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Spatio-temporal patterns of coral recruitment at Vamizi Island, Quirimbas Archipelago, Mozambique

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Spatial and temporal patterns of recruitment of reef corals were assessed for the first time in Mozambique by deploying settlement plates at various spatio-temporal scales between October 2012 and October 2013. The abundance of juvenile corals (5–50 mm in diameter) was assessed along transects. Settlement of acroporids was highly seasonal, with 97% of spat settling between July and October 2013. Pocilloporids settled throughout the year, peaking slightly between October 2012 and January 2013. The annual mean larval settlement of up to 1 135 spat m⁻² was comparable to that on other East African reefs, but was dominated by acroporids, which constituted over 80% of all spat, whereas pocilloporids settle in higher densities in Kenya and South Africa. The peak settlement season also differed from other African locations. A greater proportion of variance in settlement rates occurred at the spatial scale of kilometres (between sites) and centimetres (between settlement plates) than at the scale of metres (between subsites), implying that most patchiness occurs at those scales. The peak in acroporid settlement coincided with the period of multispecific spawning, with settlement occurring as early as nine days after a spawning event. As no similar spawning events have been reported for other reefs in the area, our results suggest that these spawning events strongly influence overall annual settlement rates and promote high levels of self-seeding at Vamizi. There was no relationship between settlement of larvae to settlement plates and juvenile density on adjacent reefs, suggesting either variable levels of early post-settlement mortality or high interannual variability in settlement.

Keywords: coral reproduction, juveniles, larval settlement, recruitment, Scleractinia, Western Indian Ocean

Introduction

Broadcast-spawning scleractinian corals have a complex life cycle in which externally fertilised larvae spend a planktonic phase in the water column before descending to the reef in search of suitable substratum to which they attach and metamorphose into primary polyps (Harrison and Wallace 1990). Newly settled corals suffer high mortality rates (Babcock 1985), a function of physical conditions at the site of settlement and biotic factors such as predation, grazing or competition (Babcock and Davies 1991; Tomascik 1991; Birrell et al. 2005; Baria et al. 2010; Penin et al. 2011; Davies et al. 2013). If corals survive to sexual maturity, generally at about 40 mm diameter (Bak and Engels 1979; Rogers et al. 1984; Wittenberg and Hunte 1992; Chiappone and Sullivan 1996), they are considered to be recruited to the population (Harrison and Wallace 1990). The process of recruitment is essential for the maintenance of healthy populations and recovery after disturbance. Thus, recruitment rates can be an important indicator of reef resilience and may predict the future state of coral communities better than does the present state of the adult community (Sale 1999).

Larvae may be recruited locally or exported to other areas by currents. The prevalence of self-recruitment or dispersal may vary geographically, among species or among cohorts of larvae of the same species (Connolly and Baird 2010).

Settlement may thus vary widely among areas even when coral reproductive output is similar. The potential for coral larvae to settle close to or disperse away from their natal reef depends on a combination of biotic and abiotic factors such as precompetency and competency periods (Richmond 1985, 1988; Harii et al. 2002; Miller and Mundy 2003; Nozawa and Harrison 2005), larval survivorship (Graham et al. 2008), larval behaviour (reviewed in Gleason and Hofmann 2011), and hydrodynamics (Reidenbach et al. 2009; Andutta et al. 2012). Although some studies have shown significant gene flow and larval connectivity over long distances (e.g. Ayre and Hughes 2000), the growing consensus is that most recruitment occurs within smaller distances than the dispersal potential of larvae would allow (Ayre and Hughes 2000; Nishikawa et al. 2003; Whitaker 2004; Baums et al. 2005; Vollmer and Palumbi 2007), and is likely to occur at scales of tens of kilometres, rather than over hundreds of kilometres (Underwood et al. 2009).

Patterns of coral settlement and recruitment have never been investigated in Mozambique. At Vamizi Island, in the north of the country, numerous coral species exhibit concentrated breeding activity over a very short, annual, multispecific and synchronous spawning event – although split-spawning over two consecutive months was also recorded in one year (Sola et al. in press) – probably

leading to increased reproductive output, but how this influences local patterns of annual recruitment is not known.

In scleractinians, survival rates immediately following settlement are usually very low and are spatially, temporally and taxonomically variable (e.g. Wilson and Harrison 2005; Glassom and Chadwick 2006). Thus, the strong influence of post-settlement processes in structuring adult communities has long been recognised (Sammarco 1991; Miller et al. 2000; Glassom and Chadwick 2006; Penin et al. 2011), although settlement rate may be a stronger determinant of community structure than post-settlement mortality in some cases. Therefore, investigating patterns of larval settlement in combination with aspects of the juvenile coral community can help clarify recruitment patterns at given locations.

We investigated how settlement rates vary along the northern side of Vamizi Island and throughout the year to determine whether they are reflected in the abundance and species composition of juvenile corals. In addition, we tested the hypothesis that high rates of coral settlement are correlated with the season of spawning. We discuss our results in the context of other studies from the region.

Material and methods

Study area and description of sites

Vamizi is a tropical island situated at latitude 11° S in the Quirimbas Archipelago, northern Mozambique (Figure 1). Approximately 12 km long and 2 km wide, the island is bound in the north and south by 500 m-deep canyons, which may provide protection from coral bleaching by supplying cooler water from depth in the Mozambique Channel (Hill et al. 2009). The island is situated where the South Equatorial Current splits into the north-flowing East African Current and south-flowing Mozambique Current, rendering Vamizi a potential source of coral larval supply to reefs both north and south of the island. The island is surrounded by a fringing reef with an associated shallow lagoon, where coral 'bommies' are interspersed with sandy patches. The coral community is dominated by *Acropora* species, especially in the lagoon and at the reef crest.

Deployment of settlement plates

Settlement plates were deployed at three sites, 1–7 km apart, at depths of 5–9 m.

Unglazed terracotta ceramic plates, 120 mm × 120 mm × 8 mm with 5 mm holes drilled in the centre, were secured individually to the reef. Two plastic push-in pins were inserted in holes drilled into natural bare substratum and each plate was attached to these with cable-ties. The plates were installed horizontally, or as close to that as possible. This way, they were located 10–20 mm above the reef's surface, allowing water to flow over all surfaces.

Seasonal larval settlement rates

At each of sites S1–S3, three sets of six settlement plates were deployed (Figure 1c). Each set was referred to as a 'subsite'. The distances between plates, subsites and sites were in the order of centimetres, metres and kilometres, respectively. The 54 plates were retrieved and replaced with new ones every three months from November 2012 to October 2013. This resulted in four sampling seasons:

November 2012–January 2013, February–April 2013, May–July 2013 and August–October 2013.

Short-term larval settlement rates

Between 10 and 11 August 2013, plates were deployed at six additional sites (S4–S9, Figure 1c) about three weeks before a multispecific spawning event that was recorded on 29–31 August (Sola et al. in press). This provided adequate time for plates to condition and acquire the biofilm that is essential for larval settlement (Erwin et al. 2008; Tebben et al. 2011; Tran and Hadfield 2011). As was the case for seasonal measurements, each site had 18 plates deployed in three sets of six plates each. Three plates were removed from each subsite at all six sites nine days after the August spawning event and the remaining plates 18 days after the event.

Retrieved plates were placed in sodium hypochlorite overnight to remove all soft tissue and expose skeletons of newly settled scleractinian recruits, referred to here as spat. Plates were then rinsed in fresh water, left to dry and inspected under a stereomicroscope. The top, bottom and side surfaces were examined and all spat detected were counted and identified to family level where possible (following Baird and Babcock 2000 and Babcock et al. 2003).

Juvenile coral community

At S1–S3, the abundance and community composition of juvenile corals were assessed once in August 2013. A total of eight transects, each covering an area of 0.6 m², were inspected at each site to detect juvenile corals of 5–50 mm diameter. A 2-m rope, with small weights every 50 cm and closely embracing the reef topography, was laid down at random. All juveniles within a band 30-cm wide and centred on the rope were identified to genus level, where possible, and their widest diameter measured.

Statistical analysis

Analyses were conducted in JMP 11 (SAS Inc.). Spatio-temporal variation in settlement rates was tested using ANOVA. A variance-component model was constructed, where subsites were nested within sites, and the interaction effect between seasons and sites was included in the model. All effects of the model were specified as random, because this is required in order to compute the variance components. The assumptions of normality and homoscedasticity were not met, so data were square-root transformed before analysis (Zar 1984). After transformation, data distribution was near-normal and variance was stable. One-way ANOVAs were used to determine whether the mean rate of settlement of acroporids and pocilloporids varied with season. *Post hoc* Tukey's HSD tests were performed when significant differences were detected. The variance-component analyses served to determine which of the temporal or spatial scales was accountable for most of the observed variation as a proxy for temporal and spatial patchiness in settlement (Glassom and Chadwick 2006; O'Leary and Potts 2011).

In the short-term settlement experiment, differences in settlement within sites, among sites and between the two immersion times were tested by a random-model ANOVA,

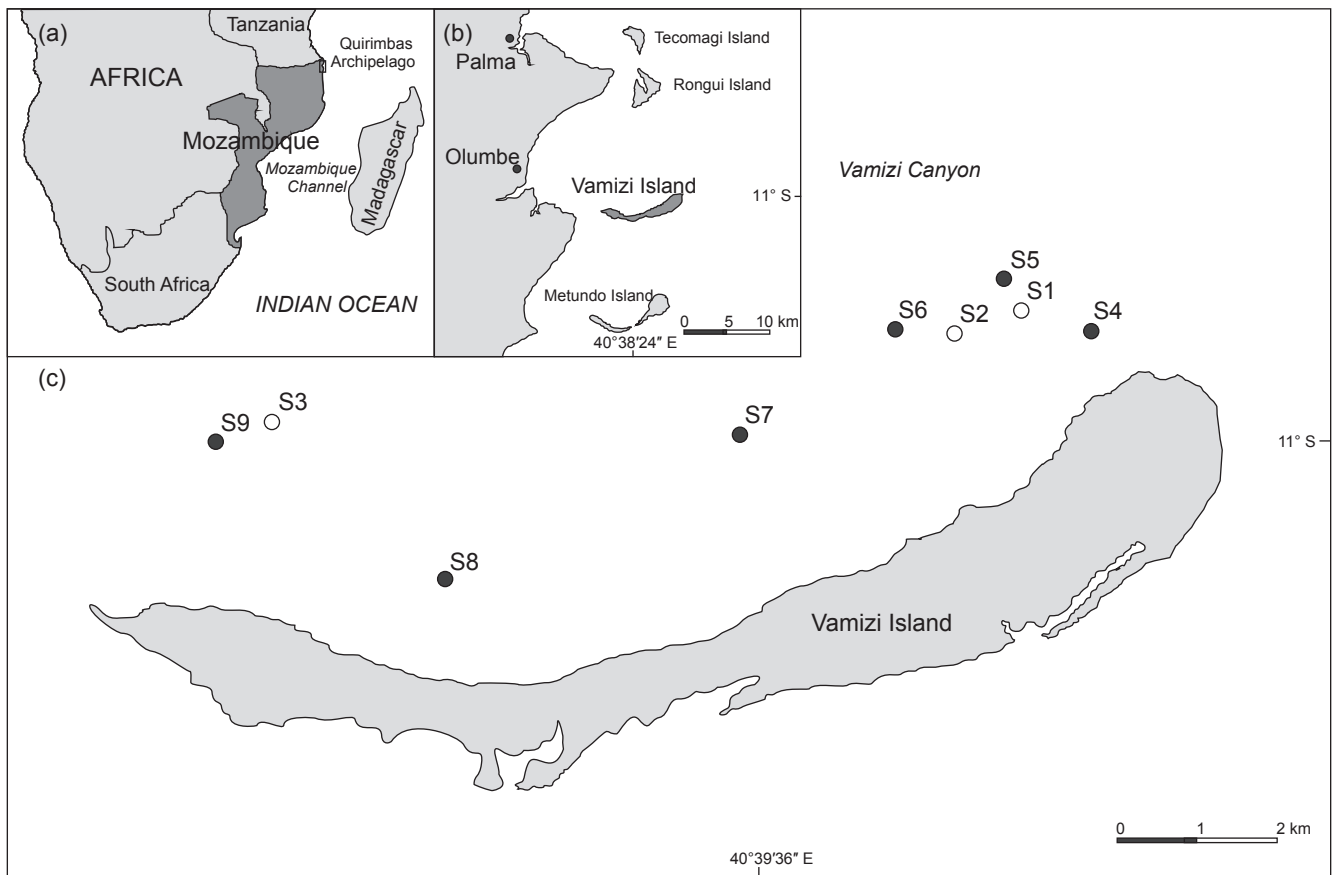


Figure 1: Map showing the location of (a) the Quirimbas Archipelago off Mozambique and (b) Vamizi Island within the archipelago, and (c) the distribution of settlement stations along its northern side. Sites used for the measurement of seasonal settlement and juvenile coral abundance are shown as open circles and sites used in the short-term settlement experiment as closed circles

where subsites were nested within sites. Tests of assumptions and data transformation were performed as described above. However, no significant spatial variation was detected, probably on account of the relatively small number of spat found in this experiment, so sites were pooled and variation between immersion times tested by a one-way ANOVA.

To compare the abundance of juvenile corals among sites, a random-model one-way ANOVA was used. The assumptions of normality and homoscedasticity were violated and could not be corrected by any transformation. A non-parametric solution was sought by ranking the data, but the variance remained unequal. Given that ANOVA is quite robust to heterogeneity of variance (Underwood 1981), especially in a balanced design, and unequal variance is more likely to result in a Type II than a Type I error, the ANOVA was performed on the untransformed data. A simple linear regression was used to determine whether density of juveniles was related directly to spat density.

Results

Annual larval settlement rates

During the year of study and across sites S1–S3, a total of 4 551 scleractinian larvae settled on the plates, equivalent

to 1 130 spat $m^{-2} y^{-1}$. The distribution of total spat found on the top, bottom and side surfaces of plates was 8.5%, 78.6% and 12.9%, respectively. Of all spat, 80.3% were acroporids, 97% of which settled between August and October 2013. During this season, spat were so numerous on the plates (with up to 285 spat on a single plate) that they often touched. Pocilloporids dominated in all other seasons, comprising 60% of spat recorded between October 2012 and July 2013. Rates of settlement varied both spatially and seasonally (Table 1). At all sites, settlement rates between August and October 2013 differed significantly from all other seasons (Tukey's HSD test, $p < 0.05$), being about 10-fold greater (Figure 2a). Differences among subsites of sites were significant (Table 1) The variance-component analysis revealed that differences between seasons accounted for the majority of observed variance, followed by the interaction between seasons and sites. Spatially, the difference in settlement among individual plates, represented by the residual term in Table 2, accounted for more variance than differences among sites and that of subsites had almost no impact on the overall variance (Table 1).

Nonetheless, exploratory statistics revealed that when the interaction term 'Season \times Site' was not included in the model, differences in settlement rates among sites were

significant. Certain types of interactions can obscure the effect of some factors and the interpretation of the significance of main effects are invalidated when such interactions are themselves significant, and thus differences among means of levels of one factor must be examined at each level of the other factor (Underwood 1981). Hence, spatial analyses for each season independently were conducted (Table 2). During each season, except between May and July 2013, settlement was significantly higher at Site 3 (Tukey's HSD test $p < 0.05$). The differences among sites accounted for the highest proportion of variance in the first and last sampling seasons, when rates of settlement were higher, whereas in the second and third seasons most of the variance could be attributed to differences at the smallest spatial scale, i.e. among individual plates (Table 2). Settlement differed significantly among seasons

both for acroporids ($F_{3,216} = 108.8276, p < 0.001$, Figure 2b) and pocilloporids ($F_{3,216} = 13.1297, p < 0.001$, Figure 2c), but whereas for acroporids this accounted for most of the observed variance (66.8%), for pocilloporids the difference among individual plates accounted for greater variance (85.5%).

Table 2: Results of a random-model ANOVA of the spatial variation in scleractinian settlement rates according to season at Vamizi Island. The Subsite effect is nested within Site. The Residual term refers to differences between individual plates

Table 1: Results of a random-model ANOVA of the spatio-temporal patterns of scleractinian settlement rates at Vamizi Island. The Residual term corresponds to individual plates within subsites. The Subsite effect is nested within Site

Source	df	F	p	Variance (%)
Season	3	6.5059	0.0258	47.715
Site	2	2.5578	0.1482	10.884
Subsite (Site)	6	3.3513	0.0036	1.461
Season × Site	6	31.3763	<0.0001	25.170
Residual				14.770

Source	df	F	p	Variance (%)
November 2012–January 2013				
Site	2	54.2026	0.0001	77.893
Subsite (Site)	6	1.2084	0.3201	0.756
Residual				21.351
February 2013–April 2013				
Site	2	14.4985	0.0051	38.873
Subsite (Site)	6	0.823	0.5582	-1.858
Residual				62.986
May 2013–July 2013				
Site	2	2.1116	0.2021	12.989
Subsite (Site)	6	3.2915	0.0092	24.393
Residual				62.617
August 2013–October 2013				
Site	2	14.6518	0.0049	67.387
Subsite (Site)	6	4.1587	0.0021	11.248
Residual				21.365

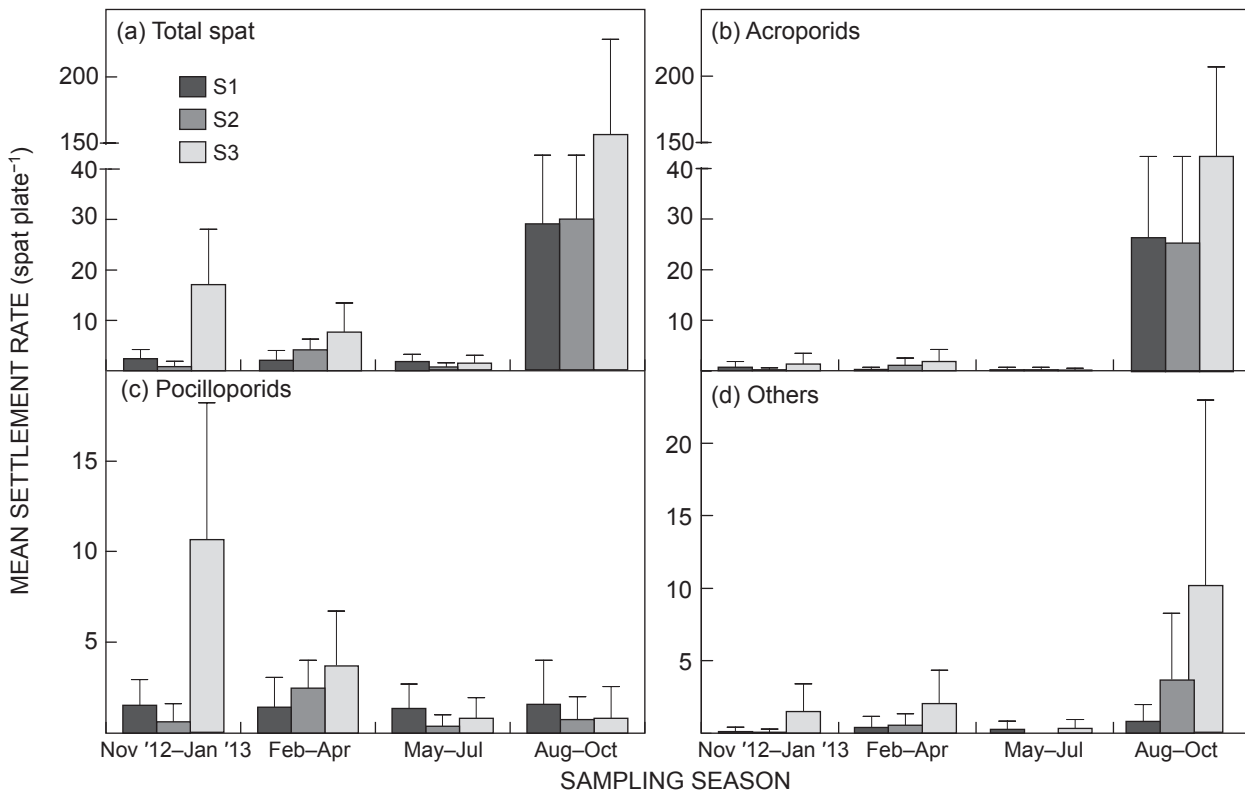


Figure 2: Variation in settlement rates at sites S1–S3 along the northern side of Vamizi Island in four different sampling seasons for (a) total spat, (b) acroporids, (c) pocilloporids and (d) other families. Error bars denote SE. Note the y-axis break for (a) and (b)

Short-term larval settlement rates

Settlement of coral larvae on plates was recorded within nine days following the spawning event. A total of 119 spat were recorded on 108 settlement plates, with the settlement rate ranging from a mean of 0.11 (SD 0.33) to 1.67 (SD 1.94) spat plate⁻¹ (Figure 3). Plates left immersed for 18 days after the spawning event had significantly more spat than 9-day plates ($F_{1,108} = 4.0136, p < 0.05$). Of all spat observed, 53% were pocilloporids, 37% were acroporids and the remainder could not be identified.

Juvenile coral community

The mean density of juvenile corals at the three sites was 17.3 (SD 12.2), 25 (SD 18.2) and 11 (SD 4.4) juveniles m⁻², respectively, but did not differ significantly between sites ($F_{2,24} = 2.7125, p > 0.05$). Differences among transects across all sites accounted for 89.9% of variance in juvenile density, with differences between sites accounting for only a small proportion. The regression analysis showed no significant relationship between spat density and juvenile density at the three sites (adjusted $r^2 = 0.39, p = 0.37$).

Juveniles of 13 genera from seven different families were identified (Table 3), but 11 colonies could not be identified conclusively. *Acropora* largely dominated the juvenile community at S1 and S2, representing 62.2% and 61.7%, respectively, of the total number of corals found at these sites (Table 3). Pocilloporids were the second most abundant family at S1 and S2, comprising 20% and 13.2%, respectively, of the total (Table 3). At S3, however, the juvenile community was dominated by merulinids and mussids, which represented 23.2% of the total.

Discussion

Annual larval settlement rates

The overall rate of coral larval settlement at Vamizi Island varied seasonally and among sites. Seasonality of settlement was also markedly different between acroporids and pocilloporids, the two dominant families found on settlement plates. The majority of acroporid species are broadcast spawners and usually have marked breeding periods, which results in seasonal patterns of settlement (Hughes et al. 2000). At Vamizi Island, acroporid settlement was generally low between October 2012 and July 2013 but increased 300-fold between August and October 2013. The peak settlement season for acroporids encompassed the two spawning events of August and September 2013, which involved numerous *Acropora* species (Sola et al. in press). The occurrence of small numbers of acroporid spat on plates throughout the year may have resulted either from other *Acropora* species and non-*Acropora* genera of acroporids breeding outside of the spawning peak, or from larval input from other reefs (Baird et al. 2012). Pocilloporid settlement peaked between October 2012 and January 2013. Spat from this family dominated plates in all seasons, except between August and October (Figure 3). Since many pocilloporids are brooders with the ability to release planulae year-round, it is often found that they settle throughout the year, despite a seasonal peak in the summer (Glassom et al. 2006; Mangubhai et al. 2007; Baird et al. 2012), which is consistent with findings in the present study. Seasonal rates

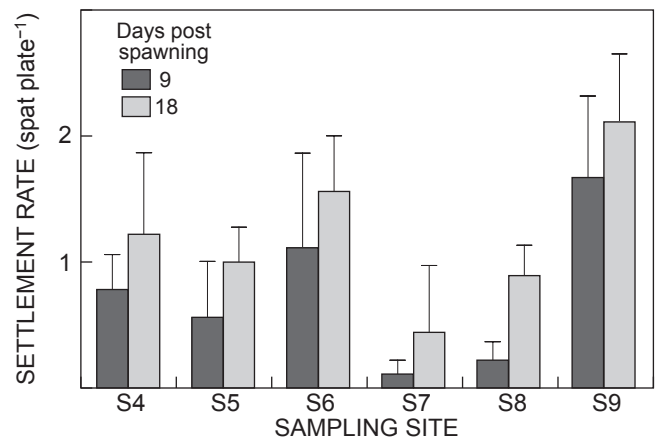


Figure 3: Variation in settlement 9 and 18 days following a spawning event, measured at six sites along the northern side of Vamizi Island. Error bars denote SE

Table 3: Summary of the number of juvenile corals found at each sampling site off Vamizi Island, according to family and genus. A total area of 4.8 m² was inspected at each site

Coral taxon	Number of juvenile corals			Total
	Site 1	Site 2	Site 3	
Acroporidae	51	76	7	134
<i>Acropora</i>	51	74	4	129
<i>Astreopora</i>	0	0	3	3
<i>Montipora</i>	0	2	0	2
Merulinidae	3	6	12	21
<i>Echinopora</i>	0	1	0	1
<i>Favia</i>	1	2	5	8
<i>Goniastrea</i>	2	3	7	12
Mussidae	1	2	8	11
<i>Acanthastrea</i>	1	0	0	1
<i>Favites</i>	0	2	8	10
Oculinidae	0	3	4	7
<i>Galaxea</i>	0	3	4	7
Pocilloporidae	22	21	7	50
<i>Pocillopora</i>	7	19	4	30
<i>Seriatopora</i>	9	2	3	14
<i>Stylophora</i>	6	0	0	6
Poritidae	2	7	7	16
<i>Porites</i>	2	7	7	16
Unidentified	3	5	3	11
Total	110	159	86	355
Mean (SD)	10.4 (7.3)	15 (10.9)	6.6 (2.6)	–

of pocilloporids only varied 4-fold, and thus the increase in total settlement between August and October 2013 was mainly due to the increase in acroporid settlers.

Most of the observed variance in settlement rates was attributable to difference among seasons. This suggests that, at Vamizi Island, variability in the overall settlement rates resulted mainly from seasonal variation in larval supply and largely reflected the highly seasonal patterns of acroporid settlement, which is likely to result from the highly seasonal patterns of spawning in *Acropora* populations. Nonetheless, conclusions on seasonal patterns of settlement must be treated with caution given the limited temporal scale of the study.

Once seasonal variation was accounted for, spatial variation among sites, subsites and individual plates contributed only 10.9%, 1.5% and 14.8%, respectively, suggesting that patchiness in settlement occurred both at the smallest scale (centimetres) and the largest scale (kilometres), but differences among subsites was of medium scale (metres), and within sites it was negligible. Spatial patchiness also varied with season. When total settlement was low, no strong contrast was apparent at the scale of kilometres and most of the patchiness occurred at the smallest spatial scale. However, in periods of abundant larval supply, most settlement was concentrated at Site 3 and differences among sites exceeded those observed within sites. A high proportion of variance attributable to individual plates within sites is common in coral settlement studies (Glassom et al. 2006; O'Leary and Potts 2011). At several other locations, the highest proportion of variance, after that between individual plates, occurred between sites that were hundreds of metres apart, but very little of the variance was associated with a spatial scale of kilometres (Dunstan and Johnson 1998; Hughes and Connell 1999; Glassom et al. 2004), implying that patchiness tends to be evened out at scales larger than 1 km. At Vamizi Island, patchiness at intermediate scales (hundreds of metres) was not assessed, but apparent patchiness at the scale of kilometres may be due to strong currents at the time of spawning and to differences in habitat conditions at widely separated sites.

Short-term larval settlement rates

In this study, substantial settlement of both acroporids and pocilloporids could be observed on plates removed nine days after the spawning event of August 2013. This is consistent with precompetency periods expected for both groups. Indeed, brooders, which most pocilloporids are likely to be, release planulae that are ready to settle within hours (reviewed in Harrison and Wallace 1990; Gleason and Hofmann 2011). Larvae from some broadcast spawners can settle as early as one day after fertilisation (Nozawa and Harrison 2005) and a peak in larval competence and settlement occurs in the week following spawning (Connolly and Baird 2010; Figueiredo et al. 2013). Plates removed 18 days after the spawning event had significantly higher spat density than after nine days (Figure 3), showing that settlement continued for at least this period. This was consistent with expected competency curves (Connolly and Baird 2010) and strongly indicative of continuous settlement of *Acropora* in the first weeks after spawning. The short-term experiment did not cover the second spawning event that took place in late September 2013 and which appeared to be of greater intensity. Thus, the high rates of settlement observed between August and October 2013 (Figure 2) may have resulted either (1) from sustained settlement over the weeks following the first spawning event, in addition to settlement following the second event, (2) mainly from settlement occurring after the second event, or (3) from the input of larval supply from upstream reefs, which may have taken place anytime during the three-month immersion period.

Regional comparison

Although it is interesting to compare estimates of settlement rates among studies from different locations,

such comparisons should be treated with caution. This is because variation in the type and size of artificial substratum, or in methods of deployment, can influence the results obtained in different studies, and the method used to standardise settlement rate to number of spat $m^{-2} y^{-1}$ can yield different estimates, even within single studies. The shape and size of settlement plates and the tendency for larvae to settle near the edges may influence the calculations of settlement density (Field et al. 2007), making meaningful comparisons between studies difficult.

Studies from East Africa, however, have mainly used unglazed ceramic tiles of similar size to those used in our study, typically 12–15 cm in length (Franklin et al. 1998; Nzali et al. 1998; Glassom et al. 2006; Mangubhai et al. 2007) and a soak time of one year, rendering the results comparable. Because these studies addressed the density of settlement on the surface preferred by spat, only the bottom surface is considered here to estimate spat density. Settlement in Vamizi was 1 130 spat $m^{-2} y^{-1}$. This is higher than the 500–600 spat $m^{-2} y^{-1}$ found along the Tanzanian coast (Franklin et al. 1998; Nzali et al. 1998), and similar to results from South Africa and Kenya where Glassom et al. (2006) and Mangubhai et al. (2007) estimated annual settlements of 976 and 1 167 spat $m^{-2} y^{-1}$, respectively. This is consistent with the hypothesis that there is no latitudinal trend in annual settlement rate along the east coast of Africa (Mangubhai et al. 2007).

Along the east coast of Australia, there is a shift in settlement dominance from broadcast spawners, mainly acroporids, at low latitudes to brooding species, mainly pocilloporids, at high latitudes (Hughes et al. 2002). On the east coast of Africa, however, pocilloporids dominate on settlement plates both at equatorial locations (Mangubhai et al. 2007) and on subtropical reefs (Glassom et al. 2006). Hence Mangubhai et al. (2007) suggested that either a gradient does not exist in East Africa or the dominance of pocilloporids in Kenya resulted from the important loss of *Acropora* species in a 1998 bleaching event. At tropical Vamizi Island, the overall annual settlement was dominated by acroporid spat. *Acropora* species dominate the adult coral community at this location (Davidson et al. 2006) and the reefs have been little affected by previous mass bleaching events (Hill et al. 2009), lending support to the hypothesised effect of *Acropora* loss from Kenyan reefs. However, acroporids did not dominate the spat composition on an equatorial Tanzanian reef, even prior to the bleaching event (Franklin et al. 1998). Thus, settlement patterns in the region cannot be explained solely by the effects of bleaching on coral communities.

Settlement patterns, however, may be influenced by the South Equatorial Current that reaches the African coast at 10–12° S, covering the latitude of Vamizi Island, and then splits into the north-flowing East African Current and south-flowing Mozambique Current. It has been suggested that the South Equatorial Current constitutes a 'functional equator', offset from the geographic equatorial line, that influences biogeographic patterns (Obura 2012). Dominance of coral settlement by acroporid spat at Vamizi Island, with shifts towards more pocilloporids to the north and south, may support this hypothesis. The data on settlement patterns along the east coast of Africa are too

Table 4: Seasonal peaks of coral larval settlement along the east coast of Africa

Location	Peak settlement season	Source
Kenya	February–May	Mangubhai et al. (2007)
Tanzania (Taa reef)	April	Nzali et al. (1998)
Tanzania (Chumbe Island)	February–April and November–December	Franklin et al. (1998)
Mozambique (Vamizi Island)	August–October	This study
South Africa (Sodwana Bay)	March–May	Glassom et al. (2006)

sparse, however, for firm conclusions to be drawn. Further studies of settlement in Tanzania and along the coast of Mozambique may clarify this matter. A notable aspect of coral reproduction at Vamizi Island was that the peak in settlement differed in season by many months from all other locations studied on the African east coast (Table 4). This seasonality, however, was driven by the seasonal variation in larval supply of acroporids, the dominance of which was also particular to Vamizi Island. The position of Vamizi Island near the so-called functional equator may underlie these regionally unusual larval settlement patterns, but measurements of settlement rates along the coast of Mozambique are needed to obtain a more complete perspective of regional settlement dynamics in East Africa.

Juvenile coral community

Measuring mortality rates of newly settled juveniles in the field is difficult, owing to their small size and cryptic nature, and was beyond the scope of this study. However, the linkage between settlement patterns and the adult community was investigated by examining the intermediary stage of juvenile corals at Sites 1–3. Contrary to spat density, juvenile density did not vary significantly among sites. This, in addition to the absence of a correlation between spat density and juvenile density at any site, suggests that post-settlement mortality was different among sites and sufficient to result in a similar number of recruits reaching a juvenile stage. Settlement rates, however, show considerable annual variation, whereas juveniles of the considered size range can be more than a year old, so their density reflects recruitment over a longer period. A similar disparity between the rate of larval settlement and the abundance of adult corals has been shown to persist over years along the Great Barrier Reef (Hughes et al. 1999). Despite the total number of larvae settling at Site 3 throughout the year being 5-fold greater than for the two other sites, the abundance of corals between 5 and 50 mm in size was not higher. This implies higher rates of mortality in corals <5 mm at Site 3, and hence either less-favourable conditions for early-stage recruits, or more sporadic settlement, with higher interannual variation than at other sites. However, patterns of settlement to tiles may not reflect those to reef substrata, especially given that corals from few families typically settle on tiles. Therefore, any conclusions about early-stage mortality rates must be made with caution.

Conclusion

This study provides the first data on coral settlement in Mozambique. Settlement patterns were closely associated with a multispecies spawning event that generally

occurs annually, although may be split between consecutive months, and largely conformed to observations from other tropical areas, but differed in seasonality and dominant family from studies to the north, in Tanzania and Kenya, and to the south, in South Africa. This raises questions about the phenology of coral reproduction along the east coast of Africa and the influence of the South Equatorial Current. In particular, the notion of this current acting as a functional equator at a different latitude from the geographical equator may be supported, although this remains somewhat speculative. Patchiness of coral settlement, revealed by components of variance, was dominated by temporal difference, but also occurred at spatial scales of kilometres and centimetres. This is similar to findings at other locations and adds to a growing global dataset on coral larval dispersal.

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References

- Andutta FP, Kingsford MJ, Wolanski E. 2012. "Sticky water" enables the retention of larvae in a reef mosaic. *Estuarine, Coastal and Shelf Science* 101: 54–63.
- Ayre DJ, Hughes TP. 2000. Genotypic diversity and gene flow in brooding and spawning corals along the Great Barrier Reef, Australia. *Evolution* 54: 1590–1605.
- Babcock RC. 1985. Growth and mortality in juvenile corals (*Goniastrea*, *Platygyra* and *Acropora*) in the first year. In: Gabrie C, Salvat B (eds), *Proceedings of the 5th International Coral Reef Symposium, 27 May–1 June 1985, Tahiti*. pp 355–360. Available at http://www.reefbase.org/resource_center/publication/icrs.aspx [accessed 21 October 2015].
- Babcock RC, Baird AH, Piromvaragorn S, Thomson DP, Willis BL. 2003. Identification of scleractinian coral recruits from Indo-Pacific reefs. *Zoological Studies* 42: 211–226.
- Babcock R, Davies P. 1991. Effects of sedimentation on settlement of *Acropora millepora*. *Coral Reefs* 9: 205–208.
- Baird AH, Babcock RC. 2000. Morphological differences among three species of newly settled pocilloporid coral recruits. *Coral Reefs* 19: 179–183.
- Baird AH, Emslie MJ, Lewis AR. 2012. Extended periods of coral recruitment on the Great Barrier Reef. In: Yellowlees D, Hughes TP (eds), *Proceedings of the 12th International Coral Reef*

- Symposium, 9–13 July 2012, Cairns, Australia*. Townsville, Queensland: ARC Centre of Excellence for Coral Reef Studies. pp 1–5. Available at http://www.reefbase.org/resource_center/publication/icrs.aspx [accessed 21 October 2015].
- Bak RPM, Engel MS. 1979. Distribution, abundance and survival of juvenile hermatypic corals (Scleractinia) and the importance of life history strategies in the parent coral community. *Marine Biology* 54: 341–352.
- Baria MVB, Guest JR, Edwards AJ, Alino PM, Heyward AJ, Gomez ED. 2010. Caging enhances post-settlement survival of juveniles of the scleractinian coral *Acropora tenuis*. *Journal of Experimental Marine Biology and Ecology* 394: 149–153.
- Baums IB, Miller MW, Hellberg ME. 2005. Regionally isolated populations of an imperiled Caribbean coral, *Acropora palmata*. *Molecular Ecology* 14: 1377–1390.
- Birrell CL, McCook LJ, Willis BL. 2005. Effects of algal turfs and sediment on coral settlement. *Marine Pollution Bulletin* 51: 408–414.
- Chiappone M, Sullivan KM. 1996. Distribution, abundance and species composition of juvenile scleractinian corals in the Florida reef tract. *Bulletin of Marine Science* 58: 555–569.
- Connolly SR, Baird AH. 2010. Estimating dispersal potential for marine larvae: dynamic models applied to scleractinian corals. *Ecology* 91: 3572–3583.
- Davidson J, Hill N, Muaves L, Mucaves S, Silva I, Guissamulo A, Shaw A. 2006. Vamizi Island, Mozambique, marine ecological assessment. Unpublished report. Maluane/Cabo Delgado Biodiversity and Tourism Project, Pemba, Mozambique and Zoological Society of London.
- Davies SW, Matz MV, Vize PD. 2013. Ecological complexity of coral recruitment processes: effects of invertebrate herbivores on coral recruitment and growth depends upon substratum properties and coral species. *PLoS ONE* 8: e72830.
- Dunstan PK, Johnson CR. 1998. Spatio-temporal variation in coral recruitment at different scales on Heron Reef, southern Great Barrier Reef. *Coral Reefs* 17: 71–81.
- Erwin PM, Song B, Szmant AM. 2008. Settlement behavior of *Acropora palmata* planulae: effects of biofilm age and crustose coralline algal cover. In: *Proceedings of 11th International Coral Reef Symposium, 7–11 July 2008, Ft. Lauderdale, Florida*. Vol. 2. pp 1225–1229. Available at http://www.reefbase.org/resource_center/publication/icrs.aspx [accessed 21 October 2015].
- Field S, Glassom D, Bythell J. 2007. Effects of artificial settlement plate materials and methods of deployment on the sessile epibenthic community development in a tropical environment. *Coral Reefs* 26: 279–289.
- Figueiredo J, Baird AH, Connolly SR. 2013. Synthesizing larval competence dynamics and reef-scale retention reveals a high potential for self-recruitment in corals. *Ecology* 94: 650–659.
- Franklin H, Muhando CA, Lindahl U. 1998. Coral culturing and temporal recruitment patterns in Zanzibar, Tanzania. *Ambio* 27: 651–655.
- Glassom D, Celliers L, Schleyer MH. 2006. Coral recruitment patterns at Sodwana Bay, South Africa. *Coral Reefs* 25: 485–492.
- Glassom D, Chadwick N. 2006. Recruitment, growth and mortality of juveniles corals at Eilat, northern Red Sea. *Marine Ecology Progress Series* 318: 111–122.
- Glassom D, Zakai D, Chadwick-Furman NE. 2004. Coral recruitment: a spatio-temporal analysis along the coastline of Eilat, northern Red Sea. *Marine Biology* 144: 641–651.
- Gleason DF, Hofmann DK. 2011. Coral larvae: from gametes to recruits. *Journal of Experimental Marine Biology and Ecology* 408: 42–57.
- Graham EM, Baird AH, Connolly SR. 2008. Survival dynamics of scleractinian coral larvae and implications for dispersal. *Coral Reefs* 27: 529–539.
- Harii S, Kayanne H, Takigawa H, Hayashibara T, Yamamoto M. 2002. Larval survivorship, competency periods and settlement of two brooding corals, *Heliopora coerulea* and *Pocillopora damicornis*. *Marine Biology* 141: 39–46.
- Harrison PL, Wallace CC. 1990. *Reproduction, dispersal and recruitment of scleractinian corals*. Amsterdam: Elsevier.
- Hill N, Davidson J, Silva I, Mucaves S, Muaves L, Guissamulo A, Debney A, Garnier J. 2009. Coral and reef fish in the Northern Quirimbas Archipelago, Mozambique – a first assessment. *Western Indian Ocean Journal of Marine Science* 8: 1–12.
- Hughes TP, Baird AH, Dinsdale EA, Harriott VJ, Moltschanivskyj NA, Pratchett MS et al. 2002. Detecting regional variation using meta-analysis and large-scale sampling: latitudinal patterns in recruitment. *Ecology* 83: 436–451.
- Hughes TP, Baird AH, Dinsdale EA, Moltschanivskyj NA, Pratchett MS, Tanner JE, Willis BL. 1999. Patterns of recruitment and abundance of corals along the Great Barrier Reef. *Nature* 397: 59–63.
- Hughes TP, Baird AH, Dinsdale EA, Moltschanivskyj NA, Pratchett MS, Tanner JE et al. 2000. Supply-side ecology works both ways: the link between benthic adults, fecundity, and larval recruits. *Ecology* 81: 2241–2249.
- Hughes TP, Connell JH. 1999. Multiple stressors on coral reefs: a long-term perspective. *Limnology and Oceanography* 44: 932–940.
- Mangubhai S, Harrison PL, Obura DO. 2007. Patterns of coral larval settlement on lagoon reefs in the Mombasa Marine National Park and Reserve, Kenya. *Marine Ecology Progress Series* 348: 149–159.
- Miller K, Mundy C. 2003. Rapid settlement in broadcast spawning corals: implications for larval dispersal. *Coral Reefs* 22: 99–106.
- Miller MW, Weil E, Szmant AM. 2000. Coral recruitment and juvenile mortality as structuring factors for reef benthic communities in Biscayne National Park, USA. *Coral Reefs* 19: 115–123.
- Nishikawa A, Katoh M, Sakai K. 2003. Larval settlement rates and gene flow of broadcast-spawning (*Acropora tenuis*) and planula-brooding (*Stylophora pistillata*) corals. *Marine Ecology Progress Series* 256: 87–97.
- Nozawa Y, Harrison PL. 2005. Temporal settlement patterns of larvae of the broadcast spawning reef coral *Favites chinensis* and the broadcast spawning and brooding reef coral *Goniastrea aspera* from Okinawa, Japan. *Coral Reefs* 24: 274–282.
- Nzali LM, Johnstone RW, Mgaya Y. 1998. Factors affecting scleractinian coral recruitment on a nearshore reef in Tanzania. *Ambio* 27: 717–722.
- Obura D. 2012. The diversity and biogeography of Western Indian Ocean reef-building corals. *PLoS ONE* 7: e45013.
- O’Leary JK, Potts DC. 2011. Using hierarchical sampling to understand scales of spatial variation in early coral recruitment. *Coral Reefs* 30: 1013–1023.
- Penin L, Michonneau F, Carroll A, Adjeroud M. 2011. Effects of predators and grazers exclusion on early post-settlement coral mortality. *Hydrobiologia* 663: 259–264.
- Reidenbach MA, Koseff JR, Koehl MAR. 2009. Hydrodynamic forces on larvae affect their settlement on coral reefs in turbulent, wave-driven flow. *Limnology and Oceanography* 54: 318–330.
- Richmond R. 1985. Reversible metamorphosis in coral planula larvae. *Marine Ecology Progress Series* 22: 181–185.
- Richmond RH. 1988. Competency and dispersal potential of planula larvae of a spawning versus brooding coral. In: Choat JH, Barnes D, Borowitzka MA, Coll JC, Davies PJ, Flood P et al. (eds), *Proceedings of the 6th International Coral Reef Symposium, 8–12 August 1988*. pp 827–831. Available at http://www.reefbase.org/resource_center/publication/icrs.aspx [accessed 21 October 2015].
- Rogers CS, Fitz CH, Gilnack M, Beets J, Hardin J. 1984.

- Scleractinian coral recruitment patterns at Salt River Submarine Canyon, St. Croix, U.S. Virgin Islands. *Coral Reefs* 3: 69–76.
- Sale PF. 1999. Recruitment in space and time. *Nature* 397: 25–27.
- Sammarco PW. 1991. Geographically specific recruitment and postsettlement mortality as influences on coral communities: the cross-continental shelf transplant experiment. *Limnology and Oceanography* 36: 496–514.
- Sola E, Marques da Silva I, Glassom D. In press. Reproductive synchrony in a diverse *Acropora* assemblage at Vamizi Island, Mozambique. *Marine Ecology*. DOI: 10.1111/maec.12348.
- Tebben J, Tapiolas DM, Motti CA, Abrego D, Negri AP, Blackall LL, Steinberg PD, Harder T. 2011. Induction of larval metamorphosis of the coral *Acropora millepora* by tetrabromopyrrole isolated from a *Pseudoalteromonas* bacterium. *PLoS ONE* 6: e19082.
- Tomascik T. 1991. Settlement-patterns of Caribbean scleractinian corals on artificial substrata along a eutrophication gradient, Barbados, West-Indies. *Marine Ecology Progress Series* 77: 261–269.
- Tran C, Hadfield M. 2011. Larvae of *Pocillopora damicornis* (Anthozoa) settle and metamorphose in response to surface-biofilm bacteria. *Marine Ecology Progress Series* 433: 85–96.
- Underwood AJ. 1981. Techniques of analysis of variance in experimental marine biology and ecology. *Oceanography and Marine Biology: an Annual Review* 19: 513–605.
- Underwood JN, Smith LD, van Oppen MJH, Gilmour JP. 2009. Ecologically relevant dispersal of corals on isolated reefs: implications for managing resilience. *Ecological Applications* 19: 18–29.
- Vollmer SV, Palumbi SR. 2007. Restricted gene flow in the Caribbean staghorn coral *Acropora cervicornis*: implications for the recovery of endangered reefs. *Journal of Heredity* 98: 40–50.
- Wallace CC. 1999. *Staghorn corals of the world: a revision of the coral genus Acropora (Scleractinia, Astroncoeniina, Acroporidae) worldwide, with emphasis on morphology, phylogeny and biogeography*. Collingwood: CSIRO Publishing.
- Whitaker K. 2004. Non-random mating and population genetic subdivision of two broadcasting corals at Ningaloo Reef, Western Australia. *Marine Biology* 144: 593–603.
- Wilson J, Harrison P. 2005. Post-settlement mortality and growth of newly settled reef corals in a subtropical environment. *Coral Reefs* 24: 418–421.
- Wittenberg M, Hunte W. 1992. Effects of eutrophication and sedimentation on juvenile corals. I. Abundance, mortality and community structure. *Marine Biology* 112: 131–138.
- Zar JH. 1984. *Biostatistical analysis*. Englewood Cliffs, New Jersey: Prentice-Hall.