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Variation in early post-settlement growth and mortality of scleractinian corals

Thesis submitted by

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In July 2013

For the Degree of Doctor of Philosophy in Marine Biology
Within the ARC Centre of Excellence for Coral Reef Studies,
James Cook University, Townsville, Queensland

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Statement on the contribution of others

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Abstract

For species with complex life histories, such as scleractinian corals, processes occurring early in life are likely to play a strong role in population regulation. A plethora of studies have examined settlement patterns of coral larvae, mostly on artificial substrata, and the composition of adult coral assemblages across multiple spatial and temporal scales. However, relatively few studies have examined the demography of small (≤ 50 mm maximum diameter) sexually immature corals on natural reef substrata, mostly due to difficulties associated with detecting small corals within natural reef environments. Mortality is often very high during the first year post-settlement, often reaching up to 99 %. However, if post-settlement mortality rates were universally high, then this would have limited influence on adult abundance. In fact, rates of juvenile mortality vary spatially, temporally and taxonomically, which will influence the structure and dynamics of populations and communities.

In order, to better understand the influence of early post-settlement processes on patterns of abundance and community structure among adult corals, I first quantified the variation in abundance, composition and size of juvenile corals (≤ 50 mm diameter) among 27 sites, nine reefs and three latitudes spanning over 1000 km on Australia's Great Barrier Reef (GBR). A total of 2,801 juveniles were recorded with a mean density of $6.9 (\pm 0.3 \text{ SE})$ individuals per m^2 , with *Acropora*, *Pocillopora*, and *Porites* accounting for 84.1 % of all juvenile corals surveyed. Size-class structure, orientation on the substratum and taxonomic composition of juvenile corals varied significantly among latitudinal sectors. The abundance of juvenile corals varied both within ($6\text{-}13 \text{ individuals.m}^{-2}$) and among reefs ($2.8\text{-}11.1 \text{ individuals.m}^{-2}$) but was

fairly similar among latitudes (6.1-8.2 individuals.m⁻²), despite marked latitudinal variation in larval supply and settlement rates previously found at this scale. Furthermore, the density of juvenile corals was negatively correlated with the biomass of scraping and excavating parrotfishes across all sites, revealing a potentially important role of parrotfishes in determining distribution patterns of juvenile corals on the GBR. While numerous studies have advocated the importance of parrotfishes for clearing space on the substratum to facilitate coral settlement, my results suggest that at high biomass they may have a detrimental effect on juvenile coral assemblages.

I next examined the effects of incidental grazing on post-settlement survival of *Acropora cytherea* recruits. Larvae of *A. cytherea* were reared in captivity and settled onto terracotta tiles. Replicate tiles were deployed within the exposed reef crest and the sheltered back reef of Lizard Island, in northern section of the GBR. Overall, survivorship was broadly comparable between habitats, ranging from 37.7 – 64.5 % per month on the exposed reef crest, and 53.1 – 64.3 % on the sheltered back reef. On the reef crest, the exclusion of herbivores increased survivorship by 22.4 %: from 42.1 to 64.5 % per month. Moreover, recruits survivorship within the reef crest was negatively correlated with the density of parrotfish feeding scars on tiles after 4-weeks. In contrast, the exclusion of herbivores had no detectable effect on survivorship within the back reef and no feeding scars were observed on tiles in this habitat. Difference in grazing-induced mortality between habitats was most likely related to differences in herbivore size and abundance, with parrotfish biomass being 5.5-fold greater on the reef crest than the back reef. Surprisingly, tile orientation had no effect on survivorship of *A. cytherea* in either habitat, despite a marked difference in the sediment cover on vertical (0 %) vs. horizontal tiles (30 %) in the back reef.

This was in marked contrast to previous studies that have reported sedimentation is a major cause of early post-settlement mortality in corals.

Ultimately, I wanted to directly measure the fate of juvenile corals on natural substratum, from small (within transect) to large scales (among latitudinal sectors of the GBR, and geographic comparisons between the GBR and French Polynesia), to better understand the role of post-settlement processes in shaping adult communities. Here, I measured growth and mortality rates of *Acropora*, *Pocillopora* and *Porites* juveniles within quadrats, over a period of 18 months. On the GBR, these processes were significantly different among the three taxa examined, and the highest variation occurred among quadrats within transect. In particular, mortality of *Acropora* juveniles (mean of 29.3 % per annum) was lower than for *Pocillopora* (33.6 % per annum) and *Porites* (43.2 % per annum); and the growth rates of *Acropora* (mean of 1.80 mm.month⁻¹) and *Pocillopora* (mean of 1.76 mm.month⁻¹) were higher than for *Porites* (mean of 0.97 mm.month⁻¹). Latitudinal patterns were not consistent among taxa; highest mortality was recorded within the central sector of the GBR for *Acropora* juveniles and lower mortality at the northern sector for *Porites* juveniles, whereas for growth rates, only those of *Pocillopora* juveniles varied at sector scale, with lower growth in the southern sector. Mortality rates decreased as the size of juveniles increased. In addition, mortality rates were positively correlated with adult cover for *Acropora* and *Pocillopora* juveniles probably due to competition for space, with adult overgrowing juveniles. However, mortality rates were not correlated with parrotfish biomass, probably due to the ability of the fish to avoid juveniles, as opposed to very small recruits. In conclusion, generic-level assemblage structure of corals on the GBR is driven largely by high variations in juvenile mortality and growth rates at small and large-scales.

When comparing post-settlement rates from Trunk reef in the central GBR with those in Moorea, French Polynesia, I found that there were no differences in the density, growth, or mortality rates of juvenile corals. However, significant regional differences exist in the taxonomic composition of coral assemblages within both adult and juvenile assemblages, with *Pocillopora* being the predominant coral genera in Moorea and *Acropora* at Trunk Reef. Most of the variations in these variables were evident at the small (within reef) scale, with exposed sites having lower densities and higher rates of mortality of juvenile corals than sheltered sites at both locations. The lack of geographic variation in the density, growth and mortality rates of juvenile corals is interesting given the cover of adult coral was 3-fold higher on Moorea (31.1 %) than on Trunk Reef (10.8 %), suggesting that adult coral assemblages are structured more by differential adult mortality, larval settlement, or very early post-settlement mortality (before colonies can be observed *in situ*), rather than demographic rates of juvenile growth or mortality.

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Table 5.5 Relationship between the density of juvenile corals and the cover of adult corals on Moorea and Trunk Reef. Pearson's correlation coefficients are given for correlations for all coral taxa collectively (i.e., total coral cover vs. total juvenile density), and the three most abundant genera independently (e.g., *Acropora* cover vs. juvenile *Acropora* density). Correlations are based on the cover of adult corals and the mean density of juvenile corals per transect (n = 9). Significant results are shown in bold..... 105

Chapter 1. General Introduction

A fundamental goal of ecology is to determine processes that influence species distributions and patterns of abundance. For marine organisms, which typically have a bipartite life cycle, where larvae develop in the plankton before settling within benthic habitats and recruiting to relatively site-attached adult populations, the distribution and abundance of adults is determined by a complex interplay of many different processes operating at different life-history stages. For some coral reef organisms (mostly, fishes) there has been considerable work linking patterns of adult abundance to spatial and temporal fluctuations in rates of settlement (e.g., Williams and Sale 1981; Doherty 1983; Wellington and Victor 1985; Doherty and Williams 1988; Hixon and Carr 1997). However, there is increasing evidence that patterns of adult abundance are decoupled from high temporal and spatial stochasticity recorded in settlement patterns (Hughes et al. 1999). Roberston (1988), for example, showed that marked inter-annual variation in settlement by Caribbean surgeonfishes was not reflected in absolute or relative abundance of adult conspecifics. Similarly, Hughes et al. (1999) showed that marked latitudinal variations in settlement rates of scleractinian corals along the length of Australia's Great Barrier Reef (GBR) were not reflected in the local abundance (percentage cover) of adult corals, which was remarkably constant among locations (see also Bak and Engel 1979; Wallace 1985b; Rylaarsdam 1983; Fisk and Harriott 1990; Baird and Hughes 1997). These findings suggest that there are additional, and as yet poorly understood, processes that influence patterns of distribution and abundance for the relatively sedentary life stages of marine organisms.

Most studies of population biology of scleractinian corals have focussed on either patterns of settlement (e.g., Babcock 1988; Fisk and Harriott 1990), or processes (such as competition, predation, and disturbance) affecting adult populations (e.g., Chornesky 1989; Connell et al. 1997). However, settlement rates, which are generally measured using experimental settlement plates made from artificial materials (e.g., Baird and Hughes 1997; Hughes et al. 1999, 2000), often show little or no relation to the local abundance of adult corals (Bak and Engel 1979; Rylaarsdam 1983; Fisk and Harriott 1990; Baird and Hughes 1997; Hughes et al. 1999). These discrepancies between patterns of coral settlement and adult abundance may be attributable to spatial and temporal variation in early post-settlement growth and survivorship (e.g., Bak and Engel 1979; Rylaarsdam 1983; Hughes et al. 1999; Penin et al. 2010), as shown for non-coral invertebrates (e.g., Hughes 1990; Stoner 1990) and coral reef fishes (e.g., Hixon and Carr 1997). However, comparatively little research has been undertaken to explicitly quantify temporal or spatial variation in demographic rates during the early post-settlement life stage of scleractinian corals, especially within the first years after settlement (Babcock and Mundy 1996). This is due, in no small part, to difficulties associated with detecting and identifying recently settled corals (Baird and Babcock 2000), which are very small (≤ 2 mm; Babcock et al. 2003) and often very cryptic, settling preferentially in crevices or on the underside of dead corals (Baird and Hughes 1997).

Early, immature life-stages of scleractinian corals are often categorized in the literature as colonies with a maximum diameter of 40-50 mm (e.g., Bak and Engel 1979; Rylaarsdam 1983; Babcock 1985; Fitzhardinge 1988; Banks and Harriott 1996; Penin et al. 2010). However, this life-stage can be further divided into two distinct phases: i) the early, post-settlement or “recruits”, represented by individuals < 10 mm,

which are not generally visible on natural substrata, and ii) later, post-settlement or “juveniles”, i.e. individuals ≥ 10 mm that are readily visible on natural substrata (Penin et al. 2010). This distinction is fundamental as corals at the recruit stage are presumed to experience very high mortality rates, often up to 99 % mortality within the first year following the settlement of the larvae (Harriott 1983; Rylaarsdam 1983; Babcock 1985; Wallace et al. 1986; Babcock and Mundy 1996; Fairfull and Harriott 1999), while later, juvenile stages exhibit decreasing mortality rates with increasing size (escape in size: often referred as size refuge in the literature, Babcock and Mundy 1996). Early post-settlement mortality of scleractinian corals is generally measured in aquaria or on artificial substrata, rather than in the field or on natural substrata (e.g., Mundy and Babcock 2000). However, recent studies are starting question to whether settlement on artificial substrata is really reflective of the number and composition of settlers on natural substrata (Penin et al. 2010), which in turn, may bias estimates of early post-settlement mortality. Studies that have measured demographic rates for small and juvenile corals that have settled on natural substrata (e.g., Bak and Engel 1979; Rylaarsdam 1983; Glassom and Chadwick 2006), are extremely limited in number, scale and scope, making it difficult to draw general conclusions on the effect of early post-settlement processes on the composition and abundance of adults coral populations.

The relative influence of pre- versus post-settlement processes is important because it determines what processes are critical in determining the structure and dynamics of coral populations and assemblages. Settlement rates of scleractinian corals on to artificial substrata are often assumed to reflect larval supply, which is influenced by i) the fecundity and fertilisation success of adult corals within the source area (Hughes et al. 2000) ii) the dispersal and delivery of planktonic larvae to

reef habitats (Harrison and Wallace 1990), and iii) larval selection of settlement habitats and substrata (Connell 1985). While coral larvae have the potential to travel vast distances (Richmond 1987; Nozawa and Harrison 2002; Graham et al. 2008), thereby contributing to recovery of reefs that have been denuded by severe acute or chronic disturbances (Sammarco 1985; Connell 1997; Van Moorsel 1988), the extent of dispersal will depend on several factors, including oceanographic conditions, larval condition and survivorship (Vermeij 2006). The active choice of substrata by the larvae following the pelagic phase has also been found to have a major influence on distribution and abundance of corals (Harrington et al. 2004), which may depend on many factors such as light availability (Mundy and Babcock 1998), depth (Baird et al. 2003), and chemical cues (Harrington et al. 2004). Therefore, if no suitable substratum is available, settlement rates and/ or post-settlement survival can be considerably reduced (e.g., Hughes et al. 2007). Following settlement, growth and mortality of corals maybe influenced by a wide range of factors: physical disturbances such as sedimentation (Sato 1985; Gilmour 1999), elevated temperature (Edmunds 2008) and/ or biological disturbances such as overgrowth by macroalgae (Box and Mumby 2007), competition with conspecifics (Vermeij and Sandin 2008), and predation (Penin et al. 2010). The relative importance of each of the above mentioned process is still poorly understood, but is likely to vary spatially, temporally and taxonomically (Babcock and Mundy 1996).

1.1 Mortality Rates of Juvenile Corals

Mortality rates of corals, and other colonial organisms, are strongly and negatively related to colony size. Small colonies are generally more vulnerable to physical and biological disturbances compared to larger adult corals, because any

given disturbance is less likely to cause whole colony mortality for increasingly larger corals (Hughes and Jackson 1985). The early post-settlement phase is therefore the most critical stage, where mortality rates often approach 99 % within the first year on the substratum, and this is true for many geographic locations: GBR (Babcock and Mundy 1996), Solitary Island (Wilson and Harrison 2005), Florida (Szmant and Miller 2006; see Table 1.1). In comparison, mortality rates of larger juvenile corals (40-50 mm) vary between 20-70 % per annum (Table 1.1). Rates of juvenile mortality are highly variable in space (Table 1.1) and time, as they are influenced by many biological and physical factors, characteristic of the environment. For example, if mortality of early stages is density-dependent (Vermeij 2005), regions with higher settlement rates (e.g. low latitude reefs on the GBR) will tend to have higher mortality rates (Hughes et al. 1999). Such variation is not surprising given marked variation in rates of mortality for adult corals (Harriott 1985b; Bythell et al. 1993; Gardner et al. 2003). Notably, juvenile corals will be highly vulnerable to many (if not all) of the same physical and biological disturbances that affect adult corals. Furthermore, juvenile mortality rates vary taxonomically (Table 1.1), and this is likely due to differences in species-specific growth rates (Bak and Meesters 1998).

Major causes of coral mortality are generally divided into chronic versus acute disturbances (Connell 1997). Chronic disturbances (e.g., predation, sedimentation, competition with algae and/ or conspecific among others) are often considered to have more influence on post-settlement mortality (Ritson-Williams et al. 2009) and may therefore greatly affect reef recovery. However, despite many studies that have quantified and compared causes of adult coral mortality, there is very limited understanding of the patterns or causes of juvenile mortality. The few studies that have quantified early post-settlement mortality of juvenile corals showed that a large

proportion of juvenile corals mortality is attributed to predation and/ or incidental grazing (e.g., Sammarco 1985; Sato 1985; Rotjan and Lewis 2008; Christiansen et al. 2009; Mumby 2009; Penin et al. 2010, 2011), which is also true for a great range of marine invertebrates (see review of Gosselin and Qian 1997). Predation on juvenile corals is attributed to both incidental grazing (mostly by herbivorous fishes) and targeted feeding by corallivorous fish, such as butterflyfishes (Penin et al. 2010). Penin et al. (2010) showed that incidental grazing by parrotfishes may account for up to 70 % mortality among newly settled corals (< 10 mm), but these fishes are much less likely to injure or kill juvenile corals once they exceed 20-30 mm diameter. The contribution of parrotfishes to early post-settlement mortality is also likely to vary spatially, in accordance with variation in abundance of parrotfishes among reef habitats and among geographical locations (Hoey and Bellwood 2008).

Sedimentation is also a major cause of mortality in small colonies (Sato 1985; Gilmour 1999), as very small corals can become quickly smothered. Therefore, juveniles occurring in habitats with high sedimentation are more likely to present higher rates of mortality than in habitats with low sedimentation, which will also contribute to spatial variations in early mortality. Competition with macroalgae (Box and Mumby 2007; Hughes et al. 2007), and conspecific (Vermeij 2005) has also been shown to reduce juvenile survival by overgrowing and/ or physical contact with the colony. For example, adult colonies harbour potential pathogenic agents that can affect and kill recruits located close to them (Knowlton and Rohwer 2003). The outcome of competition is likely to be dependent on the juvenile size, as for the other factors mentioned above. Indeed, mortality rates tend to decrease with increasing colony size (Hughes and Jackson 1985; Babcock 1991; Vermeij 2006; Doropoulos et al. 2012), therefore the probability of a coral colony to persist, changes over time

(Tanner et al. 1996). Furthermore, species with higher growth rates will be able to achieve a refuge in size faster than others, the critical recruits stage where most of the mortality bottleneck occurs (Edmunds and Gates 2004), and this is more than likely contributing to high taxonomic variations in juvenile mortality rates.

Table 1.1 Post-settlement mortality of small corals from spat size < 2 mm to 80 mm maximum diameter. Note that mortality rates were kept as shown in the studies, and were not extrapolated per month or per year as this could cause under or over-estimation of mortality. Spat describes a recently settled and metamorphosed larvae, therefore no size was applied but is usually < 2 mm (see Babcock et al. 2003).

Latitude	Location	Mortality % (sample period)	Species/Group	Maximum Size (mm)	Reference
32°46'N	Japan	50% (2 months)	<i>Acropora solitaryensis</i>	< 10 mm	Nozawa 2012
32°18'N	Bermuda	31.5% (12 months)	<i>Porites astreoides</i>	≤ 10 mm	Smith 1992
32°18'N	Bermuda	14.3% (12 months)	<i>Porites astreoides</i>	> 10-20 mm	Smith 1992
32°18'N	Bermuda	32% (12 months)	<i>Porites astreoides</i>	40 mm	Smith 1992
32°18'N	Bermuda	14% (12 months)	<i>Diploria spp</i>	40 mm	Smith 1992
29°33' N	Red Sea	27-33% (12 months)	All Community	40 mm	Glassom and Chadwick 2006
24°40'N	Florida	85-97% (1 month)	<i>Montastrea faveolata</i>	< 2 mm	Smantz and Miller 2006
24°40'N	Florida	89% (2 months)	<i>Acropora palmata</i>	< 2 mm	Smantz and Miller 2006
21°26'N	Hawaii	92% (5 months)	<i>Montipora verrucosa</i>	< 10 mm	Fitzhardinge 1988
21°26'N	Hawaii	29% (5 months)	<i>P. damicornis</i>	< 10 mm	Fitzhardinge 1988
21°26'N	Hawaii	29% (5 months)	<i>Porites compressa</i>	< 10 mm	Fitzhardinge 1988
18°28'N	Jamaica	64% (12 months)	<i>Leptoseris cucullata</i>	26 mm	Hughes 1985
18°28'N	Jamaica	71% (12 months)	<i>Agaracia agaricites</i>	25 mm	Hughes 1985
18°28'N	Jamaica	82% (12 months)	<i>Tubastrea aurea</i>	16 mm	Hughes 1985
18°19' N	US	24-57% (12 months)	All Community	40 mm	Edmunds 2000
18°12'N	Jamaica	59% (15 month)	All Community	50 mm	Rylaarsdam 1983
18°12'N	Jamaica	54% (15 month)	<i>Agaricia agaricites</i>	50 mm	Rylaarsdam 1983
18°12'N	Jamaica	82% (15 month)	Unidentified agaraciids	50 mm	Rylaarsdam 1983
18°12'N	Jamaica	67% (15 month)	<i>Leptoseris cucullata</i>	50 mm	Rylaarsdam 1983
18°12'N	Jamaica	50% (15 month)	<i>Porites astreoides</i>	50 mm	Rylaarsdam 1983
18°12'N	Jamaica	40% (15 month)	<i>Porites furcata</i>	50 mm	Rylaarsdam 1983
12°11'N	Curacao	32% (6 months)	All communities	40 mm	Bak and Engel 1979

12°11'N	Curacao	27% (6 months)	<i>Agaricia agaricites</i>	40 mm	Bak and Engel 1979
14°41'S	GBR	25-87% (3 months)	<i>Pocillopora damicornis</i>	< 10 mm	Harriott 1983
17° 30' S	French Polynesia	0-70% (1 week)	All species	< 10 mm	Penin et al 2010
17° 30' S	French Polynesia	23.6% (4 months)	All species	50 mm	Penin et al 2010
17° 30' S	French Polynesia	39.4% (14 months)	All species	50 mm	Penin et al 2010
18°49'S	GBR	30-70% (12 months)	All species	< 2 mm	Sammarco, 1991
18°37'S	GBR	86% (5.9 months)	<i>Acropora millepora</i>	< 10 mm	Babcock 1985
18°37'S	GBR	66% (5.1 months)	<i>Goniastrea aspera</i>	< 10 mm	Babcock 1985
18°37'S	GBR	74% (5.1 months)	<i>Platygyra sinensis</i>	< 10 mm	Babcock 1985
18°55'S	GBR	66% (9 month)	<i>A. loripes</i>	50 mm	Wallace 1985a
18°55'S	GBR	33% (9 month)	<i>A. granulosa</i>	50 mm	Wallace, 1985a
18°55'S	GBR	57% (9 month)	<i>A. sarmentosa</i>	50 mm	Wallace, 1985a
18°55'S	GBR	0% (9 month)	<i>A. longicyathus</i>	50 mm	Wallace, 1985a
18°55'S	GBR	66% (9 month)	<i>A. florida</i>	50 mm	Wallace, 1985a
18°55'S	GBR	0% (9 month)	<i>A. horrida</i>	50 mm	Wallace, 1985a
18°55'S	GBR	0% (9 month)	<i>A. nobilis</i>	50 mm	Wallace, 1985a
19°08'S	GBR	95% (14-15 months)	<i>Goniastrea aspera</i>	< 10 mm	Babcock 1988
19°08'S	GBR	36-44% (3-6 months)	<i>Goniastrea favulus</i>	< 10 mm	Babcock 1988
19°9'S	GBR	99.5% (4 months)	<i>Platygyra sinensis</i>	< 10 mm	Babcock and Mundy 1996
19°9'S	GBR	69.1% (4 months)	<i>Oxypora lacera</i>	< 10 mm	Babcock and Mundy 1996
23°27'S	GBR	40-83% (7 months)	All Community	< 10 mm	Dunstan and Johnson, 1998
29°55'N	Solitary Island	97.2-99.8% (12 months)	All Community	< 10 mm	Wilson and Harrison 2005

1.2 Growth Rates of Juvenile Corals

Given that the rate and cause(s) of mortality for juvenile corals is strongly size-dependent, growth rates can play a significant role in the survivorship of individuals and species (Van Moorsel 1988). Measurements of coral growth rates are mostly available for adult corals, or for coral spats on tiles, which can then be used to deduce early growth rates and determine the duration of recruits and juvenile phases (**Table 1.2**). However, similarly to post-settlement mortality, growth rates vary depending on the size, for e.g. newly settled *Acropora* recruits have very slow growth rates ($1.5 \text{ mm}\cdot\text{month}^{-1}$; **Table 1.2**) compared to larger *Acropora* juveniles ($3.2 \text{ mm}\cdot\text{month}^{-1}$,

Omori et al 2008). In addition, growth rates are also species-specific, for example, *Acropora* juvenile corals have faster growth rates than *Oxypora* juvenile corals (0.2-0.5 mm.month⁻¹; Babcock and Mundy 1996). Lastly, growth rates can also depend on water temperature, a factor known to affect reef accretion (Stoddart 1969), with optimal temperature for coral growth ~25°C to 29°C (Jokiel and Coles 1977). Therefore, juvenile coral growth rates are likely to vary among latitudes due to variations in temperature gradient. For example, coral growth rates on sub-tropical reefs such as Lord Howe Island, Eastern Australia, or the Houtman Abrolhos Islands, Western Australia, have been found to be lower than the ones on tropical reefs (Crossland 1981; Harriott 1999). Direct measurements of juvenile corals' growth rates, along with measurements of mortality rates *in situ* for different taxa and spatial scales, are needed to better understand coral population abundance and composition, as only few studies have investigated these processes as the juveniles grow larger.

Table 1.2 Size at settlement and expected age at size 5, 10, 25 and 50 mm based on growth rate of juvenile scleractinian corals. From ¹ (Babcock et al. 2003), ² (Fitzhardinge 1988), ³ (Sato 1985), ⁴ (Van Moorsel 1988), ⁵ (Babcock 1985), ⁶ (Alino et al. 1985)

Taxa	Size at Settlement (mm)	Growth rate (mm.mo ⁻¹)	Predicted age (months) at size			
			5 mm	10 mm	25 mm	50 mm
<i>Acropora sp</i>						
Mean	1.1 ⁽¹⁾	1.5 ^(1,4,5)	2.7	6.1	16.5	33.7
Range		(0.6-2.3)	(1.7-6.5)	(3.9-14.8)	(10.4-39.8)	(21.3-81.5)
<i>Porites sp</i>						
Mean	0.4 ^(1,2)	1.6 ^(2,4,6)	2.9	6.0	15.4	31.0
Range	(0.3-0.5)	(1.0-2.2)	(2.0-4.7)	(4.3-9.7)	(11.1-24.7)	(22.5-49.7)
<i>Pocillopora sp</i>						
Mean	1.4 ^(1,2,3)	1.4 ^(2,3,6)	2.7	6.4	17.5	36.0
Range	(0.8-2.0)	(1.0-1.7)	(1.8-4.2)	(4.7-9.2)	(13.5-24.2)	(28.2-49.2)

1.3 Objectives

The overarching objective of my PhD research was to quantify demographic rates (growth and mortality) of juvenile corals during the critically important and poorly studied period from settlement up until corals reached 50 mm maximum diameter. In order to understand the possible causes and consequences of differential rates of post-settlement growth and mortality, this research was conducted at a hierarchy of spatial scales, comparing among sites, reefs and latitudinal sectors on Australia's Great Barrier Reef, as well as comparing between different geographic locations within the Pacific. This is the first ever study to explicitly measure and compares rates of post-settlement growth and mortality over very large spatial scales (e.g., among reefs along the length of the GBR, or between different geographical regions). However, prior research comparing patterns of coral settlement to adult abundance (e.g., Hughes et al. 1999) suggests that there should be marked differences in the underlying population dynamics of corals at these large scales. Hughes et al (1999) showed that adult cover of scleractinian corals was very consistent along the length of the GBR, despite marked latitudinal differences in coral settlement, and suggested that there must be strong compensatory survivorship that leads to high adult abundance in the southern GBR despite comparatively low levels of input. This project does not underestimate the importance of pre-settlement (e.g., larval supply) processes in determining patterns of adult abundance, but is intended to show that differential rates of early post-settlement growth and mortality also play an important role in understanding the structure and dynamics of coral populations and communities.

The overarching aims were addressed in a series of four separate studies, presented as distinct chapters. The first of these studies (**Chapter 2**) was focused on

confirming that there is indeed strong spatial variation in the abundance of juvenile corals on the GBR, and testing whether this is related to spatial variation in the biomass of parrotfishes. If incidental grazing by parrotfishes on newly settled corals has a strong measurable effect on their survivorship, then the local abundance of juvenile corals is likely to be strongly and negatively correlated with parrotfish biomass. The second data chapter (**Chapter 3**) presents the results of a carefully conducted experiment, intended to specifically quantify rates of early post-settlement mortality attributable to both incidental grazing by parrotfishes, and smothering associated with high levels of sedimentation and/ or extensive growth of turf algae. To do this, it was necessary to rear coral larvae of a locally abundant coral species, *Acropora cytherea*, and then seed the larvae onto artificial terracotta tiles. These tiles were then placed on the reef, either inside or outside of cages (to test for effects of grazing), and orientated vertically or horizontally (to test the effect of accumulated sediment). The following chapter (**Chapter 4**) explicitly measured spatial variation in growth and mortality of juvenile corals (up to 50 mm maximum diameter) on natural substrata at a hierarchy of spatial scales on Australia's Great Barrier Reef, comparing among quadrats, sites, reefs and latitudinal sectors. The final study (**Chapter 5**), investigated even larger scales differences in growth and mortality rates of juvenile scleractinian corals (≤ 50 mm), comparing between Trunk reef in the central sector of GBR, Australia, and Moorea, French Polynesia. Both reefs are equivalent in latitude and only one habitat was examined: the exposed reef crest. Measurement of settlement rates on the reef crest at Moorea (~ 40 recruits m^{-2} year^{-1} : Adjeroud et al. 2007a) revealed that they were an order of magnitude lower than on central GBR mid-shelf reef crest (~ 200 -700 recruits m^{-2} year^{-1} : Hughes et al. 1999), despite having similar cover of adult corals (Adjeroud et al. 2007a). Therefore, large-scale variations

in early post-settlement processes were expected to compensate for marked differences established at settlement. More specifically, survivorship of juvenile corals was expected to be much higher at Moorea compared to the central GBR, which receives much higher levels of settlement.

Chapter 2. Spatial variation in abundance, size and orientation of juvenile corals related to the biomass of parrotfishes on the Great Barrier Reef*

2.1. Introduction

Most marine organisms have open populations, where rates of settlement are decoupled from local abundance and fecundity of adult individuals (Roughgarden et al. 1988; Caley et al. 1996). Replenishment and persistence of marine populations is therefore, dependent upon the supply of pelagic larvae, their successful settlement into reef habitats, and the subsequent growth and survival of individuals until they reach sexual maturity and enter the adult population (e.g., marine invertebrates: Keough and Downes 1982; Caley et al. 1996; Gosselin and Qian 1997; corals: Hughes et al. 2000; Wilson and Harrison 2005; fish: Doherty et al. 1985; Doherty and Williams 1988; Jones 1990; Schmitt and Holbrook 1996). A plethora of studies have examined settlement patterns of scleractinian corals, mostly using artificial substrata, and showed that settlement rates are highly variable, both in space and time (Wallace 1985a; Harrison and Wallace 1990; Connell et al. 1997; Hughes et al. 1999). These patterns established at settlement may however, be modified substantially by post-settlement processes such as differential growth and survivorship (Smith 1992; Dunstan and Johnson 1998; Hoey and McCormick 2004). Consequently, spatial patterns in coral settlement often bear little resemblance to patterns of adult coral abundance (Hughes et al. 1999; Edmunds 2000). Most notably, Hughes et al. (1999) found that settlement rates of scleractinian corals varied by an order of magnitude

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along 2,000 km's of Australia's Great Barrier Reef, yet adult coral cover was very consistent among the five latitudinal regions studied. Hughes et al (1999) suggested that these findings were due to large-scale variations in early post-settlement dynamics, which compensate for marked differences in settlement rates. This apparent disconnect between larval settlement and adult coral populations is poorly understood, and only few studies have focused on early life-stages of corals on natural substrata, mainly due to difficulties associated with identifying small colonies on natural substrata (Roth and Knowlton 2009).

Corals are typically very small at settlement (≤ 2 mm, Babcock et al. 2003), and very difficult to observe *in situ*. Mortality of these corals is also recorded to be very high immediately following settlement, often reaching 99 % within the first months post-settlement (Babcock 1985; Babcock and Mundy 1996; Wilson and Harrison 2005), which will have a marked influence on the distribution of later stages of juvenile corals, operationally defined as visible colonies from 10 to 50 mm diameter (Rylandsdam 1983; Banks and Harriott 1996; Penin et al. 2010). Based on size at settlement and current estimates of coral growth, the age of these juvenile corals would range from 2 to 7 years depending on the taxa (Babcock et al. 2003). Juvenile corals are also subject to high mortality (Babcock and Mundy 1996; Vermeij 2006; Penin et al. 2010), but as mortality rates often decrease with increasing size of coral colony (Hughes and Jackson 1985), the distribution of juvenile corals may be a better predictor of the distribution, abundance and composition of coral populations.

High incidences of juvenile coral mortality are often attributed to predation or incidental grazing by fishes (Sammarco 1985; Christiansen et al. 2009; Mumby 2009; Penin et al. 2010, 2011), and/ or overgrowth or smothering by macroalgae (Hughes et al. 2007). This results in a potentially complex, and probably non-linear, relationship

between juvenile survivorship of scleractinian corals and local abundance of herbivorous fishes; moderate levels of herbivory can have beneficial effects on coral survivorship in term of reducing algal cover and opening new space for coral to settle, thus maintaining coral dominated reefs (Hughes et al. 2007). However, high densities and intensive feeding activity by grazing parrotfishes may actually lead to increased levels of incidental mortality for juvenile corals (Penin et al 2010). Settlement into cryptic habitats has been suggested to be a key strategy by juvenile corals to reduce predation and susceptibility to grazing (Harriott and Fisk 1988), thereby increasing post-settlement survival (Bak and Engel 1979; Mundy and Babcock 1998). However, corals that settle within cryptic microhabitats may be sheltered from sunlight and experience reduced growth. It is possible therefore, that microhabitat preferences of juvenile corals also vary with respect to the risk of predation, due to variation in the local abundance of grazing parrotfishes.

The purpose of this study was to quantify the spatial variation in abundance of juvenile corals (≤ 50 mm) among three sectors of the Australian's Great Barrier Reef that differ in their latitude (14° S, 18° S and 23° S) and to compare these patterns to spatial variation in abundance of parrotfishes. Scraping and excavating parrotfishes (f. Labridae), unlike roving herbivorous fishes from the Acanthuridae, Siganidae and Kyphosidae, remove parts of the underlying substratum when feeding. Consequently, incidental grazing by scraping and excavating parrotfishes may be an important source of mortality for recently settled and juvenile corals. Specifically, the abundance, composition, size, and orientation of juvenile coral assemblages were compared among sites (within reefs), among reefs, and among latitudinal locations, along the Australian's Great Barrier Reef. Little is known about the juvenile life-stage

of corals on natural substrata, thus this study provides important ecological data on early life history of scleractinian corals at small and large scales.

2.2. Methods

2.2.1. Study Site

Surveys of juvenile corals were conducted in three distinct locations on the Great Barrier Reef (GBR) from north to south, separated by at least 500 km: i) northern GBR, in the vicinity of Lizard Island (14°41'S, 145°28'E), central GBR, in vicinity of Trunk Reef (18°25'S, 146°47'E), and southern GBR, in the vicinity of Heron Island (23°27'S, 155°55'E). Within each location, sampling was conducted at three reefs, and three sites per reef, giving a total of nine sites per location. Only mid-shelf reefs were sampled to minimize any effects of cross-shelf variation, and all sampling was constrained to a single habitat type, the exposed reef crest. The exposed reef crest was selected as this habitat is typically characterized by hard substratum covered by i) short sparse turf algae with a conglomeration of detritus, microbes, small invertebrates and microalgae, also referred as “epilithic algal matrix” (EAM, Wilson and Bellwood 1997), with underlying CCA (crustose coralline algae), making the distinction between turf algae and CCA very difficult, ii) high cover of adult corals (Connell et al. 2004) and iii) high rates of coral recruitment (Wallace 1985b). The biotic and abiotic processes that may influence the distribution of juvenile corals operate across a range of spatial scales (Hughes et al. 1999). Therefore, this hierarchical nested sampling design facilitates the examination of local and regional variation in juvenile coral assemblages, and provides greater insight into the processes that may be structuring these populations on the GBR.

2.2.2. *Juvenile coral census*

At each site, three replicate 10 m transects were established on the crest, parallel with depth contours and separated by 1 to 10 m. Five 1 m² quadrats were placed randomly along each transect, giving a total of 405 quadrats. Juvenile scleractinian corals were defined as any colonies visible with the naked eye with a maximum diameter of 50 mm, following Rylaarsdam (1983) and showing distinct growth and morphological characteristic (e.g., base approximately round). Care was taken to exclude colonies resulting from fission, shrinkage or fragmentation of older colonies (Hughes and Jackson 1980). To maximize detection of juvenile corals, the 1-m² quadrats were divided into a 10 x 10 grid using strings placed at 10 cm intervals along the vertical and horizontal axes. The resulting one hundred 10 cm² squares were systematically inspected for the presence of juvenile corals. All juvenile corals detected were identified to the highest possible taxonomic level (mostly genus) and the maximum diameter measured to the nearest millimetre using callipers. The smallest corals detected were 5 mm diameter, but only a very small proportion (2.4 %) of juvenile corals were < 10 mm, reflecting difficulties in detecting very small corals with the naked eye. All juveniles were also examined for any signs of damage, however, the level of partial mortality was extremely low across sectors (relative proportion: 1.4 %, 2.7 % and 1.8 % within the northern, central and southern sectors respectively) and therefore no further consideration was undertaken.

To determine if juvenile corals were associated with specific microhabitats, the orientation of each juvenile coral was recorded. The orientation was classified into one of four categories: (i) horizontal - the substratum on which the juvenile was attached had an angle < 45°; (ii) vertical - the substratum had an angle > 45°; (iii) immersed - the juvenile was positioned below the level of the surrounding substratum,

either inside a crevice or among the branches of a recently dead coral; (iv) covered - the juvenile had settled beneath an existing structure (e.g., a table coral). Depending on the major causes of juvenile coral mortality, it is possible that mortality would vary greatly with orientation. All juvenile corals were also examined for any signs of damage, predation and competition.

2.2.3. *Benthic composition*

To determine if coral cover influenced the density of juvenile corals, adult cover and composition were recorded within the same quadrats used to quantify juvenile coral assemblages. A total of 81 regularly spaced points formed by the 10 x 10 grid were surveyed within each quadrat. Any scleractinian (hard) corals underlying each survey point were identified to genus. Other benthic components such as soft corals (1.9 ± 0.35 SE %), macroalgae (0.3 ± 0.05 SE %) and sand/rubble (1.6 ± 0.21 SE %) cover were extremely low on the reef crest, characteristic of this habitat, thus they were not included in the data analysis.

2.2.4. *Herbivorous fish census*

Species-level surveys of parrotfishes were conducted using underwater visual censuses along a series of 50 m belt transects at each site. Each transect consisted of a diver swimming along the reef crest and recording all parrotfishes greater than 10 cm total length (TL) within a 5 m wide belt while simultaneously deploying a 50 m transect tape. This procedure minimised disturbance prior to censusing and allowed a specified area to be surveyed. Individual fishes were identified to species and placed into 5 cm size categories. Care was taken not to re-census fish that left and subsequently re-entered the transect area. Eight transects were surveyed within each site on each reef (total n = 216 transects). Fish densities were converted to biomass

using published length-weight relationships for each species, following (Hoey and Bellwood 2009)

Parrotfishes may be categorised into two groups based on the amount of substratum that is removed through the feeding action: 1) scrapers and excavators; 2) macroalgal browsers (Hoey and Bellwood 2008). Scraping and excavating parrotfishes (i.e., *Cetoscarus bicolor*, *Chlorurus* spp., *Hipposcarus longiceps*, and *Scarus* spp.) remove pieces of the carbonate substratum when feeding and subsequently may incidentally remove or damage recently settled or small juvenile corals. In contrast, the macroalgal browsing parrotfishes (i.e., *Calotomus* spp. and *Leptoscarus vaigiensis*) remove only algae and associated detritus and are unlikely to cause any direct mortality of juvenile corals. Browsing parrotfishes are rare on the GBR (Hoey and Bellwood 2008), and none were recorded during the visual surveys within each of the three regions. Consequently, our analyses were restricted to scraping and excavating parrotfishes.

2.2.5. *Statistical analysis*

Spatial variation in the abundance of juvenile corals, cover of adult corals and herbivorous fish biomass were examined using hierarchically nested analysis of variance (ANOVA), with sites nested within reef and reefs nested within latitudinal sectors. Juvenile coral abundance and fish biomass were $\log_{10}(x+1)$ transformed and adult coral cover was arcsine-square root transformed to improve the homoscedasticity and normality. To examine spatial variations in the assemblage structure of juvenile and adult corals a hierarchically nested multivariate analysis of variance (MANOVA) was used. The analyses were based on the abundance and cover of the three dominant genera (i.e., *Acropora*, *Pocillopora*, *Porites*) and 'other' scleractinian corals.

Bivariate correlations were used to determine if there were any relationships between the abundance of juvenile corals (≤ 5 mm) and the cover of scleractinian coral, the cover of consolidated substrata and biomass of scraping and excavating parrotfishes. The extremely low cover of macroalgae, sand and rubble, and soft corals precluded any meaningful comparisons for these benthic components.

Chi-squared tests were used to determine whether orientation (i.e., horizontal, vertical, immersed, and under) and size structure of juvenile coral assemblages differed among latitudinal sectors (i.e., northern, central, and southern GBR). For the size structure, juvenile corals were placed into 5 mm size classes: ≤ 14 , 15-19, 20-24, 25-29, 30-34, 35-39, 40-44, 45-50 mm.

2.3. Results

2.3.1. *Juvenile corals*

A total of 2,801 juvenile corals, from 28 genera and 8 families, were recorded across all sites, giving a mean of 6.92 juveniles \pm 0.25 SE per m². Densities of juvenile corals ranged from 0 to 38 per m² among quadrats, and were extremely variable even among quadrats situated along the same transect. The densities of juvenile corals varied significantly among reefs and sites, but displayed no significant variation among latitudes. Most of the variation (62.6 %) occurred within sites (Table 2.1 a). Variation among reefs was most pronounced in the southern GBR where mean juvenile density varied 3.9-fold, from 2.8 ± 0.3 ind.m⁻² on Heron Island South to 11.08 ± 1.4 ind.m⁻² on Heron Island North (**Figure 2.1 a**). Juvenile assemblages were dominated by three genera (*Acropora*, *Pocillopora*, and *Porites*) that collectively accounted for 84.1 % of all juveniles recorded. Taxonomic composition varied significantly among sectors, reefs and sites (**Table 2.2 a**), with relative proportions of

juvenile *Acropora* higher at the southern sector with 57.4 % compare to 50.6% and 39.9% at the central and northern sector respectively, *Pocillopora* corals higher at the central sector with 13.7 % compare to 11.9% and 7.1% at the southern and northern sectors respectively, and *Porites* corals higher at the northern sector with 30.5 % compare to 14.8% and 24.8% at the southern and central sectors respectively (**Figure 2.2 a**).

Table 2.1 Analyses of variance to test for variation in (a) density of juvenile corals, (b) adult coral cover, (c) biomass of scraping and excavating parrotfishes, among sectors, reefs and sites. Juvenile coral densities and fish biomass were $\text{Log}_{10}(x+1)$ transformed and coral cover data were arcsine-square root transformed.

a. Juvenile corals	SS	df	MS	F	p	Var(%)
Sector	2.340	2	1.170	0.972	0.431	0.0
Reef (Sector)	7.221	6	1.203	6.277	0.001	26.4
Site (Reef (Sector))	3.451	18	0.192	3.618	0.000	11.0
Residual	20.029	378	0.053			62.6
b. Adult corals	SS	df	MS	F	p	p
Sector	1.962	2	0.981	2.318	0.180	8.4
Reef (Sector)	2.539	6	0.423	2.163	0.096	10.4
Site (Reef (Sector))	3.522	18	0.196	6.855	0.000	22.8
Residual	10.791	378	0.029			58.4
c. Parrotfishes biomass	SS	df	MS	F	p	p
Sector	0.013	2	0.007	0.015	0.985	0.0
Reef (Sector)	2.652	6	0.442	4.234	0.008	12.7
Site (Reef (Sector))	1.879	18	0.104	1.744	0.035	7.4
Residual	11.312	189	0.060			79.9

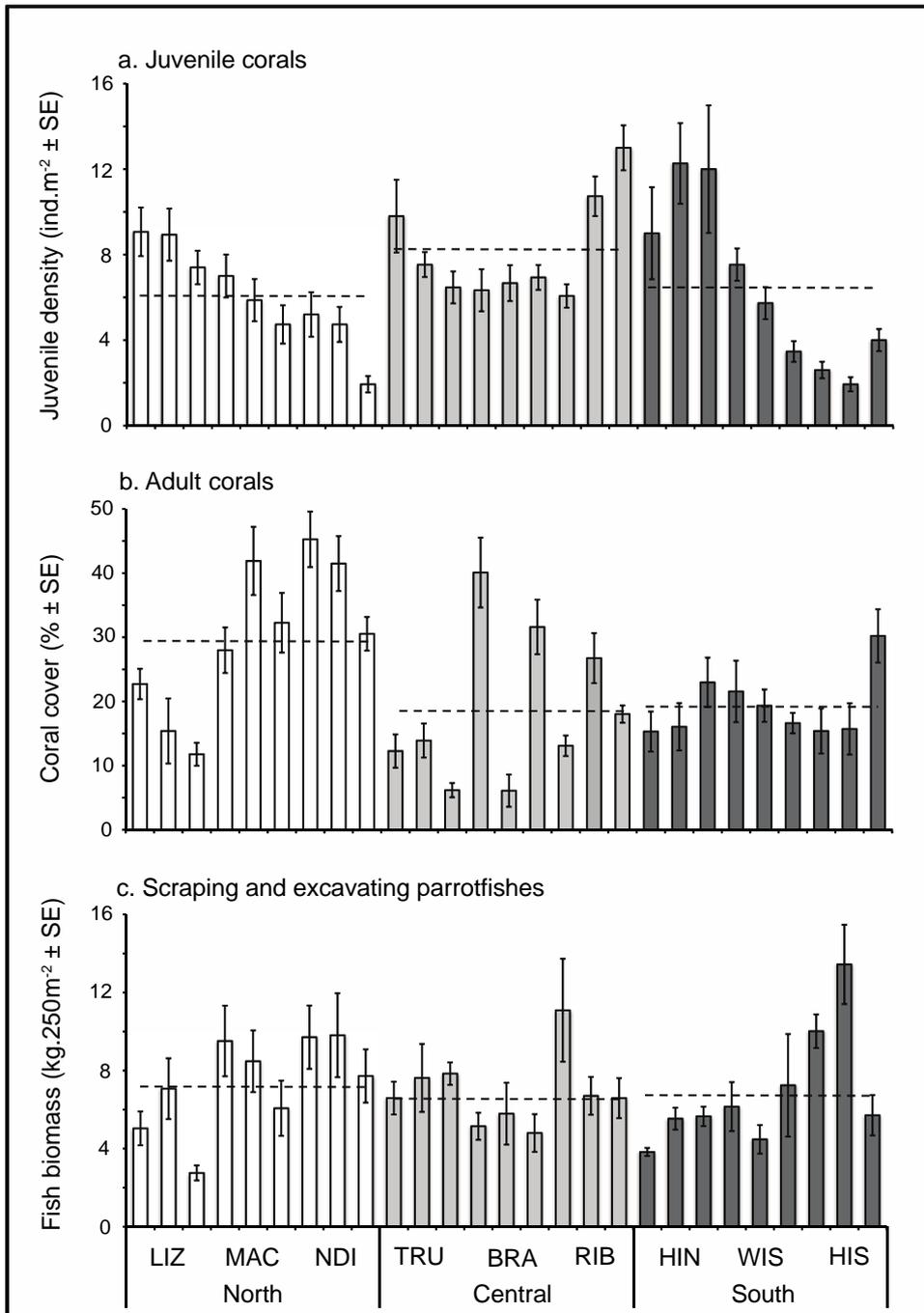


Figure 2.1 Mean (a) juvenile densities, (b) coral cover, and (c) biomass of scraping and excavating parrotfishes at Lizard Island (LIZ), Macgillivray (MAC) and North Direction Island (NDI) reefs (northern sector, *white*), Bramble (BRA), Rib (RIB), and Trunk (TRU) reefs (central sector, *light grey*) and Heron Island Nord (HIN), Wistari (WIS) and Heron Island South (HIS) reefs (southern sector, *dark grey*), for three different sites at each reef. The error bars represent 95 % confidence intervals. Dashed line represents the overall mean for each sector.

Table 2.2 Multivariate analyses of variance to test for variation in taxonomic composition of (a) juvenile corals, and (b) adult corals among sectors, reefs and sites. Juvenile coral abundances were $\log_{10}(x+1)$ transformed and coral cover was arcsine-square root transformed.

a. Juvenile corals	Pillai's Trace	F	df	Error df	p
Sector	0,264	14,314	8	752	0.000
Reef (Sector)	0,624	11,653	24	1512	0.000
Site (Reef (Sector))	0,452	2,672	72	1512	0.000
b. Adult corals	Pillai's Trace	F	df	Error df	p
Sector	0,732	54,236	8	752	0.000
Reef (Sector)	0,473	8,452	24	1512	0.000
Site (Reef (Sector))	0,567	3,470	72	1512	0.000

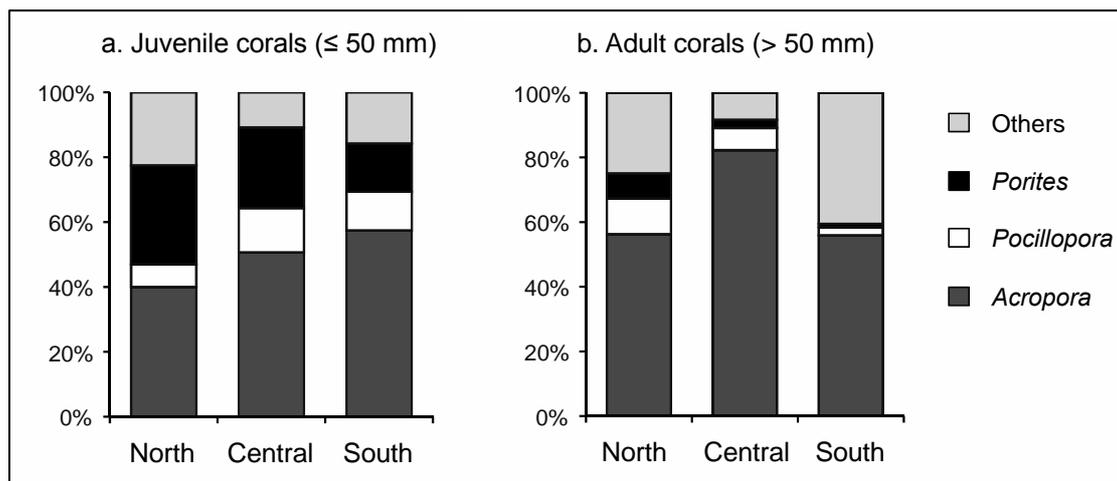


Figure 2.2 Relative abundance of *Acropora*, *Pocillopora*, *Porites* and other corals in (a) the juvenile (≤ 50 mm) and (b) adult assemblages among the three sectors.

The size structure of juvenile *Acropora*, *Pocillopora*, and *Porites* corals differed significantly among latitudinal sectors (Chi-square contingency **Table 2.3 a**, **Figure 2.3**). Juvenile *Acropora* were relatively evenly distributed among size classes in the northern and central sectors (**Figure 2.3 a & b**), whereas in southern sector the highest frequency of individuals was in the size-class 30-34 mm (relative proportion: 22 %) with few individuals in the smallest (7.9 %) and largest (2.8 %) size classes (**Figure**

2.3 c). The size distribution of juvenile *Pocillopora* and *Porites* displayed some similarities among sectors. In the northern sector juvenile *Pocillopora* and *Porites* peaked in the 25-29 mm and 30-34 mm size classes (25-29 mm: 17.2 % and 19.2 % respectively; 30-34 mm: 20.7 % and 17.6 % respectively), and the relative proportion of individuals decreased with size (**Figure 2.3 d & g**), while in the central sector frequencies were highest in the smallest size class (18.5 % and 21.6 %, respectively) and generally decreased with size (**Figure 2.3 e & h**). In the southern sector juvenile *Pocillopora* and *Porites* were relatively evenly distributed among size classes up to 40 mm, with few individuals in the two largest size classes (3.8 % and 1.5 % respectively; **Figure 2.3 f & i**).

The majority of juvenile corals surveyed in all sites, reefs and sectors were recorded on horizontal (47.5 %) and vertical (32.5 %) surfaces, but orientation of the three main genera varied among sectors (**Table 2.3 b; Figure 2.4**). In the central GBR, juvenile *Acropora*, *Pocillopora* and *Porites* were found less often on vertical surfaces (23.8 %, 19.2 %, and 29.5 %, respectively) and more often immersed in crevices (14.9 %, 31.1 %, and 21.5 %, respectively) compare to corals in the northern or southern reefs (**Figure 2.4**). In contrast, the occurrence of juvenile *Acropora*, *Pocillopora* and *Porites* under existing structures was low especially on the southern reefs (2.8 %, 3.8 %, and 0 %, respectively), compared to the central (11.8 %, 9.9 %, and 3.3 %) and northern (12.5 %, 12.1 %, and 5.2 %) reefs (**Figure 2.4**).

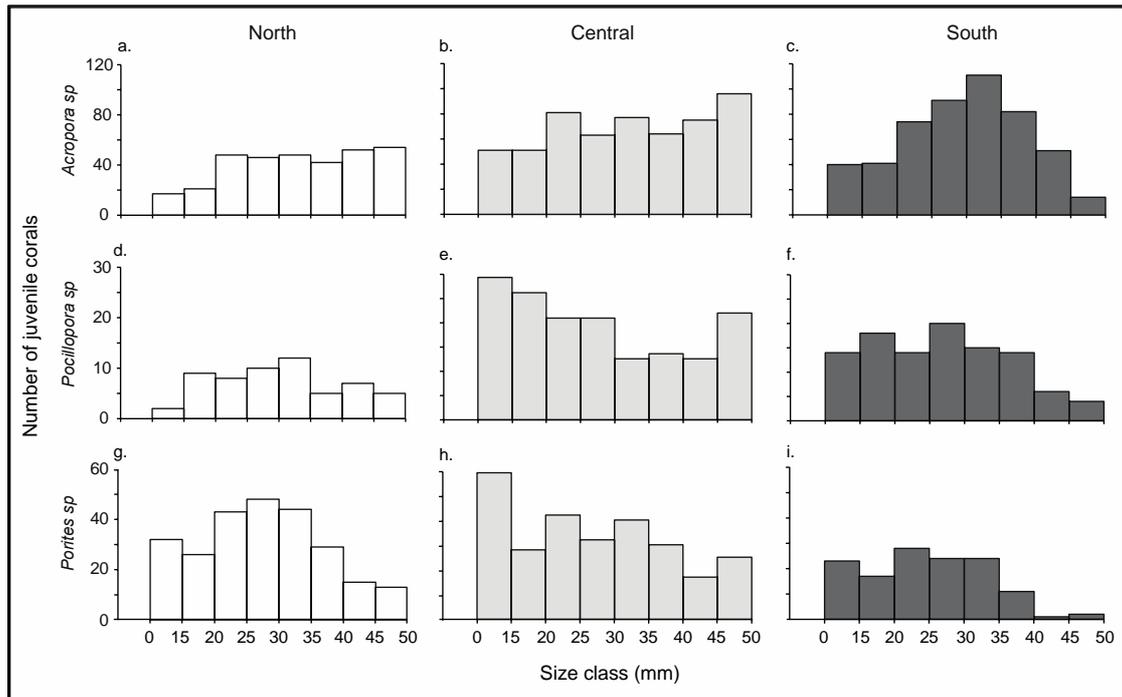


Figure 2.3 Size-class frequency distribution (mm) of juvenile corals ≤ 50 mm from the three main taxa: (A, B, C) *Acropora*, (D, E, F) *Pocillopora*, and (G, H, I) *Porites sp*, at the northern (*white*), central (*light grey*) and southern (*dark grey*) sectors of the GBR. Juveniles < 10 mm have been added to the size class 10-14 mm.

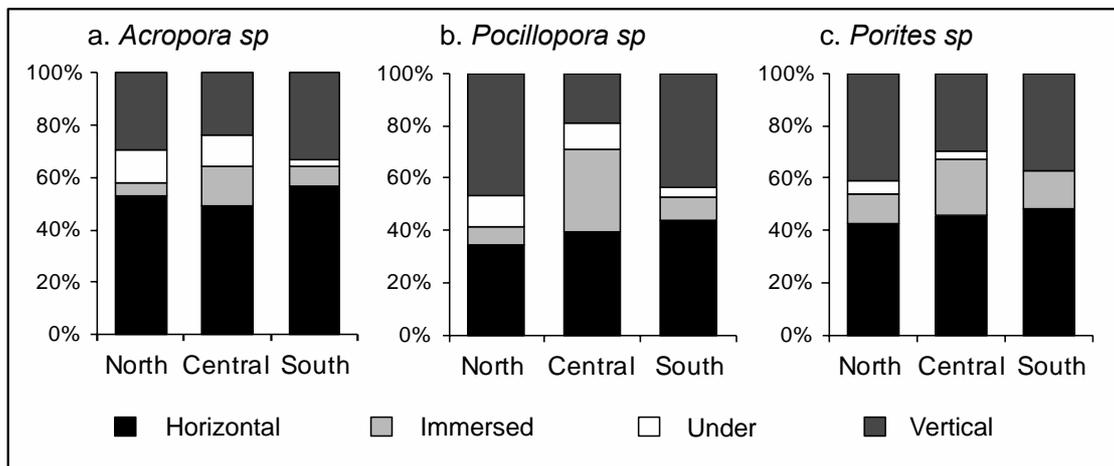


Figure 2.4 Comparison of orientation surface use by juvenile scleractinian corals across the northern ($n=135$), central ($n=135$) and southern reefs ($n=135$) on the GBR, for (a) *Acropora sp*, (b) *Pocillopora sp*, and (c) *Porites sp*.

Table 2.3 Chi-square contingency table to test for variation in (a) size-class frequencies and (b) surface orientation of juvenile corals from the three main genera *Acropora*, *Pocillopora*, and *Porites* sp.

a. Size-Class	χ^2	df	p
<i>Acropora</i>	91.20	14	0.000
<i>Pocillopora</i>	24.34	14	0.041
<i>Porites</i>	30.39	14	0.006
b. Surface orientation	χ^2	df	p
<i>Acropora</i>	67.66	6	0.000
<i>Pocillopora</i>	42.78	6	0.000
<i>Porites</i>	21.46	6	0.002

Juveniles < 10 mm have been added to the size class 10-14 mm due to the difficulty to observe such small corals on natural substrata. The size-classes are as follow: ≤ 14 , 15-19, 20-24, 25-29, 30-34, 35-39, 40-44, 45-50 mm, and the orientation on the natural substrata are: horizontal, immersed, under and vertical.

2.3.2. *Benthic composition*

Mean adult coral cover ranged from 29.9 ± 1.5 % in the northern location to 19.2 ± 1.2 % and 18.7 ± 1.4 % in the southern and central sectors respectively. However, large variation in coral cover among sites precluded the detection of any significant variation among latitudinal sectors or reefs (Table 2.1 b; **Figure 2.1 b**). *Acropora*, *Pocillopora* and *Porites* dominated the adult coral assemblages, collectively accounting for more than 80 % of total coral cover. Taxonomic composition of adult corals varied significantly among latitudinal sectors, reefs and sites (Table 2.2 b), with relative abundance of *Acropora* corals higher at the central sector (82.3 %) than in the northern (56.2 %) and southern (55.9 %) sectors (**Figure 2.2 b**). Conversely, the relative abundance *Porites* and *Pocillopora* was higher in the central and northern sectors, compared to the southern sector (**Figure 2.2 b**). Other benthic components were very sparse on the reef crest, with an overall means of 1.88

(± 0.35) %, 1.63 (± 0.21) % and 0.34 (± 0.05) % for soft corals, loose substrata (sand and rubble) and macroalgae, respectively.

2.3.3. *Parrotfish communities*

Overall, the mean biomass of scraping and excavating parrotfishes was $7.1 \pm 0.3 \text{ kg.250m}^{-2}$ (**Figure 2.1 c**). Despite significant variation in the biomass of parrotfishes among reefs and sites, there was limited variation among sectors, ranging from $6.89 \pm 0.53 \text{ kg.250m}^{-2}$ in the southern sector to 6.90 ± 0.48 and $7.35 \pm 0.54 \text{ kg.250m}^{-2}$ in the northern and central sectors respectively (**Table 2.1 c**, **Figure 2.1 c**).

2.3.4. *Relationship among variables*

Density of juvenile corals was weakly negatively correlated to coral cover at the scale of quadrat only ($r = -0.128$, $N = 405$, $p = 0.01$, **Figure 2.5 a**), but adult coral cover explained only 1.6 % of the variation in juvenile densities. Parrotfish biomass explained 21.7 % of the variation in total juvenile density ($r = -0.466$, $N = 27$, $p = 0.014$; **Figure 2.5 b**) but this was even higher (34.7 %) when considering only juvenile corals occurring on horizontal surfaces ($r = -0.589$, $N = 27$, $p = 0.001$; **Figure 2.5 c**). In contrast, there was no significant relationship between parrotfish biomass and the density of juvenile corals on immersed ($r = -0.230$, $N = 27$, $p = 0.249$), under ($r = 0.090$, $N = 27$, $p = 0.656$) and vertical ($r = -0.311$, $N = 27$, $p = 0.115$) substrata.

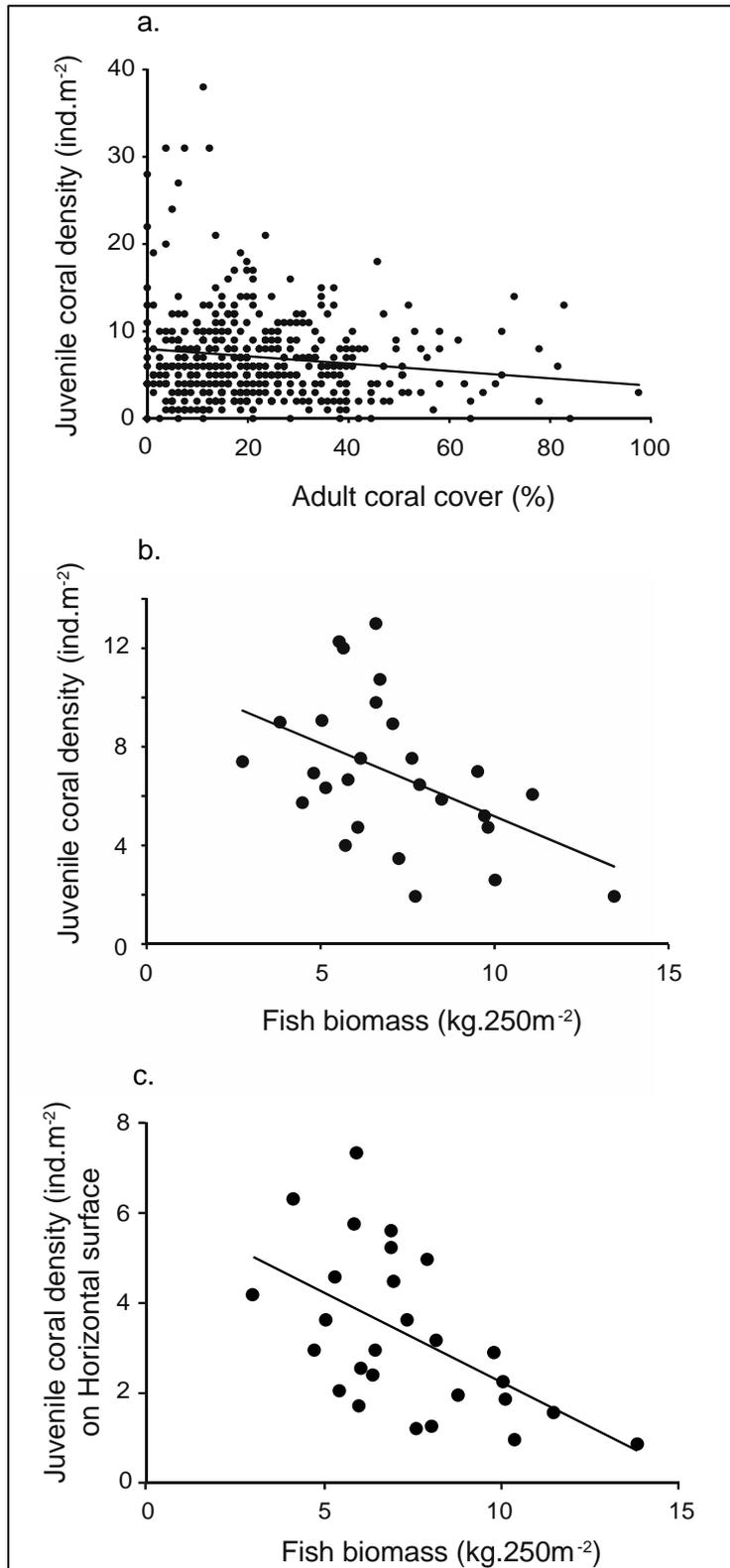


Figure 2.5 Relationship between juvenile coral density and (a) adult coral cover, and (b) biomass of scraping and excavating parrotfishes. The line represents a significant relationship.

2.4. Discussion

This study revealed significant fine-scale spatial heterogeneity in the density, taxonomic composition, size-class distribution and orientation of juvenile corals among reefs of the GBR. The density of juvenile corals was highly variable both within and among reefs, but displayed limited variation over the larger latitudinal scale. Fine-scale variation in the abundance of juvenile corals may be influenced by local scale hydrodynamic regimes (Bode et al. 2006), disturbance history (Connell et al. 1997), larval supply (Hughes et al. 1999), habitat availability (Baird et al. 2003) and predation (Penin et al. 2010). Overall abundance of juvenile corals was strongly and negatively correlated with the biomass of scraping and excavating parrotfishes, especially when considering only juvenile corals occurring on horizontal surfaces. This suggests that patterns of post-settlement mortality exert a strong influence on patterns of juvenile abundance, either augmenting or obscuring patterns established at settlement. The relative importance of larval supply versus post-settlement mortality is likely to vary temporally and spatially and would need to be explicitly tested using manipulative experiments.

Previous studies (Hughes et al. 1999, 2000) have suggested that there are strong latitudinal differences in the underlying dynamics of scleractinian corals on the GBR based on marked geographical differences in settlement rates despite similar levels of adult abundance. Both large-scale sampling and a meta-analysis of small-scale studies have found significant latitudinal variation in rates of coral settlement to artificial substrata (Hughes et al. 1999, 2002). Most notably, settlement rates in the region of Lizard were an order of magnitude higher compared to reefs in the region of Heron Island (Hughes et al. 1999, 2002). These apparent differences between settlement rates and juvenile abundance are attributable to inherent (e.g., taxonomic) biases in

coral settlement to artificial substrata, which is further confounded by failing to take account of early post-settlement mortality (Penin et al. 2010). If latitudinal differences in settlement rates (Hughes et al. 1999) reflect large-scale variation in larval supply (Hughes et al. 2002) then these differences must be offset by increased survivorship of juvenile corals with increasing latitude.

While the overall abundance of juvenile corals was very consistent among latitudinal locations, the size structure varied significantly among latitudes for *Acropora*, *Pocillopora*, and *Porites*. *Acropora* juveniles were distributed relatively evenly among size-classes in the northern and central sectors, with higher than expected abundance of larger individuals (≥ 40 mm) given expected attrition through increasing size-classes. In contrast, abundances of *Pocillopora* and *Porites* juveniles were distributed evenly in the northern and southern sectors with abundance decreasing toward the larger size classes, whereas in the central sector, *Pocillopora* and *Porites* juveniles were more abundant within the smallest size-class (< 15 mm), and still well represented in the largest size-class (45-50 mm). Large juveniles (45-50 mm) were far less abundant for all three genera in the southern sector, suggesting higher post-settlement mortality and/ or slower growth compared to juvenile corals in the northern and central sectors. If so, post-settlement growth and mortality would be expected to augment, not offset, the latitudinal variation in settlement rates, but direct measures of growth and mortality (especially among the smallest size-classes) are needed to assess large-scale variation in demographic rates from juvenile corals. However, the difficulty in detecting small corals, especially < 15 mm, significantly limits the capacity to measure early post-settlement mortality *in situ*. In this study, despite thoroughly searching for all juveniles under 50 mm diameter, we certainly under-estimated the local abundances of individuals in the smallest size classes

(< 15 mm), but this bias was assumed to be constant and should not affect overall conclusions.

Juvenile corals were found more often on horizontal surfaces, but the proportion found on vertical, under a coral or immersed surface changed greatly between sectors. This could suggest that coral larvae select different suitable orientation surfaces depending on the specific environmental conditions and habitat complexity they encounter. Studies on larval settlement choice and ultimately juvenile corals orientation on natural and artificial substrata have shown that in shallow water, coral larvae preferentially settle on vertical and under surfaces as opposed to upward horizontal substrata (Wallace 1985b; Sato 1985; Wittenberg and Hunte 1992; Mundy and Babcock 1998), probably to avoid sedimentation, incidental grazing and overgrowth by algae which are known to limit recruit survival and growth (Harriott and Fisk 1988; Oren and Benayahu 1997). However, these studies also found that once the juvenile colony reaches a certain size, growth and survival may be maximized on horizontal surfaces (e.g., escape in size: Babcock and Mundy 1996). This suggests that it may be beneficial for coral larvae to settle in cryptic microhabitats such as crevices, and then outgrow the microhabitat to become orientated horizontally on the substratum (Mundy and Babcock 2000). Although more than half of the juveniles observed in this study occurred on horizontal surface, the availability of the four different orientations was not recorded, which could have further reinforced the data. We therefore, cannot predict whether differences in size structure across sectors are function of substratum orientation, or whether larvae preferably settled on a certain orientation surface. However, we can infer that horizontal surfaces might offer a better chance for survival once the juvenile coral grow in the open, based on the literature cited above.

Similar to juvenile density and adult coral abundance, the biomass of scraping and excavating parrotfishes did not vary among latitudes but displayed considerable variation among and within reefs. A striking result was the negative correlation between the biomass of parrotfish and the density of juvenile corals across all sites. Explicitly, sites with high parrotfish biomass tended to have low juvenile densities. Although biomass does not equate to the functional impact (i.e., area grazed) of individual parrotfishes per se, it does provide a useful proxy in the absence of species- and size-specific feeding rates and bite sizes. While larger parrotfishes have been shown to scrape a disproportionately larger area of reef substratum per bite than smaller individuals (Bonaldo and Bellwood 2008; Lokrantz et al. 2008), the volume of material removed per unit body mass is relatively consistent for parrotfish greater than 10 cm TL (Bonaldo and Bellwood 2008). Incidental grazing by parrotfishes has been found to reduce the survival of corals within the first few weeks after settlement (Penin et al. 2010, 2011), but not larger more established juvenile corals (Penin et al. 2010). Therefore, parrotfishes might have indirectly influenced juvenile densities observed in this study by incidentally grazed on earlier smaller cohorts, decreasing their survival, which in turn resulted in a negative relationship between juvenile densities and parrotfish biomass.

It is widely accepted that scraping and excavating parrotfish are a key functional group on coral reefs, mediating the competition for space between corals and algae and maintaining healthy reef systems by clearing space on the substratum for new coral recruits (Hughes et al. 2007). While the positive effects of these herbivorous fishes on reef processes are well established, the potential deleterious effects are poorly understood. The vast majority of parrotfish feed almost exclusively on crustose coralline algae, algal turfs and associated detritus (Bellwood and Choat 1990; Hoey

and Bellwood 2008), also called epilithic algal matrix (EAM, see Wilson and Bellwood 1997). However, through their feeding actions parrotfish may also incidentally consume and/or damage juvenile corals. At low biomass, scraping and excavating parrotfishes have been found to enhance coral settlement on a subtropical reef (Hoey et al. 2011), however on the Great Barrier Reef, parrotfishes are far more abundant and may account for over 80 % of the total biomass of herbivorous fish in some habitats (Wismer et al. 2009; Hoey and Bellwood 2010). It appears likely that at very high biomass, high levels of incidental predation negate any positive effects of clearing space on the substratum. This was further supported by a negative correlation between parrotfish biomass and the number of juvenile corals occurring on horizontal surface, which are the most susceptible to grazing. Incidental predation of juvenile corals by parrotfish, along with many other important factors not tested in this study (e.g., abundance and type of CCA; Wilson and Bellwood 1997), may be ecologically important in structuring juvenile coral assemblages on the Great Barrier Reef.

This is the first large-scale study of coral recruitment, testing for large (latitudinal) and small (site) level differences in the abundance of juvenile corals on natural substrata, thereby complementing previous studies that looked at hierarchical patterns of coral settlement. Despite marked latitudinal variation in larval supply and settlement rates reported previously (Hughes et al. 1999, 2002), we found no large-scale differences in abundance of juvenile corals. This suggests that latitudinal variation in coral settlement may be highly modified by post-settlement processes, whereby low settlement rates in the southern sectors could be offset by high post-settlement survival. The size frequency distribution of juvenile corals actually suggests that there is lower (not higher) post-settlement survivorship and/or slower growth in the southern sector. However, direct measure of mortality and growth rates

of juvenile corals at this hierarchy of spatial scales is critical if we are to understand latitudinal variation in the population dynamics of coral population and the factors influencing replenishment and resilience.

Chapter 3. Influence of fish grazing and sedimentation on the early post-settlement survival of *Acropora cytherea* at Lizard Island*

3.1. Introduction

Like most marine organisms, scleractinian corals have a bipartite life cycle with a dispersive pelagic larval phase and a sedentary juvenile to adult phase. The structure and dynamics of coral assemblages are, therefore, influenced by factors that act upon these two distinct phases. Mortality is typically high during the larval phase (Nishikawa et al. 2003; Graham et al. 2008; Connolly and Baird 2010) and immediately following settlement, with up to 99 % of individuals dying within the first few months post-settlement (Babcock 1985; Babcock and Mundy 1996; Wilson and Harrison 2005). The early post-settlement period, therefore, represents a critical transition, or survivorship bottleneck, in the life cycle of corals and can greatly influence on abundance and composition of adult coral populations (Bak and Engel 1979; Baird et al. 2003; Vermeij and Sandin 2008; Ritson-Williams et al. 2009).

High mortality rates of recently settled corals (recruits) have been related to several factors including overgrowth or smothering by macroalgae (Box and Mumby 2007; Hughes et al. 2007), competition with conspecifics (Baird and Hughes 2000; Vermeij and Sandin 2008) or other benthic organisms (Wilson and Harrison 2005), sedimentation (Sato 1985; Gilmour 1999), and incidental grazing or predation (Sammarco 1980; Penin et al. 2010). Predation is one of the main causes of early post-settlement mortality for a range of benthic marine invertebrates in tropical and

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temperate environments (see review Gosselin and Qian 1997), and is a major source of early post-settlement mortality for scleractinian corals (Rotjan and Lewis 2008; Penin et al. 2010, 2011). While rarely tested, much of this predation is assumed to be a result of incidental grazing by herbivorous fishes (Brock 1979; Rotjan and Lewis 2008; Penin et al. 2010). Grazing by herbivores is an important process in maintaining healthy coral reefs as it inhibits the proliferation of macroalgae (Hughes et al. 2007), minimizes coral-algal competition and thereby enhances growth and survivorship of both juvenile and adult corals (Stoddart 1969; Rogers et al. 1984; Bellwood et al. 2004; Mumby et al. 2007) and provides suitable substrata for the settlement of corals and other benthic organisms (Sammarco and Carleton 1982; Hughes et al. 2007). However, excessive rates of grazing may also lead to high levels of mortality among newly settled corals (Bak and Engel 1979; Brock 1979; Mumby 2009; Penin et al. 2010).

Although grazing has often been viewed as a uniform process (reviewed by Choat 1991) there are marked differences in feeding behaviour among herbivorous fishes (e.g., Bellwood and Choat 1990; Choat et al. 2002) and this variation has important implication for the survival of recently settled corals. Herbivorous surgeonfishes (f. Acanthuridae) and rabbitfishes (f. Siganidae) tend to remove the upper portions of algae when feeding, leaving the basal portions of the algae and the substratum largely intact. Consequently they are likely to have limited effect on the mortality of recently settled corals. In contrast, scraping and excavating parrotfishes (i.e., *Cetoscarus bicolor*, *Chlorurus* spp., *Hipposcarus longiceps*, and *Scarus* spp.) remove pieces of the carbonate substratum together with the algae leaving distinctive feeding scars (Hoey and Bellwood 2008). Parrotfishes may, therefore, incidentally remove or damage recently settled corals when feeding. In support of this assertion, significant

negative correlations between parrotfish biomass and abundance of juvenile corals (≤ 50 mm) have been reported in Moorea, French Polynesia and on the Great Barrier Reef (Penin et al. 2010; Trapon et al. 2013).

The survival of recently settled corals is also strongly influenced by the specific microhabitats into which they settle (Bak and Engel 1979; Babcock and Mundy 1996; Baird and Hughes 2000). Coral larvae typically settle in crevices, on vertical surfaces, or the underside of surfaces in shallow water (Bak and Engel 1979; Birkeland et al. 1981; Babcock and Mundy 1996; Harriott 1985a; Wallace 1985b). This selection of cryptic microhabitats has been hypothesized to reduce exposure to grazing sedimentation and algal overgrowth (Brock 1979; Sammarco 1980; Harriott and Fisk 1988; Nozawa 2008), however, long-term survival is often higher on upward facing surfaces (Wilson and Harrison 2005). This differential survival has been attributed to higher light levels and subsequently higher coral growth rates on upward facing surfaces. Given mortality of corals is strongly size-dependent (Hughes and Jackson 1985; Vermeij and Sandin 2008), the faster-growing recruits will be larger and potentially less susceptible to mortality than slow growing recruits of the same age (Babcock and Mundy 1996; Wilson and Harrison 2005).

The purpose of this study was to compare rates of early post-settlement growth and survival of corals settled on to tiles that were either (i) caged or uncaged and (ii) orientated either horizontally or vertically. We hypothesized that (i) the cages would enhance the survival of coral spat, due to reduced mortality associated with incidental grazing by herbivorous fishes, and (ii) the survival of coral spat would be greater on vertically oriented as opposed to horizontally oriented tiles due to reduced accumulation of sediment. These experiments were initially (in 2010) conducted in back reef habitats, but due to unexpected (limited) effects of the caging treatment, the

study was repeated in 2011 on the exposed reef crest. Importantly, it was not clear whether the limited effects of caging in back reef habitats was due to limited effects of grazing fishes, or the generally low abundance of herbivores within these specific habitats. To test this, experiments were repeated in habitats (along exposed reef crests) where parrotfish grazing is typically greatest (Hoey and Bellwood 2008). Experiments conducted in both back reef and reef crest habitats are compared, despite being conducted in separate years, showing that processes affecting the early life history of scleractinian corals vary greatly at small spatial scales, among habitats.

3.2. Methods

3.2.1. *Study sites*

The present study was conducted during November – December in both 2010 and 2011, at Lizard Island (14° 41' S, 145° 28' E), in the northern Great Barrier Reef, Australia. To examine the effects of sedimentation and grazing on the survival of recently settled corals two habitats that were similar in depth (2 - 4m) but differed in sedimentation (Purcell and Bellwood 2001) and the abundance and composition of herbivorous fish assemblages (Hoey and Bellwood 2010) were selected; the back reef of Loomis reef and the reef crest of Bird Island. The back reef site was located on the leeward side of the Lizard Island and is characterized by high sediment load and low abundance and diversity of herbivorous fishes, while the reef crest site was located on the windward side of the Lizard Island and is characterized by relatively low sediment load and high abundance and diversity of herbivorous fishes.

3.2.2. *Larval culture*

The larvae of the broadcast spawning coral, *Acropora cytherea*, were raised following the method of (Babcock et al. 2003). Six to ten mature colonies of

Acropora cytherea were collected from the exposed reef crest of Lizard Island and placed in aquaria two days prior to the predicted spawning date in November 2010 and November 2011. The timing of the spawning events was predicted from previous observations at Lizard Island for *A. cytherea*. The colonies were held in flow-through seawater in 300 l tanks and monitored from 19:00 until 22:30 hrs every night for any sign of egg-sperm bundles release. Following spawning (25th November 2010, and 15th November 2011), egg -sperm bundles from all colonies were collected and transferred into a sterile plastic container with 0.2 micron UV sterilized filtered seawater (FSW). The egg-sperm bundles were gently agitated to tease apart the gametes to assist fertilization. After two hours following cleavage, embryos were collected from the surface and transferred into five sterile containers with FSW. Water was changed every 24 hrs. Coral larvae started swimming four days post-fertilization and were transferred to settlement tanks on the fifth day post-fertilization. *Acropora* larvae typically begin to settle 3 to 4 days post-fertilization with peak competency reached between 7 to 12 days post-fertilization (Connolly and Baird 2010).

3.2.3. *Larval settlement*

Unglazed terracotta tiles (11cm x 11cm x 1cm) were used as settlement surfaces. Forty tiles were pre-conditioned on the reef flat for three weeks in each year by laying them flat on the substratum. This allowed a biofilm to develop on the upper surface of the tile, while the under surface remained relatively bare. The tiles were collected and ten tiles placed on each of four stainless steel bars by passing the bar through a 5 mm hole in the centre of each tile. Cylindrical plastic spacers (ca. 2.5 cm in length) were placed over the bar to separate adjacent tiles. Two ‘racks’ of ten tiles were placed on the bottom of each of two 50 l settlement tanks in 2010 and 2011 ($n = 40$ tiles yr⁻¹).

The steel bars were placed horizontally within the tanks so that the surfaces of the tile with the biofilm were oriented vertically. The larvae were introduced to the settlement tanks on the fifth day post-fertilization and were left in the settlement tanks for a further eight days to allow the majority of the larvae to settle. The water in the settlement tanks was changed daily. On the thirteenth day post-fertilization most of the larvae had settled on the surface of the tile (11 x 11 cm) with the biofilm.

3.2.4. *Experimental design*

Each tile was secured to an individual stainless steel base plate with a threaded bar passed through a 5 mm hole in the centre of the tiles, and the base plate was secured to the reef substratum by two push-mounts. Within each habitat, the tiles were randomly placed within an area of approximately 400 m², with adjacent tiles being separated by a minimum of 1 m. A total of 40 tiles were deployed on the sheltered back reef in 2010 and 40 tiles on the exposed reef crest in 2011. At each site, ten tiles were randomly allocated to one of four treatments: horizontal, vertical, herbivore exclusion cage, and cage-control. Tiles within the horizontal treatment were positioned parallel to the substratum with no structure around them (**Figure 3.1a**), and tiles within the vertical treatment were attached to an L-shaped steel frame and positioned perpendicular to the substratum (**Figure 3.1b**). To manipulate access by macro grazers, ten tiles were positioned horizontally inside individual exclusion cages (25 × 25 × 20 cm) constructed from galvanised steel mesh (5 cm mesh; **Figure 3.1 c**). The remaining 10 tiles were placed horizontally inside cages in which two opposite sides were open to control for caging artefacts (**Figure 3.1 d**). Within each treatment the tiles were positioned so that the surface with the majority of the recently settled corals, was facing upward for horizontal tiles, and away from the steel frame for vertical tiles.

Tiles were collected and transported to the lab every week for four weeks. Individual tiles were removed from the base plates and held on a stainless steel bar passed through the hole in the centre of the tile. Ten tiles were placed on each bar with plastic spacers (ca. 2.5 cm) to prevent contact between adjacent tiles. Each bar was placed inside an 80 l plastic aquarium underwater and then the aquarium was carefully lifted onto the boat and slowly transported back to the lab. The density of coral spats on each tile was quantified under a dissecting microscope with UV light (following (Baird et al. 2006)). All tiles were censused blind to treatment type by a single observer (MLT) and were returned to their original base plate within six hours of collection. The tiles were also examined for sediment and algae cover by visually estimating percent coverage on each tile every week for four weeks. Any evidence of bite marks or grazing scars, typical of parrotfishes following, Bellwood and Choat (1990), was also recorded for each tile at the conclusion of the experiment (i.e., week 4).

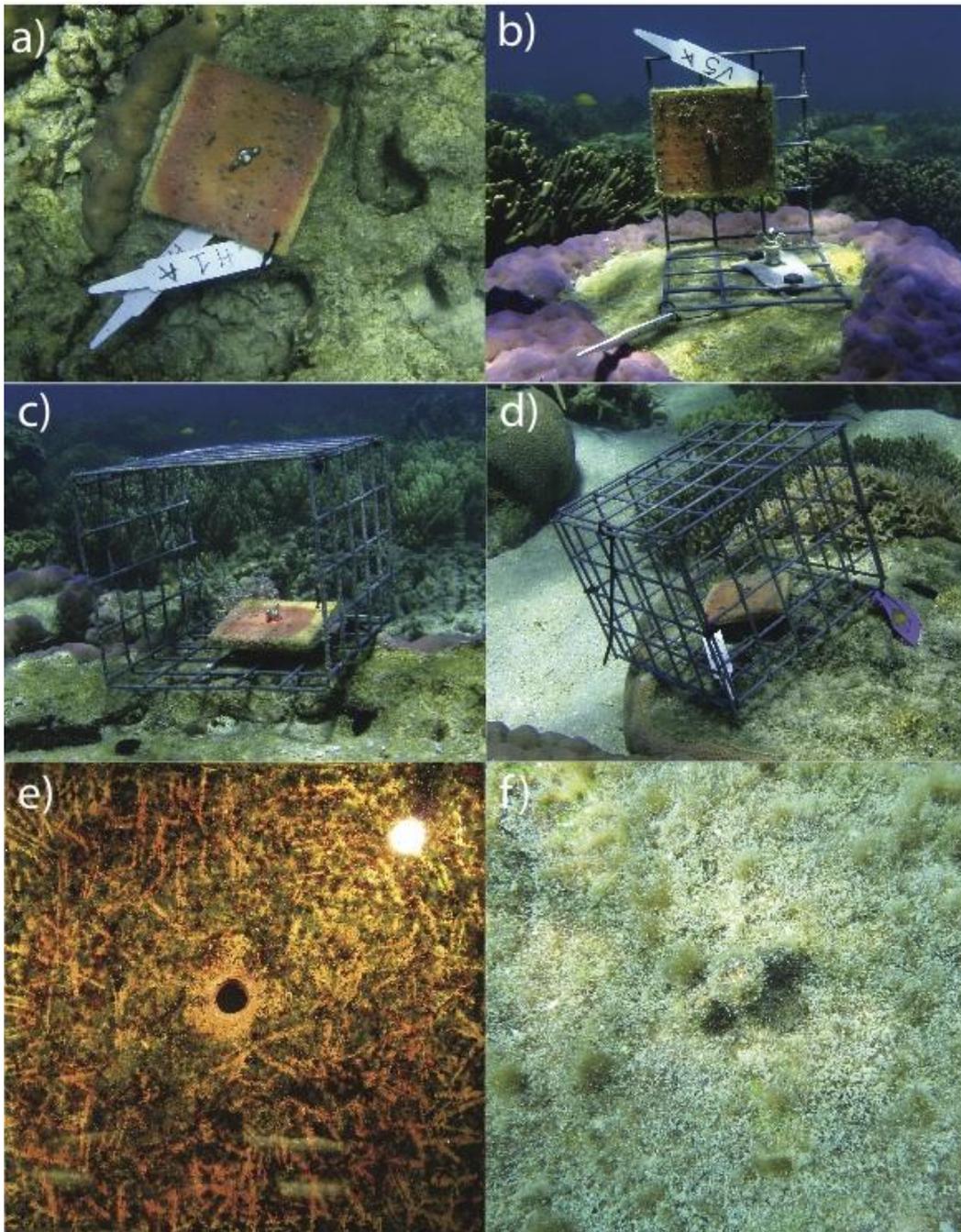


Figure 3.1 Photographs showing experimental treatments used to manipulate grazer access and the orientation of tiles seeded with *Acropora cytherea* spat: (a) horizontal, (b) vertical, (c) cage control, (d) exclusion cage, (e) an exposed reef crest tile at week 4 heavily scar by the grazing of scraping parrotfishes, and (f) sheltered back reef tile at week 4 with no feeding scars.

3.2.5. *Fish surveys*

Species-level surveys of roving herbivorous fishes were conducted along four to six 50 m belt transects within each habitat and encompassed the sites used for the coral survivorship experiment. Roving herbivorous fishes were defined as the nominally herbivorous species from the families Acanthuridae, Labridae (parrotfishes), Siganidae and Kyphosidae (Choat et al. 2002). Each transect consisted of a diver swimming along the reef and recording all nominally herbivorous fishes greater than 10 cm total length (TL) within a 5 m wide belt while simultaneously deploying a 50 m transect tape. This procedure minimised disturbance prior to censusing and allowed a specified area to be surveyed. Individual fishes were identified to species and placed into 5 cm size categories. Care was taken not to re-census fish that left and subsequently re-entered the transect area. The number of transects on the back reef ($n = 4$) was limited by the spatial extent of the reef at this site. Fish densities were converted to biomass using published length-weight relationships for each species, following (Hoey and Bellwood 2009).

3.2.6. *Statistical analysis*

Survival rates of coral juveniles were compared among treatments using the Kaplan-Meier test (Kaplan and Meier 1958), with each habitat (i.e., back reef and reef crest) being analysed separately. The Kaplan-Meier test was selected as it takes into account both individuals that died during the course of the experiment and individuals that were still alive at the end of the study (i.e., censored and uncensored data). Repeated measures ANOVAs were used to examine variation in turf algae and sediment cover on the tiles among treatments and weeks, with separate analyses performed for the two habitats due to temporal confounding. These analyses were restricted to the third and fourth weeks of the experiment as there was negligible algal

growth and sedimentation on the tiles for the first two weeks of the experiment. Assumptions of the ANOVA were examined using residual analysis and the turf algal cover on the reef crest tiles was log-transformed. An ANOVA was used to test for differences in the number of parrotfish feeding scars (log-transformed) between the four treatments on the exposed reef crest at the conclusion of the experiment (i.e., week 4). No feedings scars were observed on tiles within the sheltered back reef habitat. Bivariate correlations were used to examine the relationship between the survivorship of *A. cytherea* and the cover of turf algae and sediment, and the number of parrotfish feeding scars at the conclusion of the experiment (i.e., week 4).

3.3. Results

3.3.1. *Survivorship of coral recruits*

A total of 2,540 *Acropora cytherea* larvae settled onto the tiles and were deployed on the back-reef of Lizard Island in 2010, ranging from 26 to 173 recruits per tile (mean = 63.5 ± 5.0 SE recruits.tile⁻¹; **Figure 3.2 a**), and 799 on the exposed reef crest in 2011, ranging from 9 to 34 recruits per tile (mean = 20.0 ± 1.1 SE recruits.tile⁻¹; **Figure 3.2 b**). Overall, the survivorship of recently settled *A. cytherea* was 58.2 ± 2.2 % (mean \pm SE) after 4 weeks on the reef, pooled across habitats and treatments. Survival rates did not differ significantly among treatments on the back reef (Kaplan-Meier: $\chi^2 = 3.532$, df = 1, p = 0.06), ranging from 53.1 ± 3.8 % on the vertical tiles to 64.3 ± 4.5 % within the cage controls after 4-weeks (**Figure 3.2 c**). On the exposed reef crest, however, survivorship differed significantly among treatments (Kaplan-Meier: $\chi^2 = 11.985$, df = 1, p = 0.001, **Figure 3.2 d**). The survival rate of recently settled *A. cytherea* was higher inside the exclusion cages

($64.5 \pm 4.0 \text{ \%} \cdot \text{month}^{-1}$) than on the vertical ($43.6 \pm 8.0 \text{ \%} \cdot \text{month}^{-1}$), horizontal ($44.9 \pm 7.2 \text{ \%} \cdot \text{month}^{-1}$) or cage control tiles ($37.7 \pm 9.8 \text{ \%} \cdot \text{month}^{-1}$; **Figure 3.2 d**).

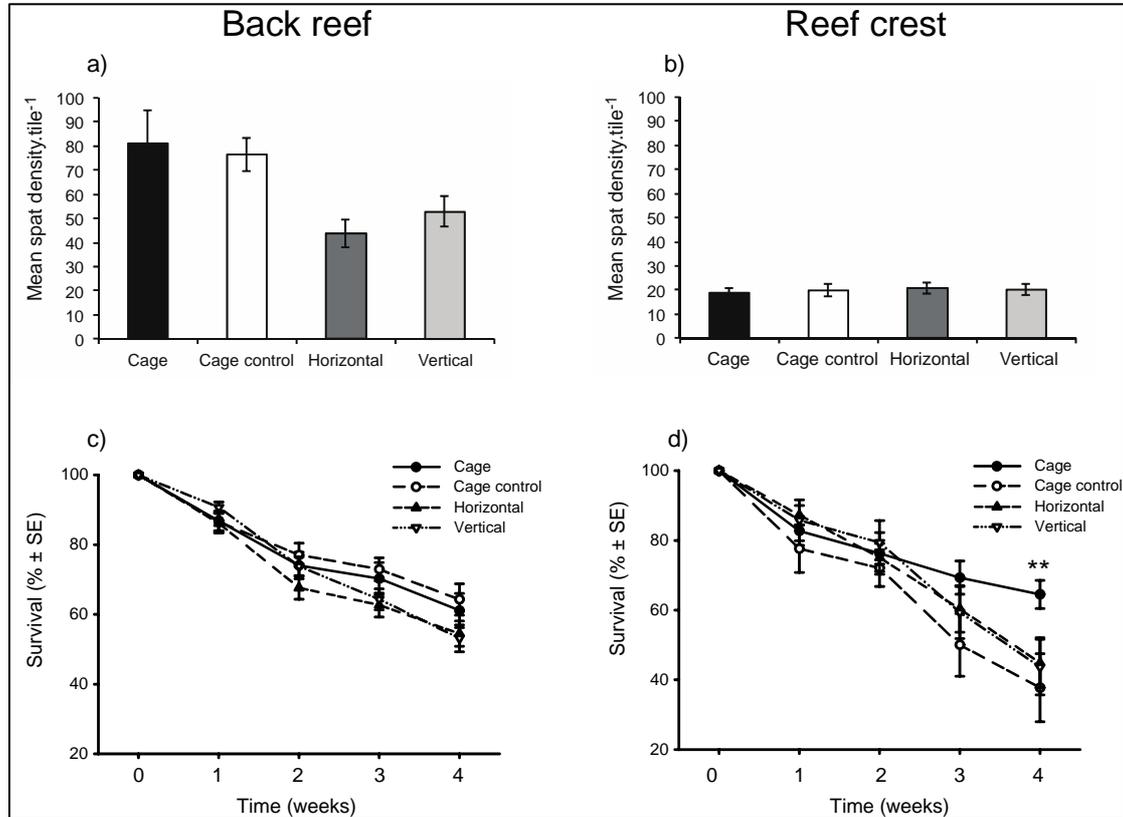


Figure 3.2 Survivorship of *Acropora cytherea* spats (mean \pm SE) after four weeks (T4) on the back-reef (a) and the fore-reef (b) for Horizontal (light grey), Open-cage (black), Cage (white) and Vertical (dark grey) treatments.

3.3.2. Abundance of algae, sediment and predation

Turf algal assemblages were first detectable on the tiles from the third week within both the sheltered back reef and the exposed reef crest habitats. Within the back-reef, the cover of turf algae on tiles did not differ among treatments ($F_{3, 36} = 1.03$, $p = 0.391$) but increased from $6.6 \pm 0.5 \text{ \%}$ (mean \pm SE) at week 3, to $12.5 \pm 1.2 \text{ \%}$ at week 4 ($F_{1, 36} = 62.18$, $p < 0.001$, **Figure 3.3 a**), with these increases being consistent among treatments (time x treatment: $F_{3, 36} = 0.289$, $p = 0.833$). On the exposed reef

crest, turf algae cover did not vary among treatments ($F_{3,36} = 0.617$, $p = 0.610$), but decreased significantly between week 3 and week 4, from $19.1 \pm 2.6\%$ to $11.0 \pm 1.9\%$ across all treatments ($F_{1,27} = 19.672$, $p < 0.001$, **Figure 3.3 b**).

Sediment was first detectable on the tiles from the third week within the back reef and reef crest habitats. Within the back reef, sediment cover increased markedly from week 3 to week 4 in the horizontal (5.0 to 30.0%), cage (4.0 to 31.0%), and cage control tiles (3.5 to 29.0%), while no sediment was observed on the vertical tiles (treatment x time: $F_{3,36} = 4.00$, $p = 0.015$; **Figure 3.3 c**). In contrast, there was no variation in sediment cover among treatments ($F_{3,27} = 2.702$, $p = 0.065$, Fig. 3d) or weeks ($F_{1,27} = 1.316$, $p = 0.261$) on the exposed reef crest, ranging from $1.4 \pm 0.4\%$ to $1.9 \pm 0.6\%$ in weeks 3 and 4, respectively (**Figure 3.3 d**).

Overall, the survivorship of coral spat was not correlated to the cover of turf algae (back reef: $r = -0.065$, $p = 0.690$; reef crest: $r = -0.073$, $p = 0.697$) or sediment (back reef: $r = -0.132$, $p = 0.418$; reef crest: $r = -0.072$, $p = 0.701$) within either habitat at the conclusion of the experiment. Very few sessile animals were observed on the tiles over the experimental period. There was, however, a weak but significant positive correlation between the initial recruit density and survivorship over the 4-week period on the back reef ($r = 0.404$, $n = 40$, $p = 0.010$), but this was driven by only one data point, and when excluded from the analysis, the relationship was no longer significant ($r = 0.307$, $n = 39$, $p = 0.055$). There was also no relationship between initial recruit densities and survivorship on tiles within the reef crest ($r = -0.265$, $n = 31$, $p = 0.154$).

The biomass of parrotfishes and all herbivorous fishes differed significantly among habitats (total herbivorous fishes: $F_{1,7} = 5.509$, $df = 1$, $p = 0.047$; parrotfishes: $F_{1,7} = 9.037$, $df = 1$, $p = 0.017$). Total herbivorous fish biomass was 6.3-fold greater

and scraping and excavating parrotfishes 5.5-fold greater on the reef crest than the back reef (**Figure 3.4**). Furthermore, parrotfish feeding scars were commonly observed on the reef crest tiles exposed to herbivores at week 4 but were absent on all back reef tiles. The number of parrotfish feeding scars on the reef crest tiles did not vary significantly among the three treatments exposed to herbivores ($F_{2,23} = 5.389$, $p = 0.445$) with an overall mean of 16.8 ± 4.4 feeding scars.tile⁻¹. The survival of *A. cytherea* in the 4-weeks post-settlement was, however, negatively related to number of parrotfish feeding scars on the reef crest tiles at the conclusion of the experiment ($r = -0.550$, $n = 31$, $p = 0.001$; **Figure 3.5**).

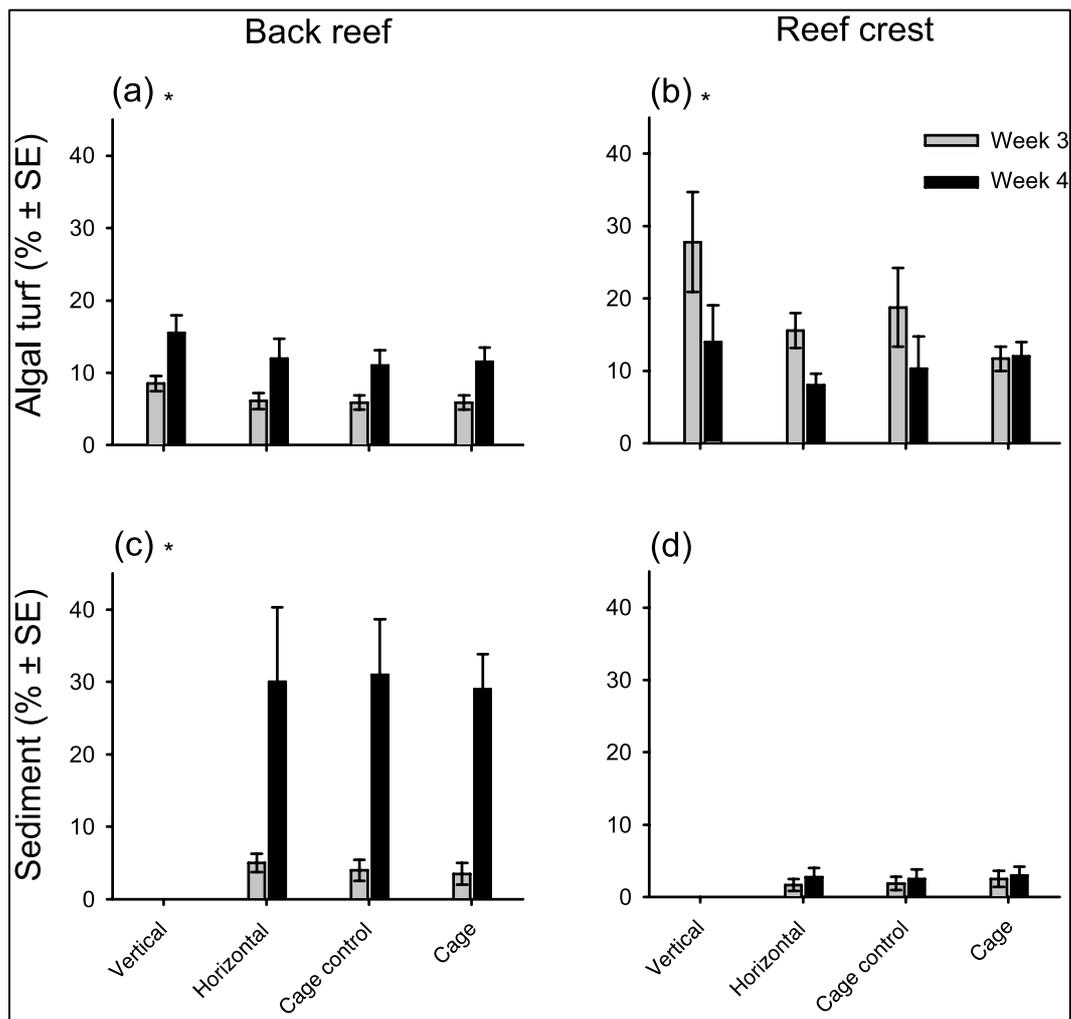


Figure 3.3 Turf and sediment cover at week 1 (T1, *white bars*), week 2 (T2, *black bars*), week 3 (T3, *light grey bars*) and week 4 (T4, *dark grey bars*) on tiles within horizontal, open-cage, cage and vertical treatments on (A) the back-reef and (B) the fore-reef.

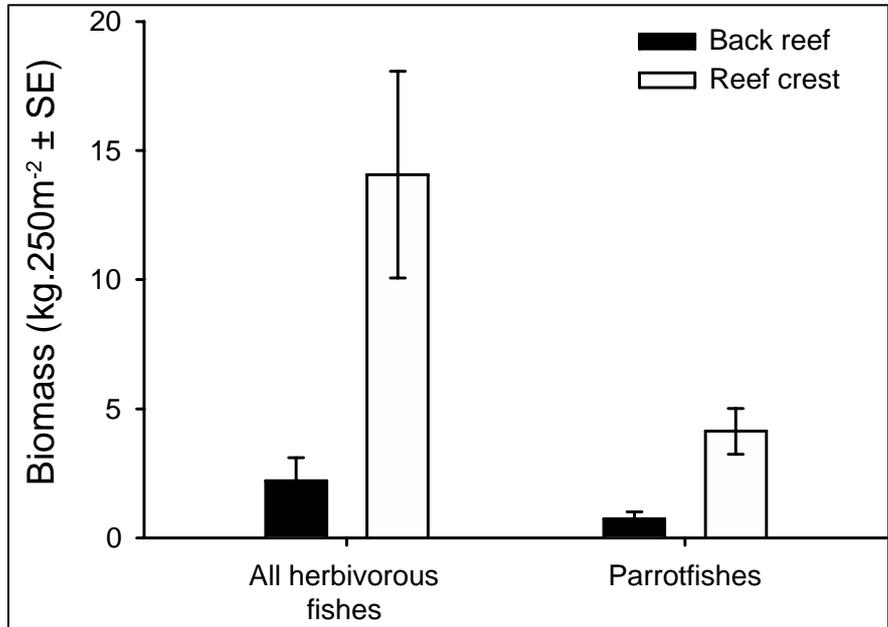


Figure 3.4 Among-habitat variation in the biomass of all roving herbivorous fishes (left) and excavating and scraping parrotfishes (right). Means are based on replicate 50 x 5m transects (back reef: n = 4; reef crest n = 6).

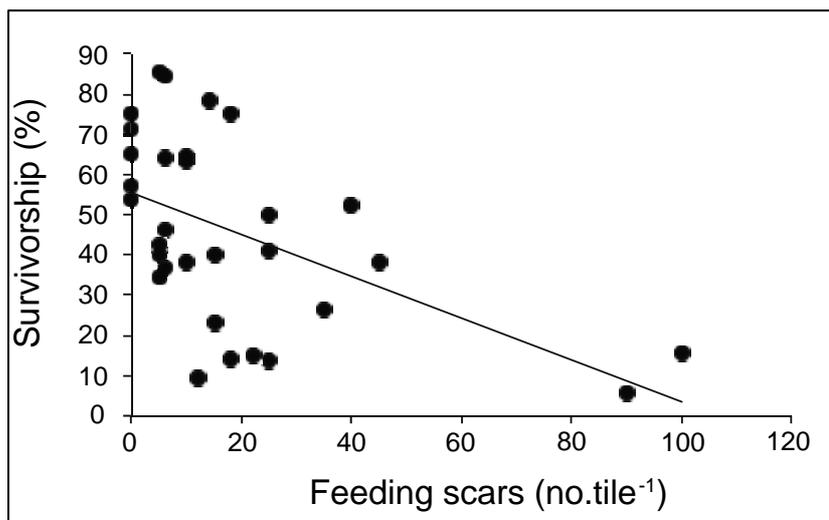


Figure 3.5 Relationship between percent mortality of juvenile corals and the number of feeding scars observed on each tiles at week 4 ($r = -0.550$, $n = 31$, $p = 0.001$).

3.4. Discussion

Mortality of newly settled corals is reported to be very high (Babcock 1985; Babcock and Mundy 1996; Raimondi and Morse 2000; Wilson and Harrison 2005), due to high levels of incidental grazing (Sammarco 1980; Penin et al. 2010), sedimentation (Sato 1985; Gilmour 1999), competition (Baird and Hughes 2000; Wilson and Harrison 2005; Vermeij and Sandin 2008), and/ or algal overgrowth (Box and Mumby 2007; Hughes et al. 2007). In this study, mean survivorship of newly settled *Acropora cytherea* was 58.2 % per month, ranging from 37.7 – 64.5 % per month, which was broadly comparable to survival rates reported for the congeners *A. solitaryensis* in Japan (36 – 55 % per month; Nozawa 2010) and *A. palmata* in Florida (44.5 % per month; Szmant and Miller 2006). The exclusion of herbivores increased survivorship by over 50 % on the reef crest (from 42.1 to 64.5 % per month), but had no detectable effect on survivorship on the back reef. Orientation, and hence sedimentation, had no detectable effect on survivorship of *A. cytherea* in either habitat, despite marked differences in sediment cover between vertical and horizontally oriented tiles in the back reef.

Predation or incidental grazing by fish is often cited as a major cause of early post-settlement mortality in corals (e.g., Raimondi and Morse 2000; Rotjan and Lewis 2008; Penin et al. 2010, 2011). In this study, the effects of macro grazers varied among habitats, coinciding with a 5.5-fold difference in the biomass of scraping and excavating parrotfishes on the reef crest compared to the sheltered back reef. Furthermore, feeding scars characteristic of scraping parrotfishes were only recorded on tiles within the reef crest habitats (**Figure 3.1 e**), with the density of these feedings scars being negatively related to survivorship of *A. cytherea* (e.g., **Figure 3.5**). Parrotfishes (Labridae) on Indo-Pacific reefs typically feed on crustose coralline

algae, algal turfs and associated detritus also called epilithic algal matrix (EAM, Wilson and Bellwood 1997) and, with the exception of the large bumphead parrotfish *Bolbometopon muricatum*, take very few bites from live coral (Bellwood and Choat 1990; Bellwood et al. 2003; Hoey and Bellwood 2008; Bellwood et al. 2012). In areas with high parrotfish biomass, such as the reef crest in the present study, grazing can be intense (Fox and Bellwood 2007; Hoey and Bellwood 2008), and appears to be a major source of mortality for recently settled corals. At low biomass, parrotfishes have been shown to be positively related to the densities of juvenile corals (Hoey et al. 2011), presumably because moderate increases in grazing activity prevents smothering of newly settled corals by algae and trapped sediments (Hughes et al. 2007; Penin et al. 2011). This effect was not observed in the back reef habitats at Lizard Island, possibly due to the early successional stage of experimental tiles. Although, tiles had been conditioned for 3-weeks, there was still only moderate growth of algae, whereas if the tiles had been left in back reef habitats for months to years it is possible that algal growth and accumulated sediments would greatly limit growth and survival of newly settled corals.

Mortality of recently settled corals is often attributed to sedimentation (Birkeland 1977; Harriott 1983; Sato 1985; Gilmour 1999) and/ or competition with algae (McCook et al. 2001; Kuffner et al. 2006; Box and Mumby 2007). In particular, higher survival of recently settled corals on vertical surfaces is often considered to be evidence of the negative effects of sediment (Loya 1976; Sato 1985; Babcock and Mundy 1996; Nozawa 2008). Within reef crest habitats, there was very limited accumulation of sediments (even on horizontal tiles), presumably due to high water flow and wave action. In back reef habitats, sediment cover was markedly lower on the vertical (0 %), as opposed to the horizontal (30 %), tiles, yet this variation had no

detectable effect on survivorship. This may be related to the relatively short duration of the experiment (28 days) or the methods used to quantify sediment cover. Sato (1985) reported marked differences in the survival of *Pocillopora damicornis* between vertical (35 – 52 %) and horizontal surfaces (100 %) during a four-week study, however in our study, sediments did not start to accumulate on the tiles until the third week. The weekly removal of tiles at Lizard Island, to score the fate of individual corals, may have prevented the longer-term accumulation of sediments. Similarly, algal turfs only started to develop on the tiles in the third week of the experiment in both habitats, and were therefore unlikely to have caused any direct mortality of corals.

Use of experimental tiles, while logistically necessary, may bias estimates of early post-settlement growth and mortality. Natural reef substrata provide settlement surfaces with a range of crevices and microhabitats that may enhance the survival of recently settled corals by protecting them from parrotfish grazing. Nozawa (2008) manipulated the availability of micro-crevices on settlement substrata and found that 100 % of corals that settled on flat surfaces (i.e., without crevices) died within the first four months, while 12 % of the corals that settled on surfaces with micro-crevices were still alive after one year. Furthermore, experimental studies that seed tiles can lead to very high densities of juveniles, which may further influence results if there is strong density-dependent mortality (e.g, Raimondi and Morse 2000). Survival of *A. cytherea* recruits was positively correlated with initial recruit densities on tiles within the back reef, but not for the reef crest. However, the positive relationship within the back reef was very weak and largely driven by one tile, where there was both a high densities of recruits (173) and unusually high survival (86.1 %) throughout our 4-week experiment. There is limited evidence that high densities of juvenile *A. cytherea*

(at least within the range of densities achieved during controlled seeding of replicate tiles) had either positive or negative effects on juvenile survivorship. It is possible however, that density-dependent mortality may be important at very high densities of juveniles, or at later stages when these juveniles are sufficiently large to directly compete with nearby conspecifics for light and space.

This study revealed relatively consistent, but moderate levels of mortality for newly settled *A. cytherea* on tiles deployed in two different habitats, and differentially subject to grazing and sedimentation. Although mortality rates were fairly consistent, the causes of mortality varied between habitats, and among treatments. On the exposed reef crests, grazing by herbivorous fishes contributed to juvenile coral mortality, but not in sheltered back reefs. Scraping and excavating parrotfish are a key functional group on coral reefs, clearing space for coral settlement and reducing algal overgrowth (Hughes et al. 2007), but they also incidentally damage recently settled corals through their feeding actions. However, mortality rates of juvenile *A. cytherea* on exposed reef crests were > 40 % even on tiles protected from grazing, and may have increased greatly over time with increased growth of both turf- and macro-algae. Even though herbivorous fishes can contribute to increased mortality of juvenile corals at high biomass, the beneficial effects of regulating macroalgae outweigh slight increases in juvenile mortality due to incidental grazing.

Chapter 4. Latitudinal variation in the growth and mortality of juvenile corals along the Great Barrier Reef

4.1. Introduction

Spatial variation in demographic rates of organisms can have a marked influence on the structure and dynamics of populations and communities (Connell 1978). While the boundaries of life history traits are generally constrained by phylogeny, individual traits may also be influenced by an organism's biological and physical environment (Hutchings 1993). Environmental conditions, and particularly temperature, vary considerably with latitude, altitude, and depth, and this variation has been related to differences in life history traits in a range of terrestrial and marine animals (e.g., Badayev 1997; Choat et al. 2003; Morrison and Hero 2003; Berner et al. 2004; Hoey et al. 2007). Although there are some differences among taxa, the majority of ectotherms (such as reptiles, fishes and many invertebrates) tend to exhibit faster growth and mature at a smaller size, but experience higher mortality in warmer environments (e.g., Pauly 1980; Houde 1989; Angilletta et al. 2004; Arendt 2011). In the marine environment, these relationships are complicated by the complex life cycle of most invertebrates and fishes, alternating between a dispersive pelagic larval phase and a sedentary juvenile and adult phase. The structure and dynamics of these communities is therefore influenced by factors acting upon these different phases (Caley et al. 1996), and how these factors vary geographically.

Scleractinian corals are the foundation species of coral reefs (Connell 1978), yet our understanding of factors that shape coral assemblages is limited to the early post-settlement and adult life history stages. The majority of studies to date have focused on processes affecting recently settled (i.e. 2-4 weeks following settlement onto the

substratum) or adult corals. The transition from a recently-settled coral to an adult coral can take several years, and has been suggested to play an important role in shaping the adult coral communities (Sammarco 1985; Hughes et al. 1999; Wilson and Harrison 2005; Roff and Mumby 2012), yet this life stage (i.e., juvenile coral) remains poorly understood due largely to difficulties in identifying small corals on natural reef substrata. For sessile organisms such as scleractinian corals, patterns established at settlement often show little resemblance to adult population patterns (Bak and Engel 1979; Rylaarsdam 1983; Fisk and Harriott 1990; Baird and Hughes 1997; Hughes et al. 1999; Penin et al. 2010) suggesting that spatial and temporal variation in recruitment has limited influence on the distribution and abundance of adult corals (Hughes et al. 1999, 2002). This is not surprising given that mortality of corals often approaches 100% in the first few weeks to months following settlement (Harriott 1983; Rylaarsdam 1983; Babcock 1985; Babcock and Mundy 1996; Chapter 3). These high rates of mortality may not only play an important role in regulating the abundance and composition of adult coral assemblages at local scales (Vermeij and Sandin 2008; Ritson-Williams et al. 2009), but may also influence larger-scale patterns in coral assemblages if rates of mortality vary predictably across environmental and/or geographic gradients.

On Australia's Great Barrier Reef (GBR) significant discrepancies have been reported between settlement patterns and the distribution of adult coral along a 1,700 km latitudinal gradient (Hughes et al. 1999). Despite adult coral cover being relatively consistent along the latitudinal extent of GBR (after accounting for cross-shelf variation), rates of coral settlement varied by an order of magnitude and were generally greater in the northern regions and lower in the southern regions. These differences in the settlement of corals, and presumably larval supply, may be linked to

variations in the fecundity of adult corals among sectors rather than adult abundance (Hughes et al. 2000), but the lack of congruence between settlement and adult abundance suggests that latitudinal variation in post-settlement processes may be compensating for marked differences established at settlement. Specifically, the lower rates of settlement in the southern GBR (Hughes et al 1999) may be compensated for with lower mortality rates in these regions compared to the northern regions of the GBR.

Few studies have effectively quantified early post-settlement growth and mortality, especially among different scales, partly due to the effort required. However, large-scale differences in demographic rates (growth and mortality) for early post-settlement coral stages: “coral recruits” (< 10 mm), and “juvenile corals” (10-50 mm, Penin et al. 2010), are likely to be influenced by several biotic and abiotic environmental factors, which often act in synergy. For example, survival rates of newly settled corals have been shown to be density-dependent (Vermeij 2005), whereby post-settlement mortality rates are highest in area with maximal rates of settlement. Similarly, cover of adult corals can affect recruits survival as they harbor potential pathogen agents that can kill recruits located close to them (Knowlton and Rohwer 2003). Incidental predation by herbivorous fish, is also known to greatly affect recruits survival (Sammarco 1985; Sato 1985; Rotjan and Lewis 2008; Christiansen et al. 2009; Mumby 2009; Penin et al. 2010, 2011), and this is also true for a great range of marine invertebrates (Gosselin and Qian 1997). Herbivorous fish abundance is typically higher on tropical reefs than subtropical reefs (Hoey et al. 2011), therefore latitudinal variations might influence spatial variations in post-settlement mortality.

All these aforementioned factors are more likely to contribute to spatial variations in demographic rates of early coral life-stage, however, their effect will also vary

upon the species and the size of the individuals, which further complicate the study of post-settlement processes and their interpretation. Indeed, mortality rates tend to decrease with increasing colony size (Hughes and Jackson 1985; Babcock 1991; Vermeij 2006; Doropoulos et al. 2012), therefore the probability of a coral colony to persist, changes over time (Tanner et al. 1996). Mortality agents such as incidental grazing by parrotfishes directly affect corals < 10 mm (Penin et al 2010, Doropoulos et al. 2012, Chapter 3) rather than bigger juveniles (Chapter 2), as fish might be able to avoid them once visible on the substratum. Therefore, coral species with higher growth rates might reach sooner a size-refuge from parrotfishes, enhancing their survival.

Growth or linear extension rates play an important role in coral population dynamic and have a critical impact on early survival (Birkeland et al. 1981; Van Moorsel 1988). Indeed, the faster the juvenile grows, the faster it will escape this vulnerable life-stage where mortality rates are high (Edmunds and Gates 2004). Measurements of colony growth have mostly been conducted on adult corals, which then were used to deduce early growth rates and determine the duration of recruits and juvenile phases (Van Moorsel 1988). However, similarly to post-settlement mortality, growth rates vary depending on the size and species-specific characteristics. Higher growth rates such as those of *Acropora* sp, might enable them a faster escape in size (Bak and Meesters 1998) and a better chance to survive until adult stage, compared to a juvenile *Porites* which will take longer time to reach a size refuge. In contrast, growth rates vary little in response to environmental conditions (Van Moorsel 1988; Babcock and Mundy 1996; Edmunds et al. 2004) as opposed to mortality rates. However, temperature is a limiting factors for reef accretion (Stoddart 1969), with optimal temperature for coral growth ~25° to 29°C (Jokiel and Coles 1977).

Therefore, coral growth rates are expected to vary among latitudes. For example, coral growth measurements on sub-tropical reefs such as Lord Howe Island, Eastern Australia, or the Houtman Abrolhos Islands, Western Australia, were lower than the ones on tropical reefs (Crossland 1981; Harriott 1999). Furthermore, seasonal variability of water temperature can also affect coral growth, with lower growth rates during winter periods (Harriott 1999). Therefore direct measurements of juvenile corals extension rates *in situ* for different taxa and spatial scales are needed to better understand coral population development along the GBR latitudinal gradient.

The aim of this study was to measure the growth and mortality of juvenile scleractinian corals across small (within reef) and large scales (among sectors) along the Great Barrier Reef latitudinal gradient. Quantifying growth and mortality for juvenile corals, which are the smallest visible size classes on natural substrata, requires explicit acknowledgement that recently settled corals will not be considered, thereby potentially missing what could be the most critical bottleneck in the life cycle of corals (Chapter 3). Moreover, it is assumed that the corals that are being surveyed are non-reproductive, but it is possible some corals that never attain large size will be reproductive at <50 mm diameter. The overarching goal of this study is to test for spatial variation in demographic rates of juvenile corals to assess whether early post-settlement processes are key to understanding apparent disparities in abundance of adult corals versus settlement rates. Given that Hughes et al. (1999, 2002) showed that coral settlement is lower at higher latitudes (but see Chapter 2) despite the relatively constant adult abundance on the GBR latitudinal gradient, we expected to find a marked latitudinal gradient in growth and mortality of juvenile corals, whereby growth is lowest and/ or mortality highest at low latitude reefs such as around Lizard Island (northern sector). This is somewhat at odds with expectations of lower growth

rates at high latitudes (e.g., Heron Island) if temperature exerts a major influence on growth, but it may be possible that both growth and mortality are significantly lower at these southern reefs. To test this, we also considered other potential drivers of large-scale variation in juvenile mortality, including competition (mostly, with corals) and predation. In chapter 2, juvenile coral densities were reduced at locations with high parrotfish biomass ($\sim 7\text{kg}\cdot 250\text{m}^{-2}$), suggesting that these fishes are responsible for a significant portion of coral mortality in early post-settlement stages (see also Chapter 3). If this effect continues into visible size classes of juvenile corals (*sensu* Penin et al. 2010), we expect mortality rates will be highest at sites with the greatest size and/ or abundance of parrotfishes, irrespective of latitude.

4.2. Methods

4.2.1. *Study sites*

Surveys of juvenile corals were conducted in three distinct sectors spanning over 2500 km on the Great Barrier Reef (GBR): northern GBR, in the vicinity of Lizard Island ($14^{\circ}41'S$, $145^{\circ}28'E$), central GBR, in vicinity of Trunk Reef ($18^{\circ}25'S$, $146^{\circ}47'E$), and southern GBR, in the vicinity of Heron Island ($23^{\circ}27'S$, $155^{\circ}55'E$) (Fig. 1). Within each sector, sampling was conducted at three reefs, and three sites per reef, giving a total of nine sites per sector. Only mid-shelf reefs were sampled to minimize any effects of cross-shelf variation, and all sampling was constrained to a single habitat type, the exposed reef crest (2-4m depth). The exposed reef crest was selected as this habitat is typically characterized by high cover of adult corals (Connell et al. 2004) and high rates of coral settlement (Wallace and Bull 1982). This hierarchical nested sampling was designed to facilitate the examination of local and regional variation in the growth and mortality of juvenile coral assemblages, and

provide greater insight into processes that maybe be structuring coral populations on the GBR.

4.2.2. *Juvenile coral census*

At each site, three permanent 10 m transects were established on the reef crest, parallel with depth contours. Adjacent transects were separated by 1 to 10 m, and the end-points of each transect marked with stainless steel bars hammered into the substratum to allow the exact positioning of transects to be relocated. Five 1 m² quadrats were placed randomly along each transect, giving a total of 405 quadrats. Juvenile scleractinian corals were defined as any colonies visible with the naked eye with a maximum diameter of 50 mm, following Rylaarsdam (1983), and showing distinct growth and morphological characteristic (e.g., base approximately round). To maximize detection of juvenile corals, the 1-m² quadrats were divided into a 10 x 10 grid using strings placed at 10 cm intervals along the vertical and horizontal axes. The resulting one hundred 10 cm² squares were systematically inspected for the presence of juvenile corals. All juvenile corals detected were identified to the highest possible taxonomic level (mostly genus), their position within the quadrat recorded to facilitate relocation during subsequent surveys, and the maximum diameter measured to the nearest millimetre using callipers. Typically, early life stage of most coral species grow first parallel to the substratum, in a 2-dimensional way to form the colony base, which allows the comparison of change in diameter of juvenile corals between different taxa (Van Moorsel 1988). The smallest corals detected were 5 mm diameter, and only a very small proportion (2.4 %) of juvenile corals were < 10 mm, reflecting difficulties in detecting very small corals with the naked eye. All quadrats were established in 2009, and resurveyed after 9 and 18 months.

Juvenile corals measured during the first survey were located during subsequent surveys using their coordinates within each quadrat. Any previously recorded juvenile corals that could not be located were assumed to have died. For all juvenile corals that were alive the maximum diameter of each coral was re-measured. Careful searching of each quadrat did reveal some new juvenile corals (not detected in the initial survey), for which the size and identity were recorded, but these newly detected (typically, < 15 mm) individuals were not considered in analyses of growth and mortality. The monthly growth of juvenile corals was calculated as the change in the maximum diameter of the colony divided by the number of months between surveys. It should be noted that partial mortality, characterized by a withdrawal of the tissue no longer extending to the base of the skeleton (Edmunds 2007) and subsequent regeneration, were likely to occur between surveys, but could not be quantified. Therefore this study examines realized growth, which accounts for both increases and decreases in the diameter of colonies, as opposed to potential growth, i.e. colonies that exhibited positive growth only (following Edmunds 2007). Mortality rates were calculated as the proportion of individuals that died or could not be relocated, divided by the number of months between surveys (% dead.mo⁻¹). Growth and mortality rates were calculated for the three main genera *Acropora*, *Pocillopora* and *Porites*, at site, reef and sector scales. Unfortunately, several of the stainless steel bars marking the end-points of the transects went missing between surveys and consequently 10 quadrats in central sector, and 15 quadrats in the southern sector could not be re-surveyed. Furthermore, one quadrat in the northern sector was omitted during the last survey, therefore a total of 26 quadrats were removed from the analysis, giving a total of 379 replicate quadrats.

4.2.3. *Scrapers and excavators fish census*

Abundances of scraping and excavating parrotfishes were quantified at each site using a series of underwater visual censuses. We specifically focused on scraping and excavating parrotfishes as they constitute the majority of parrotfish species on the Great Barrier Reef (Hoey and Bellwood 2008), and have been shown to be negatively related to the density of juvenile corals (Chapter 2) and the survivorship of recently settled *A. cytherea* (Chapter 3). Each transect consisted of a diver swimming along the reef crest and recording all scraping and excavating parrotfishes greater than 10 cm total length (TL) within a 5 m wide belt while simultaneously deploying a 50 m transect tape. Individual fishes were identified to species and placed into 5 cm size categories. Eight transects were surveyed within each site on each reef (total n = 216 transects) and encompassed the area in which the juvenile corals were surveyed. Fish densities were then converted to biomass using published length-weight relationships for each species, following (Hoey and Bellwood 2009).

4.2.4. *Statistical analysis*

Monthly growth rate or “linear extension” (mm per month) was calculated as the increase in maximum diameter between censuses, dividing by the number of months between censuses. The monthly mortality rate (% per month) was calculated as the percentage of juveniles that died between censuses, divided by the number of months between censuses.

Monthly growth and mortality rates of corals from the three main taxa (*Acropora*, *Pocillopora*, *Porites*) were compared independently among the three sectors (north, central and south), among reefs within sector (3 reefs per sector), sites within reef (3 sites per reef) and among transects within site (3 transects per site), using a four-factor

hierarchically nested ANOVA. The assumptions of the ANOVA were examined using residual analysis and monthly growth rates were log-transformed and monthly mortality rates were arcsine-square root transformed.

To determine if the growth and/or mortality of juvenile corals were density dependent, influenced by initial size of the juvenile corals, cover of adult corals, or grazing by parrotfishes a series of correlations were performed. The correlations between the growth and mortality of juvenile corals and the density of juvenile corals, initial size of juvenile corals, and the cover of adult corals were based on mean values within each quadrat. The correlation between monthly mortality rates and the biomass of scraping and excavating parrotfish was based on the mean values per site. The correlations analyses were performed for the three main genera independently (e.g. *Acropora* monthly mortality versus *Acropora* initial densities, *Acropora* monthly mortality versus *Acropora* coral cover, and *Acropora* monthly mortality versus *Acropora* initial size).

4.3. Results

4.3.1. *Juvenile coral densities*

A total of 2520 juveniles were counted within the 379 quadrats during the first survey (T1), giving a mean density of 6.65 ± 0.25 (SE) juveniles.m⁻². Nine months later (T2), 1743 of these juveniles were still alive (mean of 4.59 ± 0.21 SE.m⁻²) and 1348 juveniles were found 18 months after the first survey (T3; mean of 3.55 ± 0.19 SE.m⁻²), corresponding with overall survivorship rates of 69.2 % and 53.5 %, respectively. However, given well-established differences in the life-histories of corals (e.g., Hughes 1985), it is more appropriate to assess demographic rates within each of the most abundant genera. Juvenile coral assemblages were dominated by

Acropora (1247 individuals, relative abundance: 49.5 %), *Pocillopora* (279 individuals, relative abundance: 11.1 %) and *Porites* (586 individuals, relative abundance: 23.3 %) across the three surveys (**Figure 4.1**).

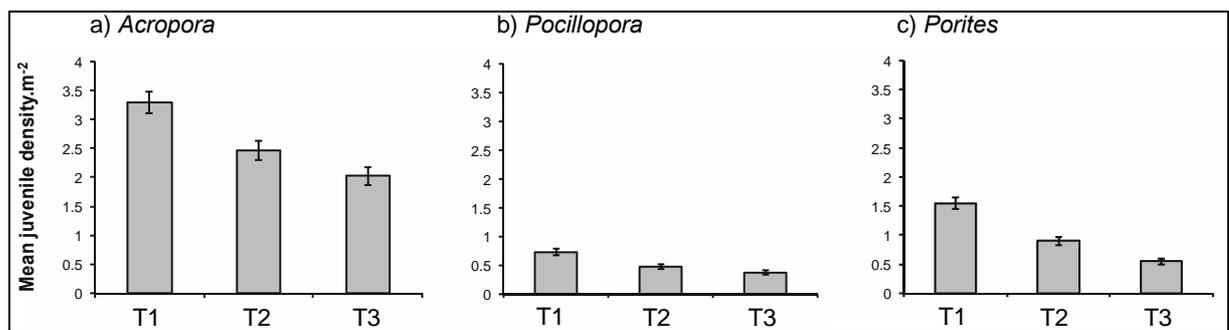


Figure 4.1 Mean densities (ind.m⁻²) of a) *Acropora*, b) *Pocillopora*, and c) *Porites* juvenile corals during the first survey (T1), nine months after (T2) and 18 months after (T3). Note that quadrats were pooled across all sectors. Error bars represent \pm SE

4.3.2. Juvenile coral mortality

Mortality of juvenile corals was relatively high during the study period, with 44.0 % (\pm 2.0 SE) of juvenile *Acropora* corals, 50 % (\pm 3.5 SE) of juvenile *Pocillopora* corals and 65.6 % (\pm 2.6 SE) of juvenile *Porites* corals dying over the 18-month period (**Figure 4.2**). The monthly mortality rates of juvenile corals varied spatially with the three main genera displaying different patterns. Mortality of juvenile *Acropora* varied significantly between sectors (**Table 4.1 a**; **Figure 4.3 a**) with mortality being greater within the central sector (3.25 % \pm 0.18 SE per month) than the northern and southern sectors (1.96 % \pm 0.18 SE per month and 2.34 % \pm 0.21 SE per month, respectively). Mortality of juvenile *Porites* also varied between sectors with monthly mortality rates lower in the northern sector (2.8 % \pm 0.2 SE per month) than in the central and southern sectors (4.2 % \pm 0.2 SE

per month and $4.8 \% \pm 0.2 \text{ SE}$ per month' respectively; **Table 4.1 c**, **Figure 4.3 c**). Juvenile *Pocillopora sp* had relatively similar monthly mortality rates across sectors, (overall mean of $2.9 \% \pm 0.2 \text{ SE}$ per month), however monthly mortality rates varied significantly between reefs within each sector (**Table 4.1 b**, **Figure 4.3 b**). For all three taxa the variation among quadrats accounted for over 70 % of the total variation in mortality rates (**Table 4.1**).

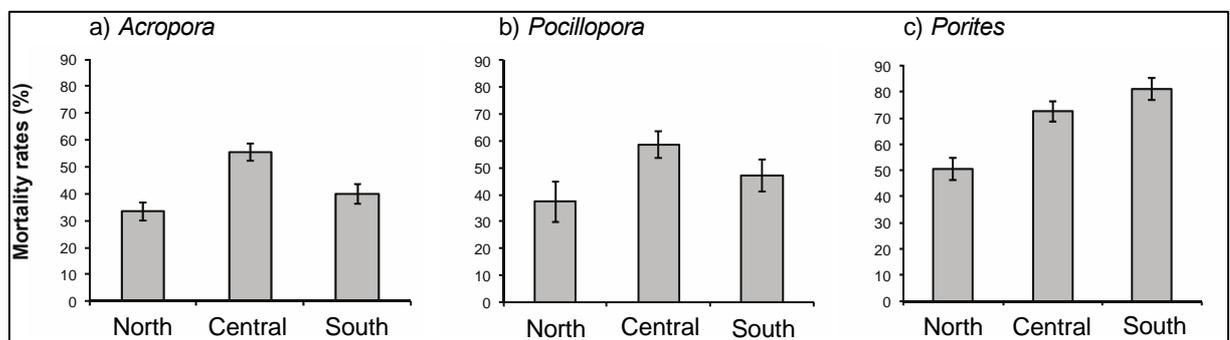


Figure 4.2 Mortality rates of juvenile corals among sectors (North, Central and South) from the three main taxa: a) *Acropora*, b) *Pocillopora* and c) *Porites*, over the 18 months study period. Error bars represent $\pm \text{SE}$

Table 4.1 Results of four-factor ANOVA's comparing mortality rates of juvenile scleractinian corals (≤ 50 mm) among sectors, reefs within sector and sites within reefs and transects within sites for (a) *Acropora* sp, (b) *Pocillopora* sp, (c) *Porites* sp. Significant results ($p < 0.05$) are shown in bold

	SS	df	MS	F	Sig.	Var(%)
a. <i>Acropora</i>						
Sector	0.223	2	0.112	5.351	0.046	9.15
Reef (Sector)	0.126	6	0.021	1.637	0.197	1.68
Site (Reef (Sector))	0.219	17	0.013	1.589	0.102	4.59
Transect (Site (Reef (Sector)))	0.399	49	0.008	1.218	0.169	3.27
Error	1.656	248	0.007			81.29
b. <i>Pocillopora</i>						
Sector	0.064	2	0.032	1.18	0.366	2.24
Reef (Sector)	0.171	6	0.028	3.375	0.020	7.99
Site (Reef (Sector))	0.132	16	0.008	0.782	0.697	0.00
Transect (Site (Reef (Sector)))	0.386	37	0.010	0.931	0.586	0.00
Error	1.099	98	0.011			89.76
c. <i>Porites</i>						
Sector	0.282	2	0.141	6.471	0.029	16.28
Reef (Sector)	0.141	6	0.024	1.883	0.137	2.96
Site (Reef (Sector))	0.221	17	0.013	1.435	0.158	2.89
Transect (Site (Reef (Sector)))	0.419	45	0.009	1.354	0.088	6.24
Error	1.143	166	0.007			71.61

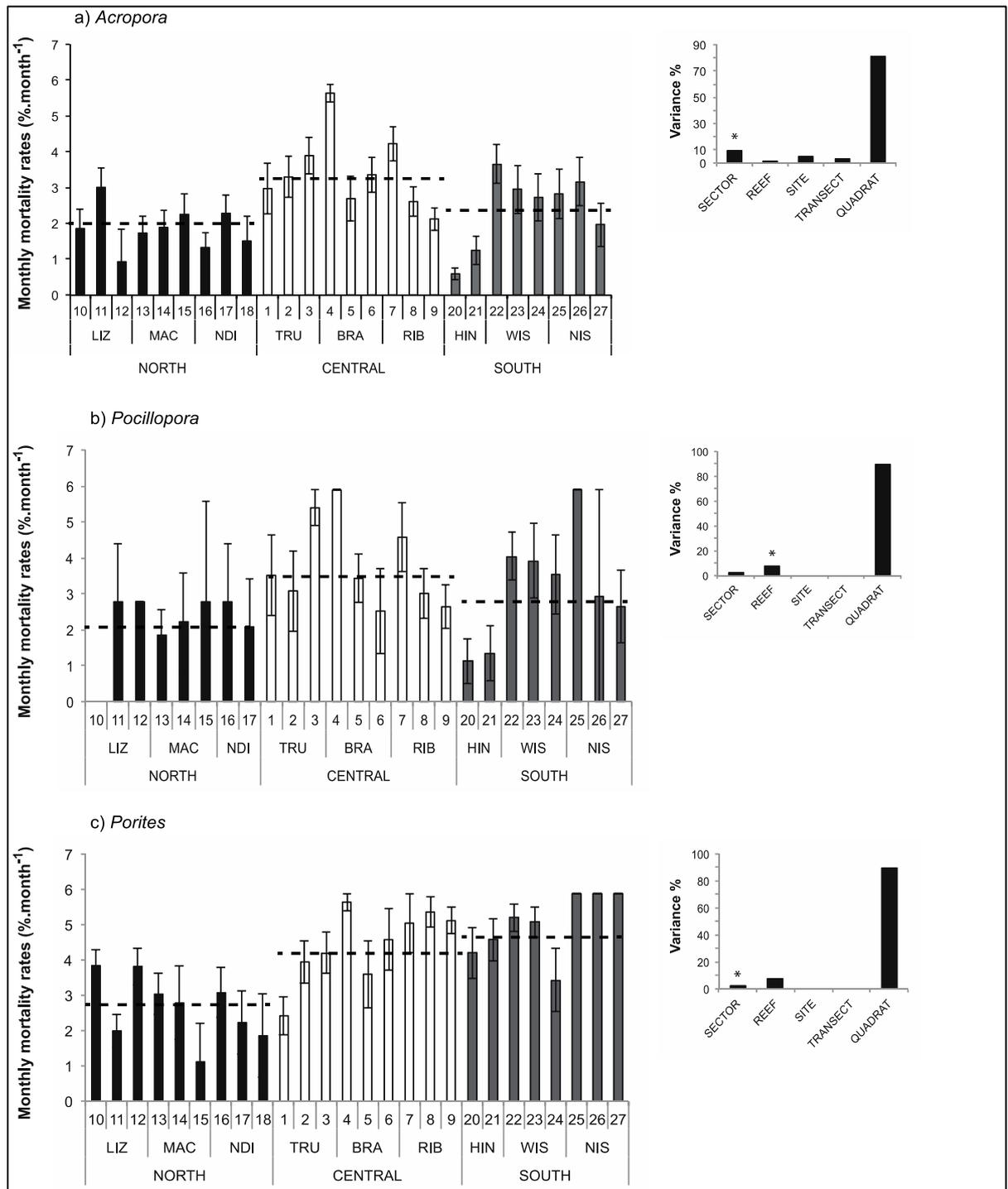


Figure 4.3 Variation in monthly mortality rates of juvenile scleractinian corals among sectors, reefs within sector and sites within reef for a) *Acropora* spp, b) *Pocillopora* spp, and c) *Porites* spp. Horizontal lines show mean monthly mortality for each sector. Monthly rates were standardised from mortality rates over 18 months. Error bars represent \pm SE. Components of variation are also shown for each taxa at five spatial scales and bars with asterisks indicate spatial scales where there was a significant variation (i.e., $p < 0.05$).

4.3.3. *Juvenile coral growth*

Mean monthly growth rate (i.e., change in maximum diameter) ranged from -0.90 to 9.20 mm.month⁻¹. Of the 1,348 juvenile colonies surveyed after 18 months only 25 colonies (in which 2 *Acropora*, 2 *Pocillopora*, and 14 *Porites*) exhibited negative growth (or a reduction in maximum diameter) and there was no change in the size of 6 other colonies (2 *Acropora*, 1 *Pocillopora*, and 2 *Porites*), which presented no growth at all (no change in maximum diameter). Juvenile *Acropora* monthly change in diameter ranged from -0.20 to 9.20 mm.month⁻¹. Monthly change in diameter of juvenile *Acropora* sp did not vary significantly at sector or site scales (overall mean of 1.80 ± 0.04 SE mm.month⁻¹; **Table 4.2 a**, **Figure 4.4 a**), but it varied at reef within sector scale. Juvenile *Pocillopora* growth rates ranged from -0.50 to 5.60 mm.month⁻¹, and were significantly different at sector scale. Growth rates of juvenile *Pocillopora* were lower within the southern sector with a mean of 1.26 ± 0.08 mm.month⁻¹, compared to 2.11 ± 0.12 mm.month⁻¹ in central sector and 1.92 ± 0.12 mm.month⁻¹ at the northern sector of the GBR (**Table 4.2 b**, **Figure 4.4 b**). Juvenile *Porites* monthly change in diameter ranged from -0.9 to 2.7 mm.month⁻¹, but did not vary significantly at any scale with an overall mean of 0.97 ± 0.04 mm.month⁻¹ (**Table 4.2 c**, **Figure 4.4 c**).

Table 4.2 Results of four-factor ANOVA's comparing monthly linear extension of juvenile scleractinian corals (≤ 50 mm) among sectors, reefs within sector and sites within reefs for (a) *Acropora* spp, (b) *Pocillopora* spp, (c) *Porites* spp. Significant results ($p < 0.05$) are shown in bold

	SS	df	MS	F	Sig.	Var(%)
a. <i>Acropora</i>						
Sector	0.074	2	0.037	0.626	0.564	0.00
Reef (Sector)	0.404	6	0.067	2.924	0.027	3.12
Site (Reef (Sector))	0.429	17	0.025	0.908	0.568	0.00
Transect (Site (Reef (Sector)))	1.519	47	0.032	2.08	0.000	8.16
Error	10.751	692	0.016	10.751		88.72
b. <i>Pocillopora</i>						
Sector	0.421	2	0.211	6.069	0.034	20.17
Reef (Sector)	0.215	6	0.036	1.825	0.160	5.50
Site (Reef (Sector))	0.278	14	0.020	1.144	0.342	9.88
Transect (Site (Reef (Sector)))	0.534	29	0.018	1.194	0.257	4.95
Error	1.465	95	0.015			59.50
c. <i>Porites</i>						
Sector	0.082	2	0.041	1.253	0.337	0.00
Reef (Sector)	0.160	5	0.032	0.733	0.606	0.00
Site (Reef (Sector))	0.698	15	0.047	1.718	0.061	6.94
Transect (Site (Reef (Sector)))	0.657	30	0.022	0.588	0.956	0.00
Error	5.779	155	0.037			93.06

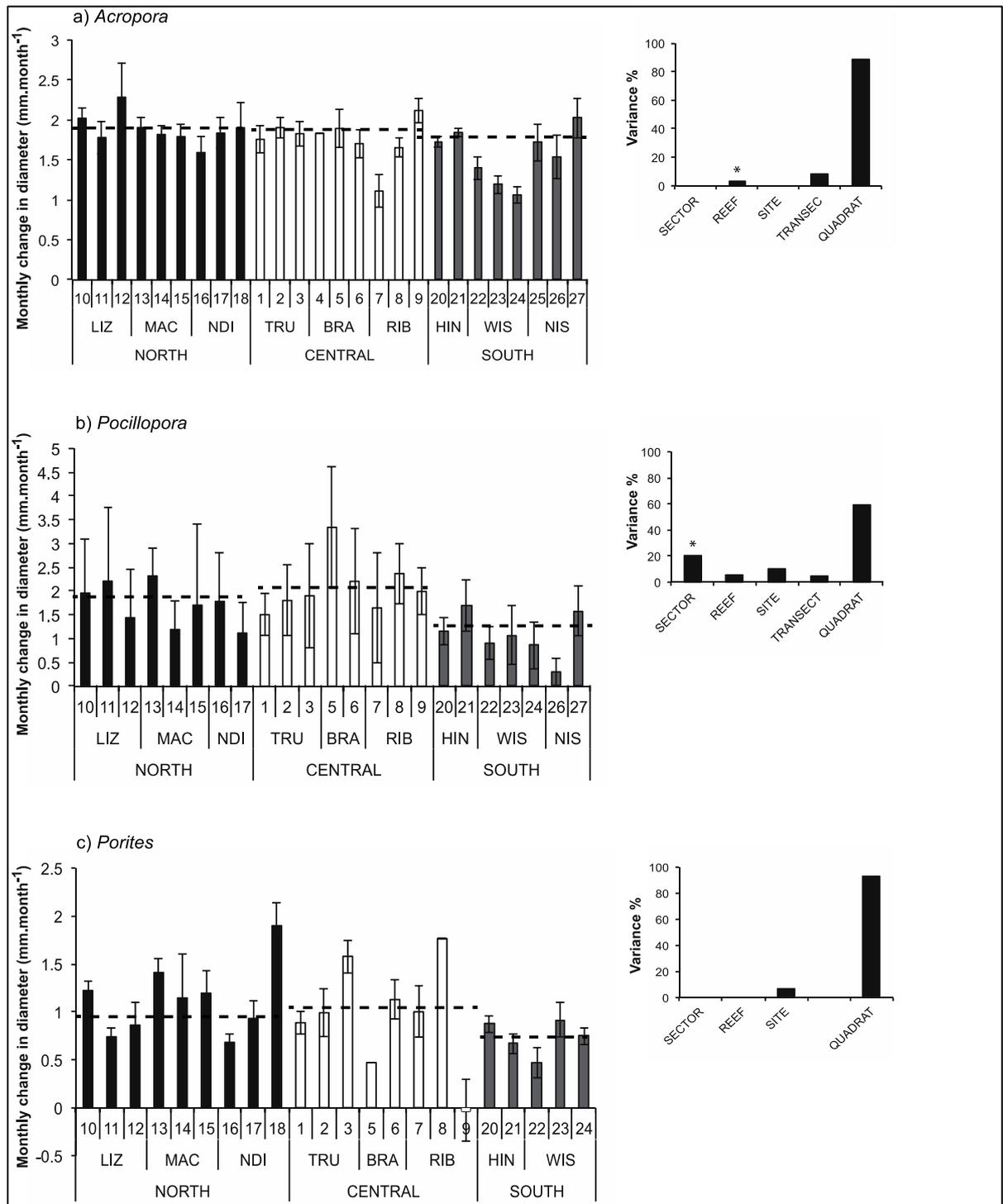


Figure 4.4 Mean change in diameter (mm.month⁻¹) among sectors, reefs within sector and sites within locations for a) *Acropora* spp, b) *Pocillopora* spp, and c) *Porites* spp. Dashed horizontal lines show mean monthly growth for each sector. Monthly rates were standardised from growth rates over 18 months. Error bars represent ± SE. Components of variation are shown for each taxa at five spatial scales. Asterisks indicate spatial scales where there was a significant variation (i.e. $p < 0.05$).

4.3.4. Correlations

Overall, the initial density of juvenile corals and the cover of adult corals were poor predictors of juvenile coral mortality, with the nature of the relationships varying between taxa. Mortality rates of *Acropora* juvenile corals were negatively correlated with *Acropora* juvenile densities and positively correlated with adult *Acropora* coral cover (Table 4.3 a & b, Figure 4.5 a & d). However, monthly mortality rates of *Pocillopora* juveniles were not correlated with either *Pocillopora* initial densities or *Pocillopora* coral cover (Table 4.3 a & b, Figure 4.5 b & e). Monthly mortality rates of *Porites* juveniles were not correlated with initial *Porites* densities (Table 4.3 a; Figure 4.5 c), but were negatively correlated with adult *Porites* coral cover (Table 4.3 b; Figure 4.5 f). Monthly mortality rates of the three taxa were not correlated with the biomass of scraping and excavating parrotfish (Table 4.3 c).

Table 4.3 Relationship between monthly mortality rates and a) initial density of juvenile corals at quadrat scale, b) initial adult coral cover at quadrat scale and c) the biomass of scraping and excavating parrotfish at site scale. Pearson's correlation coefficients are given. Significant results ($p < 0.05$) are shown in bold.

a) Mortality v. Initial density	Quadrat
<i>Acropora</i>	N = 323, r = -0.973, p = 0.000
<i>Pocillopora</i>	N = 160, r = -0.028, p = 0.724
<i>Porites</i>	N = 237, r = -0.075, p = 0.248
b) Mortality v. Adult cover	Quadrat
<i>Acropora</i>	N = 323, r = 0.150, p = 0.007
<i>Pocillopora</i>	N = 160, r = 0.016, p = 0.843
<i>Porites</i>	N = 237, r = -0.243, p = 0.000
c) Mortality v. Fish Biomass	Site
<i>Acropora</i>	N = 26, r = 0.262, p = 0.196
<i>Pocillopora</i>	N = 25, r = 0.199, p = 0.341
<i>Porites</i>	N = 26, r = 0.058, p = 0.777

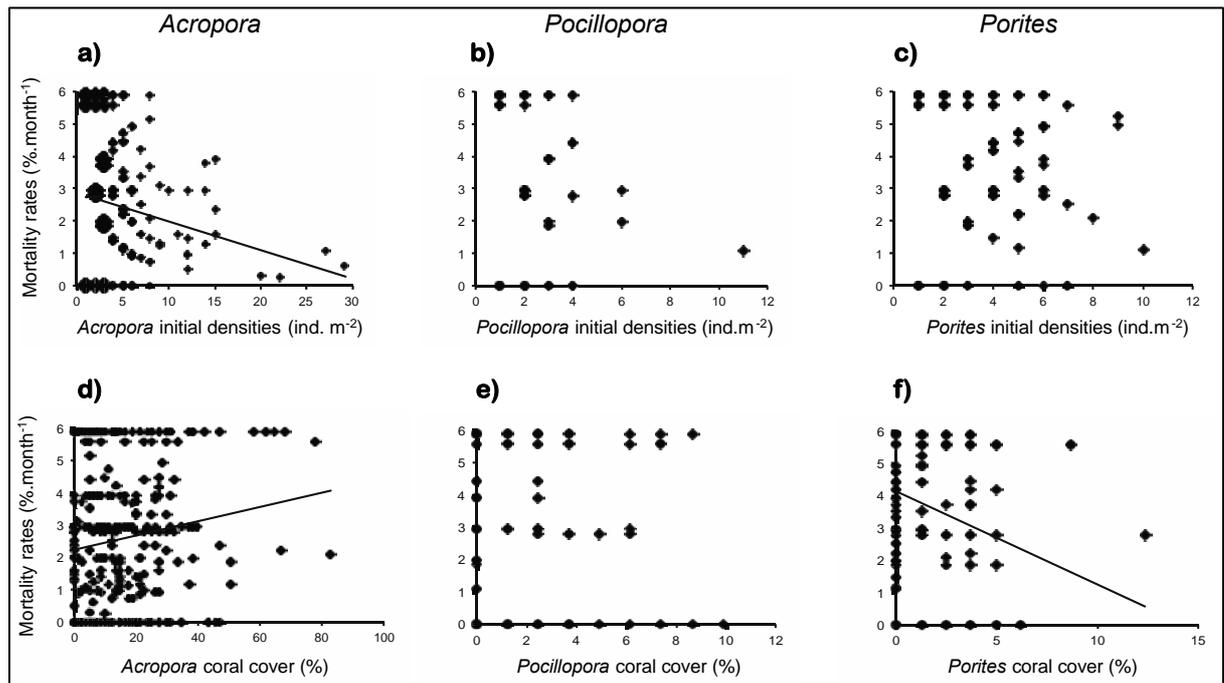


Figure 4.5 Correlation between monthly mortality rates of juvenile coral and mean juvenile initial densities (a, b, and c), and between monthly mortality rates and adult coral cover (d, e, and f). Relationships are given for the three main taxa *Acropora*, *Pocillopora* and *Porites* independently. The line represents a significant relationship. Note that for graph a) over 50 quadrats had 1, 2 or 3 *Acropora* individuals, therefore the size of the symbol is increased to show that multiple points are overlying each other.

Monthly mortality rates were negatively correlated to initial size for each of the three main taxa, indicating that mortality rates were higher among the smallest size class and declined with increasing size (**Table 4.4; Figure 4.6 a, b & c**). Monthly growth was also positively correlated to initial size for *Acropora* and *Pocillopora* juveniles (**Figure 4.6 d & e**), but negatively correlated to initial size for *Porites* juveniles (**Figure 4.6 f; Table 4.4**).

Table 4.4 Correlation between monthly mortality rates and initial juvenile size (mm) and between monthly growth rates and initial juvenile size, for the three main taxa *Acropora*, *Pocillopora* and *Porites* independently. Significant results ($p < 0.05$) are shown in bold. Note that the N values vary, as juveniles were not observed at all sizes (e.g. at 1, 2, 3, and 4 mm for all taxa, and at certain size depending on taxa)

Mortality v. Initial size	
<i>Acropora</i>	N = 44, r = -0.796, p = 0.000
<i>Pocillopora</i>	N = 44, r = -0.442, p = 0.003
<i>Porites</i>	N = 46, r = -0.481, p = 0.001
Growth v. Initial size	
<i>Acropora</i>	N = 44, r = 0.514, p = 0.000
<i>Pocillopora</i>	N = 41, r = 0.354, p = 0.023
<i>Porites</i>	N = 42, r = -0.311, p = 0.045

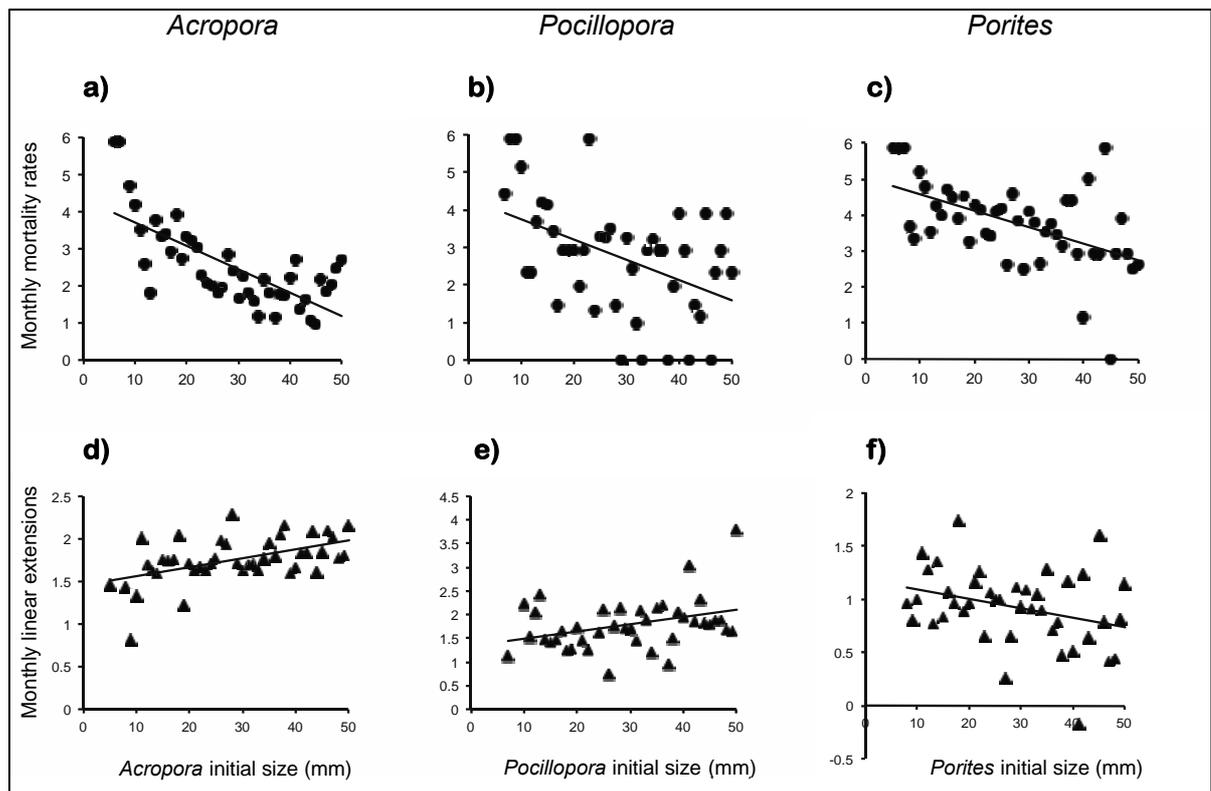


Figure 4.6 Correlation between monthly mortality rates and initial juvenile size (a, b, and c) and between monthly linear extensions (mm) and initial juvenile size (d, e, and f). Relationships are given for the three main taxa *Acropora*, *Pocillopora* and *Porites* independently, and are plotted for each individual size where a rate could be calculated.

4.4. Discussion

This study is the first to document how demographic rates (specifically, mortality and growth rates) of juvenile corals vary over large geographic scales and latitudinal gradients. At this largest spatial scale it was expected there would be a strong and consistent latitudinal gradients in both growth (e.g., Harriott 1999) and mortality of juvenile corals (*sensu* Hughes et al. 1999). Although there were significant differences in the growth and mortality of juvenile corals, there was no consistent trend with latitude apparent across all major taxa. Furthermore, growth rates of juvenile corals varied little (except for *Pocillopora*) among the three latitudinal sectors).

4.4.1. *Juvenile coral mortality*

For juvenile *Acropora*, mortality rates were higher within the central sector, while mortality rates of juvenile *Porites* were higher in the central and southern sectors of the GBR. Specific causes of mortality for individual corals were not and could not be readily established, but it is important to note that a category 5 cyclone, Cyclone Yasi, impacted the reef on the 3rd of February 2011 (Great Barrier Reef Marine Park 2011), and likely contributed for higher mortality rates in the central GBR. Ecological assessment undertaken on the aftermath of cyclone Yasi found that damages to reefs were spatially heterogeneous, but that mid-shelf reefs situated within 100-150 km from the eye of the cyclone (our study location in the central GBR), suffered severe to extreme coral damage, especially on the exposed side of the reefs (Great Barrier Reef Marine Park 2011). Furthermore, another study evaluating the potential recovery of inshore reefs (Palm Islands) after cyclone Yasi showed that the taxon *Acropora* suffered the most, with coral cover reduced to < 0.1 % on exposed

sites of the Palm Islands (Lukoschek et al. 2013). However, most of the surviving *Acropora* colonies were < 5 cm, with encrusting bases and small branches starting to erect above the substratum (Lukoschek et al. 2013). Small and juvenile corals probably escaped the significant damage from strong hydrodynamic forces, owing to their low profile, generally immersed position and boundary layer effects. Even so, mortality rates of all three taxa (*Acropora*, *Pocillopora* and *Porites*) were greatest within the immediate vicinity of the cyclone path. For all three taxa (*Acropora*, *Pocillopora* and *Porites*) however, overall mortality rates in the southern sector were lower than, or equal to, those in the northern sector. These results clearly contradict the hypothesis that post-settlement mortality will be highest in the northern GBR (Hughes et al 1999), which is where settlement rates are highest (Hughes et al. 2002).

Similarities in juvenile densities and adult coral cover found among sectors of the GBR (see Chapter 2), and the unexpected lower mortality rates in the northern sector (at least for the most abundant taxon: *Acropora* and *Porites*), suggests that either i) marked latitudinal gradients in rates of recruitment detected in 1995/1996 and 1996/1997 (Hughes et al. 1999) do not hold now, or ii) any compensatory mortality occurs during the early, and not measurable, post-settlement life-stage. Importantly, this study only measured spatial variation in juvenile corals over the size range of 10-50 mm, thereby missing the earliest, and potentially most critical, life-history stage (Vermeij and Sandin 2008). Mortality rates of newly settled corals are reported to be as high as 99% within the first year (e.g., Babcock 1985), and could therefore have a very strong influence on abundance patterns of juvenile and adult corals. Comparing rates of early post-settlement mortality across a hierarchy of spatial scales, including large-scale contrasts along the length of the GBR, is going to be very challenging, but

may be key to understanding how relatively consistent levels of adult coral cover can occur despite marked differences in population replenishment.

Major causes of juvenile coral mortality are likely to vary in time and space, but high rates of mortality are generally attributed to biotic interactions such as predation and competition. Incidental grazing by scraping and excavating parrotfishes have been found to reduce coral recruits survival on artificial substratum (Penin et al. 2010 and Chapter 3) and to negatively affect juvenile densities at high biomass (Figure 2.6 of Chapter 2). In this study, however, spatial variation in rates of juvenile mortality could not be attributed to variation in the biomass of herbivorous fishes, which are assumed to cause high levels of mortality among small and juvenile corals (Christiansen et al. 2009; Penin et al. 2010, 2011). This was likely due to the ability of the fish to detect and avoid larger juvenile on the natural substratum (Brock 1979; Doropoulos et al. 2012). Therefore, taxa with higher growth rates such as *Acropora*, would benefit by reaching a size-refuge from incidental grazing faster. Monthly mortality rates however, were positively but weakly correlated with coral cover at quadrat scale for the taxon *Acropora*. Early post-settlement mortality (recruit stage) has been found to be highly susceptible to adult coral cover immediately following settlement, probably due to high number of individuals settling close to adult colonies (Janzen 1970; Connell 1971; Vermeij 2005). Adult colonies can directly compete for light and space and will always have a major size advantage over newly settled and juvenile corals, but established corals may also harbour potential pathogens to which small and juvenile corals are highly susceptible (Knowlton and Rohwer 2003). In this study, there was a positive correlation between adult cover and juvenile mortality, whereby mortality rates of juvenile *Acropora* were highest in quadrats with highest cover of adult *Acropora*. This is most likely attributable to effects of shading (Baird

and Hughes 2000), but the specific effect of adult corals on juvenile survivorship needs to be tested by assessing the fate of individual juvenile at varying distances from adult conspecifics. No such relationship was apparent for either *Pocillopora* or *Porites*, but this may be because *Acropora* corals are very unique in their propensity to form a closed canopy that shades understorey corals (Baird and Hughes 2000). For *Porites*, mortality rates of juvenile corals actually declined with increasing cover of adult corals, but the highest cover of *Porites* recorded in quadrats was only 15 % and much lower than the highest cover recorded for adult *Acropora*.

In this study, mortality rates for *Acropora* juveniles (mean of 29.3 % per annum) were lower than recorded for juvenile *Pocillopora* (33.6 % per annum) and *Porites* (43.2 % per annum). In general, mortality rates of the three taxa were lower or similar to those reported in other studies on juvenile scleractinian corals; e.g., 32-40 % per annum for *Porites* juvenile in Jamaica, Rylaarsdam 1983; 0-88 % per annum for *Acropora* juvenile, Wallace 1985a). However, our estimated annual mortality rates are substantially lower than recorded for the same genera immediately after settlement (i.e. < 10 mm) on artificial substrata, which are generally > 60 % (e.g., 70 % per annum for Acroporidae, Babcock 1985; 60 % per annum for Pocilloridae, Harriott 1983; 70 % per annum for *Porites*, Fizharding 1988). Fine-scale variation in mortality rates may be attributable to stochasticity in biotic interactions (Jackson 1991), as well as small-scale differences in light levels, nutrient supply, sedimentation and other environmental conditions.

4.4.2. *Juvenile coral growth*

Growth rates of adult corals often vary along latitudinal gradients, whereby corals grow more slowly in higher latitudes and cooler climates (Harriott 1999; Edmunds 2000). Accordingly, growth rates for juvenile *Pocillopora* juveniles were significantly

lower at the southern sector of the GBR, compared to the central and northern sectors. For *Acropora* or *Porites*, sites where the lowest growth rates were recorded were in the southern sector, though growth rates were highly variable at smaller spatial scales and thereby obscured large-scale, latitudinal gradients. For *Acropora*, greatest variation in growth rates of juvenile corals occurred among reefs and among transects (within sites). For *Porites* growth rates varied most at the scale of individual quadrats. As Jackson (1991) pointed out, small-scale heterogeneity in the demographics of juvenile corals is to be expected given the stochasticity of biotic interactions and other fine-scale processes. What is interesting is when there are emergent patterns at larger spatial scales that swamp fine-scale variation or noise (Jackson 1991).

Spatial variation in growth rates of juvenile corals is likely to have implications for reef recovery following disturbances, such that reefs and locations with lower growth rates will take longer to recover and may therefore, be less resilient to sustained ongoing increases in the frequency, if not severity, of major disturbances. Most importantly, mortality rates are strongly size-dependent (see also Babcock 1991), such that fastest growing corals are likely to experience highest survivorship. Among adult corals, there are purported tradeoffs between growth and mortality, whereby slow growing corals benefit by having greater resistance to extrinsic sources of mortality and are more persistent (Darling et al. 2012). However, such tradeoffs do not seem to apply within the juvenile life stages. As has been shown for adult corals, juvenile *Porites* grew much more slowly (mean of 0.97 mm per month) compared to *Acropora* (mean of 1.80 mm per month) and *Pocillopora* (mean of 1.76 mm per month) juveniles. However, mortality rates of juvenile *Porites* were also higher than recorded for faster growing genera (*Acropora* and *Pocillopora*), presumably because the advantage of increased overall size in this highly sensitive stage of the life-cycle

outweighs any benefit derived from increased investment in carbonate skeleton. In support of this hypothesis, most juvenile corals initially grow in only two dimensions (regardless of adult growth form) to maximize horizontal dimensions (Van Moorsel 1985). Vertical elements are then added only when corals approach 30-40mm diameter, which may be the size at which juvenile corals are no longer susceptible to incidental grazing by fishes.

4.4.3. *Conclusion*

This study shows that demographic rates of juvenile corals (10-50 mm diameter) varied spatially, and taxonomically, and are therefore, likely to exert a significant influence on the structure and dynamics of coral populations and communities. Contrary to expectations, there was no strong and consistent latitudinal variation in the growth and mortality of juvenile corals along the length of the GBR, but spatial variation in key demographic rates of juvenile corals may nonetheless structure patterns of adult abundance and community structure of coral assemblages at smaller (and perhaps larger) spatial scales. Importantly, early post-settlement growth and mortality should not be considered in isolation, and the relative importance of pre- versus post-settlement processes in structuring coral populations and communities will vary depending on local levels larval supply, rates of settlement, as well as the specific limits on growth and survivorship of newly settled corals. In this study, there was no single over-riding mechanism (e.g., incidental grazing by herbivorous fishes) that could account for observed mortality of juvenile corals, rather these small (≤ 50 mm) corals appear susceptible to a wide range of fine-scale processes, that combine to cause significant rates of mortality, especially amongst smallest size classes. Significant further research is however, warranted to better understand the

key bottlenecks in the life history of corals, especially given widespread declines in the abundance of corals (Gardner et al. 2003; Bellwood et al. 2004).

Chapter 5. Post-settlement growth and mortality rates of juvenile scleractinian corals in Moorea, French Polynesia versus Trunk Reef, Australia*

5.1. Introduction

Scleractinian corals, like most marine invertebrates, have a bipartite life cycle in which larvae develop in the plankton before settling and attaching to the substratum. The larval stage therefore provides an important means of dispersal for sessile reef corals, enabling colonisation of new habitats, recolonization following disturbance, and genetic exchange among sub-populations (Caley et al. 1996). Ultimately, the distribution and abundance of larvae may also limit geographic distributions and regulate local populations of marine organisms (Hughes 1990; Cowen and Sponaugle 2009; Weersing and Toonen 2009). However, the abundance of new recruits (assumed to reflect variability in larval supply) often shows little or no relation to patterns of adult abundance (Bak and Engel 1979; Rylaarsdam 1983; Fisk and Harriott 1990; Baird and Hughes 1997; Hughes et al. 1999; Penin et al. 2010), suggesting that spatial and temporal variation in recruitment has limited influence on the distribution and abundance of adult corals (Hughes et al. 1999, 2002). The effects of larval input on adult abundance may be difficult to detect because adult abundance reflects the accumulation of recruits over many successive cohorts, and infrequent years of very high recruitment might have a disproportionate influence on adult abundance (Edmunds 2000). Alternatively, extreme variability in post-settlement

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growth and mortality may effectively decouple relationships between recruitment rates and adult abundance (Hughes et al. 1999, 2002).

Estimates of post-settlement mortality in scleractinian corals are rare, but mortality is known to vary with size, with the smallest size-class (< 10 mm recruits, Penin et al. 2010) experiencing up to 100 % mortality within the first year (Harriott 1983; Rylaarsdam 1983; Babcock 1985; Babcock and Mundy 1996), thereby representing a critical demographic bottleneck for coral populations (Vermeij and Sandin 2008). For example, early post-settlement mortality in *Acropora millepora*, *Goniastrea aspera* and *Platygyra sinensis*, was > 65 % during the first 8 months after settlement (Babcock 1985). High rates of mortality may therefore have an important role in regulating the abundance and composition of adult coral assemblages (Vermeij and Sandin 2008; Ritson-Williams et al. 2009). For post-settlement processes to influence patterns of adult abundance, there must be significant and consistent variation in growth or mortality among locations or habitats (Bak and Engel 1979; Rylaarsdam 1983; Hixon and Carr 1997). Studies that have explored variation in post-settlement mortality of scleractinian corals (e.g., Babcock and Mundy 1996; Mundy and Babcock 2000; Glassom and Chadwick 2006; Penin et al. 2010) have detected significant spatial and/or temporal variation in rates of mortality. Nonetheless, these studies concluded that spatial variation in abundance of corals is established mostly at settlement, due to large-scale variation in larval supply (Glassom and Chadwick 2006) or fine-scale settlement preferences of coral larvae (Babcock and Mundy 1996; Mundy and Babcock 2000). However, large-scale differences in demographic rates (growth and mortality) for early post-settlement coral stage or “coral recruits” (i.e., individual invisible to the naked eye on the substratum < 10 mm), and later post-settlement stage or “juvenile corals” (i.e., visible on the substratum > 10 mm, see

Penin et al. 2010), may contribute to geographic variation in abundance and/or resilience of coral assemblages (Sammarco 1985; Hughes et al. 1999; Wilson and Harrison 2005; Roff and Mumby 2012).

Coral populations show high spatial heterogeneity in abundance, and taxonomic composition across a range of scales, reflecting variation in biotic and abiotic processes acting on the different life stages (Connolly et al. 2005; Cornell et al. 2007; Hughes et al. 2012). In particular, the supply of coral larvae, their successful settlement, and subsequent survival and growth can have a marked influence on local population structure. These processes are expected to differ greatly across geographic scales given the dissimilarities in adult coral assemblages, local hydrodynamics, disturbances history, competition, and sources of predation (e.g., sea star, fish, sea urchin and gastropod communities) at such scales (Connell et al. 1997; Hughes et al. 2000). On the Great Barrier Reef (GBR), settlement rates of corals have been shown to be much lower on southernmost reefs (e.g., Heron Island) compared to northern reefs (e.g., Lizard Island), whereas adult coral cover did not vary over this scale (Hughes et al. 1999). The discrepancy between these two life-stages has been attributed to large-scale differences in underlying population dynamics (Hughes et al. 1999), whereby regional differences in post-settlement mortality can compensate for marked difference in settlement rates.

Few studies have specifically quantified post-settlement growth and mortality of juvenile corals, partly due to the effort required. To date, geographical variation in the status of coral reefs and particularly, coral cover and composition, is mostly attributed to differences in disturbance regimes and rates of adult mortality (Ruiz-Zárte and Arias-González 2004). It is possible however, that there are inherent differences in key demographic processes, such as post-settlement growth and mortality of juvenile

corals that would greatly influence resilience of coral populations and communities. The purpose of this study was to compare the density, taxonomic composition, growth and mortality of juvenile scleractinian corals between Moorea, French Polynesia and Trunk Reef, in the central Great Barrier Reef, Australia. Juveniles were defined as colonies visible with the naked eye with a maximum diameter ≤ 50 mm (*sensu* Rylaarsdam 1983; Miller et al. 2000; Penin et al. 2007; Penin et al. 2010; Hoey et al. 2011)). Earlier studies on settlement rates on the reef crest at Moorea, French Polynesia (~ 40 recruits m^{-2} year $^{-1}$: Adjeroud et al. 2007a; Adjeroud et al. 2007b) revealed that settlement rates were an order of magnitude lower than on the central GBR mid-shelf reef crest (~ 200 -700 recruits m^{-2} year $^{-1}$: Hughes et al. 1999), despite having similar cover of adult corals (Adjeroud et al. 2007a). Comparisons between French Polynesia and Australia's Great Barrier Reef are intended to test whether post-settlement processes should be considered in ongoing studies to understand regional differences in the vulnerability and resilience of coral assemblages (Wilkinson 2004).

5.2. Methods

5.2.1. *Field sampling*

Growth and mortality of juvenile corals were quantified at Moorea (17°29'S, 149°5'W) in the Society Islands, French Polynesia, and at Trunk Reef (18°17'S, 146°53'E), in the central Great Barrier Reef (GBR), Australia. These two locations are at equivalent latitudes, but there are significant and important differences in the environmental settings. Moorea is a large volcanic island (ca. 134 km^2) surrounded by a narrow reef (ca. 49 km^2), which can be divided into 3 distinct habitats: i) the fringing reef, separated by a sandy channel to ii) the barrier reef flat, separated by a reef crest to iii) the barrier reef slope. The north coast of Moorea is subject to

moderate swell during the summer (November-April) whereas the west coast is exposed to high amplitude swell throughout the year (Adjeroud et al. 2007a). Reefs in Moorea have been subjected several large-scales disturbances over the past three decades (Traçon et al. 2011), which have caused a dramatic shifts in assemblage structure and loss of total coral cover (Berumen and Pratchett 2006; Pratchett et al. 2011; Kayal 2012).

Trunk reef is a large mid-shelf reef in the central GBR (ca. 125 km²), located approximately 58 km from the mainland coast. Trunk reef has well-developed continuous reef along the relatively exposed east, south and western margins, partially enclosing a large shallow lagoon. Trunk reef is part of an extensive complex of reefs, with < 2 km to the adjacent reef (Bramble Reef). These reefs were subject to fairly extensive bleaching in 2001-02, which combined with outbreaks of *A. planci*, reduced coral cover to < 5 % on the reef crest and down to a depth of 6-8 m (Pratchett et al. 2006), but there was strong recovery in the aftermath of these disturbances (Linares et al. 2012).

Sampling was conducted in 2003 at Moorea and in 2009 at Trunk Reef, which corresponded to years of maximum coral cover at each of these locations over the last decade (Linares et al. 2011; Traçon et al. 2011). At each location, sampling was undertaken at three sites on the reef crest habitat, at about 4-6 m depth. At Moorea, all sampling was conducted on the outer reef crest, with two sites (Tiahura and Vaipahu) situated on the north coast and one (Haapiti) on the west coast. The west coast has the greatest exposure to prevailing trade winds, but reefs on the north coast are subject to strong swells mostly in the summer months (**Figure 5.1**). At Trunk reef, two sites were surveyed on the south (“South”) and southeast reef-crest (“East”), which are directly exposed to prevailing winds and waves. The third site was located on the

southwest reef crest (“West”), which is obliquely exposed to the trade winds (**Figure 5.1**). At each site, three 10 m permanent transects were established, delineated using steel pegs hammered into the substratum at either end of the transect. The transects were orientated parallel to depth contours with a minimum of 3 m separating adjacent transects. Juvenile corals (≤ 50 mm diameter) were surveyed within five replicate 1 m² quadrats (non-adjacent), initially positioned randomly along the transect line. Colonies ≤ 50 mm are likely to be up to 34 months old based on currently available growth estimates (see Babcock et al. 2003), and are likely to be non-reproductive according to minimum reproduction size, especially for the most common taxa *Acropora*, *Pocillopora* and *Porites*. Collectively, these taxa accounted for 77.7 % and 91.6 % of the juvenile coral assemblage in Moorea and Trunk Reef, respectively. However, this maximum size might not be appropriate for a few taxa such as *Favia* spp that can become sexually mature at sizes as small as 20 mm (Miller et al. 2000).

To maximize detection of juvenile corals, the 1-m² replicate quadrats were divided into a 10 × 10 grid using strings placed at 10 cm intervals along the vertical and horizontal axes. The resulting one hundred 10 cm² squares were systematically inspected for the presence of juvenile corals. All juvenile corals detected were identified to the highest possible taxonomic level (mostly genus) and the maximum diameter measured to the nearest millimetre using callipers. The size and condition of each coral was then assessed after 6-8 months. The total observation period (6-8 months) is not ideal, because it does not capture total annual mortality, but corresponds closely with several other studies of post-settlement growth and mortality for scleractinian corals (e.g., Babcock and Mundy 1996; Box and Mumby 2007). Colonies that were experiencing partial mortality and thus a decrease in size were characterized by a withdrawal of the tissue that was no longer extending to the base of

the skeleton (Edmunds 2007). Realized growth rates, accounting for both colonies that increase and colonies that decrease in mean diameter, were expressed as mm month⁻¹. Potential growth rates, i.e. colonies that grew ≥ 0 mm month⁻¹ (following Edmunds 2007) were also calculated to test for any differences with realized growth rates. Mortality rates were expressed as the proportion of individuals that died or were missing on the next census.

Percentage cover of scleractinian corals was recorded at each site within each location using point-intercept methods, whereby coral or substratum types were recorded directly beneath a minimum of 500 uniformly spaced points per site. In this study, we distinguished three major adult coral genera: *Acropora*, *Pocillopora*, and *Porites* that accounted for 76.0 % and 94.2 % of the adult coral assemblage in Moorea and Trunk Reef, respectively. All other coral genera were pooled into a single category ‘‘other’’.

5.2.2. *Statistical analysis*

Abundance of both juvenile and adult corals (all taxa combined) were compared between the two geographic locations (Moorea and Trunk Reef), as well as among sites (3 sites per location) using a 2-factor ANOVA. Differences in the taxonomic composition of juvenile and adult coral assemblages (*Acropora*, *Pocillopora*, *Porites* and ‘other’ corals category) were compared between locations and among sites using a 2-factor MANOVA. Although quadrats were arranged along transects, transect was not considered as a level in these analyses. The number of juvenile corals per quadrat (both collectively and the main taxa independently) was log-transformed, and percent cover of adult coral was arcsine-square root transformed to meet the parametric assumptions.

Monthly growth rates or “linear extensions” (mm per month) were calculated by subtracting the maximum diameter at census two from the maximum diameter at census one, divided by the number of months between censuses, and monthly mortality rates were calculated by dividing the number of dead juveniles by the number of months between census two and census one. Monthly growth rates or “linear extensions” were log-transformed and monthly mortality rates were arcsine-square root transformed to improve normality and homoscedasticity. A one-factor ANOVA was used to determine whether realized growth rates differed from potential growth rates, which could indicate whether partial mortality occurred between the two censuses. Realized monthly growth and monthly mortality of juvenile corals was compared among the three main genera (*Acropora*, *Pocillopora* and *Porites*), between two geographic locations (Moorea versus Trunk Reef), and among sites (3 sites nested within each location) using a three-factor ANOVA.

Juvenile corals were then separated into 5 size-classes: < 10, 10-19, 20-29, 30-39, 40-50 mm. A chi-square contingency table was used to compare juveniles’ size structure between locations for each of the three main taxa *Acropora*, *Pocillopora*, and *Porites*. Data from the different sites within each location were pooled due to the limited number of individuals within some size classes and/or genera. In addition, monthly mortality and realized monthly growth rates were compared among the five size-classes and between the two locations for each taxon using a series of 2-factor ANOVA’s. Again, data from sites within each location were pooled to increase power. Monthly mortality rates were arcsine-square root transformed while no transformations were necessary for monthly growth rates. However, due to the lack of *Porites* juvenile in Moorea (i.e. ≤ 40 mm), the two larger size classes (i.e. 30-39 and 40-50 mm) were pooled into one size class (30-50 mm). Furthermore, due to the

absence of small *Pocillopora* (i.e. < 10 mm) at Trunk, the two smaller size classes (i.e. 0-9 and 10-19 mm) were pooled (0-19 mm).

Finally, a series of correlations were used to determine if i) the mortality rates of juvenile corals were related to initial juvenile density, and ii) the density of juvenile corals was related to the cover of adult corals at each location. The correlations between mortality rates and juvenile coral density were based on individual quadrats, with data pooled across the three sites within each location (Moorea: n = 45 Trunk Reef: n = 45). Separate analyses were performed for all juvenile corals collectively and the three main genera independently (i.e., *Acropora*, *Pocillopora*, *Porites*). As total coral cover was not quantified within individual quadrats the relationship between adult coral cover and the density of juvenile corals was examined at the scale of transects (n = 9 transects per location). Separate analyses were performed for all corals collectively, and the three main genera independently (i.e., *Acropora*, *Pocillopora*, *Porites*).

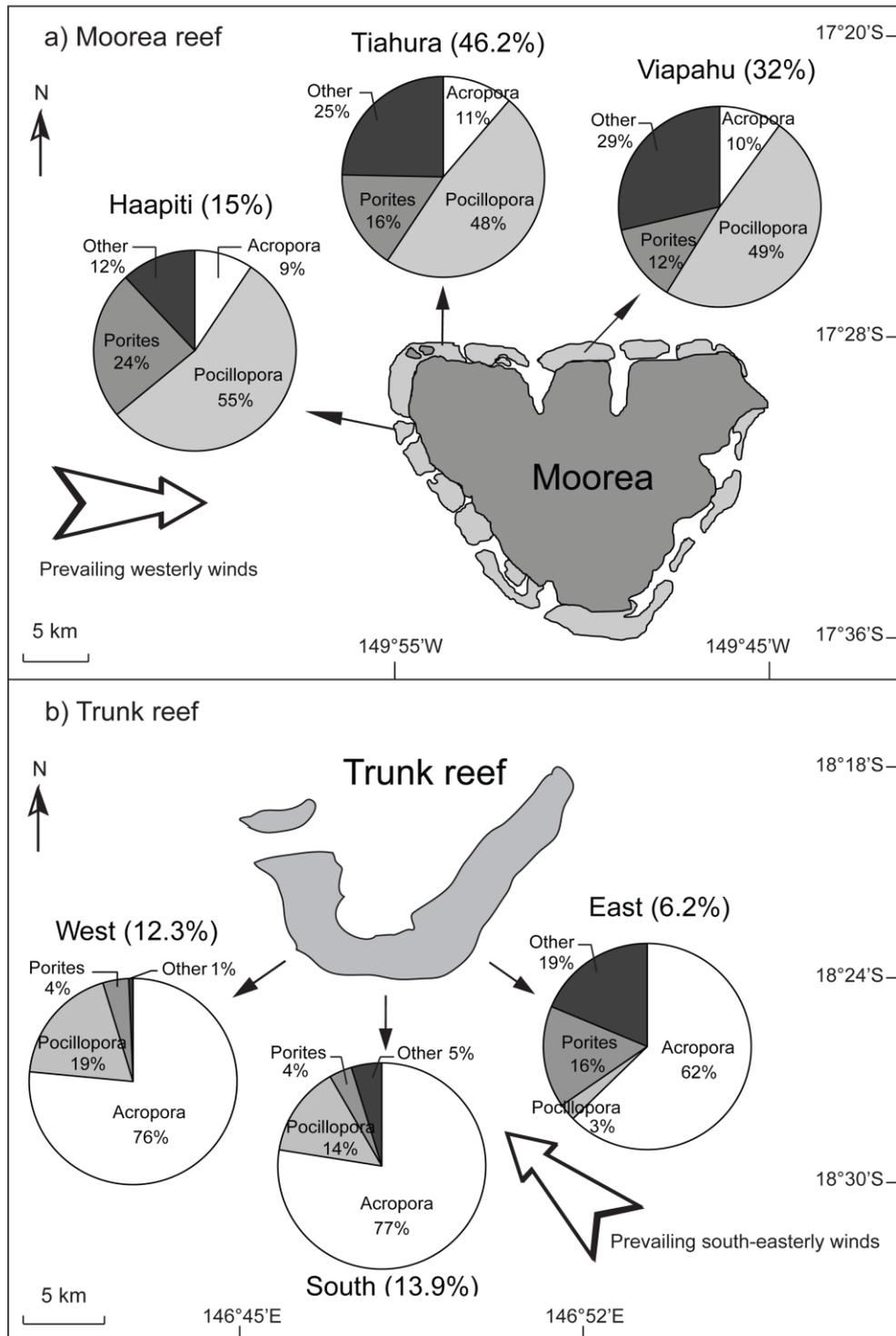


Figure 5.1 Map of a) Moorea, French Polynesia and b) Trunk Reef, central Great Barrier Reef showing the location of the study sites and the taxonomic composition of adult scleractinian corals at each site. Numbers in parentheses are the total coral cover (%) at each site. The white arrows indicate the direction of prevailing trade winds at each location. The main genera are *Acropora* (white), *Pocillopora* (light grey), and *Porites* corals (dark grey), and other genera are pooled together (dashed).

5.3. Results

5.3.1. *Abundance and composition of juvenile corals*

A total of 643 juvenile corals were recorded across both study locations (296 at Moorea; 347 at Trunk reef), corresponding with a mean density of 7.14 ± 0.42 (Mean \pm SE) juveniles per m². The overall density of juvenile corals was not significantly different between locations (Moorea: 6.57 ± 0.52 ind.m⁻²; Trunk Reef: 7.71 ± 0.64 ind.m⁻²; $F_{1,4} = 0.395$, $p = 0.564$), but did differ among sites within reefs ($F_{4,84} = 7.304$, $p < 0.001$). Most notably, the density of juvenile corals at the most exposed site in Moorea, Haapiti (3.80 ± 0.48 ind.m⁻²), was much lower when compared to sites on the northern coast, Vaipahu (8.46 ± 0.71 ind.m⁻²) and Tiahura (7.47 ± 0.98 ind.m⁻²). On Trunk reef, the density of juvenile corals was highest at the “West” site (9.20 ± 1.64 ind.m⁻²) compared to the “South” site (7.53 ± 0.58 ind.m⁻²) and “East” site (6.40 ± 0.76 ind.m⁻²).

Juvenile coral assemblages at both Moorea and Trunk Reef were dominated by the genera *Acropora*, *Pocillopora* and *Porites*. Collectively, these three genera accounted for 77.7 % (230/296) of all juvenile corals recorded on the reef crest at Moorea, and 91.6 % (318/347) of juvenile corals at Trunk Reef. Other, less abundant genera recorded at Moorea were *Acanthastrea* (0.3 %), *Montipora* (11.9 %), *Montastrea* (6.4 %), and *Leptastrea* (3.7 %), and at Trunk Reef were *Cyphastrea* (0.9 %), *Echinopora* (0.3 %), *Favia* (0.9 %), *Favites* (1.5 %), *Hydnophora* (0.3 %), *Montipora* (1.2 %), *Montastrea* (0.9 %), *Leptastrea* (0.6 %), *Pectinia* (0.3 %), *Stylocoen* (0.6 %) and *Stylophora* (0.4 %). The relative abundance of the three main genera and the remaining genera pooled together differed significantly among locations (MANOVA, $F_{4,81} = 55.55$, $p < 0.001$) and among sites nested within

locations (MANOVA, $F_{16, 336} = 3.125$, $p < 0.001$). Juvenile coral assemblages on Trunk reef were dominated by *Acropora* (39.2 %) and *Porites* (40.9 %), whereas *Pocillopora* was the predominant genus at all sites in Moorea (53.4 %, **Figure 5.2**). Variation among sites was most pronounced in Moorea, with *Acropora* and *Porites* being more abundant at Vaipahu and Tiahura than at Haapiti (**Figure 5.2**). Conversely, *Pocillopora* was more abundant at Haapiti (71.2 %) than at Vaipahu (39.8 %) and Tiahura (59.8 %; **Figure 5.2**). Densities of ‘other’ coral genera (in this case, mostly *Montipora* and *Montastrea*) were also much higher at Vaipahu (2.6 ± 0.2 SE juveniles per m^2) compared to all other sites in Moorea and at Trunk Reef.

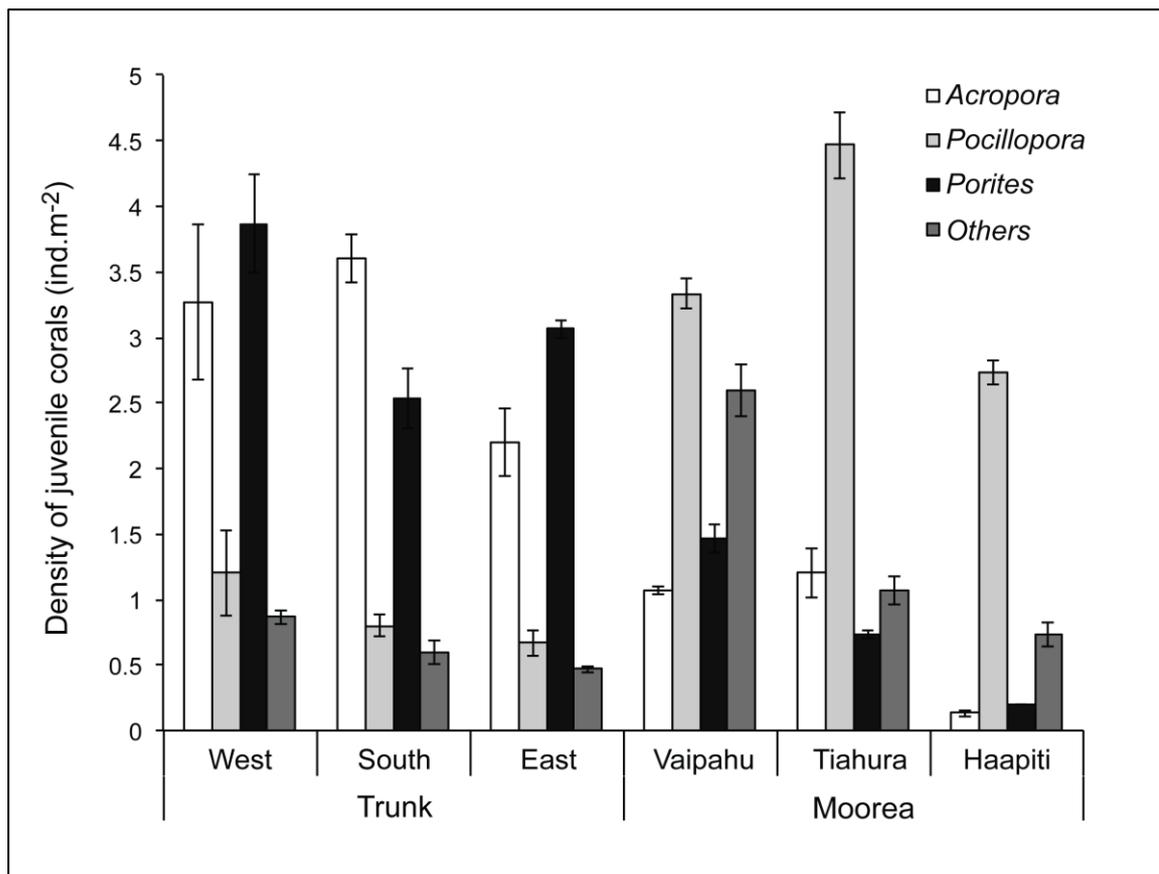


Figure 5.2 Variation in density of juvenile scleractinian corals among three reef crest sites within Trunk reef (GBR) and Moorea (French Polynesia). Mean are based on 15 replicates $1 m^2$ quadrats at each site. Error bars represents + SE

5.3.2. *Juvenile coral mortality*

A total of 175 (out of 643) juvenile corals were dead or could not be found after 6-8 months at Moorea and Trunk Reef, representing an average monthly mortality of 4.41 (± 0.51 SE) %. This corresponds to an annual average mortality rate of 52.92 (± 6.15 SE) %. Overall, monthly mortality rates of juvenile corals did not differ between the two locations or between the three main genera, however, monthly mortality differed among sites within location (**Figure 5.3; Table 5.1 a**). Within each location, mortality rates were higher at the sites directly exposed to the prevailing wind and waves. Mortality at Haapiti (7.40 % month⁻¹) in Moorea was 2-fold higher than at Vaipahu (3.80 % month⁻¹) and almost 4-fold higher than at Tiahura (2.0 % month⁻¹). On Trunk Reef mortality of juvenile corals on the relatively sheltered “West” site (3.40 %) was approximately 1.5-fold lower than at the more exposed “South” (4.85 %) and “East” sites (5.30 %, **Figure 5.3**). Lastly, there was limited evidence of density-dependent mortality (**Figure 5.4**). For *Porites*, monthly mortality rates for juvenile positively correlated with initial densities recorded at Trunk reef (**Table 5.2; Figure 5.4 h**). For all taxa and locations, there was no relationship between initial density of juvenile corals and local mortality rates, within quadrats (**Table 5.2; Figure 5.4 a-g**).

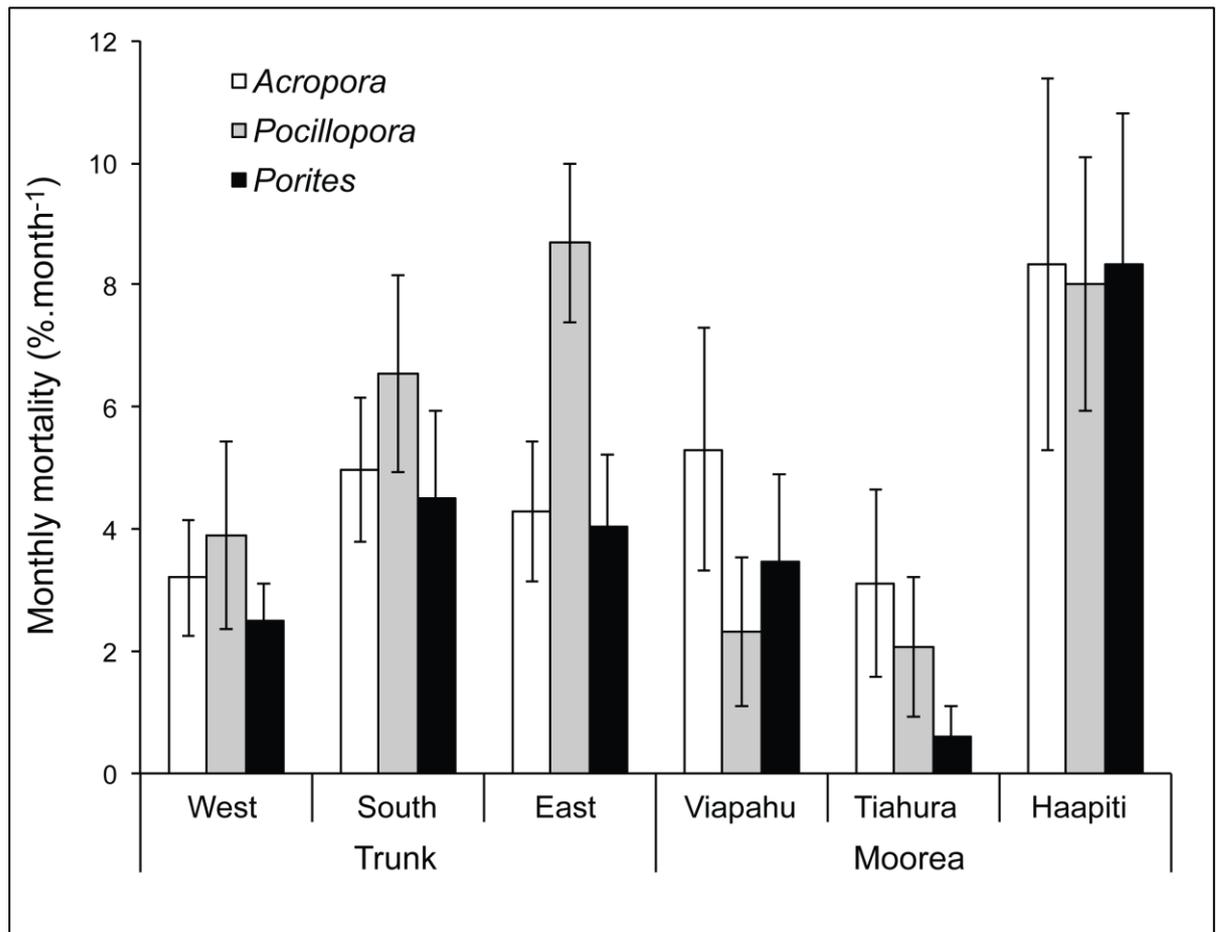


Figure 5.3 Variation in monthly mortality of juvenile scleractinian corals among three reef crest sites within Trunk reef (GBR) and Moorea (French Polynesia). Mortality rates (%.month⁻¹) for the three dominant genera are shown. Mean are based on 15 replicates 1m² quadrats at each site. Error bars represents + SE

Table 5.1 Results of three factor ANOVA's comparing (a) mortality and (b) growth of juvenile scleractinian corals (<50 mm) among genera, locations (GBR and Moorea) and three sites within each location. Mortality rates were arcsin transformed, and monthly growth were log-transformed to meet the parametric assumption. Significant results ($p < 0.05$) are shown in bold.

Source	SS	df	MS	F	Sig.
(a) Mortality					
Genus	0.034	2	0.017	1.559	0.236
Location	0.051	1	0.051	0.89	0.394
Site (Location)	0.245	4	0.061	6.531	0.006
Genus x Location	0.026	2	0.013	1.194	0.325
Genus x Site (Location)	0.067	8	0.008	0.354	0.943
(b) Growth					
Genus	0.407	2	0.204	5.319	0.005
Location	0.264	1	0.264	3.774	0.077
Site (Location)	0.282	4	0.07	3.769	0.006
Genus x Location	0.04	2	0.02	0.524	0.592
Genus x Site (Location)	0.032	8	0.004	0.058	0.999

Table 5.2 Relationship between monthly mortality of juvenile corals and initial juvenile densities (census 1) at Moorea and Trunk Reef. Pearson’s correlation coefficients are given for correlations for all coral taxa collectively (i.e., total juvenile monthly mortality vs. total juvenile density), and the three most abundant genera independently (e.g., *Acropora* monthly mortality vs. juvenile *Acropora* density). Correlations are based on monthly mortality rates and mean initial juvenile densities per quadrat (n = 45). Note that the number of quadrats varies, as juvenile corals were not always observed in each quadrat. Significant results are shown in bold.

Moorea	r	n	p
Total juvenile coral	-0.085	44	0.584
<i>Acropora</i>	-0.001	23	0.995
<i>Pocillopora</i>	0.175	43	0.704
<i>Porites</i>	-0.207	24	0.414
Trunk reef	r		p
Total juvenile coral	-0.026	45	0.868
<i>Acropora</i>	-0.156	41	0.329
<i>Pocillopora</i>	-0.117	20	0.622
<i>Porites</i>	0.541	45	0.000

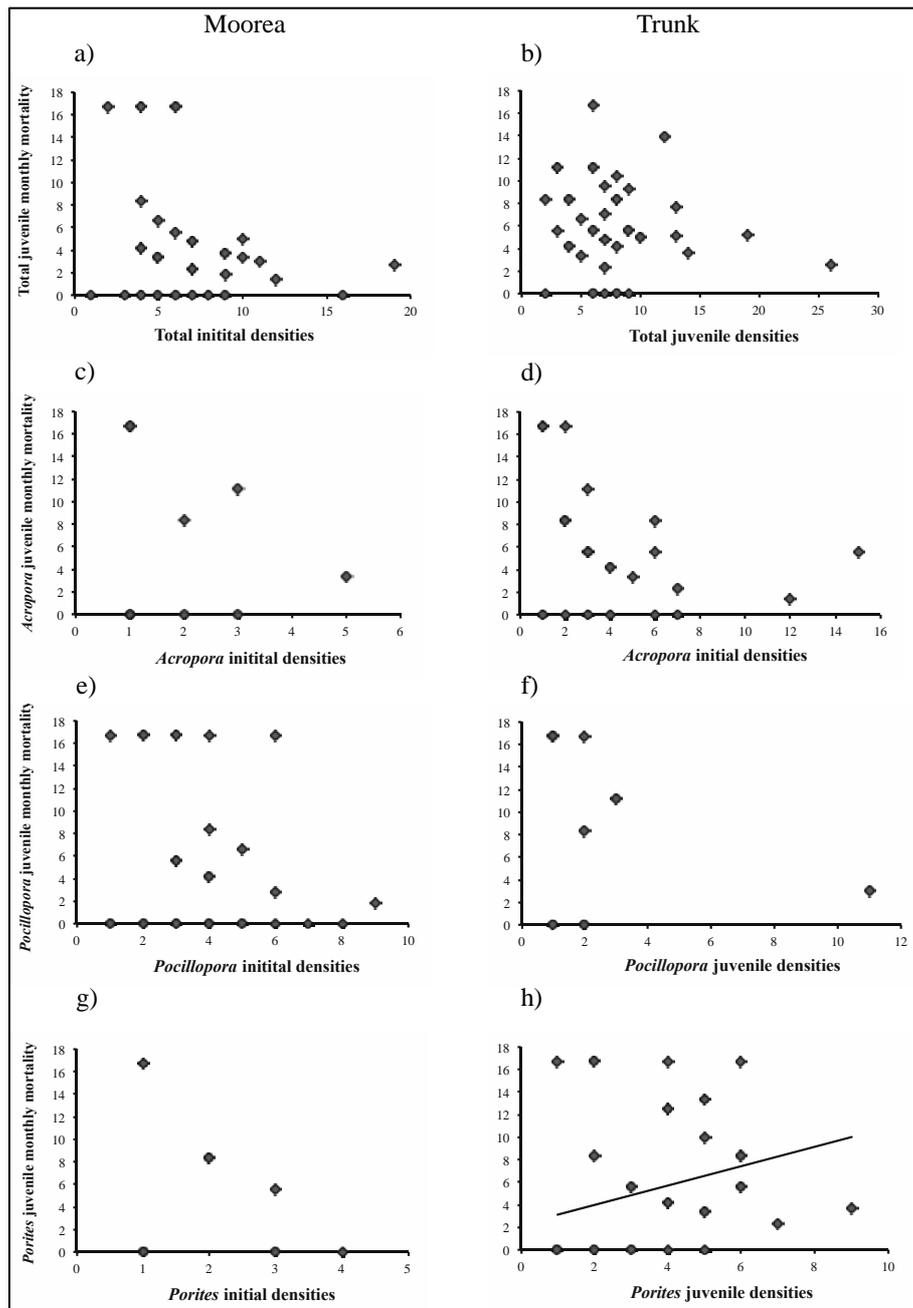


Figure 5.4 Relationship between monthly mortality rates of juvenile coral and mean initial juvenile densities on the reef crest of Trunk Reef (GBR) and Moorea (French Polynesia). (a-b) total juvenile monthly mortality versus total initial juvenile densities, (c-d) monthly mortality of juvenile *Acropora* versus initial *Acropora* juvenile densities, (e-f) monthly mortality of juvenile *Pocillopora* versus *Pocillopora* juvenile densities, (g-h) monthly mortality of juvenile *Porites* versus *Porites* juvenile densities. Analyses are based on monthly mortality rates and mean juvenile densities per transect (initially $n = 45$ for each location). Note that the number of quadrats varies, as

juvenile corals were not always observed in each quadrat. The line represents a significant relationship.

5.3.3. *Juvenile coral growth*

For the 468 (out of 643) juvenile corals that were still alive after 6-8 months, absolute growth rates (specifically, change in maximum diameter) ranged from -4.2 up to $5.0 \text{ mm.month}^{-1}$. Only 23 (out of 468) juveniles exhibited net negative growth, reflective of some partial mortality, and a further five individuals (mostly *Porites*) exhibited no change in diameter over the course of the study. Realized growth did not differ from potential growth at Moorea ($1.57 \pm 0.07 \text{ SE}$ vs $1.65 \pm 0.06 \text{ SE mm.month}^{-1}$; $F_{1,469} = 0.564$, $p = 0.453$) or at Trunk reef ($1.55 \pm 0.08 \text{ SE}$ vs $1.75 \pm 0.07 \text{ SE mm.month}^{-1}$; $F_{1,440} = 3.492$, $p = 0.062$). Realized growth rates did not vary between locations, but did vary significantly among genera and among sites within location (**Figure 5.5; Table 5.1 b**). Post-hoc tests revealed that linear extension of juvenile *Acropora* ($1.98 \pm 0.11 \text{ SE mm.month}^{-1}$) was higher than that of *Pocillopora* ($1.69 \pm 0.08 \text{ SE mm.month}^{-1}$), which in turn, was higher than that of *Porites* ($1.23 \pm 0.09 \text{ SE mm.month}^{-1}$). Within Moorea, realised growth rates were highest at Haapiti, the exposed site ($2.08 \pm 0.17 \text{ mm.month}^{-1}$), compared to and at Tiahura ($1.70 \pm 0.09 \text{ mm.month}^{-1}$) and Vaipahu ($1.31 \pm 0.10 \text{ mm.month}^{-1}$). On Trunk reef, realised growth rates were marginally higher at the southernmost (i.e., “South”) site ($1.72 \pm 0.12 \text{ SE mm.month}^{-1}$) compared to the “East” and the “West” sites (1.50 ± 0.16 and $1.45 \pm 0.12 \text{ mm.month}^{-1}$, respectively).

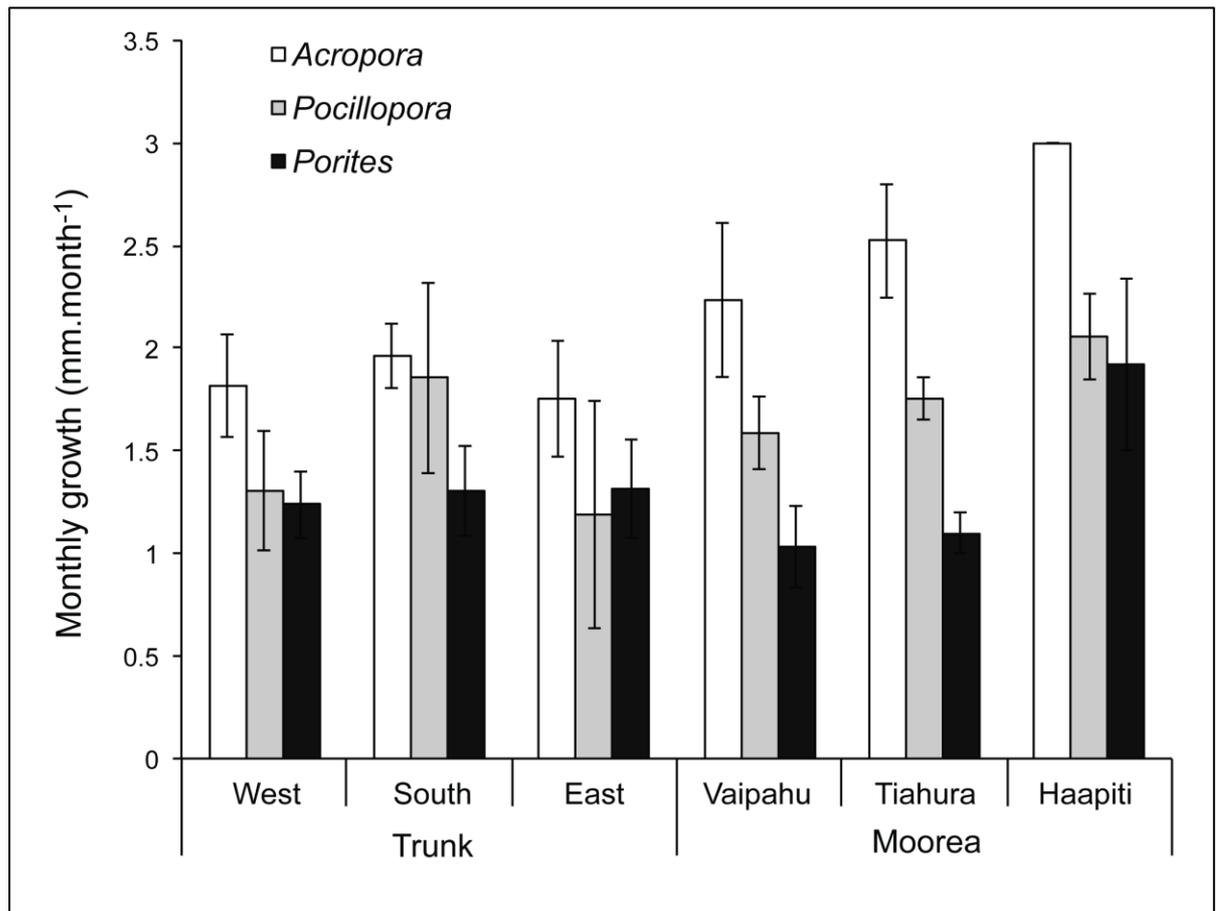


Figure 5.5 Variation in monthly growth of juvenile scleractinian corals among three reef crest sites within Trunk reef (GBR) and Moorea (French Polynesia). Growth is expressed as the linear increase in maximum diameter (mm.month⁻¹). Mean are based on 15 replicates 1m² quadrats at each site. Error bars represents + SE.

5.3.4. *Juvenile coral size structure*

The size structure of *Acropora* juvenile corals differed among locations ($\chi^2 = 23.4$, $df = 4$, $p < 0.001$, **Figure 5.6 a**), with higher proportion of smaller juveniles (10-19 mm) at Moorea (16/36 individuals) compared to Trunk Reef (23/136 individuals). Conversely, there was higher proportion of larger juveniles (30-39 mm) at Trunk reef (39/136 individuals) than at Moorea (4/36 individuals, **Figure 5.6 a**).

Porites juvenile corals size structure also varied among locations ($\chi^2 = 13.9$, $df = 4$, $p < 0.01$, **Figure 5.6 c**), with also higher proportion of smaller juvenile (10-19 mm) at

Moorea (14/36 individuals) compare to Trunk (32/142 individuals, **Figure 5.6 c**), and higher proportion of 30-39 mm juveniles at Trunk (44/142 individuals) compare to Moorea (7/36 individuals). There was no variation in the size structure of Pocillopora juveniles ($\chi^2 = 3.6$, $df = 4$, $p = 0.46$, **Figure 5.6 b**). Monthly mortality rates of *Acropora* corals differed among the five size-classes (Table 5.3) and a Fishers LSD post-hoc test revealed that mortality rates in the size-class 10-19 mm was significantly higher than the ones from the two larger size-classes 30-39 and 40-50 mm (**Figure 5.6 d**). However, monthly growth rates of juvenile *Acropora* did not differ among the five size-classes (Table 5.3; Figure 5.6 g). Furthermore, monthly mortality rates and monthly growth rates of *Pocillopora* and *Porites* juveniles did not vary significantly among size-classes or location (Table 5.3 & **Table 5.4**; **Figure 5.6 e, h** & **Figure 5.6 f, i**, respectively).

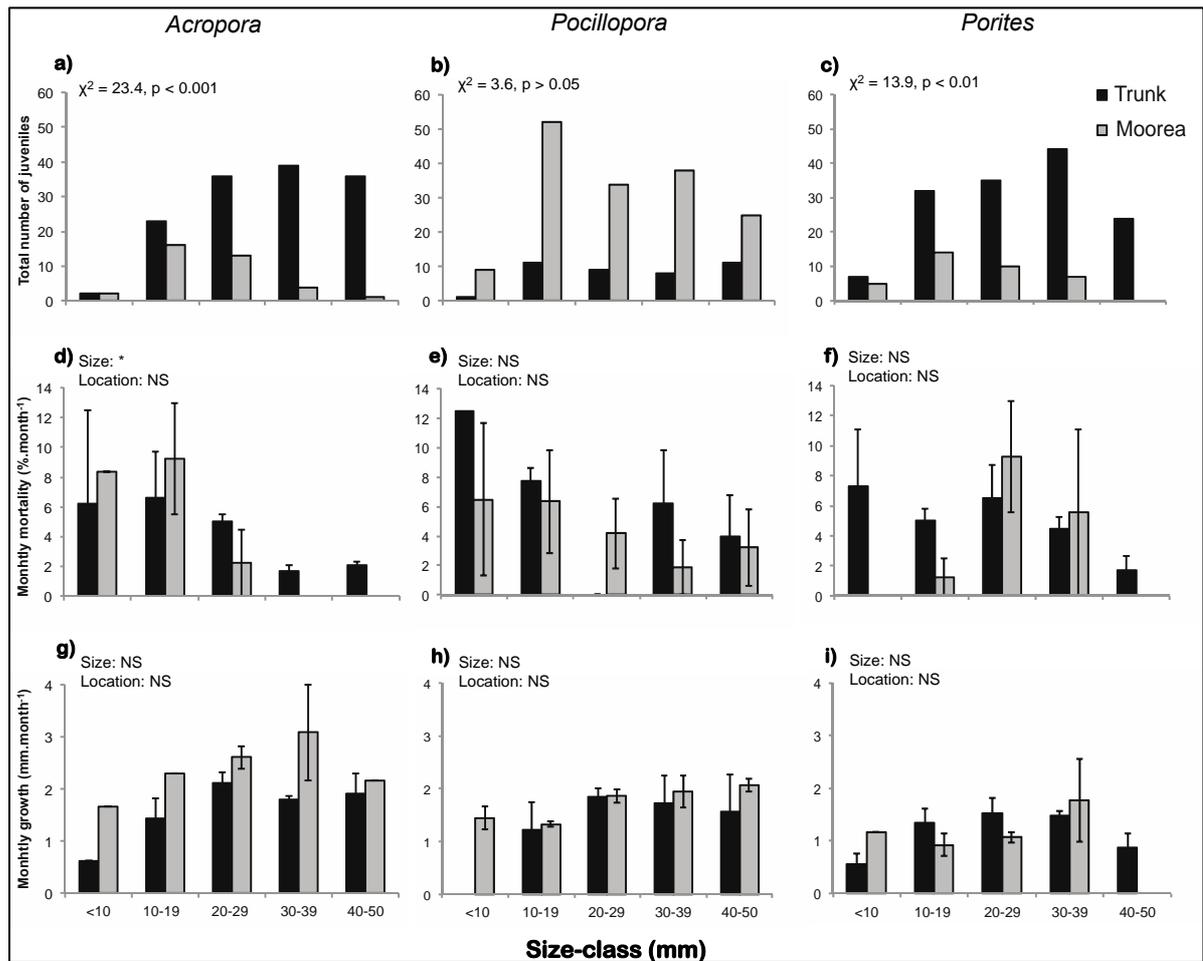


Figure 5.6 Comparisons of (a-c) size-structure, (d-f) mortality (%.month⁻¹), and (g-i) growth (mm.month⁻¹) of juvenile corals among five size-classes (<10, 10-19, 20-29, 30-39, 40-50 mm) and between locations: Trunk (347 juveniles, Black column), Moorea (296 juveniles, Grey column), for the three numerically dominant taxa *Acropora*, *Pocillopora* and *Porites*. Significant result (*: $p < 0.05$) is shown for the factor “size-class” and “location”. Error bars represents \pm SE.

Table 5.3 Results of two factor ANOVA's comparing monthly mortality (%.month⁻¹) of juveniles (≤ 50 mm) from each main taxa (a) *Acropora* (b) *Pocillopora* and (c) *Porites* corals among size-class (<10, 10-19, 20-29, 30-39, 40-50 mm) and locations (GBR and Moorea). Significant results ($p < 0.05$) are shown in bold.

Monthly mortality	SS	df	MS	F	Sig.
(a) <i>Acropora</i>					
Size-Class	0.158	4	0.039	3.439	0.037
Location	0.012	1	0.012	1.076	0.317
Size-Class * Location	0.058	4	0.015	1.273	0.327
(b) <i>Pocillopora</i>					
Size-Class	0.136	4	0.034	1.69	0.196
Location	0.009	1	0.009	0.442	0.515
Size-Class * Location	0.085	4	0.021	1.056	0.407
(c) <i>Porites</i>					
Size-Class	0.167	4	0.042	2.153	0.116
Location	7.74E-05	1	7.74E-05	0.004	0.950
Size-Class * Location	0.06	3	0.02	1.032	0.402

Table 5.4 Results of two factor ANOVA's comparing monthly growth (mm.month⁻¹) of juveniles (≤ 50 mm) from each main taxa (a) *Acropora* (b) *Pocillopora* and (c) *Porites* corals among size-class (< 10, 10-19, 20-29, 30-39, 40-50 mm) and locations (GBR and Moorea). Significant results ($p < 0.05$) are shown in bold.

Monthly growth	SS	df	MS	F	Sig.
(a) <i>Acropora</i>					
Size-Class	3.851	4	0.963	0.589	0.671
Location	2.997	1	2.997	1.832	0.179
Size-Class * Location	0.726	4	0.181	0.111	0.978
(b) <i>Pocillopora</i>					
Size-Class	4.096	3	1.365	1.504	0.216
Location	3.155	1	3.155	3.474	0.064
Size-Class * Location	1.932	3	0.644	0.709	0.548
(c) <i>Porites</i>					
Size-Class	0.916	3	0.305	0.288	0.834
Location	0.014	1	0.014	0.013	0.908
Size-Class * Location	1.800	3	0.600	0.567	0.638

5.3.5. *Adult coral cover*

The cover of adult corals varied significantly between locations ($F_{1,4} = 52.8$, $p < 0.001$) and among sites within each location ($F_{4,54} = 7.1$, $p < 0.001$). Overall, the cover of adult corals was almost 3-fold greater on Moorea (31.1 ± 3.8 %) than on Trunk reef (10.8 ± 1.3 %). Within each location coral cover was lowest within the most exposed sites. On Moorea, coral cover was the lowest at Haapiti (15.0 ± 2.9 %) compared to Tiahura (46.2 ± 3.6 %) and Viapahu (32.0 ± 3.6 %, **Figure 5.1**). Similarly, on Trunk reef, adult coral cover was lower at the “East” site (6.2 ± 1.1 %) compared to the “South” and “West” sites (13.9 ± 2.3 % and 12.3 ± 2.6 %, respectively). The taxonomic composition of adult corals differed between locations (MANOVA, $F_{4,51} = 76.22$, $p < 0.001$) with coral assemblages dominated by *Pocillopora* in Moorea (49.3 % relative abundance) and by *Acropora* at Trunk reef (74.3 % relative abundance, **Figure 5.1**). There were also significant variations in the composition among sites within each location (MANOVA, $F_{16,216} = 3.01$, $p < 0.001$). On Moorea *Porites* was relatively more abundant on the most exposed site, Hapiti (24 %) than at Tiahura (16 %) and Viapahu (12 % **Figure 5.1**). On Trunk reef, *Acropora* and *Pocillopora* were relatively less abundant and *Porites* and ‘other’ coral genera were relatively more abundant at the exposed site “East” site than the “South” and “West” sites (**Figure 5.1**). Adult coral cover pooled across all taxa was positively correlated with total juveniles’ densities at transect scale at Moorea (**Figure 5.7 a**) only. However there was no significant relationship when examining each taxon separately (**Figure 5.7 c, d, e, f, g & h**) or for total coral cover against total juvenile densities at Trunk reef (**Figure 5.7 b**).

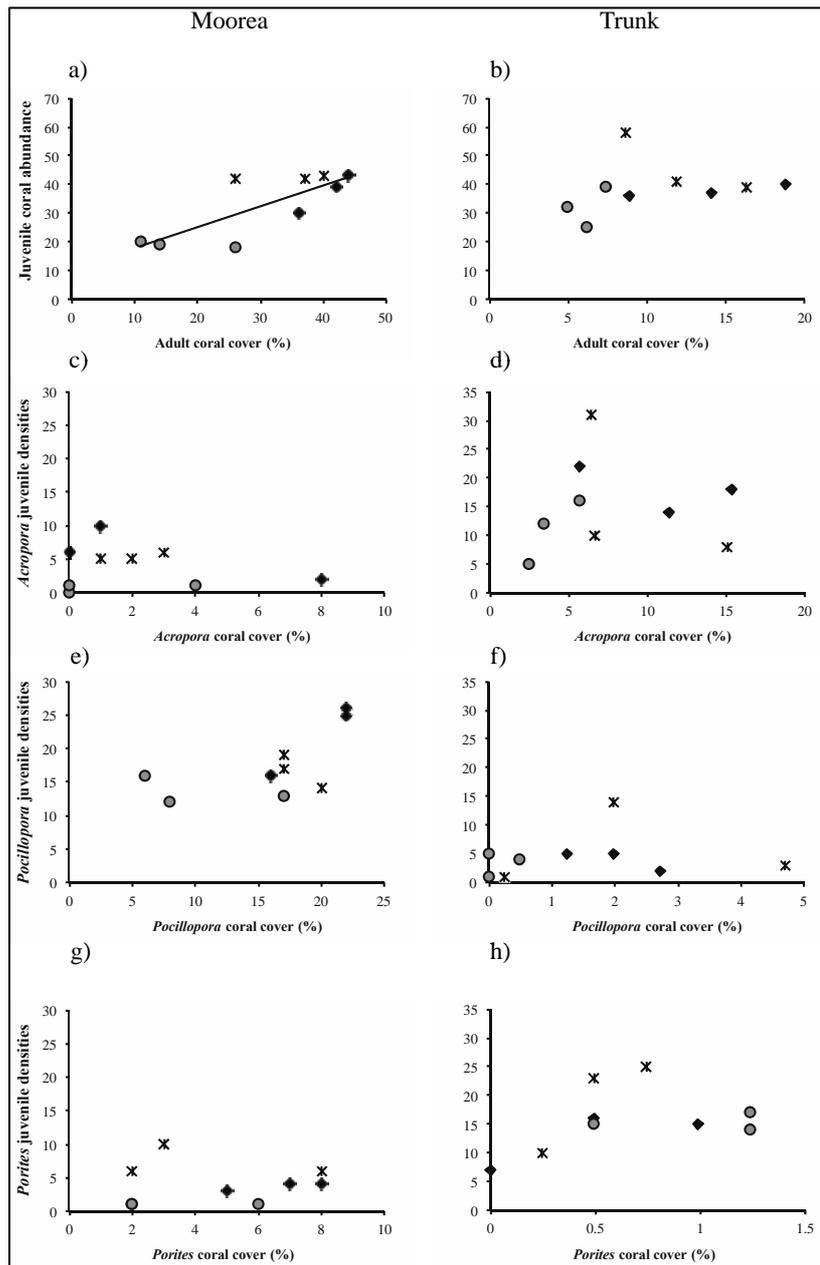


Figure 5.7 Relationship between juvenile coral densities and adult coral cover on the reef crest of Trunk Reef (GBR) and Moorea (French Polynesia). (a-b) total juvenile coral density versus total adult coral cover, (c-d) density of juvenile *Acropora* versus adult *Acropora* cover, (e-f) density of juvenile *Pocillopora* versus adult *Pocillopora* cover, (g-h) density of juvenile *Porites* versus adult *Porites* cover. Analyses are based on the adult coral cover and mean density of juvenile corals per transect ($n = 9$ for each location). The three symbols represents the three sites at each location: “round” represents Haapiti in Moorea and “East” site at Trunk, “diamond” represents Tiahura in Moorea and “South” site at Trunk, and “cross” represents Vaipahu in Moorea and “West” site at Trunk. The line represents a significant relationship.

Table 5.5 Relationship between the density of juvenile corals and the cover of adult corals on Moorea and Trunk Reef. Pearson’s correlation coefficients are given for correlations for all coral taxa collectively (i.e., total coral cover vs. total juvenile density), and the three most abundant genera independently (e.g., *Acropora* cover vs. juvenile *Acropora* density). Correlations are based on the cover of adult corals and the mean density of juvenile corals per transect (n = 9). Significant results are shown in bold.

a) Moorea	r	p
Total juveniles	0.795	0.010
<i>Acropora</i>	-0.139	0.721
<i>Pocillopora</i>	0.567	0.111
<i>Porites</i>	-0.207	0.594
b) Trunk reef	r	p
Total juveniles	0.338	0.374
<i>Acropora</i>	-0.166	0.669
<i>Pocillopora</i>	-0.299	0.434
<i>Porites</i>	0.663	0.052

5.4. Discussion

This study revealed significant differences in the taxonomic structure of juvenile coral (≤ 50 mm) assemblages between Moorea and Trunk Reef, consistent with observed adult coral assemblages at each location. Juvenile and adult coral assemblages are dominated by *Acropora* sp on Trunk reef (Linares et al. 2011; Traçon et al. 2013; this study), and by *Pocillopora* sp on Moorea (Adjeroud et al 2007a; Pratchett et al. 2011; this study). However, we did not find any differences in overall densities, or average rates of growth and mortality of juvenile corals between the two geographic locations. Furthermore, previous estimates of coral settlement suggest that it is much lower on Moorea (~ 40 recruits m^{-2} year $^{-1}$: Adjeroud et al. 2007a) than on central GBR mid-shelf reefs, including Trunk Reef (~ 200 -700 recruits m^{-2} year $^{-1}$:

Hughes et al. 1999). If these estimates are broadly representative of settlement rates at these locations, the similar densities of juvenile corals in the present study suggests that rates of early post-settlement mortality (i.e., before becoming visible to the naked eye at approximately 10 mm, Penin et al. 2010) were lower in Moorea and may compensate, at least to some extent, for the reduced larval supply at this location compared to Trunk reef. Alternatively, the similar densities of juvenile corals at the two locations may reflect a marked decline in larval supply and/or settlement rates in the central GBR compared to rates measured by Hughes et al. (1999, 2000) over a decade ago. However, determining the relative importance of larval supply and early post-settlement mortality in shaping juvenile coral populations at these two locations is difficult in the absence of recent and comparable estimates of coral settlement.

Despite systematic and focused sampling for juvenile corals, the minimum size detected on natural substratum was 5 mm, which is substantially larger than the mean size at settlement for scleractinian corals (see Babcock et al. 2003). Therefore, we almost certainly under-estimated local densities of newly settled corals in the size-class < 10 mm, and have not fully captured rates of mortality that occur within the smallest size-class. Corals are known to suffer high mortality within the first weeks to months after settlement (Babcock 1985; Wilson and Harrison 2005), and much of this mortality has been attributed to incidental predation by scraping and excavating parrotfishes (Rotjan and Lewis 2008; Penin et al. 2010, 2011; Trapon et al. 2013). Interestingly, published estimates of abundance and biomass of parrotfishes, especially the larger excavating species, are considerably greater on the GBR than in Moorea (Bellwood et al. 2003; Hoey and Bellwood 2008; Adam et al. 2011; Bellwood et al. 2012). However, the lack of variation in mortality of juvenile corals between Moorea and Trunk Reef suggests that such differences in parrotfish

assemblages may be having limited effects on the mortality rates of later stage (i.e., ≥ 10 mm) juvenile corals. There was, however, significant variation in mortality rates among size-classes of juvenile corals with mortality decreasing with increasing size, but only for juvenile *Acropora* corals. Mortality also tended to be higher within the smaller size-classes for juvenile *Pocillopora*, however, high variation in mortality estimates within size-classes precluded the detection of any differences between size-classes. This variation in mortality among juvenile coral taxa is difficult to explain, but may be related to the higher growth rates of *Acropora* compared to *Pocillopora* and *Porites* corals, enabling them a faster escape in size. (Bak and Meesters 1998) suggested once corals reach a certain size (~ 5 mm) they may be afforded a size refuge (Babcock and Mundy 1996) , especially from incidental grazing by parrotfishes (Penin et al. 2010; Doropoulos et al. 2012)

Although there were no detectable differences in the density, mortality and growth of juvenile corals between Moorea and Trunk reef, there was significant variation among sites within each reef. In general, the density of juvenile corals was lower and growth and mortality higher at exposed sites compared to the sheltered sites in both locations. For example, the exposed site on Moorea, Haapiti, had fewer juvenile corals (3.80 ind.m^{-2}) than Tiahura and Vaipahu (7.47 and 8.46 ind.m^{-2} respectively). Similar variation in abundance of juvenile corals has been reported at these sites previously (Adjeroud et al. 2007a; Penin et al. 2007), and may be related to the differential mortality among sites, as juvenile corals at Haapiti experienced 2- to 4-fold higher mortality than Tiahura and Vaipahu. Similarly, on Trunk reef, the density of juvenile corals was lower and mortality rates 1.5-fold higher on the exposed sites (“South” and “East”) than the sheltered site (“West”). The mechanistic basis for these patterns is difficult to determine but may be related to variation in

environmental conditions. For example, turbulent flows reduce the settlement of temperate macroalgae by reducing the delivery of larvae to the substratum and increasing rates of detachment (Taylor et al. 2010), and these may have similar effect on the delivery and settlement of coral larvae. Increased wave energy at exposed sites may also lead to sediment scouring of the colonies by increasing sediment re-suspension in the water column (Bak and Engel 1979; Babcock and Smith 2002).

Realized growth rates (i.e., including colonies that both increased and decreased in diameter) did not differ between Trunk reef and Moorea (mean of 1.55 mm month⁻¹ and 1.57 mm month⁻¹ respectively), and were comparable to previous estimates of both Indo-Pacific and Caribbean corals (see Babcock et al. 2003). Moreover, realized and potential growth rates were not significantly different, with only 23 out of 468 juvenile colonies experiencing partial mortality, as evidenced by a decrease in size. As damage inflicted to juvenile corals is often as large as the size of the colony, they are more likely to suffer total, rather than partial, mortality (Hughes and Jackson 1980; Meesters et al. 1997). Interestingly growth rates of juvenile corals were greatest on exposed sites within each location, coinciding with sites of highest mortality. Favourable conditions for the growth of juvenile corals may not necessarily be favourable for the survival of juvenile corals (Glassom and Chadwick 2006). For example, the higher water-flow and productivity of exposed sites may enhance coral growth (Sebens et al. 2003), but may also contribute to increased mortality through physical damage, abrasion, or associated fish communities (discussed previously).

Together with the variation in density, growth and mortality, the taxonomic composition of juvenile corals also differed among locations and sites. Overall, Pocillopora dominated the juvenile coral assemblage on Moorea (53.4 %), while *Acropora* and *Porites* were the dominant genera on Trunk Reef (39.2 and 40.9 %, respectively).

respectively. The low abundances of both adult and juvenile *Acropora* in Moorea is largely attributable to the high frequency and severity of acute disturbances. In shallow exposed reef environments, disturbances such as storms (Birkeland et al. 1981; Maida et al. 1994), bleaching related to increases in sea surface temperature, sedimentation (Gilmour 1999), and terrestrial runoff (Dubinsky and Stambler 1996) are frequent and can greatly influence taxonomic variation in mortality rates and further augment taxonomic differences in the juvenile and ultimately in the adult assemblages over region/oceanic scales. For example, *Acropora* sp are very susceptible to breakage from cyclones, climate-induced coral bleaching, as well as predation by the corallivorous sea star *Acanthaster planci* (Pratchett 2010). At Moorea, recurrent disturbances over the last three have led to the gradual replacement of *Acropora* with other genera in Moorea (Berumen and Pratchett 2006; Pratchett et al. 2011; Trapon et al. 2011). Moreover, the low abundances of large juvenile (i.e., 30-50 mm diameter) *Acropora* and *Porites* may also reflect the recent disturbance history of this location, with mortality of adult corals leading to reduced larval supply and consequently fewer juvenile corals (Gilmour et al. 2013). At Trunk Reef however, high levels of coral loss in 2001-02, have been followed by an extended period without any major disturbances enabling rapid recovery of corals, especially *Acropora* (Pratchett et al. 2009).

Superimposed upon marked regional variation in the composition of juvenile coral assemblages, there were significant differences in the relative abundance of taxa, especially on Moorea. On Moorea, the abundances of each taxon of juvenile coral was lowest at the exposed site, Haapiti, with the reductions being most pronounced in *Acropora* and *Porites*. Consequently, the relative abundance of juvenile *Pocillopora* was much higher at Haapiti, than at Tiahura and Vaipahu.

Pocillopora may be able to colonize the frequently disturbed environment of Haapiti faster than *Acropora* and *Porites*, which may need longer residence time and lower flushing rates for planula to settle on the substratum (Sammarco and Andrews 1988). In contrast, there was little variation in the relative abundance of *Pocillopora* among sites on Trunk Reef and may be related to geographical differences in their major reproductive mode; The dominant species of *Pocillopora* in Moorea (*P. meandrina* and *P. verrucosa*) are broadcast spawners (Penin et al. 2007), whereas the dominant species on Trunk Reef (*P. damicornis*) is a brooder.

This study revealed marked within-reef variation in the overall density, mortality and growth rates of juvenile corals, whereas differences at the larger geographic scale were mostly related to differences in the composition of juvenile and adult coral assemblages. Interestingly, there were no significant differences in the density of juvenile corals between Moorea and Trunk Reef, despite adult coral cover being 3-fold higher on Moorea compared to Trunk Reef. This suggests that contemporary adult coral assemblages are structured more by differential adult mortality, larval settlement, or very early post-settlement mortality (before colonies can be observed in situ), rather than juvenile growth and mortality. Both Trunk Reef and Moorea have been subject to coral bleaching and outbreaks of *Acanthaster planci*, which have caused high levels of coral mortality since 2002 (Pratchett et al. 2009; Traçon et al. 2011). There may have also been changes in settlement rates since initial surveys suggested they were much lower at Moorea than in the central GBR (Adjeroud et al. 2007a), but there have not been any recent studies of coral settlement rates at these locations. Further studies are clearly necessary to elucidate the relative importance of larval supply, settlement, and early post-settlement mortality in shaping juvenile and ultimately adult coral assemblages in different locations. Importantly, the

vulnerability and resilience of coral assemblages in different geographical regions will require an understanding and integration of key demographic processes across multiple life stages.

Chapter 6. General Discussion

6.1. Importance of Pre- Versus Post-settlement Processes

There is increasing awareness that early post-settlement processes are important in structuring populations and communities of marine organisms, including fishes (Williams and Sale 1981; Doherty 1983; Wellington and Victor 1985; Hixon and Carr 1997; Doherty and Williams 1988), corals (Bak and Engel 1979; Rylaarsdam 1983; Fisk and Harriot 1990; Baird and Hughes 1997, 1999; Penin et al. 2010), and other sessile invertebrates (Keough and Downes 1982; Hughes 1990, Stoner 1990; Caley et al. 1996; Gosselin and Qian 1997). As for pre-settlement processes (e.g., larval supply), post-settlement processes are highly variable in space and time, and are often taxon-specific. It is clear, for example, that significant variation in post-settlement growth, mortality and in some cases movement (e.g., fishes), regularly obscure any patterns established at settlement (Jones et al. 1991). This is not say that pre-settlement processes are not important in structuring populations and communities of marine organisms, but equivalent attention needs to be given to post-settlement processes in trying to understand the patterns of adult abundance (e.g., Penin et al. 2010).

For scleractinian corals, the importance of pre-settlement processes is incontrovertible (e.g., Glassom and Chadwick 2006). The number of corals settling in a given area are subject to supply and delivery of planktonic larvae, which are in turn, dependent upon patterns of adult fecundity (Hughes et al. 2000), larval dispersal (Botsford et al. 1994; Navarrete et al. 2005; Botsford et al. 2009), larval energetics (Richmond 1987; Fabricius and Metzner 2004), and many biophysical factors that

influence larval survival, such as predation (Keough and Downes 1982; Westneat and Resing 1988), water quality (Richmond et al. 2007), and temperatures (Edmunds et al. 2001). Even after the larvae arrive on the reef, the ability to settle is further conditional upon the availability of suitable settlement habitats (Babcock and Mundy 1996; Edmunds et al. 2004; Vermeij 2005), which are generally free of macroalgae (Kuffner et al 2006, Hughes et al. 2007). The extent to which settlement is limited by larval supply and/ or the availability of suitable settlement substrata varies spatially and temporally. Importantly, increasing effects of global climate change and other more direct anthropogenic disturbances are expected to reduce size, abundance and reproductive output of adult corals (Richmond 1996), thereby reducing larval supply. Moreover, increasing shifts to macroalgal dominated reef habitats (Hughes et al. 2011) are likely to inhibit the settlement of any larvae that are available. However, there are currently many locations where settlement rates remain high (e.g., Sheppard et al. 2002) where early post-settlement processes may have a significant influence on the distribution, abundance and composition of adult corals.

Throughout the past two decades, there has been an increasing awareness that post-settlement processes (growth and mortality rates) were playing a major role in the structure of coral population. This was initially suggested based on striking dissimilarities between large-scale patterns of coral settlement versus adult abundance (e.g., Hughes et al. 1999). On the Great Barrier Reef, adult coral cover is highly variable at small scales (e.g., within reef), but relatively constant at larger scales (e.g., among latitudinal sectors; Hughes et al 1999; Chapter 2), which is also true for the abundance of juvenile corals (Chapter 2). Rates of settlement meanwhile, have been found to vary mostly at largest scales, and are much more constant within or among adjacent reefs (e.g., Hughes et al. 1999). This suggests that early post-settlement

processes play a fundamental role in establishing patterns of abundance for sessile corals. Studies that have explicitly quantified post-settlement growth and mortality have also revealed marked spatial and/ or taxonomic differences in the demographic rates of juvenile corals (e.g., Bak and Engel 1979; Rylaarsdam 1983; Smith 1992; Glassom and Chadwick; Penin et al. 2010; Chapter 4 and Chapter 5). Penin et al. (2010) found a three-fold variation among sites (separated by 2-10 km) at Moorea, French Polynesia, in rates of post-settlement mortality for scleractinian corals, and attributed this mostly to variation in abundance of fishes that prey upon small corals. Until now, no one has assessed variation in rates of early post-settlement growth and mortality beyond the extent of a single reef.

The aim of Chapter 4 was to directly measure the growth and mortality of juvenile corals at a hierarchy of spatial scales, including large-scale comparisons among sectors separated by >500 km, to account for apparent disparities in patterns of settlement versus adult abundance of corals. At the largest spatial scale (among sectors) it was expected there would be a strong and consistent latitudinal gradients in both growth (e.g., Harriott 1999) and mortality of juvenile corals (*sensu* Hughes et al. 1999). However, there was no consistent trend with latitude apparent across all major taxa (*Acropora*, *Pocillopora* and *Porites*). It was expected, based on disproportionate rates of settlement (Hughes et al. 1999), that post-settlement mortality would be highest in the northern sector, but mortality rates of *Porites* were actually higher in central and southern sectors. For *Pocillopora*, mortality rates of juvenile corals were relatively constant among sectors, while mortality rates for juvenile *Acropora* were highest in central sector. Furthermore, growth rates of juvenile corals varied little (except for *Pocillopora*) among the three latitudinal sectors. Within the latitudinal extent of the GBR there did not appear to be any effect of temperature on abundance

or demographic rates of juvenile corals, but the abundance of juvenile corals is much lower on high latitude reefs, such as Lord Howe Island (Hoey et al. 2011). Hoey et al. (2011) attributed low abundance of juvenile corals at Lord Howe Island to low levels of settlement, but is also likely that low growth rates and corresponding increases in post-settlement mortality, may be responsible for the observed pattern.

Chapter 5 explored these same processes at even larger (oceanic) scales, comparing between Trunk Reef (on the GBR) and reefs surrounding the island of Moorea (in French Polynesia). There was significant regional variation in the taxonomic composition of coral assemblages within both adult and juvenile assemblages, with *Pocillopora* being the predominant coral genera in Moorea and *Acropora* at Trunk Reef. However, there were no differences in the density, growth, or mortality rates of juvenile corals between Moorea and Trunk reef. The lack of geographic variation in the density, growth and mortality rates of juvenile corals was interesting given the cover of adult coral was 3-fold higher on Moorea (31.1 %) than at Trunk Reef (10.8 %), suggesting that adult coral assemblages are structured more by differential adult mortality, larval settlement, or very early post-settlement mortality (before colonies can be observed *in situ*), rather than contrasting rates of juvenile growth or mortality. What is emerging therefore is that growth and mortality of juvenile corals (10 -50 mm diameter) are highly variable at small scales, probably due to stochasticity in biotic interactions (Chapter 4), and also vary among taxa, but cannot account for large-scale differences in the abundance of corals. It is possible that patterns of abundance for sessile corals are established by large-scale variation in growth and mortality of newly settled corals (i.e., at the size and stage before they can be readily surveyed), but this is going to be very difficult to test.

6.2. Causes of Early Post-settlement Mortality

Potential sources of mortality for small and newly settled corals are numerous (Penin et al. 2010), but high rates of mortality recorded for newly settled corals are generally attributed to overgrowth by macroalgae or smothering by sediment (Box and Mumby 2007; Hughes et al. 2007), competition with con-specifics (Baird and Hughes 2000; Vermeij and Sandin 2008), or predation, which includes incidental grazing by scraping parrotfishes (Sammarco 1980; Penin et al. 2010). In Chapter 2, I found that the abundance of juvenile corals on the GBR was negatively correlated with parrotfish biomass, suggesting that these parrotfishes may contribute to high levels of post-settlement mortality, especially in the period immediately after settlement. Chapter 3, however, showed that mortality rates of newly-settled *A. cytherea* were > 40 % even on tiles protected from grazing, and may have increased greatly over time with increased growth of both turf- and macro-algae. Scraping and excavating parrotfish are a key functional group on coral reefs, clearing space for coral settlement and reducing algal overgrowth (Hughes et al. 2007), but they also cause mortality of recently settled corals through their feeding actions. However, the beneficial effects of regulating macroalgae are likely to significantly outweigh slight increases in juvenile mortality due to incidental grazing (Chapter 3).

For each of these major sources of juvenile coral mortality (smothering, competition and predation) there is a strong size advantage (Bak and Meester 1998, Edmunds and Gates 2004, Penin et al 2010), whereby rates of mortality will decline rapidly with increasing size (Chapter 4). Above a certain size (approximately 10-20 mm) it appears that susceptibility to predation declines markedly (Doropoulos et al. 2012). Indeed, there was no correlation between juvenile mortality and parrotfish biomass on the GBR (Chapter 4). Therefore, size matters, and since mortality rates are

strongly size-dependent, there will be advantages in growing faster during juvenile stage, to reach critical size-refuges sooner and thereby reduce the probability of mortality. Accordingly, Chapter 4 showed that there was much higher survival of *Acropora* corals, which had the highest growth rates, compared to *Porites* corals, which grew the slowest. An important corollary of these findings is that where growth rates of corals are naturally constrained (e.g., on very high latitude reefs), mortality rates of juvenile corals may be even higher, thereby limiting adult abundance and/ or replenishment of coral populations (e.g., Hoey et al. 2011). Moreover, any future declines in the growth rates of corals (e.g., due to emerging effects of ocean acidification, Doropoulos et al. 2012), will significantly undermine the resilience of coral populations and communities.

6.3. Conclusion and Future Research

Studies on the population and community ecology of scleractinian corals are complicated by the complex life histories of these long-lived, and relatively slow growing organisms (e.g., Hughes and Jackson 1980). Corals are however, fundamentally important to the structure and function of coral reef ecosystems (e.g., Pratchett et al. 2008) and increased research and improved understanding is needed across all the distinct life-stages of corals, especially given widespread declines in the abundance of corals (e.g., Gardner et al. 2003; Bellwood et al. 2004). This thesis has provided direct evidence of the importance of early post-settlement processes and has for the first time empirically measured demographic rates of juvenile corals over a wide range of different spatial scales, across geographic and latitudinal scales, among reefs, among sites and between adjacent quadrats. Large-scale variation in demographic rates of juvenile corals did not account for apparent discontinuities between settlement rates and abundance of adult corals at these scales, but this

research did show that juvenile growth and mortality are spatially variable and may obscure patterns of abundance established at settlement. This research also provides an important baseline for future research on early post-settlement processes, testing for temporal changes in the structure and dynamics of coral populations and communities.

An important extension of this research is to quantify growth and mortality of newly settled corals, in the period immediately after settlement and before corals can be readily surveyed in the field, and compare these demographic rates over small and large spatial scales. There are obvious logistical constraints on studying newly settled and very small corals, especially on natural substrata (but see Schmidt-Roach et al. 2008), but this remains an important gap in our knowledge of coral life-histories. One solution may be simply compare growth and mortality of corals seeded to artificial settlement plates (e.g., Chapter 3) that are deployed over a wide range of reefs and locations. However, causes of early post-settlement mortality for corals on settlement panels maybe very different from those that cause mortality of corals on natural reef substrata (Hughes et al. 1999). This does not undermine the use of settlement panels (which are essential in studying settlement patterns), but more detailed studies of newly settled corals in their natural habitats will allow for improved understanding of the fate of different corals, relative to when and where they settle, as well as biotic interactions with a wide range of other sessile organisms.

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