

Patterns of coral larval settlement on lagoon reefs in the Mombasa Marine National Park and Reserve, Kenya

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ABSTRACT: Spatial and temporal patterns of coral larval settlement were studied on 2 lagoon reefs in the Mombasa Marine National Park and Reserve (4°S) from 2003 to 2005, to examine relationships between larval settlement and the timing and extended duration of coral spawning events in Kenya. In contrast to coral settlement in most other tropical regions, Pocilloporidae dominated on settlement tiles and comprised 93.7% of spat, while Acroporidae, Poritidae and Faviidae comprised 4.7% of spat. Coral settlement varied significantly spatially and temporally, with space–time interactions occurring. Annual mean spat densities in the park (101 spat m⁻²) were comparable to data from subtropical reefs, while densities in the reserve (908 spat m⁻²) were comparable to tropical reefs. These data suggest that there is no distinct latitudinal gradient in spat density along the East African coast. Spat settlement was seasonal, with peak settlement occurring predominantly on tiles immersed from February to May during the northeast monsoon, and was consistent with the timing of gamete release in *Acropora* and faviid species in Kenya. While non-coral fauna was 4 times more abundant than corals on settlement tiles, there was no evidence of significant competition among these spat groups. It is suggested that the relatively asynchronous and extended breeding season in Kenyan corals may result in reduced competition during settlement.

KEY WORDS: Coral settlement · Spat densities · Coral reproduction · Equatorial reefs · Kenya · East African coast

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INTRODUCTION

Knowledge of the spatial and temporal patterns of coral reproduction, settlement and recruitment is essential for understanding ecological and evolutionary processes on coral reefs (Harrison & Wallace 1990), and how well corals respond to natural and anthropogenic changes in their environment (Richmond 1997). Artificial substrata have been used widely since the early 1980s to detect coral settlement and recruitment patterns on reefs and infer larval availability (Harrison & Wallace 1990). Settlement involves initial larval attachment to the substratum, then metamorphosis to form a primary polyp ('spat'), whereas recruitment refers to the stage when newly formed

individuals ('recruits') become large enough to be censused (Harrison & Wallace 1990). During settlement and the post-settlement period, mortality may be high depending on the phototactic behaviour and 'active choices' by larvae, local physical conditions, and interactions (e.g. predation and competition) with other organisms (Keough & Downes 1982, Babcock & Mundy 1996).

Spat settlement can vary over spatial scales of region, site, depth, habitat and reef zone, and over temporal scales of months, seasons and years (Birke-land et al. 1981, Wallace 1985, Harriott & Fisk 1988, Sammarco 1991, Hughes et al. 1999) with complex space–time interactions occurring (Dunstan & Johnson 1998, Glassom et al. 2004, Adjeroud et al. 2006). Sea-

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sonal patterns of settlement appear to be linked to the timing of spawning and planulation events and the mode of reproduction of corals (Harrison & Booth 2007). On the Great Barrier Reef (GBR) spat settlement has been recorded in the months following mass spawning in the austral spring or summer (Harrison et al. 1984), with broadcast spawners such as acroporids having a more pronounced settlement period, and brooders such as pocilloporids and poritids having a more extended period (Wallace 1985, Harriott & Fisk 1988).

In some coral taxa the relative abundance of spat populations are similar to adult populations, which has led some authors to conclude that reefs may be 'self-seeding,' while for other taxa the relative abundance of spat are disproportionately higher or lower than adult populations, suggesting that dispersal and/or post-settlement processes play important roles in determining community dynamics and structure (Rylaarsdam 1983, Sammarco 1991, Smith 1992). The extent to which coral communities and reefs are self-seeding or interconnected by larval dispersal is still a strongly debated topic (Harrison 2006), as larval dispersal is influenced by mode of development (i.e. internal versus external), competency periods, mortality rates, oceanography, and the location and topography of reefs (Harrison & Wallace 1990, Harrison & Booth 2007).

Coral settlement patterns have been studied mostly in the Pacific (Birkeland et al. 1981, Hughes et al. 2002 their Table 1, Adjeroud et al. 2006) with comparatively few studies undertaken in the Western Indian Ocean and Red Sea (e.g. Franklin et al. 1998, Nzali et al. 1998, Glassom et al. 2004, 2006). The movement of the Inter-Tropical Convergence Zone across the equator results in 2 distinct monsoon seasons on the East African coast, the northeast (December to March) and southeast (May to October) monsoons, which have an influence on the timing of coral reproduction in Kenya (Mangubhai & Harrison 2006, 2007). *Acropora* and faviid species spawn over a period of 9 mo from August to April, with spawning peaking in the northeast monsoon months of January to March (Mangubhai & Harrison 2006, 2007), which contrasts markedly with the mass synchronous spawning that occurs on the GBR (Harrison et al. 1984, Harrison 1993). To date, there has been no detailed analysis of spatial and temporal patterns in settlement on equatorial reefs in Kenya. Therefore, the aim of this study was to quantify spatial and temporal patterns of scleractinian coral settlement at 2 sites within the Mombasa Marine National Park and Reserve, using artificial settlement tiles to examine relationships between larval settlement and the timing and extended duration of coral spawning in Kenya (Mangubhai & Harrison 2006, 2007).

MATERIALS AND METHODS

Study sites. The study was done at Coral Gardens (3° 59' S, 39° 45' E) and Nyali Reef (4° 4' S, 39° 43' E) within the Mombasa Marine National Park and National Reserve, respectively (Fig. 1). Since the Park and Reserve were gazetted in 1986, Coral Gardens has been protected from all extractive use, while at Nyali Reef, fishing has been restricted to traditional fishers. Both sites are patch reefs within the shallow lagoon (0 to 7 m depth) that is formed by a 200 km fringing reef that extends from Shimoni (near the border with Tanzania) to Malindi.

Benthic composition. Line intercept transect surveys were conducted in December 2003 to quantify benthic cover at Coral Gardens and Nyali Reef. Ten 10 m long transects were haphazardly placed parallel to each other on small patch reefs at each site at 0.5 to 1.5 m depth (mean low water). Cover was recorded for 11 benthic categories: corals (hard, soft), algae (coralline, *Halimeda* spp., fleshy), substrata (rock/turf, sand/rubble, rubble, sand, seagrass) and 'other.' Hard corals were further divided into 5 categories: massive, sub-massive, encrusting, branching and solitary.

Settlement on tiles. CORDIO East Africa has monitored coral settlement onto ceramic tiles at Coral Gardens since 1999 (D. O. Obura unpubl. data). For consistency with this long term dataset, the same type and number of tiles were placed at Coral Gardens and Nyali Reef from May 2003 to August 2005. Two mesh-covered metal frames (0.6 m × 0.3 m, mesh size: 0.08 m

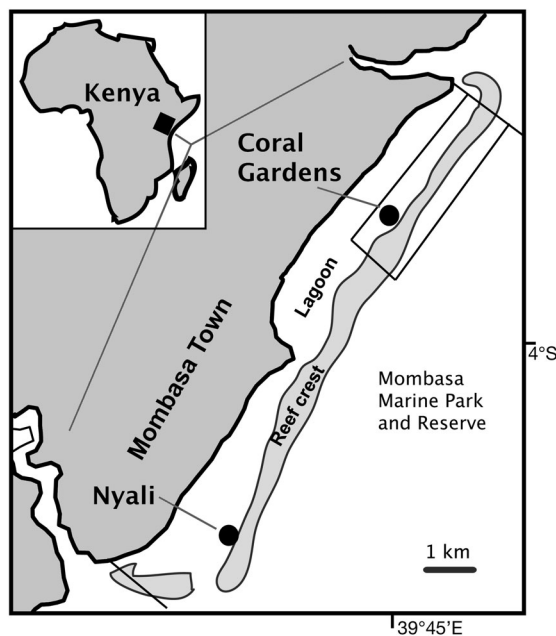


Fig. 1. Study sites in the Mombasa Marine National Park and Reserve

$\times 0.08$ m), similar to those deployed in Tanzania (Franklin et al. 1998, Nzali et al. 1998), were anchored to substrata at the 2 sites, and separated by a distance of <5 m. Ten unconditioned tiles ($0.15 \text{ m} \times 0.15 \text{ m}$) were placed on each frame at 45° with the rough surface facing down and the glazed surface up, because coral larvae preferentially settle on irregular surfaces (Carleton & Sammarco 1987) and on the underside of tiles in shallow environments (Birkeland et al. 1981, Wallace 1985, Carleton & Sammarco 1987). Given that very few 'spat' settled on upper tile surfaces or edges ($<8\%$), only those on lower surfaces are analysed in this paper.

Settlement tiles were replaced in the field every 3 mo, in February, May, August and November each year, and removed tiles were placed in household bleach for 2 to 3 d to remove organic matter, then dried and labelled. In May 2004, the majority of tiles were lost at Nyali Reef due to storm breakage and have been excluded from analyses. Additional tile data were available for Coral Gardens from August 2002 to May 2003 prior to the main study period, and these are included in this paper. All coral spat were circled, numbered, and the following information was recorded for each spat examined under a stereomicroscope: (1) identity to the family level, in accordance with Babcock et al. (2003); (2) maximum diameter to the nearest 0.1 mm; (3) number of polyps present; and (4) health status (i.e. undamaged, damaged, overgrown by other organisms). Spat were listed as 'unknown' if the identity of the coral could not be determined due to damage, and listed as 'other' if the family could not be determined with sufficient confidence. Photographs were taken of representative members of each family under a scanning electron microscope. In addition, the number of oysters, serpulids, barnacles and bryozoans on each tile were recorded to examine their potential interaction with coral spat. The interaction between coral spat and other soft-bodied fauna and flora were not documented by this study.

Statistical analyses. Data were analysed using SPSS 11.0 for Windows. Statistical analyses were done on the abundance of spat on settlement tiles from May 2003 to August 2005, which is the sampling period when data were available for both sites. The data available for Coral Gardens for 2002 to 2003 were not analysed and are only represented graphically. Homogeneity of variance in coral spat was determined using Levene's test and was found to be significant ($p < 0.001$). Although log-transformation did not fully normalize the data, the residuals had a normal distribution and, hence, a general linear model (GLM) univariate procedure was chosen because it is fairly robust to small deviations from normality (Zar 1999). Given that settlement tile data were not available for May 2004 at

Nyali Reef, a Type IV sum of squares (SS) model was used because it is designed for situations where there are missing data. Where significant differences occurred, pairwise multiple comparisons were done using Bonferroni adjusted p -values to determine which means differed significantly.

The effects of covariate variables and covariate interactions with individual factors can be tested in a GLM. The use of the term 'effect' in a GLM does not imply causality, only that variables are responding in some manner to each other. The potential for interactive effects of non-coral fauna and coral spat settled on tiles was tested by including barnacle, serpulid, oyster and bryozoan densities as covariate variables in the GLM.

RESULTS

Benthic community composition at study sites

Coral Gardens and Nyali Reef had similar benthic substrata and community composition with rock/turf areas dominating ($\sim 38\%$ mean cover) followed by hard corals ($\sim 25\%$ mean cover) (Fig. 2a). With the exception of rubble and seagrass, there were no significant differences in the mean percentage cover of major benthic categories between the sites (t -test, $p > 0.05$). The reef coral community was dominated by massive and submassive corals comprising 17 to 21% of the mean cover (Fig. 2b). Mean cover of branching corals at Coral Gardens was very low, comprising 0.6% of the benthic cover compared to 5.2% at Nyali Reef, which was about 9 times greater cover and was significantly higher ($p < 0.05$).

Total settlement on tiles

A total of 4294 coral spat were recorded on 400 tiles during the study, with representatives mainly from 4 families (Table 1, Fig. 3). The Family Pocilloporidae dominated, comprising 93.7% of all spat, while Poritidae, Acroporidae and Faviidae spat comprised 3.2, 1.4 and 0.1%, respectively. Fifty-six tiles immersed at Coral Gardens (23.2%) had no spat, compared to 2 tiles at Nyali Reef (1.3%). Coral Gardens had an annual mean density of 2.3 spat tile⁻¹ (101 spat m⁻²) and a maximum of 10 spat tile⁻¹ (444 spat m⁻²), while Nyali Reef had an annual mean density of 20.4 spat tile⁻¹ (908 spat m⁻²) and a maximum of 73 spat tile⁻¹ (3244 spat m⁻²), for the period May 2003 to February 2005. The mean density of spat at Nyali Reef in May 2004 was estimated by averaging the mean spat recorded on tiles immersed at the site in May 2003 and

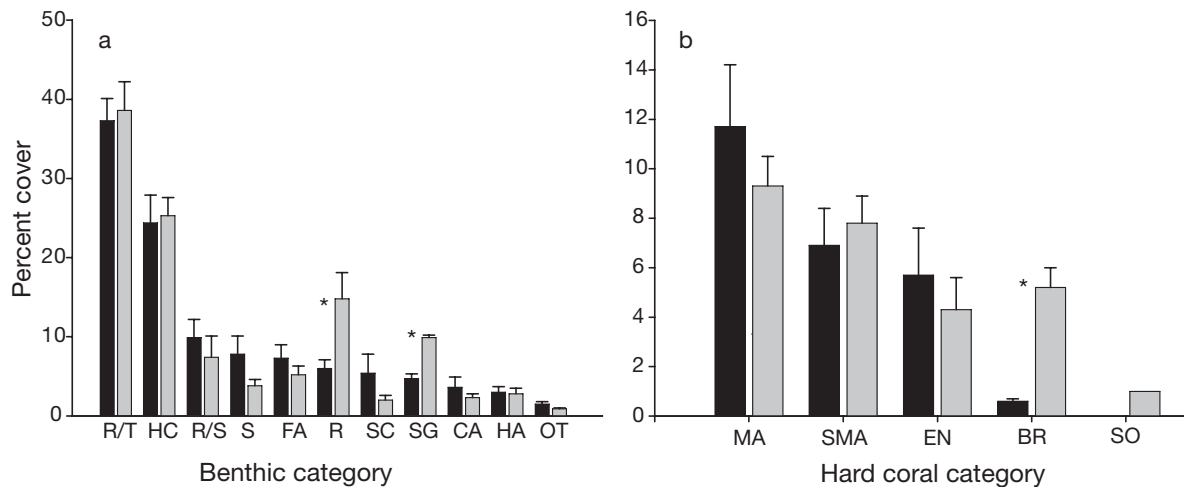


Fig. 2. Mean percent cover of (a) major benthic and (b) hard coral categories at Coral Gardens (black bars) and Nyali reef (grey bars). Error bars: +SE. *significant differences between sites (*t*-test, $p < 0.05$). R/T: rock/turf, HC: hard coral, R/S: rubble/sand, S: sand, FA: fleshy algae, R: rock, SC: soft coral, SG: seagrass, CA: coralline algae, HA: *Halimeda* spp. algae, OT: other, MA: massive, SMA: submassive, EN: encrusting, BR: branching, SO: solitary

Table 1. Number, percent composition (Comp.) and mean density of coral spat for each taxon from August 2002 to August 2005. 'Period' represents the number of times settlement tiles were placed in the field for a period of 3 mo

Taxa	Coral Gardens			Nyali Reef			All sites		
	N	Comp. (%)	Density (spat tile ⁻¹)	N	Comp. (%)	Density (spat tile ⁻¹)	N	Comp. (%)	Density (spat tile ⁻¹)
Pocilloporidae	920	88.6	3.82	3104	95.3	19.52	4024	93.7	10.06
Poritidae	87	8.4	0.36	52	1.6	0.33	139	3.2	0.35
Acroporidae	2	0.2	0.01	56	1.7	0.35	58	1.4	0.15
Faviidae	4	0.4	0.02	1	0.0	0.01	5	0.1	0.01
Other	9	0.9		5	0.2		14	0.3	
Unknown	16	1.5		38	1.2		54	1.3	
Total spat	1038			3256			4294		
No. tiles	241			159			400		
Period	12			8			20		

Table 2. Analysis of spatial and temporal variance in coral spat on settlement tiles immersed for 3 mo periods between May 2003 and August 2005 at Coral Gardens and Nyali Reef. GLM of $\log(x + 0.5)$ transformed data with Type IV SS. $r^2 = 0.81$

Source	df	MS	F	p
Site	1	313.63	754.80	<0.001
Year	2	3.77	9.06	<0.001
Period	3	9.95	23.95	<0.001
Site × Year	2	5.16	12.41	<0.001
Site × Period	3	5.50	13.23	<0.001
Year × Period	3	1.07	2.56	0.055
Site × Year × Period	2	2.39	5.75	0.004
Error	323	0.42		

May 2005. Overall, there was a 9-fold difference in the annual mean spat densities between the 2 sites.

Spatial and temporal settlement patterns

Unless stated otherwise, all the results presented in this section are for spat densities on settlement tiles from May 2003 to August 2005, which is the sampling period when data were available for both sites. Coral settlement onto tiles varied significantly spatially and temporally. There were highly significant differences in settlement between sites, years and periods when tiles were immersed in the field ($p < 0.001$), but there were interactions between Site × Year and Site × Period (Table 2). These results show that temporal

patterns were variable and not consistent from year to year or from one period to the next, and that their effect was dependent on site (Table 2). Interannual and inter-period changes in the mean density of spat at sites are shown in Fig. 4. Mean spat density was consistently higher at Nyali Reef than at Coral Gardens, and was statistically significant for all periods (Bonferroni adjusted p-values, $p < 0.001$) except for May 2003 ($p = 0.406$).

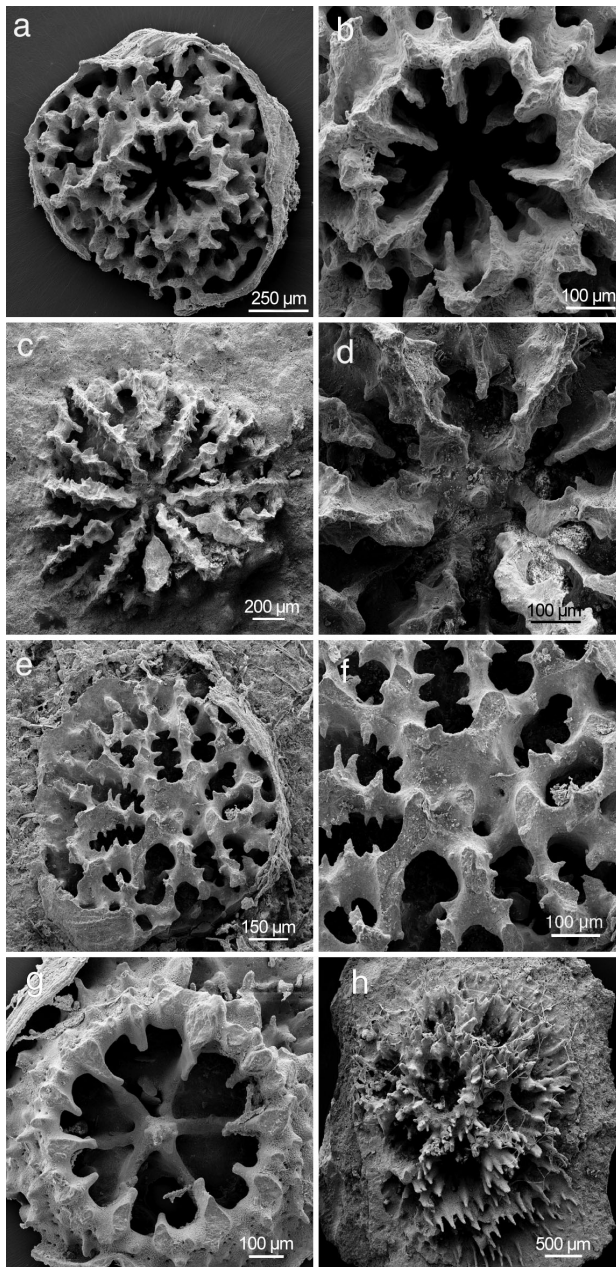


Fig. 3. Scanning electron microscope images of coral spat (maximum age 3 mo) belonging to the families (a,b) Acroporidae, (c,d) Faviidae, (e,f) Poritidae and (g,h) Pocilloporidae recorded on settlement tiles in Kenya

Overall settlement onto tiles was approximately 3 times higher during the northeast monsoon period compared to the southeast monsoon period. It is important to note that although data were missing for May 2004 from Nyali Reef, the mean density of spat recorded on tiles immersed at that site in May 2003 and May 2005 was low (≥ 4.4 spat tile⁻¹) (Fig. 4), hence proportional differences between monsoon seasons are not likely to be greatly affected by these missing data.

Peak settlement occurred in November to February (spring and summer) at Coral Gardens and in February to May (summer and autumn) at Nyali Reef, while the lowest settlement occurred in May to August (autumn and winter) at both sites (Fig. 4). The settlement tiles were dominated by Pocilloporidae spat. During peak periods, mean density of Pocilloporidae was 3.5 spat tile⁻¹ (153 spat m⁻²) at Coral Gardens and 37.5 spat tile⁻¹ (1167 spat m⁻²) at Nyali Reef. At Nyali Reef, interannual differences occurred only for the period of August to November (Bonferroni adjusted p-values, $p < 0.05$), while at Coral Gardens, interannual differences occurred during all periods ($p < 0.05$) except for February to May ($p = 0.227$). Settlement was much higher on tiles deployed in 2002 at Coral Gardens before the main study compared to the subsequent 2 yr, with a mean of 15.8 spat tile⁻¹ (702 spat m⁻²) recorded in November to February that year.

Coral settlement on tiles was generally highest in the northeast monsoon season for all taxonomic groups, and no families were found exclusively in one season (Fig. 5). Pocilloporidae dominated the spat in all seasons and occurred throughout the year at both

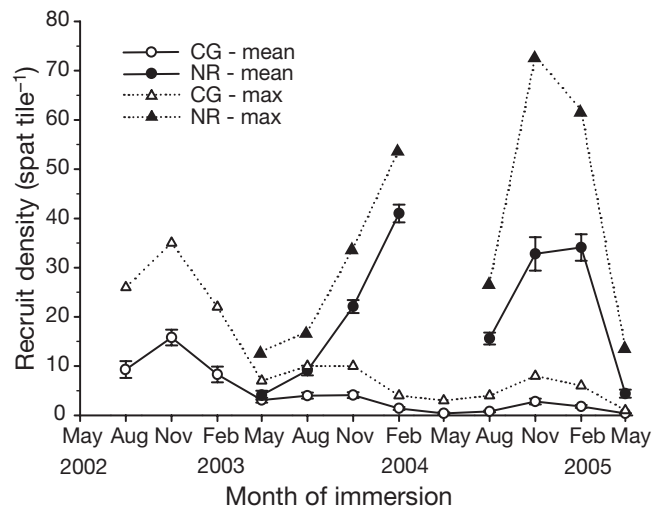


Fig. 4. Abundance of coral spat at Coral Gardens (CG) and Nyali Reef (NR) from August 2002 to May 2005. Mean and maximum values are shown. Error bars: \pm SE

sites. Peak settlement in Pocilloporidae occurred in November to February at Coral Gardens in all years. In contrast, peak settlement occurred in February to May in 2004 and over an extended period from November to May in 2005 at Nyali Reef (Fig. 5). The Family Poritidae also showed year-round settlement at Nyali Reef in both years, and at Coral Gardens in 2002 to 2003. Acroporidae spat were almost exclusively found at Nyali Reef and in all seasons during the study, with settlement peaking in February to May in both years (Fig. 5). Seasonal patterns of settlement in Faviidae cannot be determined because only 5 spat were recorded.

Size and health of coral spat

Spat size was measured using the parameters spat diameter and number of polyps spat⁻¹ for the 3 mo of tile immersion. The maximum spat diameter recorded was 7.4 mm (mean = 1.9 mm), while the maximum number of polyps recorded was 23 polyps spat⁻¹ (mean = 3.6 polyps spat⁻¹) (Table 3). Pocilloporidae spat had the highest rate of addition of new polyps, while Poritidae and Faviidae had the lowest. There was a positive linear relationship between Pocilloporidae spat diameter and number of polyps spat⁻¹ (GLM, $p < 0.001$, $r^2 = 0.82$). While there were no significant differences between tile immersion periods, there was a significant interaction between Site \times Year for both size parameters (GLM, $p < 0.001$). Multiple pairwise comparisons found significant differences in both size parameters between sites in 2003 and 2005 ($p < 0.05$). Testing for the effect of Year, there were significant differences in both size parameters between years at Coral Gardens ($p < 0.001$) but not at Nyali Reef ($p > 0.05$).

More than 95% of coral spat were undamaged on tiles at both sites. Spat that were dam-

Table 3. Spat size (maximum diameter) and number of polyps on settlement tiles (pooled for sites)

Taxa	Size (mm)			Polyps (no. spat ⁻¹)		
	Mean	SD	Range	Mean	SD	Range
Pocilloporidae	2.0	0.7	0.2 to 7.4	3.9	3.0	1 to 23
Faviidae	1.7	1.2	0.5 to 3.2	1.0	–	1
Acroporidae	1.2	0.5	0.3 to 3.5	1.4	1.3	1 to 8
Poritidae	1.0	0.5	0.4 to 2.8	1.1	0.3	1 to 3
Overall	1.9	0.7	0.2 to 7.4	3.6	3.0	1 to 3

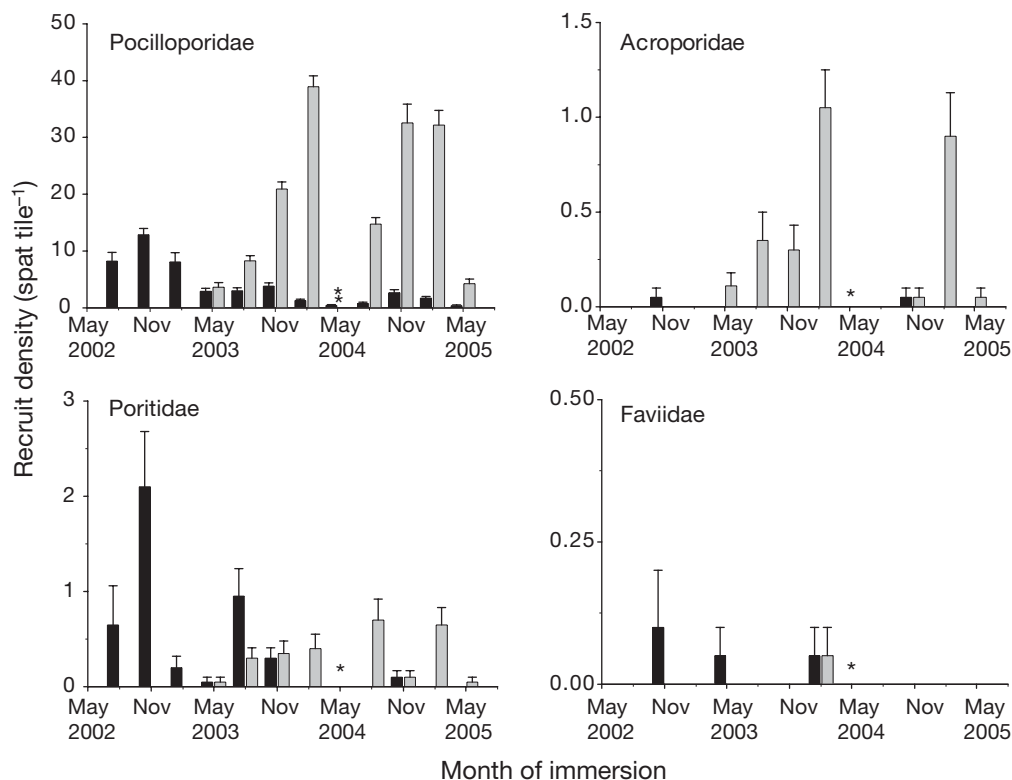


Fig. 5. Relative abundances of coral spat from 4 families at Coral Gardens (black bars) and Nyali Reef (grey bars) from August 2002 to May 2005. Error bars: +SE. Note that the y-axis scale differs in each graph. *tiles were lost for Nyali Reef during this period

aged or were overgrown by coralline algae and non-coral fauna comprised 2.5 and 1.7% of spat, respectively. While 56 coral spat (79.7%) in the 'overgrown' category were affected by coralline algae, it is not possible to determine if this interaction occurred while spat were alive, after they had died, or whether the interaction resulted in mortality. Ten spat (0.2%) were observed fused to an adjacent spat; all belonged to the Family Pocilloporidae.

Abundance of non-coral fauna

A total of 17980 non-coral fauna were recorded on tiles during the study, comprising 9457 barnacles (52.6%), 4953 serpulids (27.6%), 2400 oysters (13.3%) and 1170 bryozoans (6.5%). This equates to approximately 4 times as many non-coral fauna as coral spat. Coral Gardens consistently had a greater density of non-coral fauna, averaging 60.2 ind. tile⁻¹ (2676 m⁻²), compared to 21.8 ind. tile⁻¹ (969 m⁻²) at Nyali Reef. While all 4 categories of non-coral fauna showed year-round settlement, the timing of peak periods of settlement varied among the groups (Fig. 6). Barnacle density peaked in August to November (2528 barnacles m⁻²) at Nyali Reef in 2003 and 2004 and at Coral Gardens in 2004, while bryozoan density peaked in November to February at both sites (236 bryozoans m⁻²). There was no statistically significant interaction effect of barnacle or bryozoan density on coral settlement (GLM, $p > 0.05$). Serpulid density also peaked in November to February (946 serpulids m⁻²), and had a positive interaction effect with coral settlement when adjusted for the factors Site, Year and Period in the GLM ($p < 0.01$).

In contrast, oyster density peaked in February to May (474 oysters m⁻²) at both sites (Fig. 6), and had a more complex relationship with coral spat, with a significant interaction between oyster Density \times Year ($p < 0.05$). Parameter estimates for individual years suggested that in 2003 there was a positive interaction effect of oyster density on coral settlement when adjusted for the factors Site and Period in the GLM ($p < 0.05$), while in 2004 there was a small non-significant negative interaction effect recorded ($p = 0.623$).

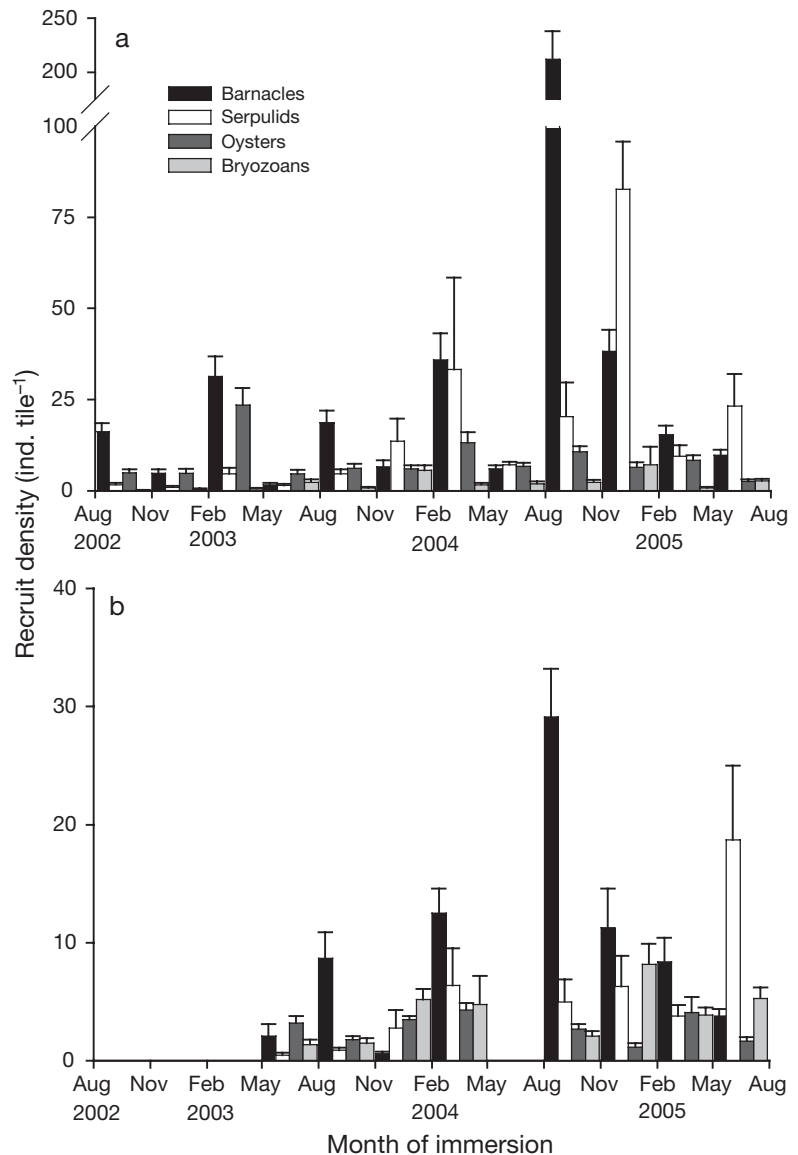


Fig. 6. Abundance of non-coral fauna recruits at (a) Coral Gardens and (b) Nyali Reef from August 2002 to May 2005

DISCUSSION

Composition of spat

The Family Pocilloporidae dominated settlement on tiles at Coral Gardens and Nyali Reef throughout the study, comprising 93.7% of spat. These results contrast markedly with studies on tropical reefs in the GBR, where Acroporidae dominate artificial settlement substrata (e.g. Wallace 1985, Harriott & Fisk 1988, Hughes et al. 2002), but are similar to those from high-latitude reefs in eastern Australia (Harriott 1992, Harriott & Banks 1995), the northern Red Sea (Glassom et al.

2004), South Africa (Glassom et al. 2006), and tropical reefs in French Polynesia (Adjeroud et al. 2006). Acroporidae spat comprised only 1.4% of spat in Kenya, compared to 9% recorded in the first year, and 35.1% in the subsequent 2 yr, of a study in South Africa (Glassom et al. 2006). The dominance of Pocilloporidae on settlement tiles on equatorial reefs in Kenya and subtropical reefs in South Africa (27 to 28° S), suggests that the transition in dominance from broadcast spawning corals to brooders on settlement tiles observed along the east Australian coast (Harriott 1992, Harriott & Banks 1995, Hughes et al. 2002), is not apparent in East Africa. However, these patterns may also reflect the loss of *Acropora* species on Kenyan reefs following the 1997 to 1998 coral bleaching event (McClanahan et al. 2001) and the slow rate of recovery occurring in this genus.

Density of spat

Coral settlement onto tiles varied significantly in space and time, with interactions occurring between the two (Table 2), which is similar to findings from other regions (Dunstan & Johnson 1998, Glassom et al. 2004, Adjeroud et al. 2006). Spat density was greater at Nyali Reef than at Coral Gardens, and this pattern was consistent for all settlement tiles from 2003 to 2005. Differences in spat density between these 2 sites were large, despite the similarity in cover of major benthic groups, and may be attributable to differences in the abundance of branching corals and their mode of reproduction, if some of these coral populations are largely self-seeding. Nyali Reef had a significantly higher mean percent cover of branching corals than Coral Gardens (Fig. 2b), mainly comprising *Pocillopora* and, to a lesser extent, *Acropora* species (S. Mangubhai & D.O. Obura pers. obs.). Given that *Stylophora* and *Seriatopora* species were absent at the 2 sites and are now extremely rare in Kenya (McClanahan et al. 2001), most spat identified as Pocilloporidae on settlement tiles are likely to be *Pocillopora* species. Site differences in branching coral cover and the overall densities of spat settling on tiles were both 9-fold, which suggests that *Pocillopora* spat availability may be a function of the relative abundance of adult colonies that brood larvae which settle soon after release, leading to locally enhanced larval settlement (Harrison & Wallace 1990).

Direct comparisons of settlement patterns between studies on different reefs or geographic locations must be made cautiously, because studies vary considerably in their choice of substrata material, method of tile immersion, length and timing of immersion relative to coral reproduction, and spatial variables such as depth,

habitat and reef zone. However, the magnitude of the settlement at Nyali Reef (908 spat m⁻² yr⁻¹) fits within the ranges recorded on the GBR, while settlement at Coral Gardens (101 spat m⁻² yr⁻¹) is comparable with levels observed in subtropical eastern Australia, the Caribbean and the Red Sea (see Table 6 in Glassom et al. 2004). On equatorial reefs in northern Tanzania (5 to 6° S), the annual mean spat density on settlement tiles was estimated to be 500 to 600 spat m⁻² (Nzali et al. 1998, Franklin et al. 1998), which is similar to densities recorded on tropical reefs in other parts of the world. However, these studies cannot be directly compared because the density and composition of spat on settlement tiles in Kenya are likely to have been influenced by the loss of corals resulting from the 1997 to 1998 coral bleaching event, whereas the 2 Tanzanian studies (Franklin et al. 1998, Nzali et al. 1998) were done in the mid-1990s, prior to the impacts of bleaching.

In a recent subtropical South African study, mean spat density was 976 spat m⁻² during peak settlement in March for tiles immersed for 3 mo or longer (Glassom et al. 2006), which is similar to the 1167 spat m⁻² recorded at Nyali Reef during peak settlement in February to May. While few studies have been conducted examining latitudinal gradients in spat density along the East African coast, the results from this study in Kenya suggest that differences in mean density between the tropics and subtropics observed along the eastern and western coasts of Australia (Harriott 1992, Harriott & Banks 1995, Harriott & Simpson 1997) do not occur in East Africa. Regional differences may be attributable to the position of Kenya's reefs and the GBR in relation to the oceanographic systems operating in both regions. The South Equatorial Current in the Pacific splits between 14 and 18° S latitude, with the southern-flowing unidirectional East Australian Current dominating along eastern Australia. The reefs of Western Australia are bathed by the southern-flowing unidirectional Leeuwin Current (Harrison & Booth 2007). In East Africa there are 2 opposite flowing current systems operating north and south of latitude 10° S. These 2 current systems result from the South Equatorial Current flowing across the Indian Ocean and splitting near the border of Tanzania and Mozambique into the northerly East African Coastal Current (EACC) and the southerly Mozambique Current, both of which run parallel to the coast. It is possible that the similarities between Kenya and South Africa may reflect a linear dispersal pattern occurring along the coast and the relative positions of the 2 countries towards the extreme ends of the northward flowing EACC and the southward flowing Mozambique Current, respectively.

Spat settlement and the timing of coral reproduction

The relationship between the timing of coral spawning and spat settlement has been shown by a number of studies (Wallace 1985, Harriott & Fisk 1988, Hughes et al. 1999, Glassom et al. 2004, Adjeroud et al. 2006). In Kenya, settlement occurred predominantly during the northeast monsoon, which coincides with the period of warmest sea surface temperatures and is consistent with the timing of gamete release in species of *Acropora* and faviids recorded at the 2 sites (Mangubhai & Harrison 2006, 2007). No information is available on the timing of reproduction in the families Pocilloporidae or Poritidae in Kenya, although data from this study suggest that reproduction in Pocilloporidae occurs throughout the year, but predominantly from November to May. It is not known why there were site differences in the timing of peak settlement, occurring from November to May at Coral Gardens and from February to May at Nyali Reef. Similar site differences were also found in South Africa, where peak settlement occurred in March and May, at southern and northern reefs, respectively (Glassom et al. 2006). In both studies, reefs were separated by a distance of 10 to 15 km. High settlement rates were observed on tiles immersed in November and in February at Nyali Reef in 2005, suggesting that spawning may have occurred over a longer period in this year, perhaps in response to the annual change in timing of the lunar reproductive periods, or perhaps due to different environmental conditions resulting in an extended period of successful settlement in 2005. Twenty-three *Acropora* and 2 faviid species commenced spawning earlier in 2005 than in 2004 (Mangubhai 2007).

Three species dominated the adult *Pocillopora* population at the study sites: *P. damicornis*, *P. verrucosa* and *P. eydouxi* (D. O. Obura unpubl. data), and it is possible that larvae of at least some of these species may have been present on settlement tiles. While its mode of reproduction in the Western Indian Ocean is currently not known, *P. damicornis* is hermaphroditic and broods sexually or asexually through derived planulae in many parts of the world, and is capable of undergoing multiple cycles of gametogenesis and planulation, with brooded larvae competent to settle within hours following release (reviewed by Harrison & Wallace 1990). *Pocillopora damicornis* spat have been shown to aggregate around adult colonies in some locations (Tioho et al. 2001), but in other areas some larvae are long-lived and have the potential for long distance dispersal (Richmond 1987). A recent genetic study by Souter (2007) found that this species has a clear population structure along southern reefs from Diani to Malindi in Kenya, with low levels of migration between reefs. Hence, there is a high likelihood that a

large portion of the reproductive output of this species is retained within or near its natal reef, and this is likely to be reflected in the settlement patterns observed in this study.

In contrast, *Pocillopora verrucosa* is a broadcast spawner in most parts of the world (Harrison & Wallace 1990) and spawns gametes annually in January in South Africa (Kruger & Schleyer 1998). Large oocytes were observed in tissue samples of *P. verrucosa* collected from Nyali Reef in December 2004 (S. Mangubhai unpubl. data), and therefore it is highly likely that this species releases gametes early in the year in Kenya. Given its mode of reproduction and genetic evidence that populations of *P. verrucosa* in South Africa are panmictic (Ridgway et al. 2001), this species may recruit onto natal reefs as well as be dispersed to other reefs. However, population genetic studies are required to confirm this hypothesis. The mode of reproduction is not known in *P. eydouxi*.

Although spat densities for Acroporidae were low (0.15 spat m^{-2}), settlement patterns generally coincided with the timing of broadcast spawning in *Acropora* species. In Kenya, *Acropora* species reproduce throughout the northeast monsoon from October to April, with reproduction peaking in February and March (Mangubhai & Harrison 2006). Settlement in Acroporidae spat occurred almost year-round at Nyali Reef, and peaked in February to May each year. The presence of Acroporidae spat on tiles in the winter months of August to October in 2003 was unexpected. Three potential explanations are: (1) winter spawning occurred in some *Acropora* species in 2003, (2) *Montipora* and *Astreopora* species (Family Acroporidae) that were present at the sites (S. Mangubhai pers. obs.) may have spawned in winter, or (3) spat were dispersed from other reefs during this period. Biannual broadcast spawning in autumn and winter months has been recorded in *Platygyra daedalea* in Kenya (Mangubhai & Harrison 2006, 2007), 3 *Montipora* species on the GBR (Stobart et al. 1992) and *Acropora* species in Western Australia (Rosser 2005), and *Acropora (Isopora) cuneata* planulates in winter on the GBR (Kojis 1986a), which provides some support for (1) and (2). Furthermore, *Acropora palifera* has been recorded south of the study sites between Kisite (near the border with Tanzania) to Diani (south of Mombasa town) (D. O. Obura unpubl. data), and if this species planulates year-round as it does on equatorial reefs in Papua New Guinea (Kojis 1986b), it may explain the presence of Acroporidae on settlement tiles immersed from August to October.

While there is no published information on the timing of spawning from other locations to support (3), tile settlement studies from Tanzania (Franklin et al. 1998, Nzali et al. 1998) suggest that spawning in *Acropora* oc-

curs predominantly during the northeast monsoon and peaks in April, with very few spat recorded in autumn and winter. This is similar to the settlement patterns recorded in Kenya. Given that the southeast monsoon winds would act in opposition to the northerly flowing EACC, long-distance dispersal of coral larvae from Tanzania to Kenya, particularly during May to August, is less likely to explain the patterns of spat settlement recorded in Acroporidae in this study.

Adult massive and submassive colonies of Faviidae and Poritidae are abundant at both Coral Gardens and Nyali Reef and both families were dominant in natural recruitment substrata surveys (Mangubhai 2007), but were poorly represented on settlement tiles. The low densities of Faviidae and Poritidae and the absence of other coral groups on tiles may be caused by the absence of appropriate cues for metamorphosis and settlement on these tiles, which has been demonstrated for some corals and other marine invertebrates (e.g. Harrison & Wallace 1990, Pawlik 1992, Baird & Morse 2004). Similar biases for and against different families have been observed on settlement tiles on the GBR (Harriott & Fisk 1988, Dunstan & Johnson 1998), the Red Sea (Glassom et al. 2004) and South Africa (Glassom et al. 2006). Poritidae showed year-round settlement with no distinct peaks, which suggests that reproduction in this family occurs over an extended period.

Interaction with other invertebrates

Non-coral fauna were 4 times as abundant as corals on settlement tiles in Kenya, but there was no evidence of significant competition between these 2 spat groups as no negative effects were detected in the GLM. While the 4 non-coral spat groups showed year-round settlement, the timing of peak periods of settlement varied among the groups. For example, barnacles (which represented 52.6% of non-coral spat) settled in August to November, before peak settlement periods for coral spat. In addition, only 1.7% of coral spat were observed being overgrown by oysters, serpulids or bryozoans during the entire study. These results contrast markedly with Dunstan & Johnson (1998), who found a significant negative correlation between coral spat density and total cover of bryozoans and oysters, and observed non-coral fauna frequently overgrowing coral spat on settlement tiles on the southern GBR. However, Dunstan & Johnson (1998) noted that standard correlation analysis was not suited to 'triangular distributions' and their results must be interpreted with caution. Growth patterns recorded in the different families in the Mombasa Marine National Park and Reserve were similar to those recorded from the southern GBR (Dunstan & Johnson 1998). The fusion of some

Pocilloporidae spat has also been observed in other studies of coral larval settlement (e.g. Hidaka et al. 1997), and may confer some advantages through increased size and decreased mortality during the critical post-settlement period.

Shlesinger & Loya (1985) suggested that the asynchronous spawning pattern recorded in the northern Red Sea may be a strategy for reducing competition among corals and other benthic organisms during settlement. The findings from our study lend some support to this hypothesis. Kenya has a more asynchronous and extended breeding season among corals compared to other regions (Mangubhai & Harrison 2006, 2007, Mangubhai 2007), with no evidence of significant competition with other organisms during settlement. Further settlement studies are required to explore this hypothesis further. The results of this study provide important baseline data for future settlement and recruitment studies that will be needed for quantifying the impacts of future disturbances and the long-term recovery and management of Kenya's coral reefs.

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