Recruitment hotspots: consistent spatial patterns in the relative abundance of coral recruits at One Tree Island, Australia

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Communicated by Saki Harii (Ecology Editor)

Abstract On coral reefs, sites that receive consistently high levels of recruitment relevant to other sites (“recruitment hotspots”) may be crucial to the persistence of populations. However, few studies of coral recruitment have the necessary replication in space and time required to detect recruitment hotspots. The aim of this study was to detect recruitment hotspots at One Tree Reef (southern Great Barrier Reef) and to explore associations between hotspots, hydrodynamics, adult abundance and reef benthos. Recruitment hotspots were detected on the reef slope and in the lagoon. Almost all hotspots were located on the leeward side of the reef, however, there was little congruence among hotspots for different families of coral recruits. Recruitment hotspots in some taxa in some habitats were correlated with water flow or adult abundance. A clear recruitment hotspot for two families (Pocilloporidae and Poritidae) in the lagoon had medium levels of water flow (~4 cm s⁻¹), but there was no relationship with water flow on the slope. In experimental aquaria, Acropora nasuta settlement was six to 10 times greater under low (2.1 cm s⁻¹) compared to medium water flow (4.6 cm s⁻¹). Abundance of pocilloporid and poritid, but not acroporid, recruits at each site was often correlated with adult cover indicating either aggregative settlement or limited dispersal. Recruitment hotspots are likely to be both sources and sinks for some taxa, and therefore identifying and protecting hotspots should be a high priority in marine reserve design.

Keywords Coral reefs, Dispersal, Hydrodynamics, Recruitment, Settlement

Introduction

Recruitment is a critical point in an organism’s life history, an important aspect of population biology, and variation in recruitment can be a major determinant of assemblage structure for reef corals (Done 1982, Connell et al. 1997, Hughes et al. 1999). Coral populations are also generally dependent on sexual recruits for recovery after catastrophic disturbances (Sammarco 1985). Since recruitment variation plays such a vital role in population and community dynamics, the causes and outcomes of recruitment variation at various scales have been evaluated in many studies (see reviews by Hughes et al. 2002, Glassom et al. 2004). In open marine populations, sites that receive consistently high levels of recruitment are known as “recruitment hotspots” (sensu Booth et al. 2000). These may play a major role in determining the abundance and persistence of sub-populations through
subsequent growth and asexual reproduction, and serve as a source for populations further downstream. Despite numerous studies on coral recruitment, few have been designed to detect recruitment hotspots.

Spatial variation in coral recruitment at the scale of individual reefs (hundreds of meters to kilometers) has been well documented (Hughes et al. 2002). The emphasis has, however, been on either very small (millimeters to meters) (Sammarco and Carleton 1981, Sakai and Yamazato 1984, Kuffner and Paul 2004) or very large (thousands of kilometers) scales (Smith 1992, Hughes et al. 1999, 2000). Variation at the scale of individual reefs, such as platform reefs or atolls is, however, often significant (Babcock 1988, Dunstan and Johnson 1998, Soong et al. 2003) and contributes to a substantial portion of overall variation (Hughes et al. 1999, Glassom et al. 2004). Understanding variations in recruitment at the reef scale are particularly important, because this is often the scale at which coral reefs are managed and marine reserve boundaries are designated (e.g. Sobel and Dahlgren 2004).

In addition, identifying recruitment hotspots is vital for the optimal placement of reserve boundaries, particularly if multiple uses are allowed within a single reef. Recruitment hotspots are a logical choice for protection because of their potential for rapid recovery from disturbance; however, they may also be suitable for extraction or tourism due to their natural resilience.

Spatial variation in recruitment will be affected by microhabitat and substratum (Baird and Hughes 2000, Baird et al. 2003) both of which vary greatly around reefs. The location of adult conspecifics may be particularly important because larvae may choose to settle in areas where adults are abundant i.e. aggregative settlement (Mundy and Babcock 2000, Carlon 2002, Vermeij 2005). A positive relationship between recruit density and adult abundance might also be expected in brooding species, which release motile planulae that often settle near their parent colonies (Harrii and Kayanne 2003, Soong et al. 2003, Vermeij 2005) and in broadcast spawning species with eggs that develop rapidly (Nakamura and Sakai 2010). Recruitment variation and the location of hotspots may also be influenced by hydrodynamics, which controls the supply of propagules to particular areas of reefs (Hamner and Hauri 1981, Black and Moran 1991, Carleton et al. 2001) and these patterns are likely to recur annually (Oliver et al. 1992, Sammarco 1994) causing recruitment hotspots. Instantaneous current speeds also affect settlement in many species of invertebrate larvae (Butman et al. 1988, Pawlik and Butman 1993, Watson and Barnes 2004) including corals (Harrii and Kayanne 2002).

The primary objective of this study was to identify recruitment hotspots for three coral families (Acroporidae, Pocilloporidae and Poritidae) at One Tree Reef and to test whether or not recruitment hotspots were associated with hydrodynamic patterns, adult abundance and/or habitat. In addition, we use a manipulative experiment to test whether larval settlement is influenced by water flow and site-specific settlement substrata.

Materials and methods

Spatial and temporal patterns in coral recruitment

Coral recruitment was monitored at 20 sites chosen to represent the range of hydrographic conditions and habitat occurring in the lagoon and on the reef slope surrounding One Tree Island (23°30′S, 153°67′E) on the southern Great Barrier Reef (GBR) (Fig. 1). Twelve sites were located in the lagoon and 8 on the reef slope. Sites were separated by 100 m to five km.

To monitor coral recruitment, 10 replicate (11×11×1 cm) unglazed terracotta tiles were attached individually to the reef (following Mundy 2000) on five occasions over the three-year study period (Table 1). Tiles were spaced randomly along the reef substratum between one and three metres apart. In the first deployment (January 2002 to March 2002) only 8 sites in the lagoon were used (sites 2, 6, 9 and 10 excluded), giving a total of 16 sites. Two of the five tile deployments (November 2002 to January 2003 and November 2003 to January 2004) coincided with the mass spawning period of corals on the southern GBR (Baird et al. 2002). The other three deployments were from January to March in the years 2002, 2003 and 2004 to monitor recruitment from corals that may spawn later in the year (Wolstenholme 2004; Baird et al. 2009a, b), or brooding species that release larvae over a longer period (Kojis and Quinn 1981, Tanner 1996). Recruitment monitored over the five month period from November to
March should capture the majority of annual recruitment (e.g. Wallace 1985). Tiles were attached at depths of 1–2 m in the lagoon and 5–7 m on the slope, 2 weeks before the full moon preceding mass-spawning events in November. Tiles were collected 8 weeks later and the next set of tiles was deployed. An 8-week interval was chosen as this is commonly accepted as a reasonable time period to minimise losses due to post-settlement mortality, but to allow sufficient development to facilitate taxonomic resolution (Babcock et al. 2003). Once removed, tiles were bleached in a dilute chlorine solution to remove all organic material and coral recruit skeletons on all surfaces (top, bottom and sides) were counted using a stereodissector microscope and identified to family level (Babcock et al. 2003).

All analyses were carried out separately for the slope and lagoon habitats and for each coral family. Two-way ANOVA was used to test for differences in mean coral recruitment among the five deployment periods (Time) and among sites (Site). Both Time and Site were random factors. Data were square root transformed to reduce heterogeneity of variances. Concordance analysis (Kendall’s Coefficient of Concordance with Correction for Tied Values) where \( \chi^2_{crit} = 19.7 \) and \( v = 11 \) for the lagoon, and

Table 1 Recruitment tile deployment and retrieval dates and sites

<table>
<thead>
<tr>
<th>Deployment</th>
<th>Retrieval</th>
<th>Sites</th>
</tr>
</thead>
<tbody>
<tr>
<td>Jan 2002</td>
<td>Mar 2002</td>
<td>1, 3, 4, 5, 7, 8, 11, 12</td>
</tr>
<tr>
<td>Nov 2002</td>
<td>Jan 2003</td>
<td>1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12</td>
</tr>
<tr>
<td>Jan 2003</td>
<td>Mar 2003</td>
<td>1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12</td>
</tr>
<tr>
<td>Nov 2002</td>
<td>Jan 2003</td>
<td>1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12</td>
</tr>
<tr>
<td>Jan 2004</td>
<td>Mar 2004</td>
<td>1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12</td>
</tr>
</tbody>
</table>

Fig. 1 Locations of study sites around One Tree Reef. Lagoon sites are labelled 1 to 12 and slope sites are labelled 13 to 20. Islands are shown in dotted outlines.
\[ \chi^2_{\text{crit}} = 14.1 \] and \( v = 7 \) for the slope, was used to determine whether relative ranks of sites according to mean recruitment were consistent among the five deployment periods (Zar 1999). Significance was taken at \( \alpha < 0.05 \) unless otherwise stated. Recruitment hotspots were determined as sites that were ranked first or second in order of greatest mean recruitment per tile on three or more occasions.

**Estimating the relative abundance of adult cover**

Two types of surveys of benthic assemblages were carried out to assess the percentage composition of each coral family: (1) Larger scale transects sampled 150 points over 160 to 200 m and represented the broad-scale habitat defining each site. Three 50 m tapes were laid parallel to the reef crest. In the lagoon, transects were 1 to 2 m deep and on the reef slope they were 5 to 6 m. The habitat type under 50 points per transect, sampled at 1 m intervals, was recorded *in situ*; (2) Smaller scale quadrats surveyed 1 m² patches directly around each tile, sampled up to 490 individual points per site over 25 to 50 m during each year of survey and represented microhabitat that could influence settlement choice. Quadrats were placed next to each tile with one corner over the tile and the remainder of the quadrat laid haphazardly, therefore, the number of quadrats varied according to the number of tiles remaining at the end of the deployment (7–10). The type of habitat was recorded at 49 points *in situ* per quadrat. For both scales, habitat was classified into 10 categories: acroporids, pocilloporids, poritids, other massive corals, other foliose and encrusting corals, dead corals, coral rock, rubble, sand, algae and other invertebrate, although here we concentrate on the three categories that could be matched with coral recruits; acroporids, pocilloporids and poritids. Both types of surveys were repeated annually for three years in the lagoon (2002, 2003, 2004) and two years on the slope (transects 2002, 2003 and quadrats 2003 and 2004). Patterns of percentage cover remained relatively consistent therefore the average cover for each coral family over three years was used in analyses.

Linear or curvilinear correlations between the mean number of recruits and mean percent cover of adults at each site were examined to detect relationships for each family at both transect and quadrat scales. Pearson’s Correlation Coefficient was used to determine the amount of variation described by each relationship and Least Squares Regression and Curve Estimation (SPSS 14.0) were used to determine significance. Residuals were examined to confirm that data was normally distributed. Use of regression assumes that recruitment is dependent on adult habitats rather than adults being dependent on recruitment.

**Estimating water flow**

The dissolution of clod cards was used to compare mass water flow among sites in the One Tree lagoon (Fulton and Bellwood 2005). This method was chosen because the integrated effect of circulation over a critical period is thought to be more important to recruitment than currents at any one time (Sammarco and Andrews 1989). Four spherical plaster balls were deployed at 12 sites in the lagoon for one week following the full moon in November 2003 to give a Water Movement Index (WMI) expressed in units of percentage weight plaster lost per day per metre of tidal movement (\( \% \text{ d}^{-1} \text{ m}^{-1} \)) and relative dissolution among sites was compared.

For the reef slope, clod cards were deployed only at the four leeward sites (sites 13 to 16) in January 2004 due to poor weather conditions. To obtain relative water flow estimates in terms of plaster dissolution for all 8 reef slope sites, data was extrapolated from a linear relationship between the dissolution results from the four leeward sites and the mean current speed at each site calculated from the output of a hydrodynamic model of the One Tree Reef region (Burgess et al. 2007). The output for this model consisted of current speeds in cm s\(^{-1}\) and directions at 30-minute intervals for 792 grid cells located over the One Tree Reef. These current patterns were modelled for reef circulation under zero wind and based on the tidal regime experienced at One Tree Reef during a 10-day period starting January 11\(^{th}\) 2001. Average current speeds in cm s\(^{-1}\) were calculated from the model output for each of the 8 grid cells where recruitment sites were located.

To convert dissolution results into a value in cm s\(^{-1}\), the average weight lost from balls in a 24-h period was converted using calibration equations from Fulton and Bellwood (2005) where \( WL = \text{weight lost in grams in } 24 \text{h and } v = \text{flow velocity in cm s}^{-1}. \) \( WL_{24h} = 0.915v + 5.395 \) was used for the November deployment and \( WL_{24h} = 0.921v \).
+10.812 was used for the January deployment in accordance with average water temperatures measured on the reef using Onset TidBits® (23.4±0.11°C (mean±SE) in November 2003 and 26.6±0.18°C in Jan 2004). Tidal movement was omitted from the data as this was not factored in for Fulton and Bellwood (2005) and is likely to be much less important to water flow on the reef slope, compared to the lagoon at One Tree.

A significant linear relationship (LSR: df=1, F=124.7, p=0.008; equation: y=0.23x+0.07) describing 98% of the variation in the data was found between the mean model current speed and the mean water flow based on dissolution of plaster balls but converted to cm s⁻¹ from the four leeward sites where both measurements were taken. To calculate y-values for water flow based on dissolution of plaster balls at the four windward reef slope sites the average current speeds for the four appropriate grid cells were input as x-values into the equation. These values were then used to examine the relationship between the mean number of recruits and the mean water flow on the slope separately for each family.

**Settlement choice of coral larvae**

To compare the relative influences of hydrodynamics and settlement substrata on rates of recruitment, *Acropora nasuta* larvae were given a choice among settlement tiles conditioned at four sites under both low (2.1 cm s⁻¹) or medium (4.6 cm s⁻¹) flow speeds. These flow speeds were equivalent to average current speeds integrated over a tidal cycle at low and medium flow lagoonal sites measured in the field (2.1 to 7.1 cm s⁻¹), but much lower than maximum current speeds, which can reach up to 130 cm s⁻¹ (Kingsford and Finn 1997). Medium flow speeds were used rather than high flow speeds due to field patterns showing greater recruitment at sites with medium flow.

Six gravid colonies of *Acropora nasuta* were collected from the leeward reef slope (near sites 15 and 16) a few days before they were predicted to spawn and held in flow-through aquaria. Five of the 6 colonies spawned and after 68 h approximately 2,500 motile larvae were added to each of 10 tanks consisting of circular plastic 35 l tubs of diameter 38 cm. Tanks were filled by a tap located at the top of each tub and drained from the centre through a 210-micron mesh sock (larvae were approximately 500
micron in diameter) that slid over a perforated 100 mm diameter PVC pipe. This created a doughnut shaped tank with water circulating in one direction (Fig. 2). Flow speeds were measured in the water column and estimated by circulating drops of red dye, while all other parameters e.g. temperature, light and water quality were kept constant between treatments. Each aquarium contained four settlement tiles that had been conditioned at different sites on the reef for the previous eight months, the maximum time available to ensure good coverage of encrusting organisms that would be representative of the sites. Conditioning commenced in March and tiles were retrieved at the end of October to avoid the peak settlement of Acropora recruits following coral spawning in November (Wallace 1985). Tiles were placed on the bottom of tubs and because of the slight curve in the base and sides of tubs a small gap between tiles and the tub bottom provided the type of “gap” habitat often preferred by coral larvae (Mundy 2000).

Part (a) of the experiment tested larval settlement choice among tiles conditioned in the lagoon, and part (b) among tiles conditioned on the reef slope. For part (a), each of six tubs, three set to each flow speed, contained one tile conditioned at each of 4 lagoon sites, 1, 4, 7 and 10 representing sites with a range of field recruitment levels. For part (b) each of four tubs, two set to each flow speed, contained one tile conditioned at each of the four leeward reef slope sites, 13, 14, 15 and 16, which also represented a range of recruitment levels. Only four tubs were used on this occasion because fewer conditioned tiles were available. Four days after larvae were introduced into the tubs, tiles were removed and the number of live coral larvae settled to all surfaces on each tile was counted under a dissecting microscope. All recruits censused were clearly of recent origin, consisting of a single primary polyp indicating they were less than 2 weeks old (Babcock et al. 2003). Data were analysed using a fully fixed orthogonal two-factor ANOVA. Data were log (x + 1) transformed following an examination of residual plots.

Results

Spatial and temporal patterns in coral recruitment

Spatial patterns of pocilloporid recruits among sites were highly consistent over time (Fig. 3). Recruit densities ranged from zero at many lagoon sites to a maximum of 6.2±1.7 (mean±SE) recruits per tile at site 14 on the leeward side of the reef slope in November 2003 to January 2004. On all occasions there were sites where no recruits were recorded, though no site had zero recruitment on all occasions. On every occasion on the reef slope mean recruitment was highest at site 14, and second highest at site 13, the two sites in the north-west location. Site 14 had 1.5 to 2.7 times the mean recruitment of site 13, and 1.8 to 8.5 times the mean recruitment of the next highest site. Site ranks were concordant among occasions (Wc =0.68; (χr)2 =23.8; p<0.005), and sites 13 and 14 had the highest summed ranks with a difference of 12.5 to the next nearest site (Table 2). Despite changes in the rank order of low recruitment sites, there was no significant interaction between Site and Time (Table 3), further indicating that the magnitude of relative differences among sites were consistent.

Pocilloporid recruitment was lower in the lagoon than on the reef slope but patterns among sites were consistent in rank order through time. Site 7 was ranked highest in mean recruitment on every occasion, and site 8, was ranked second on four out of five occasions. Both these sites are to the north of the reef. Site 7 had between 1.2 and 2.6 times more recruitment than site 8, and 2.5 to 7.2 times more than the next highest site. Site ranks were concordant among occasions (Wc =0.59; (χr)2 =32.5; p<0.001), and sites 7 and 8 had the highest summed ranks, with a difference of 13.5 to the next nearest site (Table 2), however, a significant interaction between Site and Time indicates variation in the magnitude of differences among sites depending on occasion (Table 3).

On all occasions poritid recruitment was low relative to other taxa (Fig. 4). Mean recruitment ranged from zero to 2.7±1.4 recruits per tile in November 2003 to January 2004 at site 7. Poritid recruitment approached zero in January 2002 to March 2002 in both the slope and the lagoon, and no poritid recruits were recorded at site 12.
Fig. 3  Mean pocilloporid recruitment per tile + SE at 8 reef slope and 12 lagoon sites at One Tree Reef for five 8-week deployment periods over three summer recruitment seasons. N denotes sites not included in the first deployment. ● = a recruitment hotspot i.e. the site was ranked first or second in order of greatest mean recruitment per tile on three or more occasions
during any time interval. Less than one recruit per tile was recorded at almost all sites and times. The exceptions were site 7 and two windward reef slope sites (sites 17 and 18) in November 2002 to January 2003, and two northern lagoon sites (7 and 8) in November 2003 to January 2004. Site 7 in the lagoon was ranked highest in mean recruitment and sites 17 and 18 on the reef slope were ranked either first or second on three out of five occasions and site ranks were concordant among occasions on the slope (Wc = 0.65; \( \chi^2_r = 18.3; p < 0.025 \)) and in the lagoon (Wc = 0.66; \( \chi^2_r = 29.2; p < 0.005 \)). The two sites with the highest summed ranks were sites 4 and 7 in the lagoon and 17 and 18 on the slope with differences of 4.5 and 3.5 to the next nearest sites (Table 2). Significant Site by Time interactions for both habitats (Table 3) indicated that poritid recruitment varied in the magnitude of differences among sites over time.

Overall mean recruitment of acroporids at One Tree was low at all sites and ranged from zero to a maximum of \( 5.6 \pm 1.1 \) (mean \( \pm \) SE) recruits per tile during November 2002 to January 2003 at site 17, located on the windward side of the reef slope. No site had zero recruits on all five occasions (Fig. 5). On the slope, mean recruitment was less than 2 recruits per tile at all sites on all occasions except November 2002 to January 2003 when mean recruitment ranged from 1.5\( \pm 0.60 \) per tile at site 15 to the maximum described above. Site 19 on the exposed southern corner, and site 14 on the leeward northern side (where pocilloporid recruitment was highest), were the only sites where acroporids recruited on every occasion, site 19 was ranked first or second on all five occasions, and site 14 in four of five occasions.

In the lagoon, mean acroporid recruitment was less than one recruit per tile with the single exception of site 11 during November 2002 to January 2003, where mean recruitment was 2.5\( \pm 2.5 \). Only site 5 had acroporid recruits on all occasions, and with site 6, was ranked either first or second in three of the five occasions. For both the slope and lagoon, relative site ranks were consistent among times (slope: Wc = 0.49; \( \chi^2_r = 17.2; p < 0.025 \),

Table 2: Summed ranks from five sampling occasions for recruitment of three taxa in two habitats. Bold font signifies top two sites defined here as ‘recruitment hotspots’ where ranks are consistent over time according to the Kendall’s Test for Concordance.

<table>
<thead>
<tr>
<th>Habitat</th>
<th>Site</th>
<th>Pocilloporidae</th>
<th>Acroporidae</th>
<th>Poritidae</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lagoon</td>
<td>1</td>
<td>22</td>
<td>27</td>
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<td></td>
<td>2</td>
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<td>4</td>
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<td>35</td>
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</tr>
<tr>
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<td>5</td>
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<tr>
<td></td>
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<td>21</td>
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</table>

Table 3: Two-way ANOVAs testing for difference in mean number of recruits. Data are square root transformed number of larvae per tile.

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<tr>
<th>Habitat</th>
<th>Factors</th>
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<th>MS</th>
<th>p</th>
<th>MS</th>
<th>p</th>
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<td>Lagoon</td>
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<td>0.054</td>
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<td>0.040</td>
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<td>Time x Site</td>
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<td>0.409</td>
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<td>0.178</td>
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<td>28.0</td>
<td>&lt; 0.001</td>
<td>2.277</td>
<td>&lt; 0.001</td>
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<tr>
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<td>Time x Site</td>
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<td>0.378</td>
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Fig. 4 Mean poritid recruitment per tile ± SE at 8 reef slope sites and 12 lagoon sites at One Tree Reef for five 8-week deployment periods over three summer recruitment seasons. N denotes sites not included in the first deployment. ● = a recruitment hotspot i.e. the site was ranked first or second in order of greatest mean recruitment per tile on three or more occasions.
Fig. 5  Mean acroporid recruitment per tile ± SE at 8 reef slope sites and 12 lagoon sites at One Tree Reef for five 8-week deployment periods over three summer recruitment seasons. N denotes sites not included in the first deployment. ● = a recruitment hotspot i.e. the site was ranked first or second in order of greatest mean recruitment per tile on three or more occasions.
lagoon: $W_c = 0.39; (\chi^2)_c = 21.4; p < 0.05$), with sites 5 and 6 in the lagoon and sites 14 and 18 on the slope being having the highest summed ranks with differences of 2.5 and 8.5 to the next nearest sites respectively (Table 2). There was no significant interaction between Site and Time (Table 3) indicating that recruitment patterns among sites were consistent. Exceptionally low recruitment rates overall, however, meant that these results may reflect similarly low recruitment at all sites on all occasions, rather than similar patterns of high and low recruitment among sites during each occasion.

The role of adult cover on patterns of coral recruitment

Mean recruitment of pocilloporids was positively exponentially correlated with percent cover of conspecific adults at quadrat and transect scales in the lagoon, and linearly correlated with adults at the transect scale for the slope. There was no relationship between mean pocilloporid recruitment and cover of adults in quadrats on the slope. In the lagoon (Fig. 6a), adult cover described 73 and 55% of the variation in mean recruitment in quadrats and transects respectively. The mean percent cover of pocilloporid adults in transects explained 82% of the variation in mean pocilloporid recruitment on the slope.

Poritid recruitment was positively linearly correlated

![Figure 6](image)

**Fig. 6** Relationship between mean site recruitment and the mean percent cover of adult corals for (a) lagoon and (b) slope.
with poritid adult cover at the quadrat scale on the slope (Fig. 6b). The mean percent of poritids comprising the coral habitat in quadrats explained 68% of the variation in mean poritid recruitment. No relationships were found between recruitment and the cover of poritid adults in transects, or between poritid recruits and adults at either scale in the lagoon. Acroporid recruitment and acroporid adult cover were not correlated in either habitat or at either scale.

**Relationships between water flow and patterns of field recruitment**

Mean recruitment and water flow were not linearly related for any of the three coral families in either the slope or lagoon. However, in the lagoon (Fig. 7a) recruitment patterns were similar between pocilloporids and poritids: recruitment was highest at a site with medium flow (~0.35% d⁻¹ m⁻¹ or 4.5 cm s⁻¹), and was low at sites with low (~0.27% d⁻¹ m⁻¹ or 2.1 cm s⁻¹), medium or high (~0.43% d⁻¹ m⁻¹ or 7.1 cm s⁻¹) flows. In contrast, on the reef slope (Fig. 7b) there were no clear relationships between water flow and mean recruitment for pocilloporids and poritids. Water flow was not correlated with acroporid recruitment for either the slope or lagoon.

**Experimental recruitment in response to water flow**

*Acropora nasuta* recruitment was 10 times higher under low (2.1 cm s⁻¹) compared to medium (4.6 cm s⁻¹) flow [61.0±23.0 (mean±SE) and 6.0±2.0 respectively (ANOVA: df=1, 16, F=11.9, p=0.003)] where tiles were conditioned in the lagoon (Fig. 8a), and 6 times higher under low flow (40.0±14.0) compared to medium flow (6.0±3.0) (ANOVA: df=1, 8, F=30.3, p=0.001) where tiles were conditioned on the slope (Fig. 8b). The site of tile conditioning had no effect for either the slope or lagoon nor was there any interaction between the factors.
Recruitment hotspots were identified for all taxa in both lagoon and slope environments. This suggests that the rank order of recruitment among sites within a reef may be highly predictable, even though the magnitude of differences may vary from year to year. Clearly both deterministic and stochastic processes affect recruitment variation at reef scales.

Recruitment hotspots were most prominent for pocilloporids and all of these hotspots were located on the western side of the island (adjacent sites 7, 8 in the lagoon, adjacent sites 13 and 14 on the slope: see Fig. 1). Consistency in spatial patterns of pocilloporid recruitment between years also occurred in the Red Sea (Glassom et al. 2004) and other studies have found greater spatial variation in recruitment in pocilloporids at reef scales (Babcock 1988, Baird and Hughes 1997, Dunstan and Johnson 1998) when compared to acroporid recruitment. Hydrodynamics may be influencing pocilloporid hotspots at One Tree since hotspots sites were adjacent in both habitats, and also because one site in the lagoon (site 7) was a hotspot for both pocilloporids and poritids and one site on the slope (site 14) was a hotspot for both pocilloporids and acroporids. Pocilloporid recruit abundance was, however, also positively correlated with adult cover in the lagoon and slope. The importance of adult cover may be driven by the development times of propagules. Higher local retention would be expected to occur in taxa which brood larvae that are capable of settlement immediately on release, like the most abundant pocilloporids on the GBR which include *Pocillopora damicornis*, *Stylophora pistillata* and *Seriatopora hystrix* (Baird and Babcock 2000; Baird and Morse 2001, Tioho et al. 2001) and also in taxa with smaller eggs that develop rapidly (Nakamura and Sakai 2010), which include the locally abundant spawning species *Pocillopora verrucosa* and *P. eydouxi* (Baird et al. 2009a). Planulation in these three pocilloporid species co-occurs with the mass spawning period in the southern GBR (Tanner 1996) and the recruitment tiles were placed at the correct time to captured this event. Whether or not these recruits persist and ultimately maintain the adult population is unknown, however, because DNA analyses suggest that sexual recruits may not substantially contribute to adult populations at One Tree Reef (Sherman et al. 2006).

In addition to the combined pocilloporid and poritid
recruitment hotspot at site 7 in the One Tree lagoon, poritid hotspots were also located at adjacent sites 17 and 18 on the slope (see Fig. 1). A relationship between recruits and adults was found for poritids on the reef slope, however, there was no relationship between recruits and adults for this family in the lagoon. While the majority of poritids are broadcast spawners, some species brood larvae, including the locally abundant Porites murrayensis, which planulates from November to April on the southern GBR (Kojis and Quinn 1981). Differences in poritid recruit-adult relationships between the lagoon and slope may reflect differences in poritid species assemblages between habitats and the prevailing reproductive strategies of these species.

Recruitment hotspots were also evident in the Acropora at adjacent sites 5 and 6 in the lagoon (see Fig. 1) and sites 14 and 19 on the reef slope; however, the factors driving these patterns were not clear. Adult cover and recruit abundance was not correlated, so self-recruitment is unlikely to explain these patterns, and nor would we expect a relationship given all acroporid recruits were from spawning species (i.e. there were no isoporan recruits censused on recruitment tiles). Similarly, given that the two hotspots observed on the slope were on opposite sides of the reef, prevailing currents are also unlikely to explain this pattern. Two sites that ranked consistently high in the lagoon were, however, located in close proximity on the eastern side of the lagoon and so it is possible that hydrodynamics may play a role in driving these patterns, including factors that were not tested here, such as flow direction.

In the lagoon, recruitment hotspots were commonly areas of medium water flow, however, not all sites with medium water flow were recruitment hotspots. High recruitment at medium flow sites may also be related to larval supply: sites with the lowest levels of water flow may receive very little input of larvae (Black and Moran 1991, Harriott and Simpson 1997), while at sites with high levels of flow, larvae are can’t settle. Because our flow measurements were time-integrated, medium flow sites may have tidally driven periodic high flows to bring larvae to the site, alternating with periodic low flow periods during which larvae can settle. On the reef slope, recruitment hotspots were not correlated with the flow regimes. In this habitat, ambient flow is on average very fast (greater than 10 cm s$^{-1}$), so recruitment of spawned larvae may depend entirely on unpredictable settlement windows afforded by infrequent low wind and current conditions.

In addition to average water flow, hydrodynamic features such as turbulence, boundary layers and complex micro-topography may affect the ultimate settlement of coral larvae and therefore have an important influence on recruitment patterns. Pelagic larvae accumulate in fronts: the border zones between two bodies of water with different physical and chemical properties (Kingsford 1990, Willis and Oliver 1990, Kingsford et al. 1991, McCulloch and Shanks 2003) such as those observed between the lagoon and inter-reef waters at One Tree. During the course of this study, we observed fronts forming along the reef margin in the location of sites 7 and 8 in the lagoon and sites 13 and 14 on the reef slope, corresponding with recruitment hotspots for pocilloporids.

In experimental aquaria, Acropora nasuta larvae settled in densities up to 10 times greater in low (2.1 cm s$^{-1}$) compared to medium flow (4.6 cm s$^{-1}$). This may reflect either poor powers of locomotion or limited capacity to adhere to the substratum in higher flows, or it may reflect larval choice. Coral larvae swim at speeds of only 0.1 to 0.5 cm s$^{-1}$ which is very slow when compared to most other marine invertebrate larvae (Chia et al 1984). However, swimming abilities and/or settlement preferences may differ considerably among taxa. In experimental aquaria (Harii and Kayanne 2002), the highest settlement rates in Pocillopora damicornis larvae (70%) occurred under high flows (9.8 cm s$^{-1}$) while greatest settlement in Heliopora coerulea larvae (50%) occurred in still water. Our results suggest that greatest recruitment of acroporids may occur under very low flow conditions, and so hydrodynamic features and neap tides may be of more importance for recruitment in this taxon. We recommend examination of such flow events on the reef slope rather than the measurement of average current speed for future studies.

In conclusion, recruitment ‘hotspots’ were identified for three coral families in the lagoon and on the slope at One Tree Reef. Recruitment hotspots were correlated with adult cover for pocilloporids and poritids but not acroporids, possibly reflecting differences in the development
times of propagules among these taxa. In the lagoon, recruitment hotspots were located in areas with medium levels of water flow relative to other sites in the same habitat, and flow speed was a good predictor of settlement density of *Acropora nasuta* larvae in controlled aquaria. However, due to the inherent differences between laboratory and field condition, careful assessment of the relationship between flow and settlement in the field is required. Further work is required to determine whether recruitment hotspots occur at predictable sites on other platform reefs within the GBR and in other locations and to further examine other factors that may cause recruitment hotspots such as depth, sedimentation and the presence of benthic algae.

**Acknowledgements**

Many thanks to One Tree Island managers P., K. and A. Beinssen, O. Heutschal, M. Smith and A. Marshall and field assistants D.P. Thomson, P. Costello, S. Adams, S. Walker, M. Kospartov, S. Burgess, D. Betts, N. Pressman, B. Murphy, and K. Nash. Thanks to S. Piromvaragorn and D.P. Thomson for their expertise and two anonymous reviewers for improvements to the manuscript. This research was supported by funding awards from CRC Reef, PADI Aware, Linnean Society of NSW, American Museum of Natural History, Royal Zoological Society of NSW, James Cook University Graduate Research School, and an Australian Postgraduate Award and Nancy Vernon Rankine Write-Up Scholarship to J.V.E. and Australian Research Council Discovery Grants to M.J.K. and G.P.J.

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Received: 29 June 2011
Accepted: 14 March 2012
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