0.581	0.513	- 0.068	- 11.70
17	Control	0.643	0.479	- 0.164	- 25.51
18	Control	0.643	0.429	- 0.214	- 33.28
19	Control	0.489	0.452	- 0.037	- 7.57
20	Control	0.584	0.464	- 0.120	- 20.55
21	Control	0.566	0.537	- 0.029	- 5.18
22	Control	0.625	0.377	- 0.249	- 39.76
23	Control	0.535	0.422	- 0.114	- 21.21
24	Control	0.595	0.506	- 0.089	- 14.96
25	Control	0.623	0.471	- 0.152	- 24.40
26	Control	0.557	0.455	- 0.102	- 18.31
27	Control	0.656	0.547	- 0.109	- 16.62
28	Control	0.612	0.406	- 0.206	- 33.61
29	Control	0.643	0.490	- 0.153	- 23.79
30	Control	0.617	0.640	**0.023**	**3.73**
31	Control	0.663	0.647	- 0.015	- 2.31
32	Half-cage	0.511	0.378	- 0.133	- 25.98
33	Half-cage	0.432	0.294	- 0.138	- 32.00
34	Half-cage	0.608	0.428	- 0.180	- 29.66
35	Half-cage	0.675	0.418	- 0.257	- 38.09
36	Half-cage	0.643	0.659	**0.016**	**2.49**
37	Half-cage	0.677	0.641	- 0.036	- 5.27
38	Half-cage	0.623	0.674	**0.051**	**8.13**
39	Half-cage	0.620	0.626	**0.006**	**0.97**
40	Half-cage	0.630	0.674	**0.044**	**6.98**
41	Half-cage	0.672	0.658	- 0.014	- 2.13
42	Half-cage	0.667	0.516	- 0.151	- 22.63

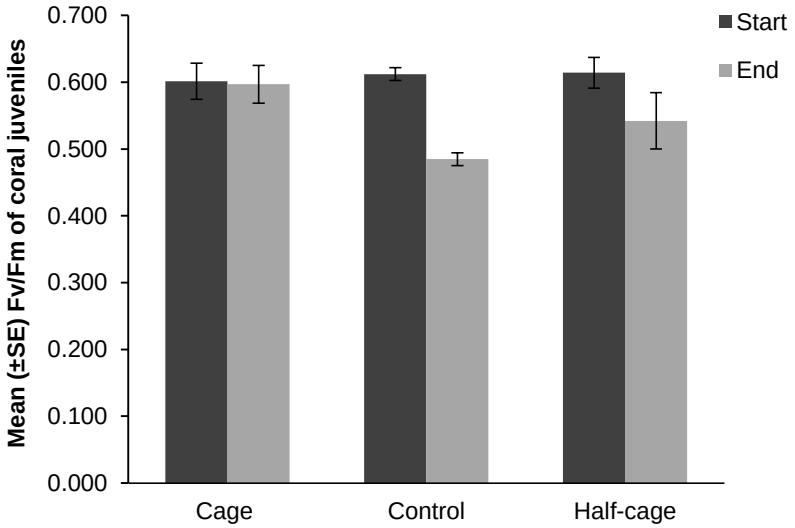


Figure 4.7 Mean (± Standard Error) photosynthetic efficiency (Fv/Fm) values for coral juveniles placed in three treatments (cage, half-cage and control) at 6 m depth at Buoy 3 and Buoy 4 in a fish exclusion experiment that lasted 6 weeks. Values were measured at the beginning (dark gray bars) and at the end (light gray bars) of the experiment. A decrease in the mean Fv/Fm values was recorded across all treatments and was more evident in the control and half-cage treatments

Table 4.8 Result of the PERMANOVA analysis assessing variations in photosynthetic efficiency (Fv/Fm) values in coral juveniles kept in three different treatments (cage, half-cage and control) occurred in a fish exclusion experiment lasted 6 weeks and conducted at 6 m depths

Factor	df	SS	MS	Pseudo-F	P
Treatment	2	51.6	25.8	8.0415	**0.0014**
Residual	39	125.0	3.21		
Total	41	176.6			

Table 4.9 Pair-comparisons between variation in average Fv/Fm values of coral juveniles between the beginning and end of a fish exclusion experiment using three different treatments (cage, half-cage and control)

Groups	t	P
Cage, Control	4.56	**0.0003**
Cage, Half-cage	1.63	0.1223
Control, Half-cage	1.93	0.0600

4.4.4 Assessment of the main benthic categories overgrowing coral juveniles

A total of 134 (58.51%) of the juveniles initially identified were overgrown by other benthic organisms. These colonies were unevenly distributed between treatments: 56 juveniles were on the caged tiles (72.8% of the colonies found at the beginning of the experiment in the cage treatment), 25 juveniles on the control tiles (32.5% of the initial number of colonies) and 56 colonies on the half-caged tiles (74.7% of the initial number of colonies). Algae were covering

73.86% of the 134 overgrown juveniles, bryozoa 10.82%, and the remainder were covered by sponges, tunicates and other organisms. Among the algae category, the most common taxa found overgrowing juveniles were turf algae (30.52%), green algae (or macroalgae) (15.8%) and CCA (11.09%) (Figure 4.8).

Only 66 of the 134 coral juvenile colonies were overgrown during the experiment; 25 colonies in the cage treatment, 36 in the half-cage and 5 in the control. 80.3% of the coral colonies were overgrown by algae: 36.36% by turf algae, 16.67% by green algae, 18.18% by red algae and 9.01% by CCA (Figure 4.8).

The proportion of benthic groups overgrowing coral juveniles before the beginning of the experiment, measured at the first laboratory analysis, and during the experiment was similar. Benthic groups colonised exposed tiles similarly to before being exposed, however this finding can be due to grown of benthic organisms already present on the tiles. Sponge did not overgrown coral juveniles during the experiment duration; this could be due to their preferences for more cryptic habitat, such as the lower part of the settlement panel. There are few differences between treatments; tunicates overgrown juveniles only in the cage treatment, red algae and turf algae did not overgrown and juvenile in the half-cage treatment. These differences are more likely due to different exposition of the tiles rather than to cage effect.

During the experiment an increase in turf algal coverage was observed on the tiles, which was consistent between treatments (PERMANOVA, df=2, $P>0.05$).

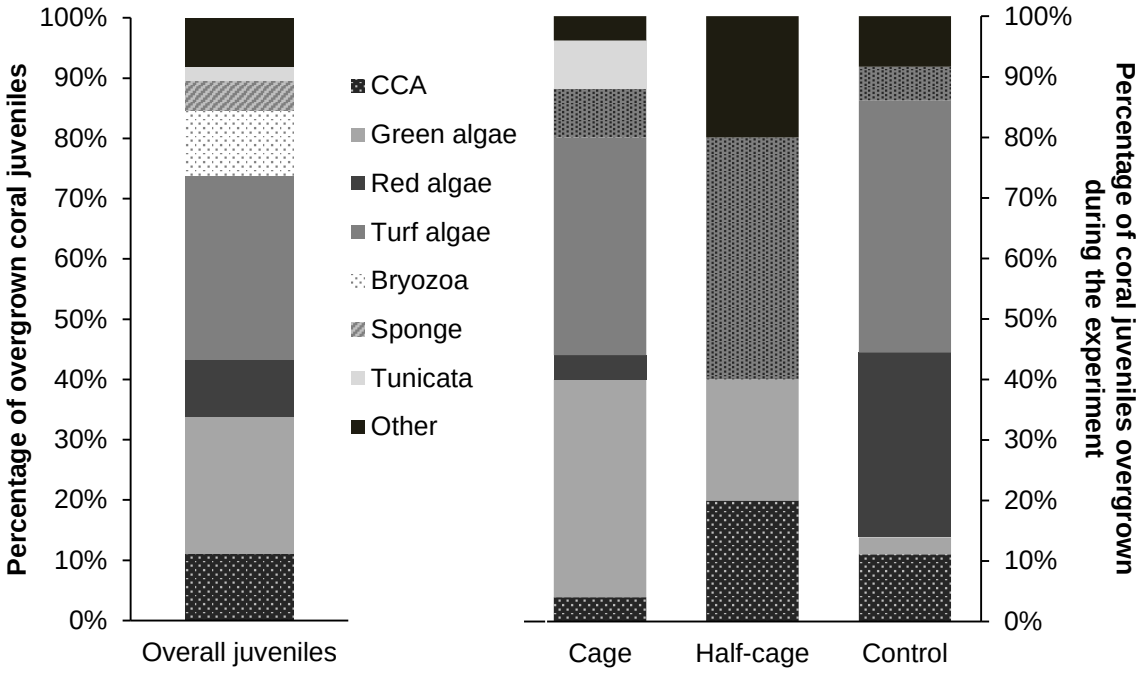


Figure 4.8 Percentages of the coral juveniles colonies overgrown by benthic families in three treatments (cage, half-cage and control) during a fish exclusion experiment conducted at 6 m depth. On the left: overall juvenile colonies found overgrown at the end of the experiment; on the right: juveniles colonies overgrown during the 6 weeks of experimental period.

Effect of overgrowing benthic organisms on variation in Fv/Fm in coral juveniles

Analysis of photosynthetic efficiency was assessed only on coral juvenile colonies not completely overgrown and where the Fv/Fm values were recordable both at the beginning and at the end of the experiment (Table 4.10).

Overall, a decrease in Fv/Fm values occurred in all the three treatments and there were no differences between treatments (Figure 4.9).

Table 4.10 Variation in Fv/Fm values between the beginning and the end of the experiment in coral juveniles overgrown by different benthic groups. Coral juvenile colonies were divided by treatment (cage, control and half-cage) and overgrown benthic group

N.	Treatment	Overgrown by	Start mean	End mean	Δ	Variation (%)
1	Cage	Bryozoa	0.519	0.664	0.145	- 0.15
2	Cage	Bryozoa	0.549	0.690	0.141	- 0.14
3	Cage	CCA	0.617	0.643	0.026	- 0.03
4	Cage	Green algae	0.635	0.643	0.008	- 0.01
5	Cage	Green algae	0.630	0.252	- 0.378	0.38

N.	Treatment	Overgrown by	Start mean	End mean	Δ	Variation (%)
6	Cage	Green algae	0.667	0.000	- 0.667	0.67
7	Cage	Green algae	0.608	0.165	- 0.443	0.44
8	Cage	Green algae	0.611	0.000	- 0.611	0.61
9	Cage	Green algae	0.631	0.682	0.051	- 0.05
10	Cage	Green algae	0.651	0.725	0.074	- 0.07
11	Cage	Green algae	0.518	0.420	- 0.098	0.10
12	Cage	Green algae	0.604	0.616	0.012	- 0.01
13	Cage	Green algae	0.557	0.243	- 0.314	0.31
14	Cage	Green algae	0.671	0.651	- 0.020	0.02
15	Cage	Green algae	0.651	0.000	- 0.651	0.65
16	Cage	Green algae	0.659	0.000	- 0.659	0.66
17	Cage	Tunicata	0.631	0.671	0.040	- 0.04
18	Cage	Turf	0.671	0.592	- 0.079	0.08
19	Cage	Turf	0.639	0.616	- 0.023	0.02
20	Cage	Turf	0.651	0.647	- 0.004	0.00
21	Cage	Turf	0.622	0.675	0.053	- 0.05
22	Cage	Turf	0.651	0.498	- 0.153	0.15
23	Cage	Turf	0.243	0.235	- 0.008	0.01
24	Control	Bryozoa	0.571	0.630	0.059	- 0.06
25	Control	Bryozoa	0.578	0.510	- 0.068	0.07
26	Control	CCA	0.447	0.361	- 0.086	0.09
27	Control	CCA	0.572	0.374	- 0.198	0.20
28	Control	Green algae	0.650	0.000	- 0.650	0.65
29	Control	Green algae	0.635	0.482	- 0.153	0.15
30	Control	Green algae	0.617	0.646	0.029	- 0.03
31	Control	Sponge	0.552	0.341	- 0.210	0.21
32	Control	Sponge	0.094	0.180	0.086	- 0.09
33	Control	Turf	0.715	0.671	- 0.044	0.04
34	Control	Turf	0.710	0.631	- 0.079	0.08
35	Control	Turf	0.591	0.391	- 0.200	0.20
36	Control	Turf	0.676	0.663	- 0.013	0.01
37	Control	Turf	0.658	0.000	- 0.658	0.66
38	Control	Turf	0.575	0.528	- 0.048	0.05
39	Half cage	Ascidian	0.573	0.404	- 0.169	0.17
40	Half cage	CCA	0.628	0.480	- 0.148	0.15
41	Half cage	CCA	0.651	0.640	- 0.011	0.01
42	Half cage	CCA	0.580	0.608	0.028	- 0.03
43	Half cage	Green algae	0.627	0.510	- 0.117	0.12
44	Half cage	Green algae	0.533	0.424	- 0.109	0.11
45	Half cage	Green algae	0.549	0.435	- 0.114	0.11
46	Half cage	Green algae	0.624	0.000	- 0.624	0.62
47	Half cage	Turf	0.533	0.000	- 0.533	0.53
48	Half cage	Turf	0.639	0.518	- 0.121	0.12

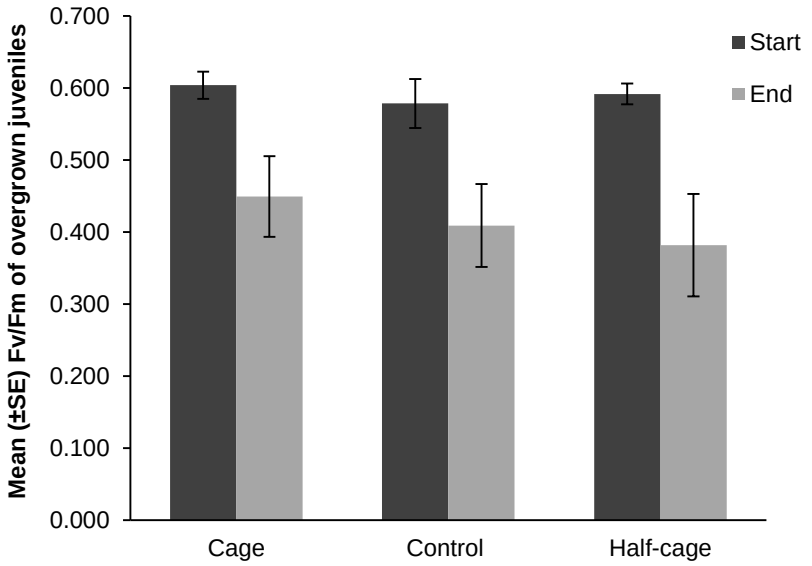


Figure 4.9 Variation in mean (± Standard Error) Fv/Fm values in coral juveniles overgrown by benthic organisms and subjected to three different treatments (cage, control and half cage) in a fish exclusion experiment for 6 week at 6 m depth

Table 4.11 Summary of the average values of Fv/Fm recorded in coral juveniles subjected to three different treatments (cage, half-cage and control) and overgrown by different benthic organisms during a fish exclusion experiment. Because of the nature of this study, cases are distributed haphazardly between treatments and benthic groups

Overgrown by	Treatment	Between benthic groups		Benthic groups by treatment	
		Start	End	Start	End
Ascidian (1)	Half-cage	0.573	0.404	0.573	0.404
Bryozoan (4)	Cage (2)			0.534	0.677
	Control (2)	0.554	0.624	0.574	0.570
CCA (6)	Control (2)			0.510	0.368
	Cage (1)			0.617	0.643
	Half-cage (3)	0.583	0.518	0.620	0.576
Green algae (20)	Cage (13)			0.623	0.338
	Control (3)			0.634	0.376
	Half-cage (4)	0.616	0.345	0.583	0.342
Sponge (2)	Control (2)	0.323	0.261	0.323	0.261
Tunicate (1)	Cage	0.631	0.671	0.631	0.671
Turf algae (14)	Cage (6)			0.580	0.544
	Control (6)			0.654	0.481
	Half-cage (2)	0.612	0.476	0.586	0.259

The samples were divided by the benthic organism that had overgrown them and by treatment to investigate the effects of interactions between treatment and benthic group on the photosynthetic efficiency of coral juveniles (Table 4.11).

Overall, the variation in Fv/Fm values was evident by benthic groups overgrowing the coral juvenile colonies. Especially green and turf algae affected the photosynthetic efficiency of the colonies (Figure 4.10), losing 44% and 22.2% of their initial Fv/Fm value.

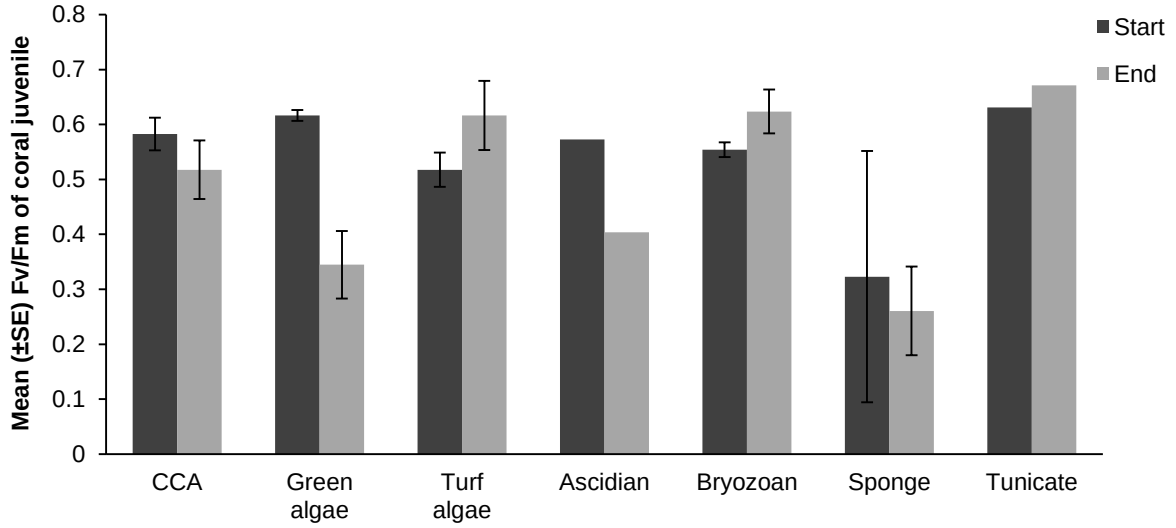


Figure 4.10 Mean (± Standard Error) Fv/Fm values in coral juveniles overgrown by different benthic organisms during a fish exclusion experiment for 6 weeks. Ascidian and tunicate data are based on only one sample and therefore do not have error bars. The difference between the bars at the beginning and at the end of the experiment show the variation in Fv/Fm value that occurred for each benthic group involved in the interaction with coral juveniles

Despite the evident fluctuation in the Fv/Fm values, the PERMANOVA analysis of the differences in variation between treatment or benthic organisms overgrowing the coral did not show any significant differences (Table 4.12). This result might be due to the small number of samples or the absence of samples from some groups.

Table 4.12 Results of the PERMANOVA analysis assessing the variation in Fv/Fm in coral juveniles subjected to three different treatments (cage, control and half cage) and overgrown by different benthic organisms during a fish exclusion experiment

Factor	df	SS	MS	Pseudo-F	P
Treatment	2	39.05	19.52	13.99	0.3388
Overgrown by	6	186.59	31.1	13.79	0.2482
Treatment * Overgrown	5	60.94	12.19	0.54	0.7436
Residual	34	766.66	22.55		
Total	47	1098.50			

4.5 Discussion

In this chapter, I investigated the impact of predation on coral juvenile survivorship. The fish exclusion treatment conducted did not increase juvenile survivorship rates. Mortality due to grazing activity, either full or partial (damaged colonies), affected only 3.49% of the juvenile. Juvenile mortality was found in all the treatments and the size of juvenile did not influence mortality rate. Changes in size were detected in the juvenile colonies not affected by predation; colony growth or reduction in size was also consistent between treatments. Initial colony size was important in determining differences in change in size between treatments. Differences in decrease in photosynthetic efficiency values between treatments suggest that coral juveniles exposed to fish grazing are more stressed. At the end of the experiment, 28.38% of the colonies initially identified were found overgrown by other benthic organisms, mostly algae. However, only green algae and turf algae caused significant stress in coral colonies.

Overall, grazing and corallivours fish did not induced mortality in coral juvenile population, although the grazing activity caused some stress to the colonies. The impact of the coral juvenile overgrowing process by other benthic organisms, particularly with algae, was likely to affect coral juveniles survivorship.

4.5.1 Low impact of grazing fish on juvenile survivorship

Predation by fish did not appear to be the main cause of mortality in young coral populations in the Wakatobi; the exclusion of grazers did not significantly affect coral survival between different treatment groups. Mortality between treatments was similar: only four recruits were completely missing at the end of the experiment and five were affected by partial mortality that was likely connected to grazing activity. In previous caging experiments conducted with recruits that were only a few weeks old, the mortality rate was correlated with exposure to grazers, with corals on control tiles having the highest mortality compared to those protected by cages (Penin *et al.* 2011; Trapon *et al.* 2013c). The authors suggested that grazing fish were the main group responsible for recruit mortality. However in my study, full mortality, despite its low rate, was found only in the cage and half-cage treatments, while no recruits were missing from the control tiles, despite them being fully exposed and available to predators.

A fish survey conducted in the Wakatobi in 2011 found the overall grazing fish biomass on the reef crest of my research site to be 83.71 (±10.89) kg/250m^2 with this values increasing to 102.55 (±15.02) kg/250m^2 when occasional grazers and corallivores were included (Curtis-

Quick 2013). These values are much higher than those found at other locations: on the Great Barrier Reef parrotfish abundance was found to be up to 7.1 (±0.3) kg/250m^2 (Trapon *et al.* 2013c), while the overall grazing fish was 5 kg/250m^2 (Hoey & Bellwood 2008). At Lizard Island it was between 10.5 (±3.0) kg/250m^2 and 21.8 (±3.8) kg/250m^2 (Brandl *et al.* 2013) and in the Caribbean it was over 5.25 kg/m^2 (Sandin & McNamara 2012). Trapon *et al.* (2013c) found a correlation between parrotfish abundance and recruit mortality. In the Wakatobi, Achanturidae and Scaridae were the most common families, however unlike Trapon *et al.* (2013c) I did not observe scars left by bigger grazers like parrotfish on my experimental tiles. The lack of scars suggest that grazing could be due mostly to small fish that were able to move through the cage mesh. In my experiment, the corals on the caged tiles were apparently affected similarly to those in the control treatment, suggesting similar grazing effects between treatments. This result contrasts with the findings of a study by Hughes *et al.* (2007), who found the abundance of grazers in the cages to be lower than for other treatments, such as control and open cages, by up to seven times.

Baria *et al.* (2010) found that the exclusion of predators in cage treatments actually increased coral recruit mortality due to competition with algae. At the same time, they found that tiles in half-cages were accessible only to small fish and grazing invertebrates. These grazers were likely regulating the algal growth without removing recruits, resulting in low coral mortality (Miller & Hay 1998). In my experiment the number of damaged colonies in the cages was low and might be due to the low abundance of small fish, such as blennies and wrasses, in the Wakatobi, however data on small size fish in the Wakatobi were not available.

For all of the treatments, size of the juveniles apparently did not influence the possibility of their being accidentally removed from the tiles or damaged by grazing fish. Differences in size were low between colonies, although the juveniles belonged to different families and settled at different times, as a consequence there was not really a sufficient number of colonies of different sizes to test the effect of the size.

In my experiment the complex substratum on the tiles presented several cryptic microhabitats that offered protection to the coral colonies. The efficiency of refuges in enhancing recruit survivorship against predation has been assessed in multiple studies (Nozawa 2008; Brandl *et al.* 2013; Cooper *et al.* 2014; Edmunds *et al.* 2014b). However, the benefit of refuges was available only to small recruits, which were the optimal size to occupy the more effective refuges (Gleason 1996), and the colonies that exceeded this size were more easily accessible

by grazers and predators (Brandl *et al.* 2013). In my research most of the colonies were small and had only a few polyps, however I did not assess their position on the tiles to detect the effect of refuges on juvenile survivorship.

Overall, the small number of juveniles and their similarity in size did not allow me to obtain robust results and assess any correlation between mortality, colony size, and treatment. However I assessed that grazing might have a role on variation of coral Fv/Fm values; coral juveniles in fish exclusion treatment did not showed decline in Fv/Fm. This finding needs to be further investigated to assess the impact of grazing activity on coral juvenile physiology.

4.5.2 Consistent change in size in coral colonies between treatments

I also found that the change in coral colony size was not affected by the treatment but it was correlated with the size of the colonies. Despite smaller colonies being more likely to increase in size and bigger colonies being more likely to reduce in size, it was not possible to assess any specific correlation in my experiment.

Different benthic organisms, known to interfere with the coral growth rates, were present on the experimental tiles; for example, algae such as CCA and turf algae. During my study I found an increase in turf algae of approximately 15% on the experimental tiles and this was consistent between treatments. When algal regulation is missing (e.g. from grazers), algae increase in abundance and compete for the available space. In cases of contact between algae and coral colonies, often the first response of corals is to shrink before being eventually being overgrown by the algae (Davies *et al.* 2013). However, in my study I did not measure the interaction between benthic organisms and juveniles in order to assess the nature of their relationship (see Chapter 5).

4.5.3 Low competence of coral juveniles for competition with other benthic organisms

Over the course of my experiment, 28.38% of the juveniles initially identified were covered by other benthic organisms. Overgrowth was common in all the treatments. In accordance with previous studies (see Lirman 2001; Box & Mumby 2007; Trapon *et al.* 2013c), a large proportion (73.9%) of the overall overgrown juveniles were found partially or completely covered by algae, especially by turf algae and CCA. It was not possible to determine if overgrowth was the cause of colony death or if the coral died as a result of other stressors before being covered.

Adult corals are stronger competitors than turf algae, and when turf algae was found overgrowing corals it usually indicated death from other causes (Hughes 1989; Coyer *et al.* 1993). It is also possible that coral juveniles are overgrown by turf algae only after colony death due to other reasons (reviewed by McCook *et al.* 2001). However, juvenile colonies overgrowth by either turf and green algae showed a decrease in Fv/Fm; it is not excluded that juveniles death is a consequence of overgrown, but full mortality takes longer than 6 weeks, which was the duration of this study. It is possible that initially coral juveniles are more resistant to overgrowing organisms and use their energy to react; this behaviour would explain the decrease in Fv/Fm without either mortality or overgrown. However, this study do not inform about later stages of the overgrowing process, so it is not possible to assess if the coral juvenile died and if this happens before or after being completely covered.

4.5.4 Limitations of the experimental design

The experimental design used in this study was improved after a preliminary study conducted in 2012 in order to assess the effect of predation and sedimentation on coral recruit survival (see Appendix I). In the present study I enhanced the previous experiment design with a new set-up and minimised disturbance. However, despite the precautions taken, it is possible that a certain amount of disturbance was still present.

The distribution of juveniles was unbalanced between my treatments. Coral larvae were left settling naturally on the submerged panels and the panels were randomly distributed between treatments to avoid any bias. As a consequence there was a high variability in abundance and species between experimental tiles. Although the overall number of juveniles was similar between treatments, it was different between sites. At the end of the experiment the number of juveniles available for the data analysis was unequal between treatments.

The age of the tiles had an impact on the outcome. In previously published experiments clean tiles were used to carry out similar studies with few-week old recruits, mostly settled in controlled conditions. Those tiles were first pre-conditioned in seawater in order to obtain a biofilm on the surface, which promoted larvae settlement (Baria *et al.* 2010; Penin *et al.* 2011; Trapon *et al.* 2013b) and also algal growth. In contrast, the panels used in my experiment presented a complex substratum after being submerged for two years; many benthic invertebrates and algae occupied the surfaces, sometimes overgrowing each other. The advantage of using older tiles was that they were more similar to natural conditions (Brandl *et*

al. 2013), but as a consequence my results are not directly comparable with those of previous studies.

It is known that artefacts used in manipulative experiments can have an impact on the results (Hall *et al.* 1990; Lewis 1996; Connell 1997b; Cooper *et al.* 2014). In particular, the use of cages in order to examine the effect of predators on benthic invertebrate survivorship, such as that of coral, sponges and barnacles (Jenkins *et al.* 1999; Powell 2013; Cooper *et al.* 2014), has been long discussed. Half-cages are largely used to test the effect of the artefact; their open side allows access to big fish and other predators to the tiles, while small fish have the freedom to move within the cages in the half cage and control treatments. As a consequence, differences found between the half-cage and control treatments are likely to be due to the cage artefact.

Cages have also been criticised for their potential to modify water flow, reduce light availability, and change the amount of nutrients inside the cage (Connell 1997b; Box & Mumby 2007). In order to minimise any effect due to the cages, in my experiment the full and half-cages were cleaned weekly to remove fouling organisms and algae that had settled on the mesh, which were likely to trap sediments and shade light from the tiles.

There were some impediments to the collection of data on photosynthetic efficiency of the coral colonies. Despite the great potential of the I-PAM I could not detect any variation in the photosynthetic efficiency of part of the coral juveniles. Panels were mostly covered by benthic organisms and, despite the 0.5 mm resolution of the I-PAM camera, it was difficult to localise juveniles on the images recorded by the I-PAM because of their short distance from the benthos. Some images, especially those taken at the end of the experiment, presented some noise, for example the fluorescence of the seawater in the tank might have disturbed the recordings. Despite the adjustment of the I-PAM settings, noise was still present. To improve the use of the I-PAM for a future experiment, more precise mapping of the position of the coral juveniles could be undertaken before the beginning of the experiment and the neighbouring benthic organisms could be scraped off from the tiles.

Some improvements were identified to enhance this experimental design for a future study. A longer duration for the experiment that included additional time for the initial examination of the tiles would allow more precise counts and measurements of the juveniles to be made, and would enable a more balanced redistribution of the juveniles between sites and treatments. In addition, I would also examine the position of the juveniles to see if they were located in crevices or in more exposed locations on the tiles. Furthermore, in order to better assess the

effect of grazing, I would consider scraping off organisms that could interfere with juvenile survivorship, such as ascidians and sponges, from the tiles. This action would also improve the efficiency of the I-PAM measurements on the smaller juvenile colonies. During the experiment, periodic measurements of light availability and sedimentation rate inside the full and half-cages would also help to better understand the role of light in juvenile mortality.

This study explored the role of grazing on juvenile corals (as opposed to coral recruits or adults) using colonies grown *in situ* that had not been exposed to grazing before. Based on the outcomes (and the limitations identified above), predation is unlikely to be the driver of juvenile mortality and other factors apparently play a role in regulating the life history of corals in the post-settlement phase. The relationship with other benthic organisms likely influenced the juvenile growth and the mortality processes. Algae were the most common organisms associated with overgrown juvenile colonies, although I did not recorded mortality in overgrown coral colonies, green and turf algae cause high stress to juveniles and impacted their survivorship.

Chapter 5 Influence of ecological succession on coral recruitment

5.1 Abstract

During the colonisation of new substrates, associative and competition processes occur that shape the benthic assemblage. Coral recruitment patterns are influenced by the development of the benthos and some benthic groups, such as crustose coralline algae (CCA), promote or inhibit coral settlement and growth. The interactions between juvenile corals and benthic organisms can influence coral survivorship. In this chapter, I investigated the initial colonisation of artificial bare substrate, the impact of the developing benthic assemblage on coral recruitment and the interactions occurring between benthic organisms and juveniles. Settlement panels were deployed for one and two year periods on reefs in the Wakatobi Marine National Park (South Sulawesi, Indonesia) to examine changes in the benthic community over time. Marked changes occurred in the relative coverage of the benthic organisms across years and on the sides of the panels. The front sides of panels were characterised by algae, especially CCA and turf algae, in both years, while on the back of the panels there was a shift from invertebrate dominance, mostly bryozoans, to equal coverage of invertebrates and algae. In the second year, benthic organisms grew both horizontally and vertically, and consequently the assemblage complexity increased, especially on the back of the panels. Approximately 10% of the panel substrate remained bare in the second year. The benthic coverage was not correlated with coral recruitment patterns, however in the second year recruitment rates were higher on the back side of the panels, where the benthic structure was more complex. There was an increase in the number of interactions between coral juveniles and benthic organisms in the second year, but this was not linearly correlated with the increase in juvenile abundance. The highest number of spatial interactions involving coral juveniles occurred with CCA and the most common outcomes were stand-offs, where no organism was prevailing on the others. Coral juveniles were rarely found overgrowing CCA, bryozoans and bivalves, but they were partially overgrown by CCA, sponges and tunicates, despite the high coral survival rate suggests that overgrowth was unlikely to be the main cause of juvenile mortality. Overall, my study showed that changes in the benthic assemblage was not correlated with coral recruitment rates, however changes in benthic structural complexity may promote coral juvenile survivorship.

5.2 Introduction

Coral reefs support many organisms with complex interactions and species associations that are fundamental for maintaining diversity (Jackson & Buss 1975). For example, reef fish diversity, abundance and biomass, and coral cover are positively correlated with reef complexity (Pratchett *et al.* 2014). High reef complexity provides refuges to many marine species from predation, shelters, and resources to reproduce and feed (Graham & Nash 2013). Loss of reef complexity due to different stressors, such as bioerosion caused by high densities of sea urchins, leads to degradation and modification of the habitat (McClanahan & Shafir 1990). Algal cover increases on bare reef substrate freed by the loss of other benthic organisms, such as corals; these changes affect the existing interactions and associations (Hughes *et al.* 2010). Therefore, the structure of the reef is considered an indicator of the health of the reef ecosystem.

Benthic assemblage composition is influenced by a range of physical and biological factors and the relationships, both intra- and inter-specific, between the different populations (Vermeij 2006). The processes that shape benthic assemblages are dynamic and vary in the time; they include seasonal abiotic and biological factors, such as larvae availability (Fairfull & Harriott 1999; Glassom *et al.* 2004), fluctuations in environmental parameters (Haas *et al.* 2010), climatic events (Ban *et al.* 2014), associations between benthic organisms (Diaz-Castaneda & Almeda-Jauregui 1999; Vermeij 2006; Easson *et al.* 2014), and competition for space and resources, such as light and nutrients (Tanner *et al.* 2009; Price 2010).

During the early developmental stages of benthic assemblages, new species join the benthic community until the maximum density/coverage is reached, however, the diversity continues to change over time through changes in dominance (Diaz-Castaneda & Almeda-Jauregui 1999; Brandl *et al.* 2013; Williams *et al.* 2013). The succession of benthic assemblages is determined by the order of colonisation, growth rate, life span, and relationships between the benthic organisms (Connell 1997a; Fairfull & Harriott 1999).

Recruitment is variable between species, but the interactions between benthic organisms are fundamental for successful recruitment. For example, some organisms have been found to recruit only next to adult conspecifics, while others require biological cues or the presence of specific conditions, such as specific light conditions or the presence of refuges (Maida *et al.* 1994; Brandl *et al.* 2013). The benthic groups present on a reef together create a complex three-

dimensional structure with trophic webs that can also influence recruitment (Diaz-Castaneda & Almeda-Jauregui 1999).

Competitive networks are thought to connect different populations in benthic communities and maintain reef diversity (Buss & Jackson 1979). The associations between organisms are established at different life history stages (Bruno *et al.* 2003; Idjadi & Edmunds 2006); these relationships can be temporary or last for the entire lifetime of the organisms involved and can bring individual or mutual benefits. For example, a tropical sponge has been found in a stable mutualistic association with a red algae; together they are able to live and persist in shallow water; the sponge is never found alone (Carballo & Ávila 2004); the benefits of this associations are the transfer of nutrients and protection against predators (Wulff 1997).

The relationships between corals and other benthic organisms are important for coral recruitment patterns and coral survivorship; interactions with the benthos affect coral distribution patterns and determine survivorship through association and inhibition. Most of the previous studies in this area have investigated the relationships between adult corals and benthic groups, such as sponges and algae (for example Norström *et al.* 2009; González-Rivero *et al.* 2011). Only a few studies have examined the relationship between the reef benthic assemblages and the recruitment rate during the early stages of ecological succession (Fairfull & Harriott 1999; Perkol-Finkel & Benayahu 2007).

Coral colonisation can only occur through successful recruitment; available substrata and optimal conditions are needed that are free from sediment or other benthic organisms, with the exception of crustose coralline algae (CCA) that can promote settlement. Several aspects of the settlement and post-settlement phase have been widely investigated, such as the choice of an optimal space to settle (Edmunds 2007), chemical cues that promote settlement (Price 2010), preference for certain substrata (Harrington *et al.* 2004), and accidental mortality resulting from grazing (Sammarco 1981; Trapon *et al.* 2013c). Coral juvenile neighbours, benthic organisms bordering on the juveniles, are particularly important in the post-settlement processes, when mortality is usually high (Dunstan & Johnson 1998). Different benthic groups promote coral recruitment, while others inhibit settlement or survivorship in the post-settlement phase. CCA has been widely studied; it promotes coral settlement by releasing biological cues, although it can also overgrow coral colonies (Buenau *et al.* 2011, 2012; O'Leary *et al.* 2012).

Some benthic organisms have associations with coral colonies and offer protection that promote coral recruitment and enhance survivorship. These other organisms can affect coral

growth rates and survivorship, particularly for coral juveniles, which are more affected than adults. For example, macroalgae can affect coral growth, but at the same time offer protection against predation (Ferrari *et al.* 2012). Growth rates are usually lower in coral early life history stages (Zilberberg & Edmunds 2001); small colonies are more easily overgrown by other organisms, which normally would not affect adult colonies (Box & Mumby 2007; Venera-Ponton *et al.* 2011). Vermeij *et al.* (2010a) showed that an increase in nutrient levels increased the growth rate of turf algae. When the growth rate of the turf algae was higher than the juvenile coral growth, the algae overgrew the juveniles.

Despite the importance of the processes that drive benthic community composition, little is known about how changes in benthic community assemblages affect associations with coral juveniles. There is little information about how the interactions between juvenile corals and benthic organisms vary during the initial phases of the colonisation process. In this chapter, I investigated the role of benthic community composition in shaping coral recruitment patterns. I focused on the initial stage of colonisation and on the impact of benthic community composition on the coral recruitment abundance. Specifically I have: 1) described the initial ecological succession of a benthic coral reef community; 2) determined the associations between coral recruitment rates and benthic assemblage composition; and 3) analysed the spatial interactions that occurred between juveniles and neighbouring benthic organisms by identifying for each interaction if there was any dominant organism (winner) prevailing on the other.

5.3 Methods

This study was carried out in the Wakatobi Marine National Park (WMNP) (see Chapter 2 for further information about the study area).

All of the data used in this chapter were collected from settlement panels deployed at two replicate sites, Buoy 3 (B3) and Buoy 4 (B4), at 6 m depth in June–August 2011, following the method described in Chapter 2.

Thirty-three panels were collected in June 2012 (15 panels at B3 and 18 B4) and a further thirty panels (15 panels at B3 and 15 at B4) were retrieved in June 2013. I examined both sides of the panels to identify any effect of orientation on the benthic organisms and coral juveniles; the front sides were more exposed to light and disturbance, while the back sides were more protected and comparable to a cryptic reef habitat.

5.3.1 Assessment of benthic community coverage

The photographs taken from fresh tiles were analysed with Coral Point Count with Excel extension (CPCe, v. 4.1; Kohler & Gill 2006) in order to determine the coverage of different benthic groups.

Two hundred points per tile (100 points for 100 cm^2) were used on each tile. Three major benthic categories were used: Coral, Algae and Invertebrates. Each of them included different sub-benthic groups, such as type of algae or invertebrate 'group'. A further 'Unknown' group was defined, which included all the points where it was not possible to determine the organism present under the point, while points placed on the bare settlement tile were recorded as 'Substrate'. Points positioned in areas where the surface was shaded by other organisms or fragments or cable ties stuck to the tiles were recorded as 'Tape' and were not included in the subsequent analysis.

5.3.2 Coral recruitment rate

All the settlement tiles collected were analysed in order to assess the coral recruitment rate following the method described in Chapter 2. All the tiles were photographed when taken to the laboratory before and after the bleaching process. The abundance, position on the tile, size, and species of each coral colony were recorded.

Figure 5.1 The digital images show the settlement panels at the moment of the analysis in the laboratory. Panels were deployed for one or two years at 6m depths; after collection both front and back side of the panels were analysed in order to identify the benthic organisms and their coverage and all the coral recruits and juveniles present on the tiles (here showed in light blu circles). Graph paper in the image shows one line per 2 millimeters

5.3.3 Interactions between coral juveniles and benthic neighbours

All the coral colonies found on the settlement tiles were examined and all the cases where the coral colonies were either touching or were less than 1 mm away from another benthic organisms were considered to be interacting. These interactions were recorded in a contact matrix (Figure 5.2).

	Benthic groups	
Coral juveniles	Total number of stand-off events	Total number of interactions won by the benthic organisms (coral overgrown)
	Total number of interactions won by the coral (coral overgrowth)	Total number of interactions

Figure 5.2 Example of a cell of the contact matrix. Interactions between coral juveniles and benthic organisms were recorded. Each cell of the matrix corresponded to the sum of the different interactions between coral colonies and benthic organisms. Rows represent each coral family, while columns represent the different non-coral benthic organisms

The total number of interactions was recorded along with the outcome of the interactions; these included the number of events when the coral was winning over the benthic organism (defined as 'won'), the number of events when the other benthic organism was winning and the coral was the 'loser' (defined as 'lost'), and the overall stand-off interactions ('stand-off'), when the coral and the benthic organisms were touching but no dominance was recorded. 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 & Todd 1994; Barnes & Rothery 1996; Bell & Barnes 2003).

5.3.4 Data analysis

Canonical analysis of principal coordinates (CAP) was conducted in PRIMER v6 (Kohler & Gill 2006) to identify any differences in community composition. The same sides of tiles from each years were compared in order to assess any changes in community composition along with the different sides of tiles collected in the same year to assess variability in community composition between the front and back of the tiles. Vectors representing Spearman's rank correlations (>0.6) with the axes of the CAP analysis used to determine the individual benthic groups that characterised the benthic assemblage in each year.

Any differences in benthic assemblage composition between years were assessed further using PERMANOVA. Assemblage data were separated by panel side and PERMANOVA was performed with two factors: side of the panel (fixed, with two levels: front and back) and year (random with two levels).

Coral recruitment data were analysed separately in order to assess differences in coral recruit and juvenile (see definition of coral recruit and juvenile in the methods section of Chapter 2) abundance between years. The data were transform by square root and a dissimilarity matrix was produced. PERMANOVA analysis was then performed with two factors: side of the panel (fixed) and year (random). To detect any relationships between overall benthic assemblage composition and patterns of coral recruitment, the data on recruitment rates on the CAP plots were represented as 'bubbles'. The size of the bubble varied from 0 to 20 and corresponded to the recruitment rate, with bigger bubbles corresponding to higher recruitment rates.

The data obtained from the assessment of the interactions between coral colonies and benthic organisms were used to identify any relationships between the number of interactions and the coverage of benthic organisms. The recruitment rate on each tile was also correlated with the coverage of the benthic organisms that were interacting with the coral colonies. The number of

interactions was correlated with the coverage of the same group at each tile level to assess if higher coverage was correlated with a higher number of interactions.

5.4 Results

5.4.1 Benthic community composition

Overall, total coverage of benthic organisms increased over time and benthic assemblage was variable between years and sides of the panels. Algae dominated the front sides in both years. On the back sides invertebrates dominated in the first year, but in the second year algae and invertebrate coverage was similar. All benthic groups identified were found in both years; some of them, such as bryozoans, sponges and tunicates, showed a preference for the back side of the panels. After one year approximately 15.77% (±1.51 SE) of the panel substrate was still bare; this declined to 11.95% (±0.93 SE) in the second year. This reduction in bare space was more pronounced on the back side of the panels, where bare substrate was half of the value found in the first year (Table 5.1).

Algae were the most abundant group in both years, and CCA, live and dead, was the most abundant taxa in this category, covering 27.46% (±3.00 SE) and 28.0% (±3.17 SE) of the tiles in the first and second year, respectively. On the front side of the panels, overall algae coverage was consistent between years, however the assemblage composition was different. In the first year the algal assemblage was composed mostly by live CCA, while in the second year live CCA coverage was low. Dead CCA coverage was fivefold higher in the second year. In contrast, on the back side of the panels, live CCA almost tripled in coverage, unfortunately the nature of this study do not allow to know if this increase was due to growth of already existing CCA or to new CCA on bare artificial substrate. Turf algae and non-coralline encrusting algae coverage was consistent between years on the front sides of the panels, while it increased on the back sides. Other algae taxa, including cyanobacteria, green encrusting algae and other macroalgae, covered less than 8% of the tiles in both years.

Thirteen different groups of invertebrates were found on the tiles (see Table 5.1). They occupied 7.01% (±0.80 SE) and 16.97% (±1.77 SE) of the surface on the front side in year one and year two, respectively, and 56.11% (±2.20 SE) and 44.82% (±22.17 SE) on the back side in year one and two, respectively. Both tunicates and sponges had higher coverage in year two, while bryozoan coverage had decreased. All other taxa did not cover more than 2.5% of the

tiles in either year. In addition, bivalves and hydrocorals were only recorded on the back side of the panels.

Coral coverage was low in both years, although there was a slight increase in the second year and a preference for corals to settle on the back side in year two. Pocilloporidae was the most common coral family (Table 5.1).

Table 5.1 Summary of the percentage of average benthic coverage across sites on settlement panels deployed at 6 m on the reef for one and two year periods respectively

	Year 1		Year 2	
	Front	**Back**	**Front**	**Back**
Corals	**0.95 (± 0.18)**	**0.10 (± 0.04)**	**1.07 (± 0.32)**	**1.27 (± 0.27)**
Dendrophilliidae		0.01 (± 0.01)		0.18 (± 0.06)
Faviidae		0.04 (± 0.04)	0.11 (± 0.10)	0.40 (± 0.22)
Fungiidae				0.02 (± 0.01)
Pocilloporidae	0.37 (± 0.08)	0.04 (± 0.03)	0.85 (± 0.28)	0.07 (± 0.03)
Poritidae	0.09 (± 0.04)		0.04 (± 0.03)	0.15 (± 0.05)
Other corals (dead, unknown)	0.48 (± 0.18)		0.07 (± 0.07)	
Algae	**82.83 (± 1.50)**	**21.42 (± 2.84)**	**68.27 (± 2.04)**	**43.66 (± 2.51)**
Turf Algae	13.04 (± 1.52)	0.66 (± 0.32)	17.08 (± 1.31)	5.30 (± 0.40)
CCA	38.44 (± 2.30)	8.63 (± 1.26)	7.72 (± 0.85)	23.57 (± 1.86)
Dead CCA	5.78 (± 1.23)	2.06 (± 0.67)	23.64 (± 1.79)	1.07 (± 0.29)
Cyanobacteria	7.88 (± 0.99)	0.55 (± 0.10)	4.48 (± 0.88)	0.19 (± 0.09)
Green encrusting algae	0.63 (± 0.22)	4.14 (± 0.66)	0.57 (± 0.24)	2.77 (± 0.67)
Macroalgae	0.55 (± 0.17)	2.21 (± 0.65)	0.20 (± 0.14)	0.83 (± 0.35
Non-coral encrusting algae	16.50 (± 1.88)	3.18 (± 0.66)	14.58 (± 0.82)	8.78 (± 1.03)
Invertebrates	**7.01 (± 0.80)**	**56.11 (± 2.20)**	**16.97 1.77)**	**44.82 (± 2.17)**
Amphipod tubes		0.06 (± 0.03)	0.02 (± 0.02)	0.18 (± 0.08)
Ascidean	0.31 (± 0.11)	0.03 (± 0.02)	0.12 (± 0.02)	0.28 (± 0.15)
Barnacle	0.09 (± 0.03)	0.03 (± 0.01)	0.12 (± 0.06)	0.00 0.00
Bivalve		0.35 (± 0.16)		0.47 (± 0.35)
Bryozoan	0.71 (± 0.27)	29.83 (± 2.16)	1.45 (± 0.77)	8.33 (± 0.57)
Foraminifera		0.19 (± 0.09)		0.08 (± 0.07)
Hydrocoral		0.11 (± 0.05)		0.36 (± 0.27)
Hydroid		2.25 (± 1.08)		2.10 (± 0.62)
Snail	1.29 (± 0.47	0.11 (± 0.06)	1.16 (± 0.31)	0.14 (± 0.04)
Sponge	0.53 (± 0.29)	7.05 (± 1.28)	2.91 (± 1.46	12.89 (± 2.01)
Tubeworm	0.05 (± 0.03)	0.51 (± 0.12)	0.04 (± 0.02)	0.07 (± 0.04)
Tunicate	3.63 (± 0.41)	14.81 (± 1.20)	9.59 (± 0.80)	18.93 (± 1.74)
Vermetid	0.27 (± 0.10)	0.77 (± 0.14)	0.62 (± 0.14)	0.73 (± 0.12)
Other Invertebrate	0.11 (± 0.06)	0.02 (± 0.02)	0.94 (± 0.31)	0.44 (± 0.34)
Substrate	**9.21 (± 1.03)**	**22.33 (± 2.35)**	**13.69 (± 1.31)**	**10.20 (± 1.25)**

There were significant differences in community composition for the same side of the panels between the two year periods (PERMANOVA, df=1, P>0.2883) (Table 5.2).

Table 5.2 Result of the PERMANOVA analysis examining differences in community composition between the front and back sides of settlement panels submerged at 6m depth for one and two year periods respectively

Factor	df	SS	MS	Pseudo-F	P
Year	1	39528	39528	1.90	0.2548
Side	1	15519	15519	38.53	**0.0001**
Year * Side	1	20717	20717	51.44	**0.0001**
Res	122	49135	402.75		
Total	125	1.2625E5			

5.4.2 Coral recruitment rates

In the first year, a total of 84 coral colonies were found on the settlement panels: 43 on the front side (65.15 col. m^{-2}) and 41 on the back (60.61 col. m^{-2}). In the second year, a total of 302 coral colonies were found on the settlement panels: 71 on the front side (118.34 col. m^{-2}) and 231 on the back side (385 col. m^{-2}). Excluding three back tiles collected in the second year that had 29, 50 and 64 coral juveniles respectively as outliers, overall recruitment rate was 162.96 (±0.44) col. m^{-2}.

The relative percentages of different coral families in the first and second years respectively, were: 52.38% and 27.48% Pocilloporidae, 17.86% and 11.92% Faviidae, 9.52% and 7.95% Poritidae, 4.76% and 1.76% Acroporidae, 1.19% and 0.99% Agariciidae, 0.66% Fungiidae in the second year only, 1.99% Dendrophylliidae in the second year only, and 25.58% and 47.35% others. On the back side of the panels there was a higher number of coral families in both years; in the second year there were two new coral families on the back sides and one on the front sides not found in the first year (Table 5.3).

Abundance of the coral colonies was higher in the second year and there was a significant difference in coral juvenile abundance between the two year periods (Table 5.4).

Table 5.3 Summary of the overall coral juvenile colonies recorded in the Wakatobi MNP (Indonesia) on settlement panels submerged for one and two year periods respectively (data combined from two sites). Columns report the abundance and relative percentage values on different sides of the panels (front and back) and total values.

Coral juvenile families	Abundance and relative percentage					
	Year 1			Year 2		
	Front	Back	Total	Front	Back	Total
Pocilloporidae	34 79.07%	10 24.39%	44 52.38%	48 67.61%	35 15.15%	83 27.48%
Poritidae	2 4.65%	6 14.63%	8 9.52%	5 7.04%	19 8.23%	24 7.95%
Acroporidae	3 6.98%	1 2.44%	4 4.76%	2 2.82%	3 1.30%	5 1.66%
Faviidae		15 36.59%	15 17.86%	2 2.82%	34 14.72%	36 11.92%
Agariciidae		1 2.44%	1 1.19%		3 1.30%	3 0.99%
Fungiidae					2 0.87%	2 0.66%
Dendrophylliidae					6 2.60%	6 1.99%
Others	4 9.30%	8 19.51%	11 14.29%	14 19.72%	129 55.84%	143 47.35%
Total	43 100%	41 100%	83 100%	71 100%	231 100%	302 100%

Table 5.4 Result of the PERMANOVA analysis examining differences in coral recruitment rates between the two sides of settlement panels submerged for one and two year periods respectively

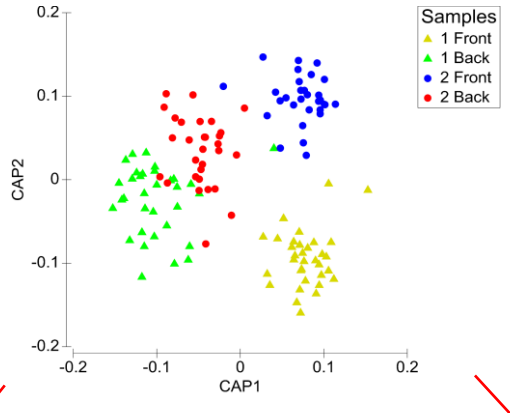
Factor	df	SS	MS	Pseudo-F	P
Year	1	437.89	437.89	0.45	0.4986
Side	1	4193.3	4193.3	10.09	0.0007
Year * Side	1	985.06	985.06	2.37	0.1088
Res	122	50702	415.59		
Total	125	56304			

5.4.3 Relationship between benthic community and coral recruitment pattern

There was variability in community composition between tiles from different years and of different orientation (Figure 5.2). In order to better visualise differences, the analysis was conducted separately for each side of the panels. Recruitment occurred on most of the tiles in both years, with higher values in year two due to the accumulation of two years of recruitment and a preference for settlement on the back side of the panels (Figure 5.3).

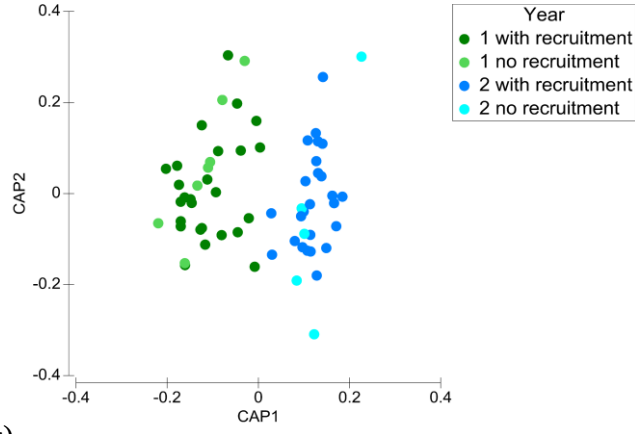
Different benthic organisms characterised the community in each year. While in first year only one group was identified for each side of the panel, in year two more groups of organisms were found (Figure 5.2c). Despite this finding, coral recruitment rates were not correlated with the abundance of any benthic group found associated in the CAP plots and known to be previously associated with coral recruitment (CCA, sponges, turf algae and bryozoans) or with the percentage of the available bare substrate on the settlement panels (see Appendix II).

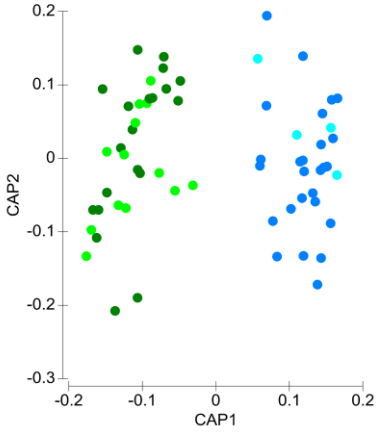
a)



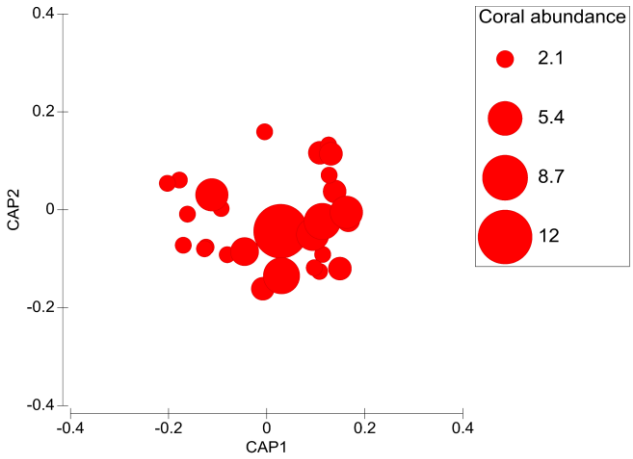
Front side **Back side**

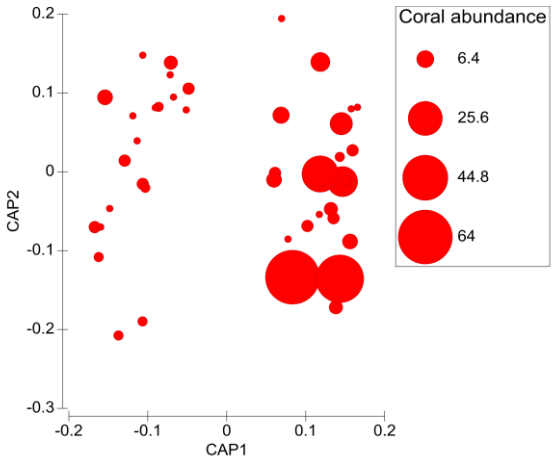
b)



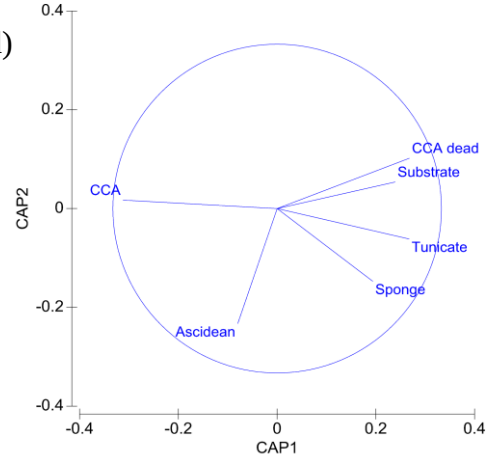


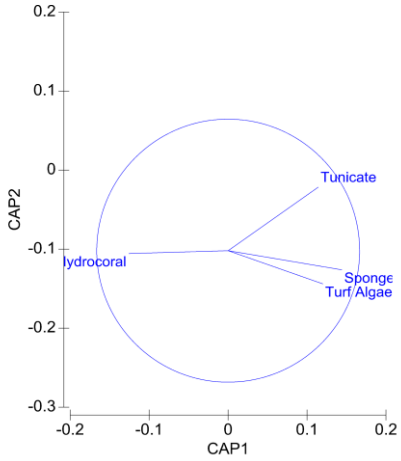
c)





d)





5.4.4 Interactions between coral juveniles and benthic neighbours

Overall, 442 interactions were observed: 118 on tiles deployed for one year (73 on the front sides and 45 on the back sides) and 324 on tiles deployed for two years (95 on the front sides and 229 on the back sides). No interactions with juvenile corals were found with foraminifera, hydrocorals, hydroids and barnacles. The average number of interactions per coral colony in the first year was 1.34 (± 0.08 SE): 1.43 (±0.129 SE) on the front side and 1.19 (±0.09 SE) on the back side; in the second year the average number was 1.05 (±0.05 SE): 1.62 (±0.12 SE) on the front side and 0.87 (±0.05 SE) on the back side.

In both years, the overall highest number of interactions occurred with algae. There was a predominance of interactions between corals and CCA; in the first year they represented 40.68% of the total interactions and they were mostly on the front sides, while in the second year they represented 29.32% of the total interactions and were mostly on the back sides (Table 5.5). Of the total interactions between CCA and corals, 71.33% were stand-offs, while only 20.28% resulted in a win for the coral, either by overgrowing or settling on CCA. In the second year there was also an increase in the number of interactions with dead CCA on the front side.

Table 5.5 Summary of the overall outcomes of the interactions occurring between coral juveniles and benthic organisms on both sides of settlement tiles submerged for one and two year periods respectively at 6 m (data of two replicate sites combined)

Year	Side	Outcome of the interactions			
		Won	Lost	Stand-off	Total
1	Front	7	7	59	73
	Back	4	11	30	45
2	Front	15	15	65	95
	Back	40	27	162	229

Front page:

Figure 5.3 CAP plots showing a) the differences between benthic community composition on settlement panels submerged for one and two year periods respectively in the Wakatobi MNP. CAP axes discriminate between the samples data and show the maximum variability (see correlation of axes to data cloud inAppendix II); b) the benthic community composition separated by side of the panel in order to better visualise the differences in benthic communities on the front and back of panels; plots on the left side represent the front side of the panels, while those on the right side represent the back side. Samples (tiles) with and without recruitment are coloured differently; c) recruitment rates which have been imposed as bubbles on the CAP plots; and d) vectors representing Spearman's rank correlation of individual benthic groups with the CAP axes showing which factors are characteristics of the benthic community in each year

Turf algae-coral interactions represented 9.4% of the overall interactions with algae. The number of interactions was higher in the second year and they were mostly stand-offs, where the algae was often surrounding the whole colony or where turf algae was overgrowing the coral. There were only a small number of interactions between green encrusting algae and corals in the first year and no interactions on the front sides in the second year. Few interactions between macroalgae and coral were found in either year, while interactions between corals and non-coralline encrusting algae were more abundant in the second year, especially on the back side of the panels. The outcome of most of the interactions with algae was a stand-off or algae overgrowing the corals.

Interactions between bryozoans and corals were found only on the back side of the panels; outcome of the interactions was mostly a stand-off or coral overgrowing the bryozoan. Bivalves were only recorded on the back side of the panels and interacted more with corals in the second year; in all the cases the coral colonies were found settling on the top of the shells. There were few interactions with sponges in the first year, but they increased in the second year on the back side of the panels. The outcome of most of these interactions was a stand-off or sponge overgrowing the coral. Colonial tunicates and vermetids interacted with corals mostly in the second year and most of the outcomes were stand-offs for both groups, or tunicate overgrowing the coral. Foraminifera and hydroids did not have any interactions with corals; this was probably due to these benthic organisms having low coverage (Table 5.6).

The coverage of the benthic organisms was not correlated with the number of interactions between coral juvenile abundance and coverage of different benthic groups, such as turf algae, CCA, sponge and bryozoans (Figure 5.4).

Table 5.6 Summary of the interactions between coral colonies families and benthic organisms. Data were collected from settlement panels deployed at 6 m at two replicate sites (Buoy 3 and Buoy 4) in the Wakatobi MNP

	Coral juvenile			
	Won	Lost	Stand-off	Total
Algae	**36**	**40**	**200**	**276**
CCA	29	12	102	143
CCA Dead	4	6	35	45
Cyanobacteria	1	2	9	12
Green Encrusting Algae	0	3	18	21
Macroalgae	0	3	3	6
No Coralline Encrusting Algae	2	6	15	23
Turf Algae	0	8	18	26
Invertebrates	**30**	**19**	**111**	**160**
Bivalves	7	0	4	11
Bryozoans	10	2	14	26
Hydroids	2	0	0	2
Sponges	3	10	54	67
Tubeworms	1	0	4	5
Tunicates (colonial)	1	5	15	21
Tunicates (solitary)	0	2	2	4
Vermetids	1	0	15	16
Other Invertebrates	5	0	3	8

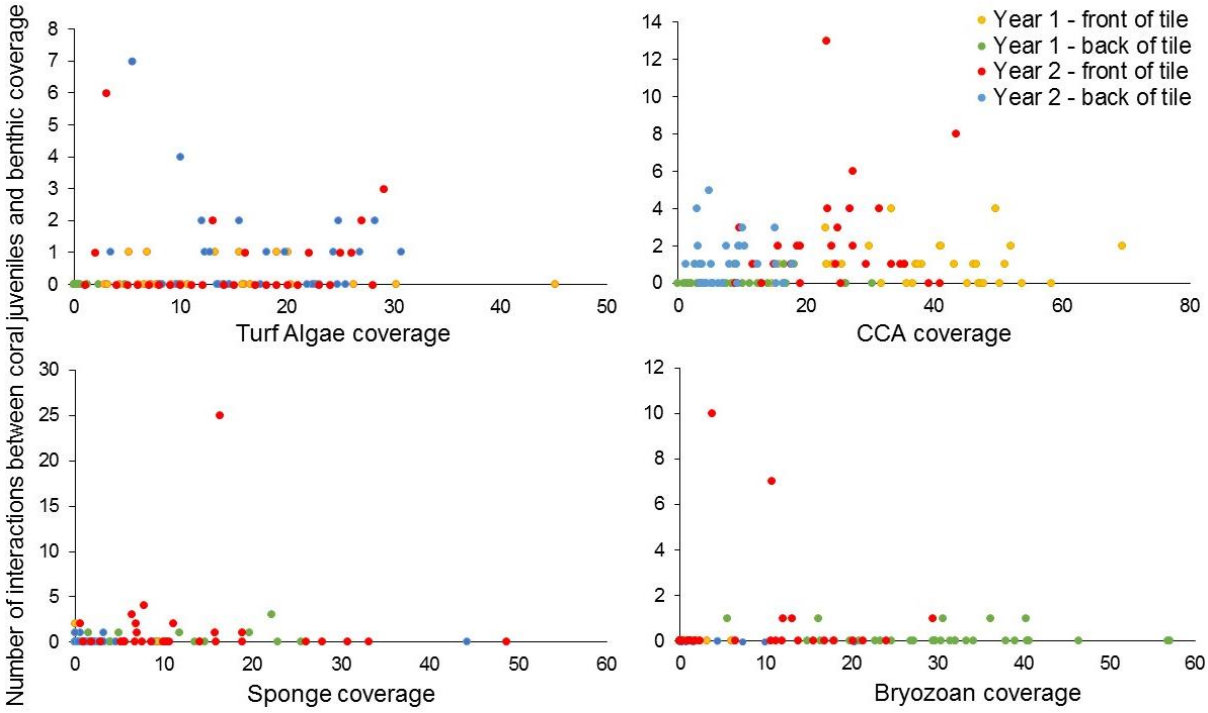


Figure 5.4 Correlations between the main benthic groups present on the settlement tiles and known to interact with corals, and the overall number of interactions with coral juveniles

5.5 Discussion

In this study I investigated the impact of the initial colonisation process of a benthic coral reef community on coral recruitment. Benthic assemblage was significantly different between panel orientations and for panels deployed for one or two year periods on the reef. Higher coral juvenile abundance was recorded in year two and on the back side of the tiles, and this was probably due to two years of coral colony accumulation. Coral juvenile abundance was associated with different benthic assemblages on the two sides of the tiles for each time period and was not correlated with the coverage of the more abundant benthic groups. The number of interactions between coral juveniles and other biota was higher in year two; CCA and sponges were the principal benthic groups interacting with coral juveniles. The majority of these interactions were stand-offs, although juveniles were found to be overgrown rather than to have settled on other biota.

5.5.1 Succession of benthic assemblages

The benthic community changed significantly from the first to the second year. The overall number of benthic groups differed consistently across the duration of my study and there was a marked change in the relative coverage between years and orientation of the tiles (Figure 5.5). The front side of the tiles was dominated by algae, mainly CCA, while invertebrate coverage was higher on the panels collected in year two. The back sides of the panels were characterised by invertebrates, such as colonial tunicates, sponges and bryozoans. In the second year, algae coverage was similar to invertebrate coverage; CCA coverage was higher on the back side compared to year one. This finding could be due to light still reaching the back side of the panels and promoting algal growth. Some groups showed preferences for the front or back side of the panels. For example, bivalves and foraminifera were not found on the front side in the second year, while tubeworms had disappeared from the back sides by that point. This pattern could however be the result of post-settlement mortality rather than orientation choice at settlement time.

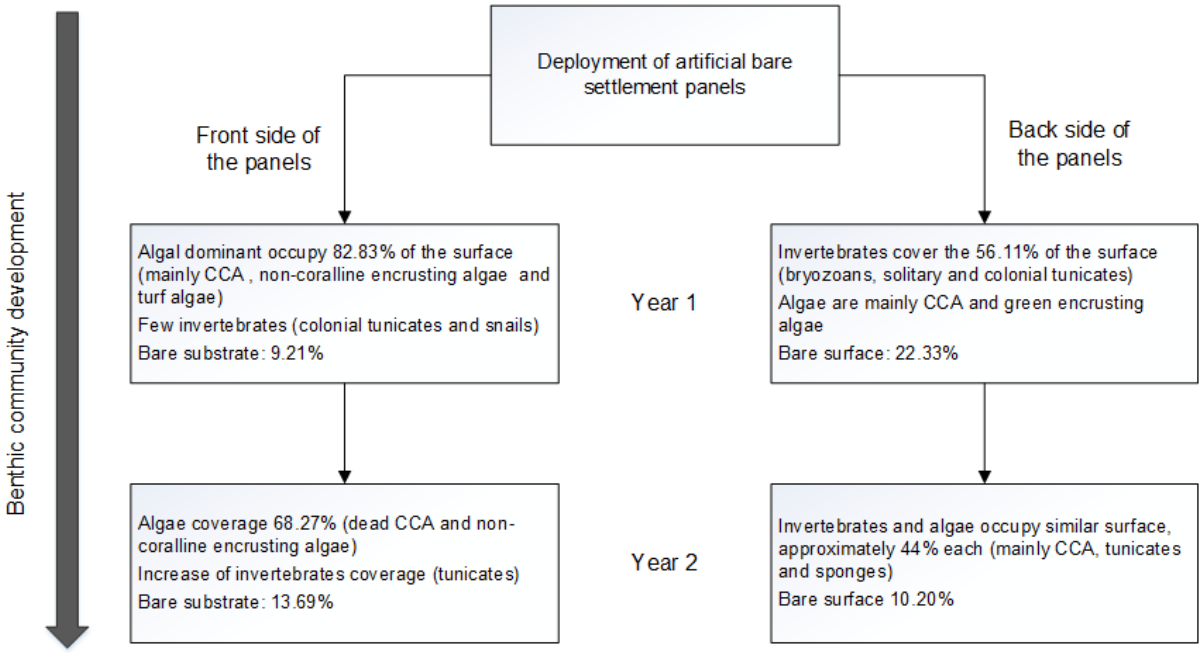


Figure 5.5 Diagram of the development of the benthic community on the artificial settlement panels deployed on the reef for one and two year periods respectively in the Wakatobi MNP (Indonesia).

All benthic groups found in this study were present in both years and it was not possible to assess if the availability of bare substrate on the panels was correlated with the number of benthic groups on the panels. Despite different species succeeding each other during the development of benthic communities, as described by Tanner *et al.* (1996) and Connell (1997a), in my study I was unable to record the order in which benthic organisms settled on the tiles or the time required to occupy the tile. Field *et al.* (2007) found that colonisation was faster in the first month, and then declined when free space decreased. In my research, the interval of 12 months between sampling times prevented fine temporal scale recording of the organisms that appeared and disappeared. Such groups might have had a short life span but could have still influenced the community development, as suggested by Sutherland (1974). Therefore, more than two sampling points would be recommended in future studies to assess correlations between colonisation and free space. In addition, the taxonomic level used for identification pooled several species, and did not allow any assessment of differences at species level.

Previous studies on ecological succession on both natural and artificial substrates in different environments (Tanner *et al.* 1996; Diaz-Castaneda & Almeda-Jauregui 1999; Bowden *et al.* 2006) have identified various factors that affect the development of the community. These factors include time of tile deployment (Field *et al.* 2007), seasonal supply of larvae (Bowden

et al. 2006), presence of biological cues (Price 2010), specific assemblages that promote recruitment (Carballo & Ávila 2004; O'Leary *et al.* 2012), and time when the panels were analysed after deployment (Martinez & Abelson 2013). In order to better understand the trends of ecological succession, data from more consecutive years would be useful. In addition, frequent observations and identification of biota to a higher taxonomic level would improve the understanding of the dynamics and order of colonisation.

5.5.2 Relationship between coral recruitment and benthic community composition

The overall coral recruitment rate in the first year was similar for the front and the back sides of the settlement panels (43 and 41 respectively). In previous surveys conducted in the same area, recruitment rates have always been higher on the back side (see recruitment rates in Chapters 2 and 3). Panels with higher recruitment on the front side rather the back side were found occasionally. In year two, higher coral juvenile abundance was recorded on both sides compared to year one, probably due to the accumulation of juveniles that survived from the first year and new recruits that settled in the second year (Perkol-Finkel & Benayahu 2007). The high coral recruitment rate on the back side was mostly due to three tiles, which had 29, 50 and 64 juveniles respectively and together accounted for 62% of the total recruits on the back side in that year. In addition, two new families, not commonly found on settlement panels deployed for one year, were recorded on the back side of the panels in the second year.

Higher coral recruitment rates were associated with specific benthic assemblage compositions, which differed between sides of the panels; however, individual benthic groups that characterised those assemblages were not correlated with coral recruitment rates. This result is consistent with studies conducted in the Red Sea (Glassom *et al.* 2004; Field *et al.* 2007) and in the Caribbean (Birkeland 1977). In contrast, on the Great Barrier Reef, the coverage of the dominant benthic groups (bryozoan, ascidians and barnacles) were negatively correlated with coral recruitment (Harriott & Banks 1995).

In this study I did not find any correlation between CCA and coral juvenile abundance, which has been reported in other areas, such as in the Antilles Islands in the Caribbean (Morse *et al.* 1994), in the Mombasa Marine National Park in Kenya (O'Leary *et al.* 2012), and at Lizard Island in the Great Barrier Reef (Harrington *et al.* 2004). In other locations, such as Bonaire in the Caribbean (Morse *et al.* 1994), in the Gulf of Aden in Yemen (Benzoni *et al.* 2011), at Pelorus Island located in the central Great Barrier Reef (Baird & Morse 2004) and at Moorea in French Polynesia (Price 2010), CCA is not considered important for high coral recruitment

rates. Other studies have shown that although some species of CCA promote coral recruitment by releasing chemical cues, others release inhibiting cues that affect coral survivorship (Raimondi & Morse 2000; Harrington *et al.* 2004; Ritson-Williams *et al.* 2009b; Benzoni *et al.* 2011; O'Leary & Potts 2011). Harrington *et al.* (2004) investigated the relationship between two coral species and five CCA species and found a positive correlation between recruitment and post-settlement survivorship, while O'Leary *et al.* (2012) found that coral density was correlated with the abundance of only one CCA species.

My study did not consider the recruits that died or were removed from the tiles, or potentially scraped off by predators before the sampling time. It is possible that initial coral recruitment was correlated with either CCA or available space, but early mortality occurred and modified the initial pattern. As a consequence, coral recruitment patterns at the observation time may have been different from the original settlement pattern (Kuo & Soong 2010).

Studies by Coyer *et al.* (1993) and Davies *et al.* (2013) highlighted the importance of macroalgae in protecting young corals from fish grazers and at the same time competing with coral juveniles. Erect macroalgae, found also on my settlement tiles, affects the growth rate of coral juveniles by contact and induces tissue loss by abrasion (Sammarco 1980; Birrell *et al.* 2005; Diaz-Pulido *et al.* 2010). However, the declining fish abundance found in the Wakatobi and low coverage of macroalgae on the back surfaces suggest that macroalgae were not important for juvenile survivorship (see Chapter 4 for information on fish abundance).

The abundance of new coral recruits in year two was higher than in year one, when benthic assemblage complexity was higher, but also when spatial competition was likely to be more intense as there was less free space. This is in accordance with research conducted by Kuo & Soong (2010), who showed that coral recruitment and juvenile survivorship were higher on older tiles, which probably produced cues that promoted recruitment not present on younger tiles.

5.5.3 Interactions between coral juveniles and benthic neighbours

The number of interactions between coral colonies and benthic organisms was not correlated with the number of colonies. Despite the increase in coral colony abundance and community assemblage complexity, the average number of interactions per colony was similar across years. In both years there were coral colonies without interactions with other benthic organisms, however in year two, more coral juveniles were in contact with only one benthic organism; in these cases juveniles were mostly overgrowing or surrounded by it.

Benthic group coverage was not positively correlated with the total number of interactions between benthic groups and coral juveniles. For example, bryozoans had no interactions on the front side of the panels in both years, while on the back side, despite the coverage in year two being a quarter of the coverage in year one, the interactions tripled. While CCA coverage tripled in year two compared with year one, the number of interactions was seven times higher. Similarly, while sponge cover almost doubled in year two, their interactions with coral juveniles were almost sixfold higher.

Stand-off events occurred in the majority of the interactions between coral juveniles and algal groups and sponges. This is in contrast with research conducted on the Great Barrier Reef, where the most common outcome on the back side of settlement panels was mortality of coral juveniles caused by overgrowth by bryozoan, sponges and tunicates (Fairfull & Harriott 1999; Wilson & Harrison 2005). Some stand-off interactions benefit coral juveniles, for example by offering protection, but at the same time the benthic organisms, such as macroalgae and vermetids, can affect coral growth rate (Coyer *et al.* 1993; Lenihan *et al.* 2011). A study conducted with adult *Montastrea* coral colonies found that stand-offs between coral colonies and sponges were the most common outcome of the interactions, however sponge promoted slow mortality in coral polyps engaged in the interaction (Suchanek *et al.* 1983; Aerts 2000).

In my study, the majority of the interactions occurred between coral juveniles and CCA. Most of these were stand-offs, where CCA was touching the juveniles or surrounding it. Only in a few cases was CCA partially overgrowing the coral juveniles. Buenau *et al.* (2011) suggested that CCA overgrows only corals smaller than a specific threshold size, beyond which they are less vulnerable. In contrast, Harrington *et al.* (2004), using a manipulative experiment, assessed the relationship between coral recruits and five different CCA species. CCA was rarely overgrowing recruits, suggesting the limited role of CCA in young coral survivorship. Only coral recruits settled on CCA, while juveniles were never found on CCA. Chemical cues that promote coral larval settlement might have a negative effect on coral juvenile post-settlement survivorship (Harrington *et al.* 2004). In addition, other factors, such as epithelial shedding that occurs in some CCA species, might remove coral recruits from the surfaces before they reach a bigger size (Keats *et al.* 1997; McCook *et al.* 2001). More coral juveniles were recorded as having settled on dead CCA in year two, although it is unknown if the CCA was still alive at the time the larvae settled. Heyward & Negri (1999) suggested that dead CCA releases chemical cues that both inhibit coral recruitment and induce mortality in coral juveniles that had settled on the CCA when it was still alive. It is possible that juvenile mortality occurred in

coral colonies settled on already dead CCA and could not be detected by this study. Additional juvenile mortality can occur in juveniles settled on living CCA, in case of death of the coralline algae.

In this study, size of the coral colony, growth rates, and amount of coral colony perimeter in contact with other benthic organisms were not investigated. Therefore, it is unknown how these factors affect the number and outcome of the interactions over time. Previous investigations found that larger organisms usually win in competitive interactions (Zilberberg & Edmunds 2001; Box & Mumby 2007). Aerts (1998), Lirman (2001) and Ferrari *et al.* (2012) investigated the effect of the amount of coral colony perimeter involved in interactions with benthic organisms. Ferrari *et al.* (2012) found that, in small corals, the percentage of perimeter in touch with another organism did not change the intensity of the interaction. In this study, I only examined interactions between coral juveniles and other benthic organisms less than 1 mm apart, however some interactions occur without the necessity of contact. For example, erect macroalgae affect coral growth rate by abrasion with algal filaments, reducing the growth rate in coral juveniles and causing tissue loss and variations in size (Lirman 2001; River & Edmunds 2001; Box & Mumby 2007).

In this chapter, I have assessed the effect of the succession of benthic assemblages on patterns of coral recruitment. I found that coral recruitment rates were higher on tiles where benthic community was more developed. Despite higher coral recruitment rates being associated with specific benthic assemblage compositions, recruitment rates were not correlated with the individual benthic groups that characterised those assemblages.

Chapter 6 General discussion

In this thesis I have investigated patterns of spatio-temporal variability in coral recruitment and examined the abiotic and biological factors that affect the distribution of coral recruits and juveniles. I then focused on the impact of fish grazing on the young coral population and I have studied the associations between benthic community composition and coral recruits and juveniles during the initial phases of colonisation of bare substrate.

The key findings of my research are: 1) the identification of high levels of variability in coral recruit and juvenile abundance across space and time (Chapters 2 and 3); 2) that coral recruit and juvenile abundance patterns are not easily explained by individual factors, but seem to be the result of multiple factors resulting in complex interactions (Chapter 2); 3) that predation is not an important factor influencing coral post-settlement mortality in the Wakatobi Marine National Park (Chapter 4); and 4 that the benthic assemblage influences coral recruitment abundance through interactions that promote or inhibit coral survivorship (Chapters 4 and 5).

In this chapter I discuss the variability in the scale of variation in coral recruits and juveniles in the Coral Triangle and the Indo-Pacific area. I also explain the contribution of my research to our understanding of the environmental factors that affect the coral recruitment processes, focusing particularly on the role of fish predation and spatial competition. Finally, I discuss the implications of my results for coral reef management.

6.1 Changes in spatial variability in coral population along recruitment

Earlier research on coral population dynamics has suggested that coral larvae can travel both long and short distances, depending on the species (Christie *et al.* 2010; Saenz-Agudelo *et al.* 2012). This larval dispersal maintains reef connectivity and generates spatial variability between coral reefs at most scales (Dunstan & Johnson 1998; Graham *et al.* 2008; O'Leary & Potts 2011). For example, at wide scales, reefs at high latitude in the Pacific have lower coral recruitment rates compared to tropical reefs, while on the Great Barrier Reef a latitudinal gradient in spatial variability was found in coral recruit abundance and assemblage composition across 1700 km (Hughes *et al.* 1999b, 2002). At smaller scales, high levels of spatial variability in coral recruitment rates was found between islands 5 km apart in Moorea, but not within sites on the same island, 5–8 km apart (Penin & Adjeroud 2013), generating a more patchy

distribution. Variability in coral recruitment rate is correlated to the scale of variability of biological and abiotic factors driving the recruitment process. The correlation between coral recruitment rate spatial variability and scale of variability in factors was examined Moorea (Penin *et al.* 2010), at Ryukyu Island (Nakamura & Sakai 2009) and Fiji (Quinn & Kojis 2008) with different results, highlighting the high variability existent between and within locations.

A number of studies (for example, Bak & Engel, 1979; Fairfull & Harriott, 1999; Perkol-Finkel & Benayahu, 2007) have suggested a correlation between physical and biological factors and coral recruit distribution, however only a few, such as this one, have investigated and described the strength of this correlation (for example Lirman 2001; Harrington *et al.* 2004; Buenau *et al.* 2012). My research also highlights the high variability in environmental factors at small localised scales and in the relationship between coral recruit and juvenile distributions, regardless the distance between sites, which varied from a few hundred meters up to 5 km. Howerver, despite sites sharing similar abiotic and biotic conditions were expected to have similar distribution patterns and coral composition (Chapters 2 and 3), this was not what I found.

A prevalence of self-recruitment on coral reefs would support a correlation between adult coral cover and young coral colony density (Tioho *et al.* 2001; Carlon 2002). However, this correlation has only been found at the coral family level, at Seychelles (Chong-Seng *et al.* 2014), Moorea (Edmunds *et al.* 2010), Ryukyu Island (Nakamura & Sakai 2009) or when only considering seasonal coral recruitment data, such as in the Wakatobi (Salinas De León *et al.* 2012a) and in Singapore (Bauman *et al.* 2015). I did not find a linear correlation between coral cover and coral recruit or juvenile density (Chapter 2). Furthermore, the patterns of spatial variability in coral densities were consistent across the seven years of my study for both recruit and juvenile populations, despite the high fluctuations in the actual coral density values between years (Chapter 3).

Studies conducted in Moorea (Penin & Adjeroud 2013), Taiwan (Nozawa *et al.* 2013) and the Wakatobi (Salinas De León *et al.* 2012a) and this thesis) have assessed the differences in coral density and assemblage composition between corals in early life history stages and adult coral populations. Correlations between coral recruits, juveniles and adults are variable across locations; in Japan (Nakamura & Sakai 2009), Moorea (Edmunds *et al.* 2010) and the Seychelles (Chong-Seng *et al.* 2014) coral recruit abundance was found to be correlated with adult distribution or with juveniles. In Tonga (Adjeroud *et al.* 2013), Taiwan (Nozawa *et al.*

2013), Moorea (Penin *et al.* 2007) and the Wakatobi (Salinas De León *et al.* 2012a) juvenile abundance was similar to the adult coral distribution patterns. The only case were all coral life hisoty stages, recruit, juvenile and adult, were correlated, was in Taiwan, where apparently coral recruitment apparently is not strongly affected by post-settlement mortality(Nozawa *et al.* 2013). This is supported by fact the majority of the coral recruit were found on the exposed side of the panels

Some coral families had higher mortality rates than others. Coral post-settlement mortality was selective and not consistent across years and spatial variability in coral colony distribution was maintained, with differences in coral assemblage composition at each site (Chapters 2 and 3). However, these correlations are biased by the time the measurements were taken. For example, in a coral recruitment study a longer time period left between the main spawning event and the coral density measurement do not mean a higher mortality rate. From the time of settlement, coral recruits are immediately affected by post-settlement mortality, which might cancel any observable correlations existent between the coral spat at settlement time and physical and biological factors (e.g. coral cover) (López-Pérez *et al.* 2007; Penin *et al.* 2010; Martinez & Abelson 2013).

Spatial and temporal changes in coral assemblage composition between recruit and juvenile stages highlighted the action of selective mortality. Although Pocilloporidae is the most common family on settlement panels in most coral reef studies, at the juveniles and adult stages other families have greater dominance. Pocilloporidae was the most common coral recruit family in most locations, with exceptions for Ryukyus Island (Nakamura & Sakai 2009), Taiwan (Ho & Dai 2014) and Fiji (Quinn & Kojis 2008) with Acroporidae, and Moorea with Poritidae (Edmunds *et al.* 2010), while other coral families were represented in different proportions at each location. In the Caribbean, coral recruit assemblage was mainly comprised of Agariciidae, while Pocilloporidae was rare.

Coral juvenile assemblage composition is more varied than recruit composition and similar results have been found across in the Indo-Pacific, where coral recruit populations were dominated by Pocilloporidae, Poritidae and Acroporidae colonies that varied by location. Faviidae and Agariciidae colonies tend to dominate at juvenile coral populations, despite being rarely found at recruitment time (Arnold *et al.* 2010). In the Caribbean, coral recruit assemblage was mainly comprised of Agariciidae, while Pocilloporidae was rare.This finding suggests that

different processes drive coral recruitment across wide areas, such as the Indo-Pacific and the Caribbean, and smaller regions.

Tables 6.1 and 6.2 summarise the studies on coral recruitment conducted in the last 10 years and mentioned previously in this chapter, with a focus on the Pacific Ocean. Studies were divided by coral early life history stage, recruit and juvenile, and examined by the locations where studies were conducted, depth of the surveys, time of deployment of settlement panels and distance between sites.

Overall the Pacific area, coral recruitment means were highly variable and it was not possible to find any existent pattern or trend. This studies suggest that different processes drive coral recruitment across wide areas, such as the Indo-Pacific and the Caribbean, and smaller regions. However, I could not identify any observable distribution pattern in coral recruit assemblage at different locations in the Indo-Pacific.

Comparisons with other studies are difficult because of differences in definitions of coral life history stages vary by authors and there is a wide variability in data collection. Surveys conducted in the same locations in different years with different protocol, such as different depth, variable duration of panel deployment, gave different results, such as in Moorea (Edmunds *et al.* 2010; Penin & Adjeroud 2013) and Taiwan (Nozawa *et al.* 2013; Ho & Dai 2014).

The high variability found highlight the lack of information about the coral recruitment process. Better identification of coral recruits, continuous monitoring of different life history stages of corals and the choice of study sites by using information about spatial variability of ecological factors could improve the current knowledge about coral recruitment and provide a better understanding of the overall process.

Table 6.1 Summary of the studies on coral recruitment conducted in the last decade in the Indo-Pacific regions and the Caribbean. Since the Coral Triangle is known for its richness and high diversity in corals, research from this area was separated from the rest of the Indo-Pacific region in order to more easily compare the data. For each study I report location, the depth at which the settlement panels were deployed, the distance between sites used in the study, the mean coral recruit density, the outcome of the analysis on the differences in spatial variation in coral recruits between sites, the preference for orientation (side of the settlement panels presenting more settled coral recruits) and the assemblage composition of the coral recruit population

Author	Location	Depth (m)	Duration (months)	Site distance	Mean (m^2)	Spatial variability	Correlations	Orientation preference	Assemblage
Coral Triangle									
This study	Wakatobi (Indonesia)	6; 12	12 (repeated for 3 years)	200m - 5 km	61.09	Spatial variability across sites, not across depths. Temporal variability not always found	No correlations found	64.15% on the back side of the tiles, rarely front and back side presented similar abundance	Pocilloporidae 25.47%; Poritidae 19.18%; Faviidae 15.72%; Acroporidae 8.5%; Agariciidae 4.71%
Sawall et al. (2013)	Sulawesi SW (Indonesia)	3 - 4	4 (repeated for 2 years)		705 -286	Temporal variability. Seasonal variability	No correlation with benthic community, although recruits mostly settled next to complex benthic community (back side)	Preference for back side of tiles	Pocilloporidae 63%; Acroporidae 14.6%; Poritidae 7.8%.
Salinas De León et al. (2012)	Wakatobi (Indonesia)	5 - 7	12 (repeated for 2 years)	1.5 km	89 (2008); 209 (2009)	Spatial and temporal variability. Seasonal variability	Positive correlation between recruits/coral cover	Back, both sides were counted	Acroporidae 25-12%; Pocillopora 21-10%; Poritidae 13-16%.
Fox (2004)	Komodo (Indonesia)	6 - 10	6 (repeated twice)	9 blasted and 6 unblasted sites up to 20 km apart	285 - 772	Spatial and seasonal variability between blasted and unblasted sites.	No correlation with coral juvenile abundance at blasted sites.	Overall preference for back side of the panels. Acroporidae mostly on front sides.	Pocilloporidae 44.7%; Acroporidae 27.1%; Poritidae 12%
Indo-Pacific region									
Bauman et al. (2015)	Singapore	3 - 4	3 (repeated for 2 years)	7 sites along 15 km	54.74	Consistent spatial pattern amongst sites. Seasonal variability	No correlation between recruits/coral cover during peak season (found only for Poritidae).	Lateral sides 41%, back 30.7% and front 27.6%	Pocilloporidae 84%; Poritidae 4%; Acroporidae 1%; others 10%
Chong-Seng et al. (2014)	Seychelles	4	3	From few to several km		Variation between reefs, not between sites on same reef	Correlation between Pocilloporidae recruits and adults, no with juveniles		
Ho & Dai (2014)	Taiwan	6-8, 8-10; 12-13	3 and 12 (repeated for 2 years)	3 sites about 500-700 m apart	86-116	Yes, but only in the first year Seasonal variability	Abundance negatively correlated with depth	Both sides counted, preference for front 53%, 42% vertical, 5% back	Acroporidae 77%, Pocillopora 18 %, Poritidae 6%

Author	Location	Depth (m)	Duration (months)	Site distance	Mean (m^2)	Spatial variability	Correlations	Orientation preference	Assemblage
Nozawa & Chung (2013)	Taiwan	5; 15	4	Up to 10 km apart		Yes, no differences between different depths at same site	At 5 m no correlation with juvenile and adult composition; at 15 m similar composition	Preference for front side	At 5 m: Pocilloporidae and Poritidae (80%). At 15 m: Acroporidae (48-65%) and Pocilloporidae
Penin et al. (2013)	Moorea (French Polynesia)	6, 12 and 18	3 (repeated twice)	5 km between islands; 3-8 km within islands	568.54	Yes, at regional and island levels	Abundance variable with depth, no pattern found	Both sides counted, no preference specified	Pocillopora 67%, Acroporidae 23%, Poritidae 10%. Seasonal variability
Edmunds (2010)	Moorea (French Polynesia)	1.5 - 2	5 - 7 (repeated for 2 years)	10 sites along 20 km coast	23.74	Only seasonal variability	Coral cover correlated only with part of the seasonal data	96% on back, 4% on lateral sides and 1% on front	Poritidae 34%, Acroporidae 27%; Pocilloporidae 23%
Kuo (2010)	Taiwan	4 - 5	2 years, panels of different age		32.5	Age of the tile and seasonal variability	Older panels have more Pocilloporidae recruits	Tiles fixed in vertical position, only back side included	Pocilloporidae 51%, Poritidae 31%, Astrocoeniidae 6%, Acroporidae 2%
Nakamura (2009)	Ryukyu (Japan)	5	8 weeks	Between location: 0.3-0.6; between sites: 0.5-2 km	N/A	Yes, across sites and years	Pocilloporidae: correlation recruit/adult. Correlation between surface and current direction/recruitment pattern	No recruits found on the front side	Acroporidae 78.8%-61.3%, Poritidae 10%-16%, Pocilloporidae 10.7-13.7%
Kojis & Quinn (2008)	Fiji	5, 15 and 25	6 (repeated for 2.5 years)	Few km within site, 70-200km between sites	570 (summer); 93 (winter)	Yes, between sites 5 (winter) - 1749 (summer)	Correlation with depth, Poritidea mostly in deep water and with coral cover	All sites counted, no data on orientation preference	Acroporidae 52.2%, Pocillopora 30.3%, Poritidae 3.4%, Faviidae 0.5%
Mangubhai et al. (2007)	Kenya	0 - 7	3 (repeated for 27 months)	Two sites 7 - 8 km apart	101 (degraded reef) 908 (healthy reef)	Spatial and temporal variability Seasonal variability	No latitudinal gradient in recruit density. Seasonal correlation with serpulids and oysters. Weak interaction with oyster density.	Only recruit on back side (92% of total recruits) included in analysis.	Pocilloporidae 93.7%; Poritidae 3.2%; Acroporidae 1.4%; Faviidae 0.1%
Adjeroud et al. (2007)	Moorea (French Polynesia)	6, 12 and 18	3 (repeated for 3 years)	Three sites about 10 km apart	40.77 Overall decrease in recruitment rates over 3 years	Spatial and temporal variability. Variability in depth not consistent across years. Seasonal variability		57.1% on back, 28.4% on lateral sides and 14.5% on front	Pocilloporidae: 60.4%, Poritidae: 18.8%, Acroporidae: 11.2% Pocilloporidae and Poritidae decrease over 3 years.

Author	Location	Depth (m)	Duration (months)	Site distance	Mean (m^2)	Spatial variability	Correlations	Orientation preference	Assemblage
López-Pérez et al. (2007)	Huatulco (Pacific coast) Mexico		11-13 (some tiles replaced every second month)	1.5 - 6	0.85 - 20.4 (higher recruitment rate on two-months tiles)	Yes	No correlation in assemblage composition between recruit and adult		290 out of 291 Porites and one Pocillopora
Dunstan & Johnson (1998)	Heron island (GBR, Australia)	9-12 or 2-3 (lagoon)	3 and 10 months after spawning peak (for 4 years)	Three zones with three sites (400-600m apart) each		Spatial and temporal variability No spatial variability within sites in 10 months old recruits	No consistent pattern within zones across years Negative correlation between coral recruit abundance and bryozoan and oyster cover		Pocilloporidae 80.1%; Acroporidae 16.4%
Caribbean									
Green & Edmunds (2011)	Virgin Island	5 - 6	6 (repeated for 2 years)	10 sites randomly distributed along 10 km	76	Yes, across sites, years and seasons	Correlation with water motion (analysis of temperature and flow)	All on the back side of the tiles	Poritidae 43%, Agariciidae 29%, Faviidae 17%. Seasonal variability
Arnold et al. (2010)	Bonaire	10	Repeated for 7 years	Few km apart	128 (± 32)		Correlation with juvenile density	Mostly on back side	Agaricia 88.8%, Porites 8.3%
Irizarry-Soto & Weil (2009)	Puerto Rico	0-3, 3-5, 5-10 and >15	Up to 2 years		2.24				

Table 6.2 Summary of studies on coral juvenile abundance conducted in the last decade in the Indo-Pacific region and the Caribbean. For each study I report location, the depth where the survey was carried out, the definition of juvenile used in the data collection (maximum diameter in mm), the mean coral juvenile density, the outcome of the analysis on differences in spatial variation in coral juveniles between sites, the number of families/genera/species detected and the assemblage composition of the coral juvenile population

Author	Location	Depth (m)	Juvenile size (mm)	Mean (juv.m^{-2})	Spatial variability	Correlations	Families (Genera)	Assemblage
Indo-Pacific								
This study	Wakatobi (Indonesia)	6; 12	<40	9.63 (±0.24 SE)	Spatial and temporal variability Pocilloporidae and Acroporidae varied across sites, Faviidae and Agariciidae across depths	No correlation with coral cover or recruits,	13 (28)	Agariciidae 20.84%; Faviidae 19.85%; Poritidae 13.77%; Pocilloporidae 12.16% and Acroporidae 4.59%
Chong-Seng et al. (2014)	Seychelles		<50	2.4 (±1.1) - 33.1 (±7.3)	Between reefs dominated by coral, macroalgae or rubble	No correlation with adult assemblage	3	Faviidae, Agariciidae, Poritidae, Siderastreidae, Astrocoenidae, Acroporidae and Meandrinidae
Adjeroud et al. (2013)	Tonga	2-3	10 - 50	5.5	Yes	7 dominant genera correlated between juvenile and adult stage	(28)	Acropora 22%; Porites 21%; Montipora 18%; Favia 10%
Nozawa et al. (2013)	Taiwan	5; 15	10 - 50		Not specified, but high variability between sites	At 5 m similar composition to adult (p=0.01);but different from recruits; at 15 m no differences. Strong recruits-adults-correlation for broooding species.	3	At 5 m: Pocilloporidae and Poritidae (80%). At 15 m: Acroporidae (48-65%) and Pocilloporidae (12-38%)
Salinas De León et al. (2012)	Wakatobi (Indonesia)	6	<40	24.8	Yes	Juvenile abundance correlated with coral cover	5	Faviidae 28.3%; Poritidae 24.5%; Agariciidae18.9 %; Acroporidae 10.7% Pocilloporidae 4.22%
Penin et al. (2007; 2010)	Moorea	6; 12 and 18	<50	7.9 (higher density at 18m)	Yes	Correlation with coral adults	(14)	Acropora, Fungia, Montipora, Pavona (no: Pocillopora and Porites)
Roth & Knowlton (2009)	Palmyra	10; 14 and 18	<50	Range: 0-59.5 (higher at 14 m on fore reef)	Yes (p<0.001)	Pattern not correlated with depth, juveniles mainly on CCA or bare substrate		Montipora; Acropora; Porites: 55.9-61.4%

Author	Location	Depth (m)	Juvenile size (mm)	Mean (juv.m^{-2})	Spatial variability	Correlations	Families (Genera)	Assemblage
Caribbean								
Lozano-Cortés & Zapata (2015)	San Andres Island (Colombia)	1 - 6	<40	5.75 (±3.47 SD)		No correlation with adult corals abundance and assemblage	7 15 species	Favia, Agaricia and Porites: 85.8%
Arnold et al. (2010)	Bonaire	10	<40	13.2 (± 2.2)		Correlation with recruit density		
Green et al. (2010)	Virgin Islands	5	<40	36.82	N/A	Correlation with the substratum (igneous or carbonate)		
Irizarry-Soto & Weil (2009)	Puerto Rico	0-3; 3-5; 5-10 and >15	<50	4.8 ± 0.24	Spatial and temporal variability (excluded 10 m)		31 species	

6.2 Importance of different environmental factors at different phases of the coral recruitment process

Several studies have investigated the causes of the selective mortality that affects coral recruitment, resulting in a decrease in coral densities between the recruit and juvenile stage and changes in assemblage composition (Hughes & Jackson 1985; Quinn & Kojis 2008; Penin & Adjeroud 2013). Fish predation and spatial competition have been identified as two of the main drivers that influence the recruitment process (Lewis 1986; Lirman 2001; Mumby 2009; Lenihan *et al.* 2011; Brandl *et al.* 2013). For example, on the Great Barrier Reef, parrotfish abundance was correlated with coral recruit densities (Trapon *et al.* 2013c), while associations of different strength were found between the abundance of young coral colonies and benthic organisms, such as serpulids and oysters in Kenya (Mangubhai *et al.* 2007), serpulids, bryozoans and bivalves in the Red Sea (Glassom *et al.* 2004) and bryozoans and oysters in the Great Barrier Reef (Dunstan & Johnson 1998). However, most of these studies focused on coral colonies that had recently settled, which are known to be affected by high mortality rates because of their vulnerability, and did not investigate the later phases of the recruitment process.

Despite the use of statistical and experimental methods, the drivers of coral recruitment process remain poorly understood. In Chapter 2, using a modelling approach, I did not find any dominant factor or combination of factors that adequately explained the spatial variability in either coral recruit or juvenile distribution. Furthermore, in a complementary manipulative experiment, fish predation or accidental removal from the reef was not found to be a cause of mortality in coral colonies aged up to two years (Chapter 4). However, this result does not exclude the possibility that overall fish abundance, or grazer abundance, might have a major influence in the first few days or weeks after the corals initially settle.

Spatial competition was expected to affect coral juvenile distribution and survivorship only in later stages when there was a lack of available substrate necessary for growth, expansion and competition for resources (e.g. nutrients, light). However, I found coral recruits began interacting with other benthic organisms, such as CCA and turf algae, very soon after settlement, when there was still a large proportion of free space on the settlement panels (Chapter 5). Although CCA is known to promote coral settlement (Price 2010; O'Leary *et al.* 2012), I found no specific association between CCA or the common benthic organisms present on the panels, such as bryozoans, turf algae, sponges, and coral colony density (Chapter 5).

However, the succession of organisms interacting with coral colonies, the outcome of these interactions, and the impact on coral survivorship and coral growth rate still need further investigation (Figure 6.1).

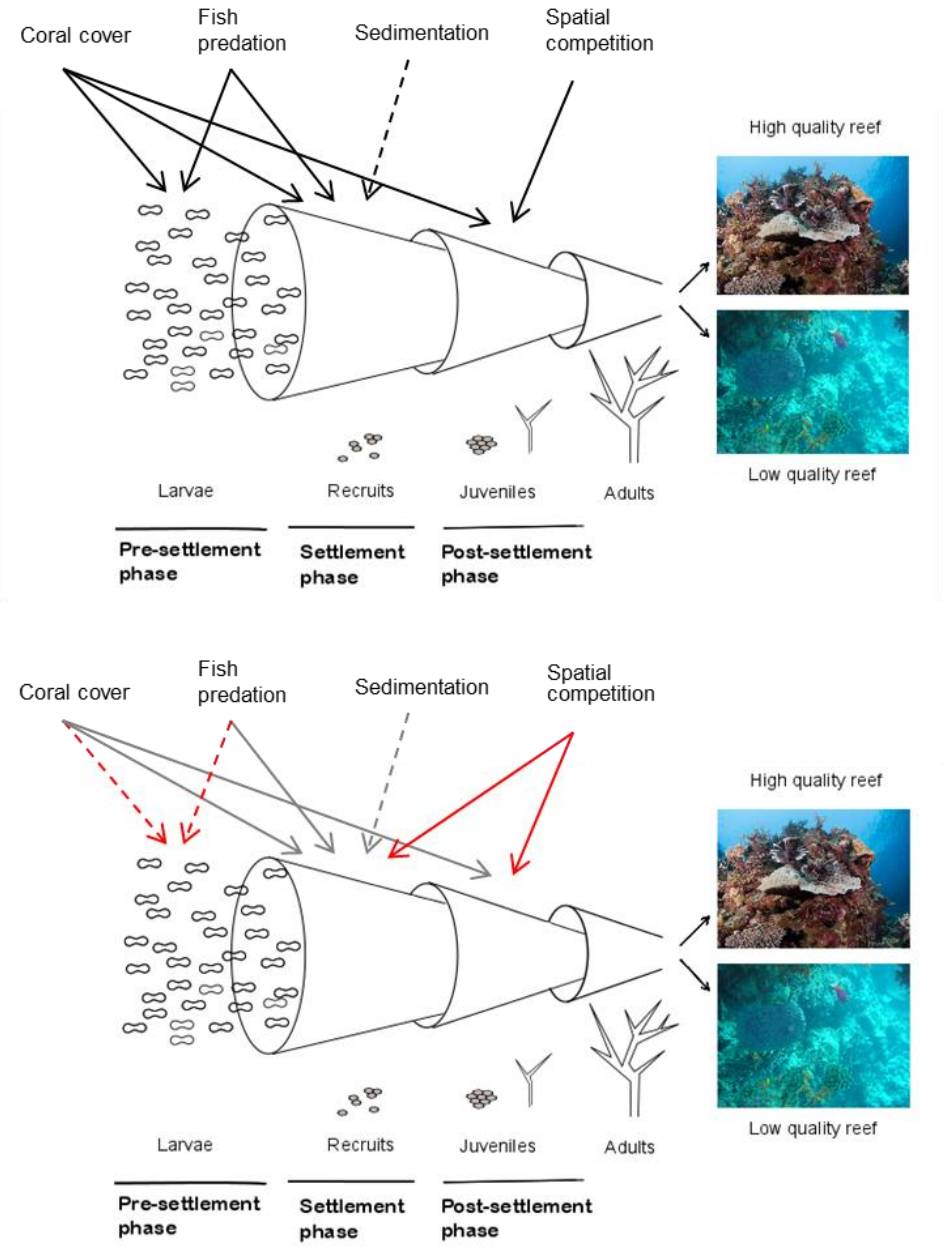


Figure 6.1 Summary of the main findings of my research (modified from Pineda *et al.* 2008). In the top half of the figure, the arrows show the correlations that were already known to exist before my study between environmental factors with coral populations at different stages of the coral recruitment process. The lack of studies were coral life history stages were studied separately did not allowed to understand the role and impact of factors, such as coral cover , fish predation, sedimentation and spatial competition, at different stages of the recruitment process. In the bottom half, the arrows show the outcomes of my study. No clear correlation was found between coral cover and recruitment rates, no evidence of self-recruitment, although coral cover might be correlated to the larvae availability. Mortality by fish grazing activity is likely to impact on coral recruit, no information about predation of coral larvae by fish. Sedimentation might have a role at coral settlement, but more investigations are needed about further effects on coral recruit survivorship. Spatial competition influences coral spatial variability from settlement across all the life history stages. Interactions and correlations between coral colonies and benthic organisms play an important role in determining the final composition and pattern of coral population. Black lines: knowledge before my study. Black dotted line: suggested correlation. Red lines: findings of this study; grey lines: correlations not found. Red dotted line: correlations that need more investigation.

6.3 Implications for reef management

My data for coral recruit and juvenile abundances collected over a seven-year period represent an important step in the development of a monitoring program for coral recruitment in the Wakatobi. My data can be compared with data collected in the future to assess longer temporal coral recruitment trends and identify range fluctuations in coral recruit densities. Any future decreases in coral densities or change in coral assemblage composition can then be compared with my time series data to determine if it falls within patterns of previously observed variability or if it is a cause for greater concern. In addition, if there were ever a major bleaching event or other major disturbance, my data can serve as a reference point for the coral recruitment state in normal conditions when planning a coral recovery project.

Overall, my research provides a better understanding of the role and importance of grazing activity and spatial competition in regulating coral recruitment. It highlights the importance of investigating local ecological factors at different localities on small scales (e.g. a few hundred meters), since even small distances between sites can result in high variability in recruitment patterns. My study shows that fish predation is not an important cause of mortality in coral recruits and juveniles in the Wakatobi. As a consequence, any future changes in coral densities in these early coral life history stages are not likely to be attributable to fish activity, but rather to other or factors that remain currently unidentified.

Interactions with other benthic organisms, especially algae, need to be monitored through time. Although my study did not find any specific organisms that affected coral recruits and juvenile distribution and survivorship, on more complex surfaces such interactions between coral colonies and organisms might have a higher impact than what I found in a developing community. More studies are required to understand the association between environmental disturbances with different stages of coral recruitment in the Wakatobi.

My study identified sites with higher recruitment rates which are important for conservation purposes and need to be maintained healthy through a monitoring program repeated in time in order to prevent declines in recruitment rates.

At the same time, degraded sites, which present low recruitment rates, need proactive management to implement plans to reduce stressors, such as sedimentation caused by coral mining and land-based pollution, and avoid further deterioration of the current reef conditions.

Once disturbances have been reduced and reef status is continuously monitored, a coral restoration project could improve reef recovery at degraded sites in order to increase

recruitment possibility. Decrease of disturbances promotes the growth of coral colonies artificially deployed on reef substrate, but also of the natural coral colonies.

In addition to these suggestions, reef managers could improve the site selection for development or conservation and implement more strategic and proactive approach that delivers long-term benefits. For example implementation of a fish zonation plan in the overall Wakatobi could protect the area important for coral reproduction and recruitment, especially during the spawning season. A better regulation of fisheries could benefit grazing fish population and they important role in regulating algae growth.

In the last decade, genetic and environmental data have been combined in order to investigate the scale of connectivity and variability in coral recruitment and model the patterns of coral recruitment variability. A genetic study on reef connectivity in the Wakatobi would give insight into the sources and movement of coral larvae. These genetic data combined with my data on spatial variability could provide important information on the regulation of the recruitment process occurring in the Wakatobi. Measuring relationships between reef connectivity, scale of variability in coral recruitment, and environmental factors would make it possible to predict recruitment trends (Golbuu *et al.* 2012) and identify areas that should be given priority for conservation and reef restoration.

6.4 Conclusions

The results of my study provide important insights into the processes regulating coral populations in the Wakatobi and the changes occurring over time. My research demonstrates that there is a high variability in abundance and assemblage composition between coral early life history stages and this variability is likely driven by local environmental factors.

In the future, the establishment of a regular coral recruit and juvenile monitoring program, combined with my seven-year dataset, will prove invaluable for conserving and managing coral populations in this region, and would generate useful information for assessing the health of the coral reef.

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Appendix I

Effect of predation and sedimentation on coral recruits: Pilot study for Chapter 4

Predation and sedimentation are two of the main detrimental environmental factors that affect coral reefs (Lenihan *et al.* 2011; Erftemeijer *et al.* 2012). Sedimentation has been increasing in recent years as a result of changes in land use (Rogers 1990) and it can slow the growth of corals and increase mortality. Prolonged exposure to high levels of sedimentation induces chronic stress, decreasing coral recovery potential and coral density, and resulting in changes to coral community composition (Bellwood *et al.* 2004). A preliminary experiment to investigate the effect of fish predation, sedimentation, and their interaction on coral recruits was conducted between June–August 2012.

Experimental design

Fifty settlement panels were used that had been submerged for 10 months at 6 m depth at two replicate sites on the Hoga reef: Buoy 3 and Buoy 4 (see map in Chapter 2). Four treatments were applied: control, increased sedimentation, fish exclusion, and increased sedimentation combined with fish exclusion. According to my findings (see results from Chapter 3) and previous research in the area (Salinas De León *et al.* 2011, 2012a), coral recruits settle mostly on the back and cryptic side of the panels rather than on the front and exposed side. Therefore, I performed my experiment using the back side of the panels. While still submerged, the panels were removed from the reef, turned upside down and fixed to the reef at the same depth. Six panels were assigned to each treatment and all the coral colonies visible to the naked eye were counted. Fish exclusion was achieved by fixing a plastic frame with 12 wooden spikes around the tiles using cable tiles. The spikes were positioned on the top side of the frame pointing up, in order to prevent big herbivorous fish reaching the tiles. Small fish were still able to access the tiles and feed on them (Figure 1).

Figure 1 Set-up of the fish exclusion treatment on a settlement panel deployed on the reef at 6 m

Sediment addition was carried out by pouring a measured amount of sediment, prepared in advance, onto the panel. The amount of sediment required to cover the surface of one side of the panel was assessed prior to conducting the experiment. Sediment was collected from the reef and taken to the lab to be filtered by sieves until the sediment particles with a diameter smaller than 0.63 µm (silt) were separated. This size fraction was chosen because it was found in previous surveys to be the predominant size fraction in sediment from the Wakatobi (Operation Wallacea, unpublished data). Then the sediment was dried in an oven for 24 hours, weighed and separated in quantities of 2g, 5g, 10g and 15g into small plastic ziplock bags, three for each quantity. Ten grams were found to be a sufficient amount to cover the entire tile surface with a thin layer that had a good resilience to water flow (Figure 2).

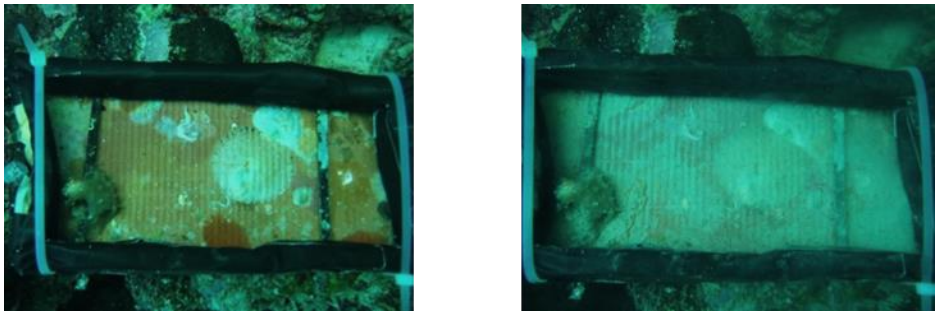


Figure 2 Standardisation of the amount of sediment to use for the sediment addition treatment. Digital images represent the experimental tile before (left) and after (right) the sediment addiction

Sediment was added to the experimental tile with care in order to obtain a thin and equal layer on the surface. All the panels were checked every second day and digital images of the tiles were taken in order to record variations in coral recruit patterns and sediment distribution.

At the end of the experiment, the tiles were collected and taken to the laboratory in seawater and analysed using the procedure described in Chapter 2.

Results

When analysing the tiles, I did not observe variation in the status of the recruits identified at the beginning of the experiment. Recruits in the sediment addition treatment did not show detectable signs of bleaching or mortality and I did not observe bites of herbivorous fish on the tiles without fish exclusion or the controls. In addition, during the laboratory analysis, I found recruits not recorded in the initial count *in situ*.

The lack of any effect of fish predation and sedimentation on the tiles could be due to a number of reasons, including the limited abundance of recruits on the tiles, the small size of the recruits that makes them difficult to detect *in situ,* and the low presence of algae.

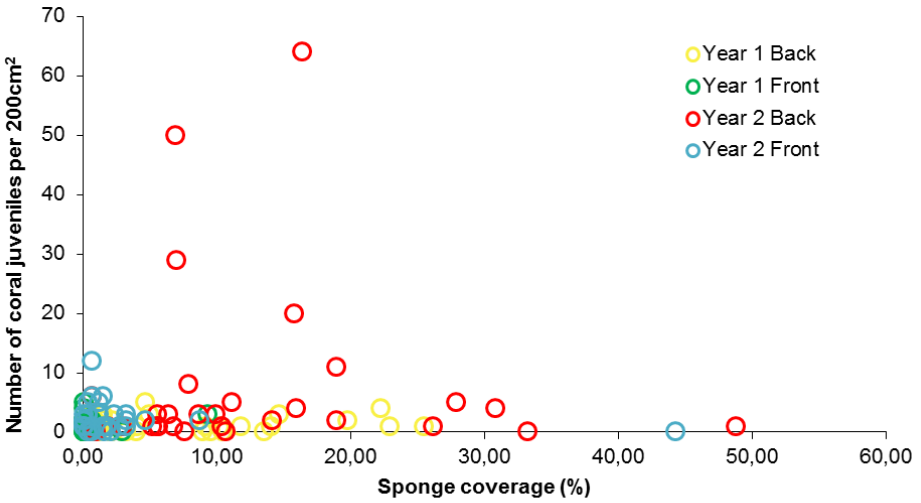
This experiment was conducted in a year characterised by low coral recruitment rates compared to recruitment data collected in 2008 and 2009 in the same area of the WMNP (see Chapter 3). The number of coral recruits found on the experimental tiles was lower than expected and there was not a sufficient number to generate robust results. Recruits were not easily detectable on the panels *in situ* and not all of them could be mapped at the beginning of the experiment because of their small size. Furthermore, the duration of the experiment of seven days was found to be insufficient to measure the effects of sedimentation on the corals, such as colony bleaching or mortality.

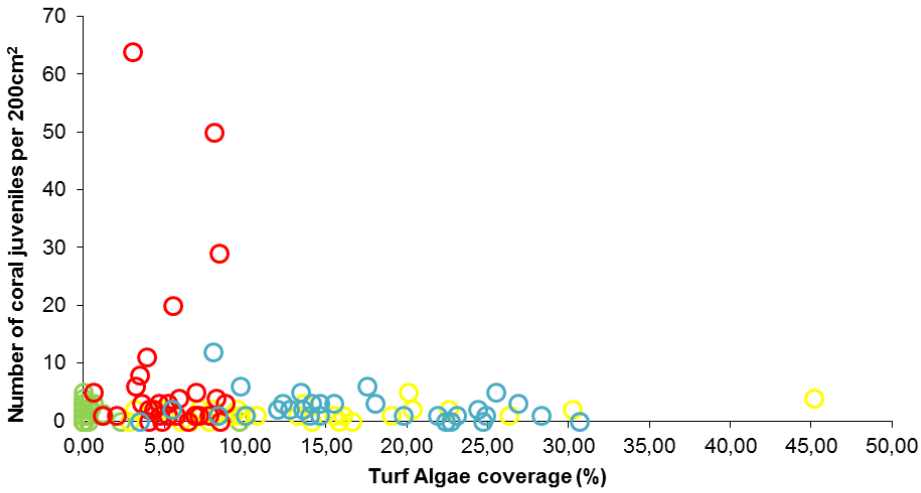
The observations collected at the end of this experiment were used to enhance the experimental design for the manipulative experiment conducted in the following year (see Chapter 4). The new experimental design included the use of settlement panels submerged for a longer time (up to 2 years) with older coral colonies settled on them and the use of a longer experiment duration.

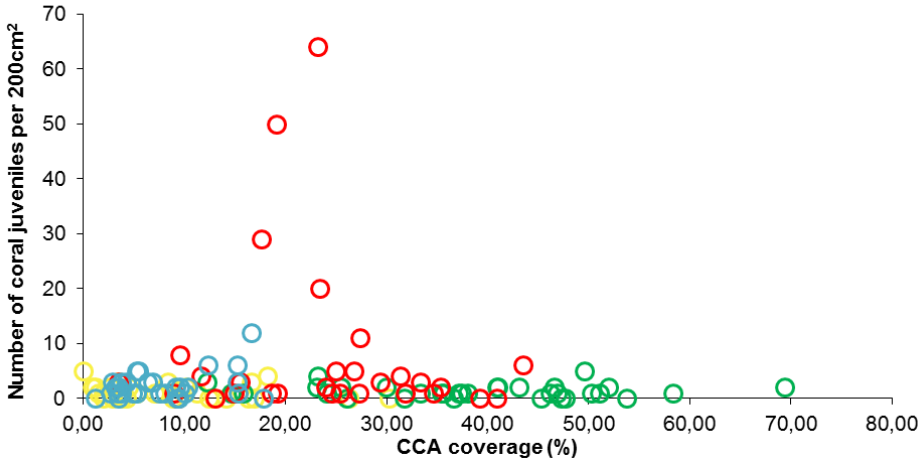
Appendix II

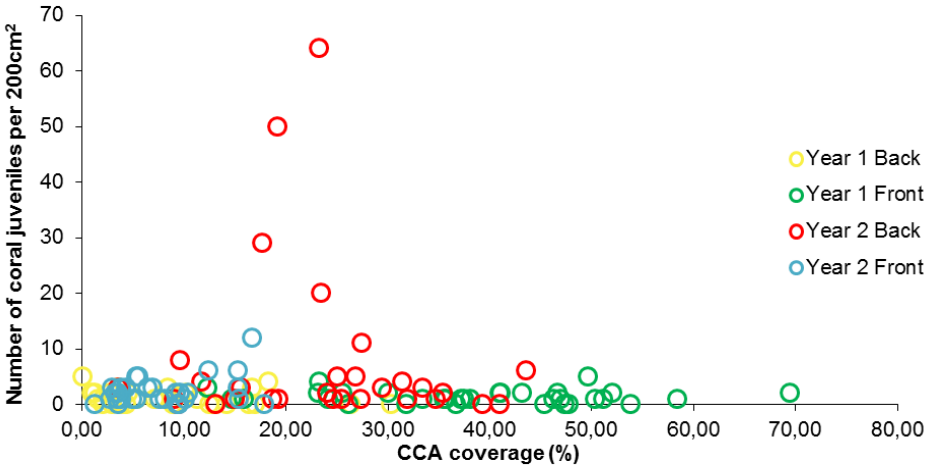
Supporting data for Chapter 5

Figure 1 Correlation between the coverage of four benthic groups (sponges, turf algae, CCA and bryozoans) and recruitment rates recorded at Buoy 3 and Buoy 4. Circles indicate different tiles








Number of coral juveniles per 200cm²
70
60
50
40
30
20
10
0
0,00
10,00
20,00
30,00
40,00
50,00
60,00
70,00
80,00
CCA coverage (%)
Year 1 Back
Year 1 Front
Year 2 Back
Year 2 Front

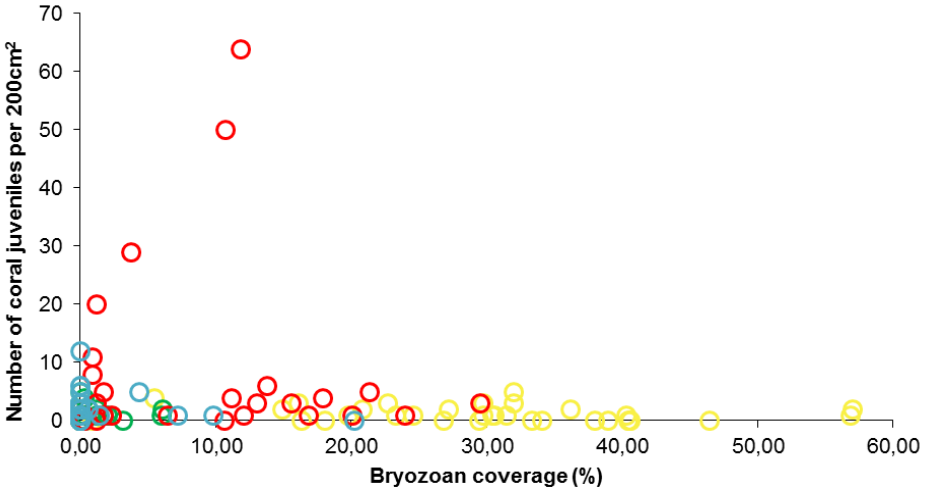

Number of coral juveniles per 200cm²
70
60
50
40
30
20
10
0
0,00
10,00
20,00
30,00
40,00
50,00
60,00
Bryozoan coverage (%)

Table 1 Summary of the interactions between the coral juveniles and the benthic organisms. Data were pooled for Buoy 3 and Buoy 4 and data are divided by year (one or two) and side of the settlement panel (front or back). Coral families are in the rows and the benthic organisms in contact with the coral colonies in the columns. Explanations about how to read the table are in Methods in Chapter 5

Year 1 – Front side

Year 1 Front	Algae										Invertebrate									
	Turf Algae	CCA	CCA Dead	Cyanobact.	Green Encr. Algae	Macroalgae	No Corall. Encr. Algae	Barnacles	Bivalve	Bryozoan	Foram.	Hydrocoral	Other Invert	Snail	Sponge	Tubeworm	Ascidean individual	Ascidea colonial	Vermetid	Unknown
Acroporidae		3 0 0 3			1 0 0 1		1 0 0 1													
Pocilloporiidae	5 1 0 6	25 4 3 32	8 2 0 10		5 0 0 5		3 0 0 3								3 0 0 3			1 0 1 2	2 0 0 2	
Poritidae		0 0 1 1	0 0 1 1																	
Faviidae																				
Dendrophyllidae																				
Fungiidae																				
Agaricidae																				
Other		2 0 1 3																		
Total		30 4 5 39	8 2 1 11		6 0 0 6		4 0 0 4								3 0 0 3			1 0 1 2	2 0 0 2	

Year 1 – Back side

Year 2 Front	Algae										Invertebrate									
	Turf Algae	CCA	CCA Dead	Cyanobact.	Green Encr. Algae	Macroalgae	No Corall. Encr. Algae	Barnacles	Bivalve	Bryozoan	Foram.	Hydrocoral	Other Invert	Snail	Sponge	Tubeworm	Ascidean individual	Ascidea colonial	Vermetid	Unknown
Acroporidae		1 0 0 1	1 0 0 1																	
Pocilloporiidae	6 3 0 9	18 2 4 24	15 4 2 21	5 0 0 5		0 1 0 1							0 0 1 1	3 0 3 6	2 1 0 3			5 1 0 6		
Poritidae																				
Faviidae		1 0 0 1																1 0 0 1		
Dendrophyllidae																				
Fungiidae																				
Agaricidae																				
Other	0 2 0 2	5 0 2 7	2 0 0 2	0 1 0 1									0 0 1 1	0 0 2 2						
Total	6 5 0 11	25 2 6 33	18 4 2 24	5 1 0 6		0 1 0 1							0 0 2 2	3 0 5 8	2 1 0 3			6 1 0 7		

Year 2 – Front side

Year 1 Back	Algae							Invertebrate												
	Turf Algae	CCA	CCA Dead	Cyanobact.	Green Encr. Algae	Macroalgae	No Corall. Encr. Algae	Barnacles	Bivalve	Bryozoan	Foram.	Hydrocoral	Other Invert	Snail	Sponge	Tubeworm	Ascidean individual	Ascidea colonial	Vermetid	Unknown
Acroporidae		1 0 0 1	1 0 0 1		1 0 0 1															
Pocilloporiidae		3 0 0 3	2 0 0 2		2 0 0 2		1 0 0 1		2 0 0 2	1 0 0 1					0 1 0 1			1 0 0 1		
Poritidae		1 0 2 3				0 1 0 1									0 1				1 0 0 1	
Faviidae			1 0 0 1	0 1 0 1		1 1 0 2				2 1 2 5					2 3 0 5		1 1 0 2			
Dendrophyllidae																				
Fungiidae																				
Agaricidae																		0 1 0 1		
Other		2 0 0 2													3 0 0 3			1 1 0 2		
Total		7 0 2 9	4 0 0 4	0 1 0 1	3 0 0 3	1 2 0 3	1 0 0 1	0 0 0 0	2 0 0 2	3 1 2 6					5 4 0 9	0 0 0 0	1 1 0 2	2 2 0 4	1 0 0 1	

Year 2 – Back side

Year 2 Back	Algae							Invertebrate												
	Turf Algae	CCA	CCA Dead	Cyanobact.	Green Encr. Algae	Macroalgae	No Corall. Encr. Algae	Barnacles	Bivalve	Bryozoan	Foram.	Hydrocoral	Other Invert	Snail	Sponge	Tubeworm	Ascidean individual	Ascidea colonial	Vermetid	Unknown
Acroporidae		2 0 1 3					0 0 1 1								1 0 0 1					
Pocilloporiidae		6 1 5 12		1 0 0 1	2 0 0 2		1 1 0 2		0 0 2 2	0 0 1 1					6 0 0 6		0 1 0 1	1 0 0 1		
Poritidae		5 0 2 7			0 1 0 1				0 0 4 4	4 0 0 4					3 1 0 4	1 0 0 1				
Faviidae	9 1 0 10	20 4 4 28	3 0 0 3	3 0 0 3	6 0 0 6	1 1	6 1 1 8		0 0 1 1	5 0 2 7					26 1 3 30	3 0 1 4		5 2 7	5 0 1 6	
Dendrophyllidae	1 0 0 1	1 0 1 2			1 0 0 1				1 0 0 1	1 0 0 1					2 0 0 2				1 0 1	
Fungiidae		0 1 1								0 0 2 2										
Agaricidae	1 0 0 1	2 1 0 3	1 0 0 1						1 0 0 1											
Other	1 2 0 3	4 0 2 6	1 0 1 2	0 0 1 1	0 2 0 2	1 0 0 1	3 4 0 7			1 1 3 5					6 3 0 9		1 0 0 1		6 0 0 6	
Total	12 3 0 15	40 6 16 62	5 0 1 6	4 0 1 5	9 3 0 12	2 0 0 2	10 6 2 18		2 0 7 9	11 1 8 20					44 5 3 52	4 0 1 5	1 1 0 2	6 2 0 8	12 0 1 13	

Table 2 Summary of the interactions between the coral juveniles and the benthic organisms. Data were pooled for Buoy 3 and Buoy 4 and divided by year, one or two. Coral families are in the row and the benthic organisms in contact with the coral colonies are in the columns. Explanations about how to read the table are in Methods in Chapter 5

		Algae															
		Algal Turf		CCA		CCA Dead		Cyanobacteria		Gr.Encr.Algae		Macroalgae		No Cor.Encr. Algae	
1	Front	0	0	30	4	8	2	0	0	6	0	0	0	4	0
		0	0	5	39	1	11	0	0	0	6	0	0	0	4
	Back	0	0	7	0	4	0	0	1	3	0	1	2	1	0
		0	0	2	9	0	4	0	1	0	3	0	3	0	1
2	Front	6	5	25	2	18	4	5	1	0	0	0	1	0	0
		0	11	6	33	2	24	0	6	0	0	0	1	0	0
	Back	12	3	40	6	5	0	4	0	9	3	2	0	10	6
		0	15	16	62	1	6	1	5	0	12	0	2	2	18

		Invertebrate																									
		Barnacles		Bivalve		Bryozoan		Foraminifera		Hydrocoral		Hydroids		Other Invert		Sponge		Tubeworm		Ascidean ind		Ascidea col		Vermetid		Unknown	
1	Front	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	1	0	2	0	0	0
		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	1	2	0	2	0	0
	Back	0	0	2	0	3	1	0	0	0	0	0	0	0	0	5	4	0	0	1	1	2	2	1	0	0	0
		0	0	0	2	2	6	0	0	0	0	0	0	0	0	0	9	0	0	0	2	0	4	0	1	0	0
2	Front	0	0	0	0	0	0	0	0	0	0	0	0	3	0	2	1	0	0	0	0	6	1	0	0	0	0
		0	0	0	0	0	0	0	0	0	0	2	2	5	8	0	3	0	0	0	0	0	7	0	0	0	0
	Back	0	0	2	0	11	1	0	0	0	0	0	0	0	0	44	5	4	0	1	1	6	2	12	0	0	0
		0	0	7	9	8	20	0	0	0	0	0	0	0	0	3	52	1	5	0	2	0	8	1	13	0	0

Figure 2 Correlation between CAP axes to data cloud from Figure 5.2 (Page 103). The results of the CAP analysis show that there is very strong and significant correlation between the benthic community composition and coral recruitment rates (P=0.0001). The strength of this association is indicated by the size of correlation of the axes to the data cloud, where values greater than 0.9 indicate strong correlation. The first axis is reasonably large (δ_1>0.9373).

Correlations		
Eigenvalue	**Correlation**	**Corr.Sq.**
1	0.9373	0.8785
2	0.8895	0.7912
3	0.833	0.6938