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Spatial and temporal variation in fecundity among populations of *Acropora millepora* on the Great Barrier Reef

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ABSTRACT: Sexual reproduction is vital for population persistence, even in organisms that can reproduce asexually, such as corals. Yet, information on spatial and temporal variation in reproductive traits is surprisingly rare. Here, we examined spatial and temporal variation in fecundity, defined as the number of oocytes per polyp, in the staghorn coral *Acropora millepora* over 2 yr among 6 populations separated by over 700 km on inshore reefs on the Great Barrier Reef. Variation in fecundity was greatest at small spatial scales: there were pronounced differences in fecundity within and among colonies at each site but little variation at the site or regional scale. This suggests that fecundity is affected by environmental variables that also vary at small scales, such as light and water flow, rather than variables that vary on a regional scale, such as temperature. Colony fecundity in the first year was a good predictor of colony fecundity in the second year, suggesting that some genotypes are more fecund than others. This research suggests that factors operating at the scale of the individual, such as microhabitat differences in flow or light, or genetic identity, are the main cause of variation in fecundity among coral colonies.

KEY WORDS: Coral reefs · Demography · Life histories · Reproduction

INTRODUCTION

Sexual reproduction is generally considered essential to population persistence, even for organisms such as corals that are capable of non-sexual reproduction (e.g. Richmond & Hunter 1990). However, surprisingly few studies have measured reproductive traits in healthy coral populations. Consequently, there is limited information on natural variation in reproductive traits within and among coral species, without which it is difficult to assess the role of sexual reproduction in regulating coral populations. For example, very little is known about how coral reproductive traits vary in space and time within species because few, if any, studies have quantified reproduction across populations or species at more than one site at more than one time using similar methods. Wallace (1985) followed 6 *Acropora* spp. over 2 yr at one site on the Great Barrier Reef (GBR) and found that annual fecundity estimates differed in only 2 of the species. There are few estimates of fecundity from more than one location for a small number of species (e.g. Wallace 1999), and these data have never been rigorously examined and therefore it is difficult to draw any conclusions about spatial variation in this trait. Only a single study has followed reproductive traits of individual colonies through time, finding that fecundity and sexuality varied between years, possibly in response to available energy reserves in individuals (Loya & Sakai 2008). However, the fungiid species studied by Loya & Sakai (2008) are not typical of scleractinian coral

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because they are gonochoric and solitary rather than hermaphroditic and colonial (Baird et al. 2009).

Despite the lack of empirical studies on natural variation in reproductive traits, the response of these traits to stress, including competition (Tanner 1995), injury (Hall 1997), disease (Burns & Takabayashi 2011) and bleaching (Michalek-Wagner & Willis 2001a, Mendes & Woodley 2002), suggests that these traits are labile. For example, the proportion of colonies breeding was significant lower following bleaching on the GBR in 1998 in 2 *Acropora* spp. (Baird & Marshall 2002) when compared to 2 non-bleaching years. Similarly, gonad size and number were reduced in *Orbicella annularis* following bleaching in the Caribbean (Mendes & Woodley 2002). In addition, the number of oocytes per polyp and the number of gravid polyps were lower in tumorous tissue versus healthy tissue in coral colonies with tumors (Yamashiro et al. 2001, Burns & Takabayashi 2011). These studies provide evidence for plasticity in reproductive traits and therefore suggest that these traits should be affected by prevailing environmental conditions, particularly those that might influence resource acquisition such as light and water flow (Hoogenboom & Connolly 2009).

The aim of this research was to document spatial and temporal variation in fecundity of the coral *Acropora millepora* at 2 sites in each of 3 regions separated by over 700 km on the inshore GBR, and to examine the relationship between colony size and fecundity.

MATERIALS AND METHODS

Study sites, selection of colonies and sampling frequency

This study was conducted on the fringing reefs at 2 sites in each of 3 inshore high island groups separated by 5° of latitude along the GBR: Orpheus Island (18.62° S, 146.48° E) and Pelorus Island (18.55° S, 146.48° E) in the Palm Island group; Hook Island (20.17° S, 148.90° E) and Mid-Molle Island (20.23° S, 148.82° E) in the Whitsunday Island group; and Miall Island (23.15° S, 150.90° E) and Halfway Island (23.20° S, 150.97° E) in the Keppel Island group (Fig. 1). All sites were less than 20 km from the mainland and located on the leeward side of islands at depths of between 1 and 3 m (Fig. 1). *Acropora millepora* is a corymbose species that is common in shallow water on most inshore reefs and in protected areas on mid- and outer-shelf reefs along most of the length of the GBR (Veron & Wallace 1984, Wallace 1999). At each site, 30 *A. millepora* colonies were tagged in April or May 2009 and then revisited on another 4 trips over the next 2 yr, with the final trip occurring in April 2011. Only colonies likely to be reproductively mature (maximum diameter >16 cm; Hall & Hughes 1996) and with no tissue damage were tagged. The track that was swam on the first sampling trip was logged using a GPS towed on a body board, and the position of each colony was recorded on this track.

Quantifying polyp fecundity

Samples for reproductive analysis were collected in the week before the full moon in October 2009 and 2010 to ensure the samples were collected before spawning, which typically occurs in either November

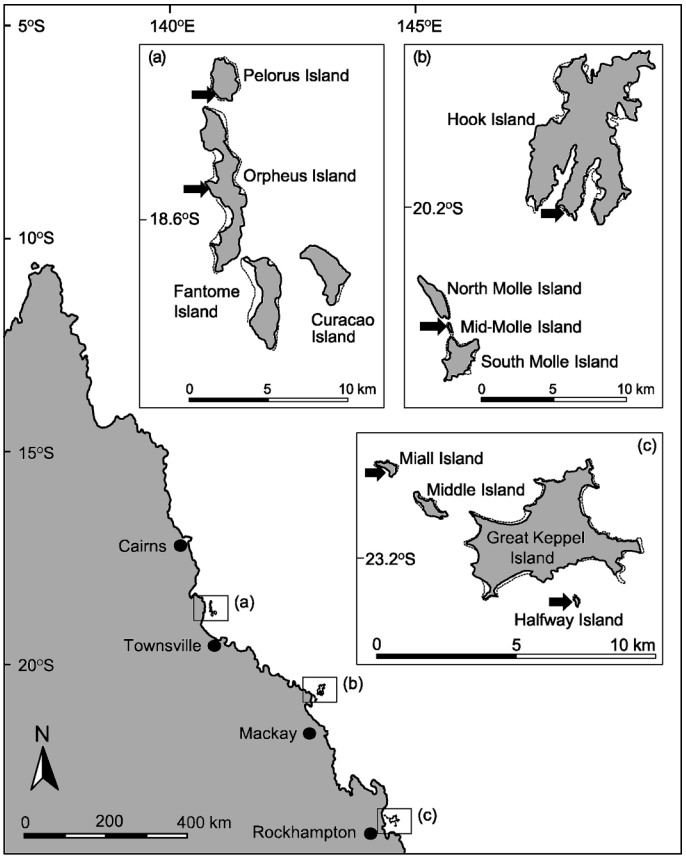

Fig. 1. Sampling regions on the Great Barrier Reef: (a) Palm Islands (18° S), (b) Whitsunday Islands (20° S) and (c) Keppel Islands (23° S). Arrows in the insets indicate the position of sampling sites within regions

or December at these sites (Willis et al. 1985, authors' unpubl. data). One branch, at least 5 cm long, was collected from the centre of each colony to avoid the sterile zone on the periphery of colonies (Wallace 1985). Branches were placed in individual zip-lock bags labelled by colony number while underwater, then transferred to labelled containers containing 10% seawater formalin immediately upon surfacing. In the lab, branches were decalcified in 10% formic acid and then placed in 10% seawater formalin until dissection.

Branches were dissected under a stereo-dissecting microscope. First, each branch was cut in half along the sagittal plane to allow visual inspection of the distribution of polyps containing oocytes. Typically, there is an area commencing at the tip where no polyps contain oocytes, known as the sterile zone (Wallace 1985). Any polyps without oocytes below the sterile zone were visibly smaller than the others, presumably because they had recently been budded, and were therefore deemed immature (Sakai 1998) and excluded from sampling. A total of 10 mature polyps were selected haphazardly from below the sterile zone and dissected out of the branch. Next, each polyp was dissected, and the number of oocytes recorded. Finally, 30 oocytes from each branch were selected haphazardly from those that had been dissected out of the polyps, and the maximum diameter was measured using a stage micrometer under a compound microscope at 40× magnification.

Estimating colony size

On each sampling occasion, all tagged colonies were photographed using a Canon Powershot G11 from approximately 1.5 m above and perpendicular to the surface of the colony to quantify horizontal planar surface area. A pre-calibrated 10 × 10 cm white Perspex scale bar was placed on the surface of each colony and included in each photograph. Photographs were corrected for barrel distortion and then horizontal planar surface area was quantified for each coral colony using the software package ImageJ (http://rsbweb.nih.gov/ij/).

Statistical analysis

Contingency tables were used to test for differences in the number of colonies that were and were not breeding at each site and in each year. A 3-way ANOVA was used to test for differences in the mean number of oocytes per polyp. Factors were (1) region, (2) site nested within region and (3) colony nested within site and region. All factors were treated as random. Variance components were also calculated using the same model. The analysis was done separately for each year to allow partitioning of variance among the 3 scales of spatial variation. Only colonies with oocytes were used in the analysis. The fit of the models was explored graphically by comparing the predicted values to the residuals, and there was no evidence of bias in the models.

The relationship between colony size and fecundity was tested using linear regression, as was the relationship between fecundity in 2009 versus fecundity in 2010. Colony size was $\log_{10}$ transformed, and separate regressions were performed for each site in each year. All ANOVAs were performed with the statistical software SPSS v.20 (IBM), and all regressions in R (R Core Team 2015).

RESULTS

Table 1. Number (n) and percentage of coral colonies with oocytes in 6 populations of *Acropora millepora* on the Great Barrier Reef in October 2009 and 2010

Region	Site	2009		2010	
		n	Percent with oocytes	n	Percent with oocytes
Palm Islands	Orpheus	26	88	11	82
	Pelorus	26	96	13	100
Whitsunday Islands	Hook	29	97	6	100
	Mid-Molle	28	93	24	96
Keppel Islands	Miall	28	89	27	96
	Halfway	27	96	28	96
	Total	164	93	109	95

A high percentage of tagged colonies were breeding at all sites in both years, ranging from 82% at Orpheus Island in 2009 to 100% at Pelorus and Hook Islands in 2010 (Table 1). The proportion of colonies breeding did not vary among sites in either year (2009: $\chi^2 = 2.91$, df = 5, p = 0.71; 2010: $\chi^2 = 5.68$, df = 5, p = 0.34), or between years ($\chi^2 = 0.21$, df = 1, p = 0.6403).

Mean fecundity differed between sites and among colonies in both years, and there were no regional differences in

Table 2. Summary of ANOVA testing for spatial differences in the mean number of oocytes per polyp in populations of *Acropora millepora* in 2009 and 2010. Variance components (Var (%)) are used to apportion variance to different levels

Source of variation	df	MS	*F*-value	p-value	Var (%)
2009					
Region	2	20.811	0.385	0.729	0.0
Site (Region)	3	5066	3.512	0.018	5.4
Colony (Site × Region)	147	15.395	13.141	<0.001	51.2
Error	1377	1.172			43.4
2010					
Region	2	70.019	1.026	0.454	5.9
Site (Region)	3	7190	841	0.003	7.2
Colony (Site × Region)	98	15.325	17.379	<0.001	53.9
Error	936	0.882			33.0

either year (Table 2, Fig. 2). The majority of variation in fecundity occurred among colonies: 51.2% of the total variation occurred at this scale in 2009 and 53.9% in 2010 (Table 2). Only 5.4 and 7.2% of the variation in 2009 and 2010 respectively occurred at the site level (Table 2).

Mean fecundity did not vary with respect to colony size, except at Pelorus Island in 2009, where fecundity increased with colony size (Fig. 3, Table 3).

Mean colony fecundity in 2009 was a good predictor of mean fecundity in 2010 at 3 of the 6 sites (Fig. 4, Table 4).

Table 3. Linear regression model results for *Acropora millepora* colony size versus fecundity at each site

Region	Site	2009				2010			
		Slope	r^2	Intercept	p-value	Slope	r^2	Intercept	p-value
Palm Islands	Orpheus	0.91	0.02	3.45	0.50	0	0.18	−6.33	0.26
	Pelorus	2.24	0.24	−0.88	0.01	−0.37	0.01	6.55	0.68
Whitsunday Islands	Hook	0.63	0.02	32	0.49	–	–	–	–
	Mid-Molle	−0.34	0.01	7.46	0.65	−1.15	0.05	9.88	0.32
Keppel Islands	Miall	−0.05	0.00	6.12	0.98	−1.27	0.03	9.85	0.42
	Halfway	0.82	0.02	30	0.44	−1.25	0.04	10.65	0.32

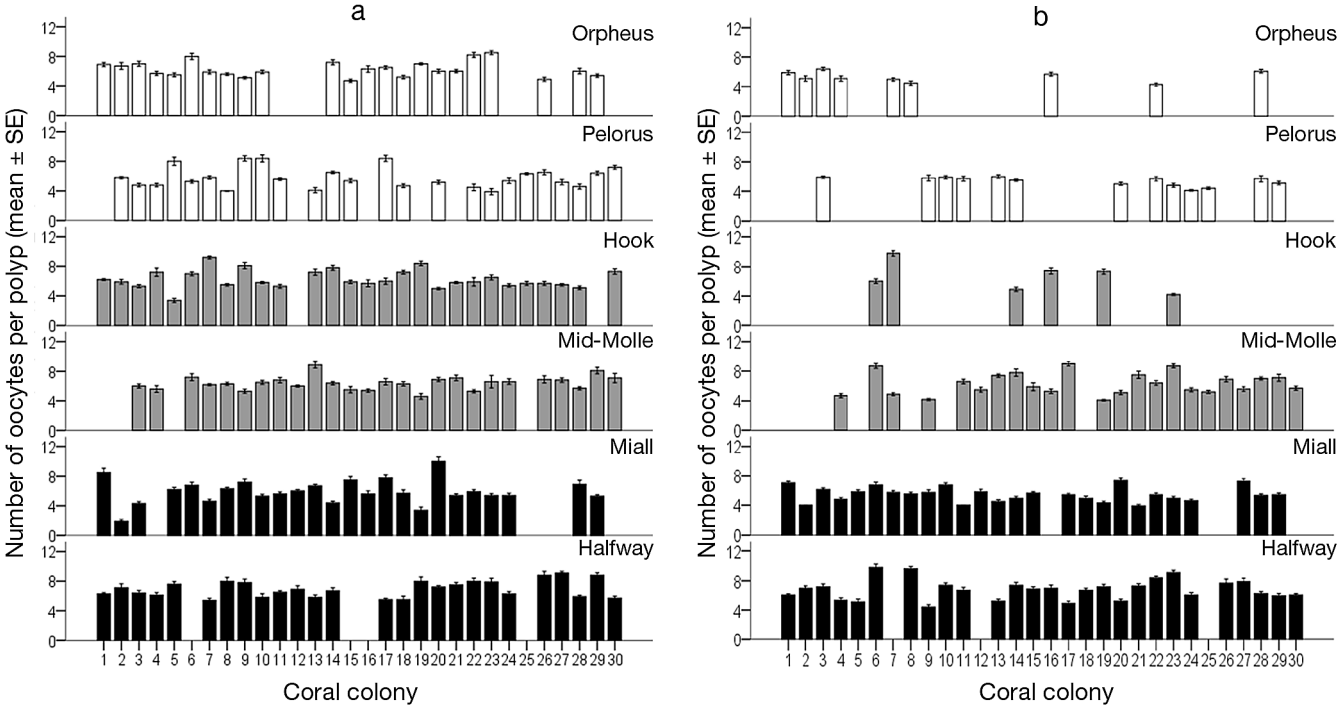

Fig. 2. Fecundity of *Acropora millepora* colonies in (a) 2009 and (b) 2010. White bars: Palm Islands; grey bars: Whitsunday Islands; black bars: Keppel Islands. Areas with no bars represent dead or missing colonies

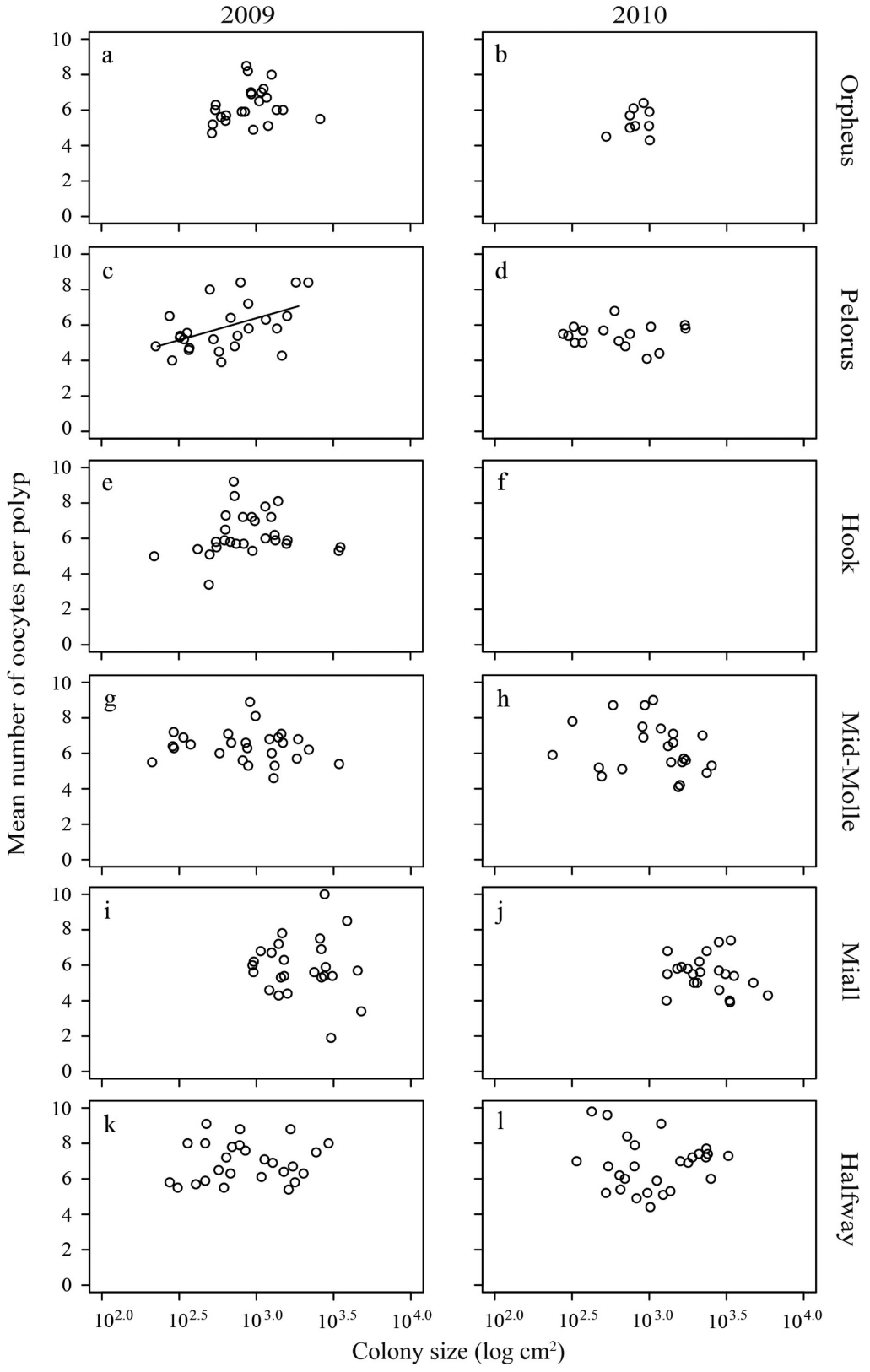

Fig. 3. Relationship between *Acropora millepora* colony size in April and mean number of oocytes per polyp in October for each year at each site. Note no size data exists for Hook Island in 2010 because the colonies could not be located during the April survey. A regression line was drawn when the relationship was significant

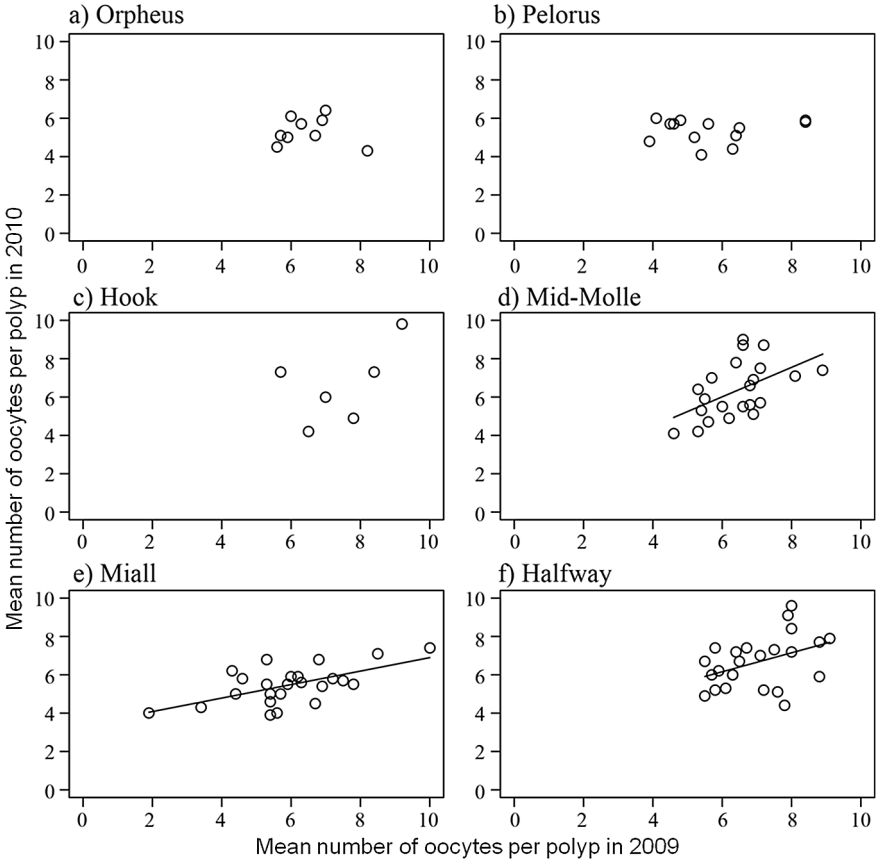

Fig. 4. Mean number of *Acropora millepora* ooctyes per polyp in 2009 versus 2010 at each site. A regression line was drawn when the relationship was significant

Table 4. Linear regression model for the relationship between *Acropora millepora* fecundity in 2009 versus 2010

Region	Site	Slope	r^2	Intercept	p-value
Palm Islands	Orpheus	–0.07	0.01	5.77	0.846
	Pelorus	0.05	0.01	5.08	0.710
Whitsunday Islands	Hook	0.85	0.29	0.28	0.267
	Mid-Molle	0.77	0.28	1.40	0.012
Keppel Islands	Miall	0.35	0.37	3.38	0.002
	Halfway	0.49	0.17	3.19	0.045

DISCUSSION

Despite the large spatial scale of this study, which compared colonies separated by over 700 km on inshore reefs of the GBR, the fecundity of *Acropora millepora* varied mostly at small spatial scales. Fecundity did not vary among regions in either of the 2 yr, and the difference among sites was small and inconsistent — with the possible exception of Halfway Island, which had the highest mean fecundity in both years. Fecundity was, however, often very different among colonies within the same site. Furthermore, the best predictor of colony fecundity was fecundity in the previous year. All of these results suggest that factors operating at the colony scale (such as microhabitat differences in flow or light, or genetic differences among colonies) are the main cause of variation in fecundity among colonies of *A. millepora* on inshore reefs on the GBR.

These results suggest that there are individualistic differences among colonies, caused by intrinsic (e.g. genotype) or extrinsic (microhabitat) factors, which lead to marked differences in fecundity between neighbouring colonies. The importance of microhabitat on colony physiological performance is supported by models suggesting that energy acquisition is strongly influenced by the light and flow regime (Hoogenboom & Connolly 2009, Hoogenboom et al. 2011), and that small differences in colony position, such as distance from the reef crest, can affect colony performance and population abundance (Madin et al. 2012).

The high level of variability in fecundity among individuals suggests that this is not an ideal variable with which to test or monitor the effects of stress because a large number of individuals or replicates would need to be sampled to detect an effect. Alternatively, differences in the biochemical composition of oocytes (Michalek-Wagner & Willis 2001b) that might affect vital rates, such as acquisition of competence and larval mortality, might be more informative.

Colony size had no consistent effect on fecundity in *A. millepora* despite theoretical predictions. Kim & Lasker (1997) predicted that average fecundity per polyp of larger colonies should be reduced due to self-shading effects in the centre of colonies. Hoogenboom & Connolly (2009) predicted that larger colonies would have a greater net energy balance over a wider range of light and flow regimes and inferred that this should lead to an increase in colony fecundity with colony size. Neither of these predictions was supported by the relationships between

size and fecundity in *A. millepora*. In contrast, the differences among colonies within sites and the fact that fecundity in the first year was a good predictor of fecundity in the second year suggest that genetic or microhabitat differences are the major driver of variation in fecundity. It is, in fact, rare to find a relationship between colony size and reproductive variables in corals. For example, of 6 species examined by Hall & Hughes (1996) on the reef crest at Lizard Island, a positive relationship between colony size and the size of oocytes was found in only 2 species. Colony size had no effect on oocyte or testes number per polyp, or testes volume per polyp, for any species (Hall & Hughes 1996).

In conclusion, in this study we found that variation in reproductive variables was greatest at small scales and likely to be driven by genetics or microhabitat differences in light and flow based on colony position. Similarly, theoretical predictions with respect to the relationship between colony size and reproductive variables appear to be overwhelmed by genetic or microhabitat differences among colonies.

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