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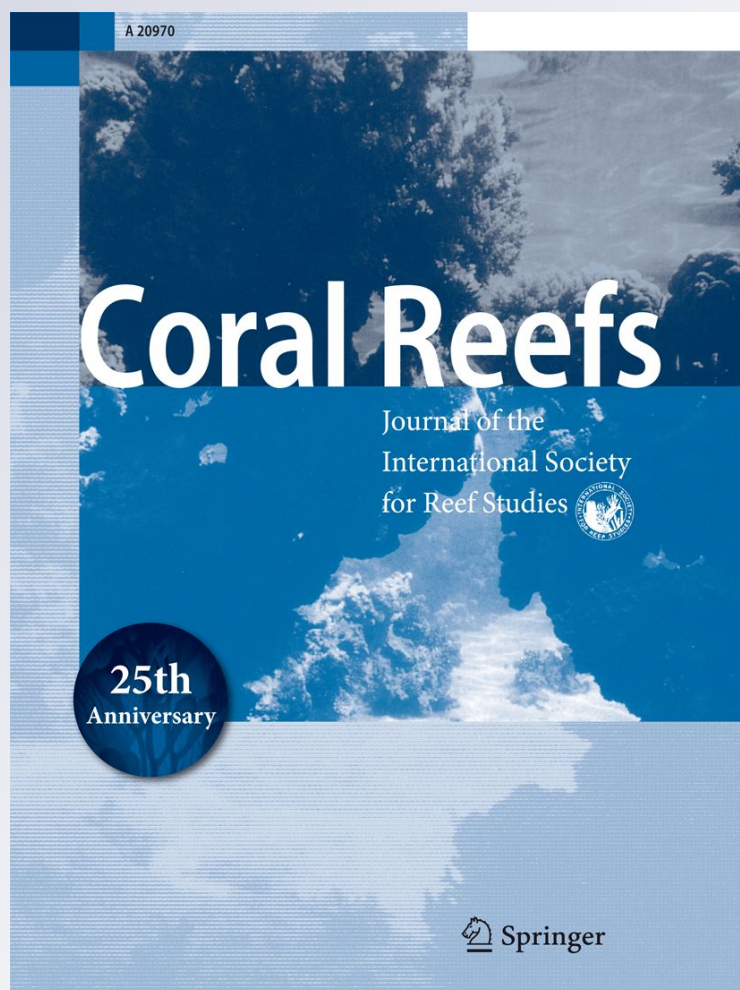
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Using hierarchical sampling to understand scales of spatial variation in early coral recruitment

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Abstract Ecological patterns are created by processes acting over multiple spatial and temporal scales. By combining spatially explicit sampling with variance components models, the relative importance of spatial scale to overall variability can be determined. We used a spatially structured experimental design in the Mombasa Marine National Park in Kenya to quantify variation in coral recruitment across four spatial scales (~1–1,000 m) and to generate hypotheses about processes affecting recruitment and potential sources of post-settlement mortality during early life history. For the dominant recruiting corals (*Pocillopora* spp.), variation in recruitment on surfaces protected from fish grazing was greatest at the largest spatial scale examined (1,000 m). We hypothesize that recruitment on protected surfaces varies mainly with larval delivery due to different lagoonal circulation and water flow between sites. Conversely, variation on surfaces exposed to fishes was greatest at the smallest spatial scale (1 m). We hypothesize that recruitment on exposed surfaces mainly reflects local differences in the scale and intensity of fish grazing, which may obscure larval delivery patterns. Spatial variation in recruitment can affect many

ecological processes and factors, including growth, survival to maturity, the distribution of habitat, and variation in species interaction strengths. This study demonstrates how spatially explicit sampling, followed by variance components modeling to partition variance across scales, can help to identify potential drivers of patterns at each relevant scale.

Keywords Variance components modeling · Post-settlement mortality · Larval dispersal · Early life history · *Pocillopora* · Indian Ocean

Introduction

Ecological and population patterns are driven by processes spanning a range of spatial and temporal scales (Levin 1992; Levin and Pacala 1997; Collinge 2001). Identifying the scales with the greatest variation can indicate when and where key ecological processes are operating and help to isolate the range of potential processes most important for determining patterns in populations and communities (Wiens 1989; Underwood and Chapman 1996; Nathan and Muller-Landau 2000). For species with complex life histories that include both an early dispersive phase (seed, spore, egg, or larva) and a sessile adult phase, factors affecting recruitment to the adult site are likely to play major roles in driving spatial variability in adult populations.

Recruitment is often defined empirically as survival up to the time of first census and thus includes pre-settlement, settlement, and post-settlement mortality (Keough and Downes 1982; Pineda et al. 2009). The early life-history period prior to recruitment (or first census) is often the least understood of all life stages (Wenny 2000; Vermeij and Sandin 2008). This is partly because of the difficulty of

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observing small dispersive stages and early recruits in field settings, and partly because recruitment is a dynamic process with potentially high variability across spatial and temporal scales (Sammarco and Andrews 1988; Nathan and Muller-Landau 2000).

Understanding the scales of variation inherent in settlement and post-settlement processes can help to identify the scales at which recruitment is most strongly regulated (Caffey 1985; Carr and Syms 2006; Pineda et al. 2009). One statistical approach is variance components modeling, which estimates the amount of variation in a dependent variable (e.g., recruitment) that is associated with one or more independent factors (e.g., spatial scale). This approach is typically applied to spatially explicit hierarchical sampling or experimental designs, and the outputs of such models estimate the proportions of total variance (components of variation) attributable to each factor. Spatially explicit studies encompassing several scales provide insights into the range of potential processes that may be operating and allow quantification of the relative importance of different scales to the overall variation (Underwood and Chapman 1996; Hughes et al. 1999).

Successful recruitment is critical for the persistence and resilience of sessile benthic marine organisms and involves multiple processes: spawning, larval transport (dispersal), settlement, metamorphosis, and post-settlement survival. Characterizing the scale-specific nature of processes and mechanisms underlying successful recruitment should enhance understanding of the distributions of adult populations and therefore of their communities (Heyward et al. 2002). Two particularly important aspects of recruitment that can be quantified using a spatially explicit approach are dispersal success (i.e., arrival at settlement sites) and post-settlement mortality. Dispersal is a biophysical process dependent on attributes of larvae (e.g., pelagic duration, behavior, larval competency), species interactions in the pelagic environment (e.g., predation), and hydrodynamic transport processes (Gaines and Bertness 1992; Strathmann et al. 2002; Levin 2006; Pineda et al. 2009). Dispersal can be either short or long distance, with populations being either primarily self-seeding or dependent on larval arrival from distant sources (Kinlan and Gaines 2003; Jones et al. 2009). Outcomes of dispersal can be determined by recording recruitment on identical surfaces in the absence of most causes of post-settlement mortality. However, in non-experimental settings, post-settlement mortality can greatly alter apparent settlement patterns through a number of processes including predation, competition (e.g., overgrowth), and physical factors (Hunt and Scheibling 1997). Post-settlement mortality due to predation can be isolated by holding other factors constant across spatial scales.

Reef-building corals are major constructors of biogenic habitat, and coral recruitment patterns can drive

community-wide patterns on coral reefs in cm to km, and daily to millennial scales. However, the magnitude of variation in coral recruitment at various spatial and temporal scales is relatively poorly documented (Dunstan and Johnson 1998). We found and reviewed 28 studies focusing on spatial patterns in coral recruitment, and only eight of them used a spatially explicit hierarchical approach (Table 1). The others were mainly small-scale studies or experiments (\leq tens of m) that did not span multiple spatial scales. The spatial scope of the eight studies that used spatially explicit hierarchical approaches ranged from meters to thousands of kilometers (Table 1), but only one study (Dunstan and Johnson 1998) also considered the effects of spatial variation in post-settlement mortality on recruit distribution. If the mechanisms behind post-settlement mortality are spatially variable, there should be strong correlations between the spatial variability of mortality mechanisms and observed recruitment patterns at relatively small scales (<1 – $1,000$ m).

We used a spatially structured, hierarchical experimental design to demonstrate how this technique can help to elucidate patterns and potential drivers of early coral recruitment (up to 1.5 months post-settlement) at relatively small scales of 1– $1,000$ m. By using a hierarchical design, we replicated the typical small-scale measurements of recruitment across several larger scales. Our design included protected and exposed surfaces at each scale, allowing us to form hypotheses about how various ecological processes may alter spatial scales of variation in early coral recruitment. We hypothesized that in the absence of fish grazers and predators, variation in recruitment would correspond to differences in hydrodynamics within the study site. In contrast, we hypothesized that where fishes are present, variation in recruitment would occur at smaller scales similar to those of variation in fish grazing.

Methods

Study area

The Kenyan coral reef system consists of 450 km of fringing reefs lying ~ 0.5 – 2 km offshore that protect a back-reef lagoon containing numerous patch reefs (McClanahan and Arthur 2001). This study was conducted in the Mombasa Marine National Park, a marine protected area (MPA) that has been closed to fishing since 1991. The park is within a shallow lagoon that is 1– 3 m deep at low tide, with a tidal range of 4 m during spring tides and 1 m during neap tides (McClanahan et al. 2008). The estimated residence time for lagoon waters is 1 day during spring tides and 2 days during neap tides (Angwenyi and Rydberg 2005). Within the lagoon at Mombasa MPA, flow rates are

Table 1 Summary of eight studies (of 28 reviewed) that used a spatially explicit hierarchical approach to understanding coral recruitment

Scale	Post-settlement mortality measured	Citation
Kilometers to thousands of km	No	Hughes et al. (2000)
Meters to thousands of km	No	Baird and Hughes (2000)
Meters to thousands of km	No	Hughes et al. (1999)
Meters to kilometers	No	Connell et al. (1997)
Meters to kilometers	Yes	Dunstan and Johnson (1998)
Meters to kilometers	No	Glassom et al. (2004)
Meters to kilometers	No	Sammarco and Andrews (1988)
Meters to kilometers	No	Soong et al. (2003)

highest near a channel that forms a break through the fringing reef in the NE region of the park, and flow rates are lower with longer water residence times farther from the channel (Tamelander et al. 2000).

The Mombasa MPA covers an area of $\sim 6 \text{ km}^2$. Much of the substratum consists of seagrass beds, but there are two main sites $\sim 1,000 \text{ m}$ apart are dominated by corals: Coral Gardens ($3^\circ 60' \text{ S}$, $39^\circ 45' \text{ E}$) and Starfish ($3^\circ 59' \text{ S}$, $39^\circ 44' \text{ E}$). Coral Gardens is located near the channel and has high flow rates and short water retention times; Starfish is located farther from the channel and has relatively low flow rates and longer water retention times. Water depths (1–3 m at low tide) at both sites are similar to those throughout the park.

In coral-dominated areas (i.e., both main sites), scleractinian corals comprise approximately 25% of the total benthic cover, with massive and submassive coral morphologies dominating (17–21% of total cover; Mangubhai et al. 2007). Since a major coral bleaching event in 1998, massive *Porites*, *Pocillopora*, and various faviids have been the dominant corals on protected reefs in Kenya (McClanahan et al. 2008). The dominant coral type in the Mombasa MPA in 2007–2008 was massive *Porites*, which accounted for approximately 23% of total substrate (T. McClanahan, pers comm). In the same time period, pocilloporids accounted for <1% of the substrate (T. McClanahan, pers comm).

Peak coral settlement in Kenya occurs between November and March (Tamelander et al. 2000), during and following the northeast monsoon season, and coincides with the warmest sea surface temperatures (Angwenyi and Rydberg 2005; Mangubhai et al. 2007). Synchronized multi-species mass-spawning events of the magnitude of those documented on the Great Barrier Reef have not been reported in Kenya (Mangubhai and Harrison 2008).

Recruit collectors

We deployed recruit collectors in the two coral-dominated sites within the Mombasa MPA: Coral Gardens and

Starfish. Each collection unit (collector) consisted of two $16.5 \times 16.5 \times 0.2 \text{ cm}$ sanded PVC tiles attached by a stainless steel bolt to a 30-cm-high and 1.5-cm-diameter PVC pipe in a “sandwich” configuration with the tiles 3 cm apart (Fig. 1a). The spacing was created using stainless steel washers on the bolt between the PVC pipe and the tile. Washers (3 cm diameter, 7.1-cm^2 area) were in contact with both inner and outer tile surfaces, so the effective settlement area on each tile surface was 265.2 cm^2 . The pairing of tiles in a “sandwich” design allowed analysis of coral recruitment patterns on two surfaces: an inner surface protected from large grazers and predators unable to access those surfaces, and an outer surface exposed to grazing and predation (Fig. 1a). This design required minimal maintenance while creating a major difference in grazing pressures. While the design may have modified some physical or light conditions on the inner compared with the outer surfaces, evaluating such effects was beyond the scope of this study.

We fixed each collector to the substrate by drilling a 5-cm-deep hole in dead coral and inserting a 30-cm-long, 1.5-cm-diameter metal stake into the hole. Each collector's PVC pipe fitted tightly onto its stake, and both the stake and PVC pipe were cemented at their joint base to the substrate with a 50/50 mix of masonry cement and sand mixed with seawater. This design kept settlement tiles immobilized in a vertical position and approximately 20 cm above the substratum. All collectors were placed with openings between tiles oriented in an east–west direction.

Experimental design

We used a four-level hierarchical design to determine variation in settlement and post-settlement mortality at spatial scales ranging from $\sim 1 \text{ m}$ to 1,000 m, which encompasses the full spatial range of coral-dominated habitat within the MPA. The largest scale was between the two sites, separated by $\sim 1,000 \text{ m}$ of seagrass habitat. Within each site, we established 4 locations, each 55 m apart. Within each

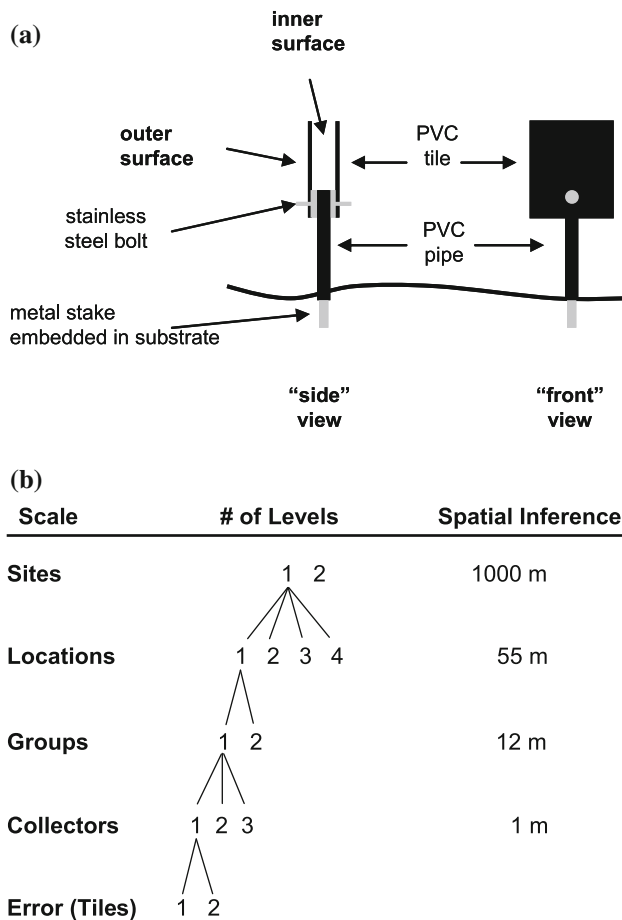


Fig. 1 a Collector design. b Experimental design showing spatial array of collectors across 4 spatial scales (1–1,000 m). Each spatial scale is nested within the scale above it (only left-hand nesting is shown)

location, we established 2 groups, spaced 12 m apart. Each group contained 3 collectors, spaced ~ 1 m apart. Thus, each site had a total of 24 collectors arranged in 4 locations, with 2 groups per location and 3 collectors per group (Fig. 1b). Spacing ranged from 55 m (locations) to 1 m (collectors, Fig. 1b). This arrangement covered the horizontal extent of coral-dominated reef at each site.

We placed clean, dry (unconditioned) PVC tiles on the collectors during the peak coral settlement period for two consecutive periods of 1.5 months (15 Nov 2007–1 Feb 2008 and 1 Feb 2008–14 Apr 2008). Tiles were replaced after 1.5 months to: (1) determine whether settlement patterns changed during the recruitment season and (2) investigate the roles of settlement and post-settlement mortality during the very early life history (≤ 1.5 months following settlement). Tiles were individually numbered with small stainless steel tags attached with a small plastic zip tie through a hole drilled in the upper corner. The numbers on tags always faced the outside of each tile when flush with the tile, to allow identification of inner versus

outer surfaces after collection. We collected tiles after each sampling period in individual plastic bags, transported them to shore, and air-dried them in the sun.

Recruit abundance

Two independent observers searched each tile for coral recruits under a dissecting microscope. Each coral individual (recruit) was circled with an indelible pen, numbered, and identified to family level (Babcock et al. 2003). To characterize general patterns of recruit abundance at the two sites, and on the inner versus the outer tile surfaces, we tested differences in recruit numbers between sites and treatments (inner versus outer surfaces) using a two-way ANOVA. Recruit counts were square root transformed to meet assumptions of normality. We tested for differences in overall recruitment between time periods using a one-way ANOVA.

Spatial variation in recruitment

To determine the characteristic spatial scales of variation in recruitment, we built a hierarchical variance components model using a nested ANOVA (in Systat 12) with 4 levels of random effects: site, location nested within site, group nested within location, and collector nested within group. The two tiles per collector provided the error term. We treated any negative variance components as zero (Quinn and Keough 2002). More than 97% of coral recruits (from both inner and outer surfaces) belonged to the family Pocilloporidae, so we only used this family in analyses. We ran the model for inner and outer tile surfaces separately for each time period to determine whether spatial patterns of recruitment differed by time period. Patterns of recruitment among spatial scales were very similar in both time periods, so we averaged the variance components percentages for the two time periods at each spatial scale. The full data set is provided in the Electronic Supplemental Material, ESM Appendix 1.

Adult coral populations

We used existing data on adult coral cover (T McClanahan, unpublished data) to estimate the density of adult populations to: (1) provide an indication of whether recruit densities between sites corresponded with adult densities and (2) assess whether patterns in early recruitment were correlated with distribution patterns in adult communities. The coral cover data were collected in February 2009 from the two study sites using 10-m line-intercept transects, with coral family and colony size recorded along 18 randomly placed transects at Coral Gardens and 9 randomly placed transects at Starfish. A greater number of transects was

used at the Coral Garden site to cover the larger coral-dominated area. We used a one-way ANOVA to compare adult coral cover between sites.

Potential effects of fish grazing and predation

Large grazers and predators could only access outer tile surfaces. While the two dominant grazer groups in Kenya are fishes and sea urchins, sea urchin densities are very low within Kenyan MPAs (McClanahan and Shafir 1990; O'Leary and McClanahan 2010). Therefore, any mortality attributable to grazing was most likely due to feeding by large fishes. To investigate this hypothesis, we used two approaches.

First, we compared the size-structure of recruits on inner and outer surfaces. If recruits on outer surfaces were substantially smaller than on inner surfaces, this might indicate greater mortality on outer surfaces. To estimate recruit colony size, we counted the number of polyps per recruit colony for 209 recruits on a random subsample of 65 tiles from the Coral Gardens site (which had a higher recruitment rate) collected during the sampling period (15 Nov 2007–1 Feb 2008). We used separate one-way ANOVAs to compare the number of polyps per recruit on inner and outer tile surfaces.

Second, we evaluated spatial variation in fish grazing by counting fish bite scars on the outer surfaces of both tiles from every collector from the first sampling period. Bites were identified as areas where the microbial/algal film that uniformly covered both inner and outer plate surfaces had been removed. Most bites were characteristic of parrotfish, with paired scars (~ 3 mm wide and 1 cm long) corresponding to the two upper plates of the teeth. Bite widths were larger than most coral recruits (mean width of 2 mm). To count bites, we superimposed five evenly spaced, horizontal lines across each tile and counted bite scars intersecting each line. We used the same hierarchical nested model (described above for recruit counts) to determine the characteristic spatial scale of fish grazing (using counts of bites/tile, square root transformed for normality). Therefore, the model included 4 levels: site, location nested within site, group nested within location, and collector nested within group.

Results

Recruit abundance

A total of 1,099 coral recruits were found on the 192 tiles (from 96 collectors—48 in each sampling period) of which 97% were Pocilloporidae. The remaining corals were Poritidae (0.8%), Acroporidae (0.3%), and unidentifiable

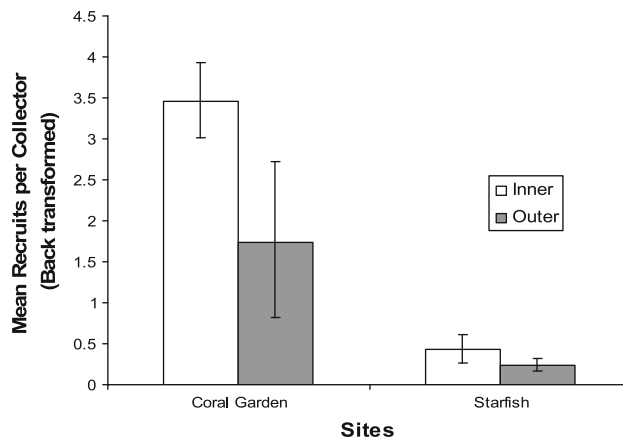


Fig. 2 Mean number of recruits per collector at the two sites on inner (*open bars*) and outer (*solid bars*) tile surfaces ± 1 SE (values back-transformed from square root transformation used in two-way ANOVA)

(1.5%). The number of recruits at Coral Gardens (938) was significantly higher than at Starfish (161; Table 1, Fig. 2). Thus, the mean number of recruits/tile was ~ 3.5 at Coral Gardens and 0.5 at Starfish, which translates into 132 and 19 recruits per m^2 , respectively. The mean number of recruits was also significantly higher on inner than on outer surfaces at each site (Table 2, Fig. 2). The interaction between tile surface and site was not significant (Table 2). Recruits were widely spaced on every tile surface, suggesting no competition for space between recruits.

Spatial variation in recruitment

The spatial scales of variation in recruitment were very similar between the first and second time periods, but were very different between inner and outside surfaces of tiles. On protected inner surfaces, the largest components of variation were at the largest (1,000 m) spatial scale (39%) and in the error term (40%; Fig. 3). In contrast, on exposed outer surfaces, the largest component of variation was at the smallest (1 m) spatial scale (51%) and in the error term (33%; Fig. 3).

Plots of the frequency distributions of numbers of recruits per collector on inner and outer surfaces at each site (dates pooled) provide a visual representation of differences in variance structure (Fig. 4). Within each site, the distribution of collectors with large numbers of recruits on the outer surfaces was right-skewed compared with the inner surfaces (Fig. 4). This pattern was strongest at the Coral Gardens site, which had higher overall coral recruitment (inner surfaces: median = 4, kurtosis = 2.3; outer surfaces: median = 0.5, kurtosis = 5.8; Fig. 4a). At Coral Gardens, the maximum number of recruits per collector was 44 on outer surfaces and 23 on inner surfaces. There were also more collectors (48)

Table 2 Results of two-way ANOVA of numbers of pocilloporid recruits (square root transformed) by site and by treatment

Source	df	F	P
Site	1,380	72.6	<0.0001
Treatment (inner vs. outer)	1,380	8.7	0.003
Site by treatment interaction	1,380	2.4	0.12

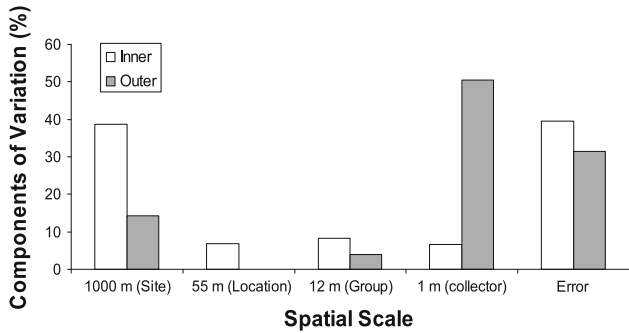
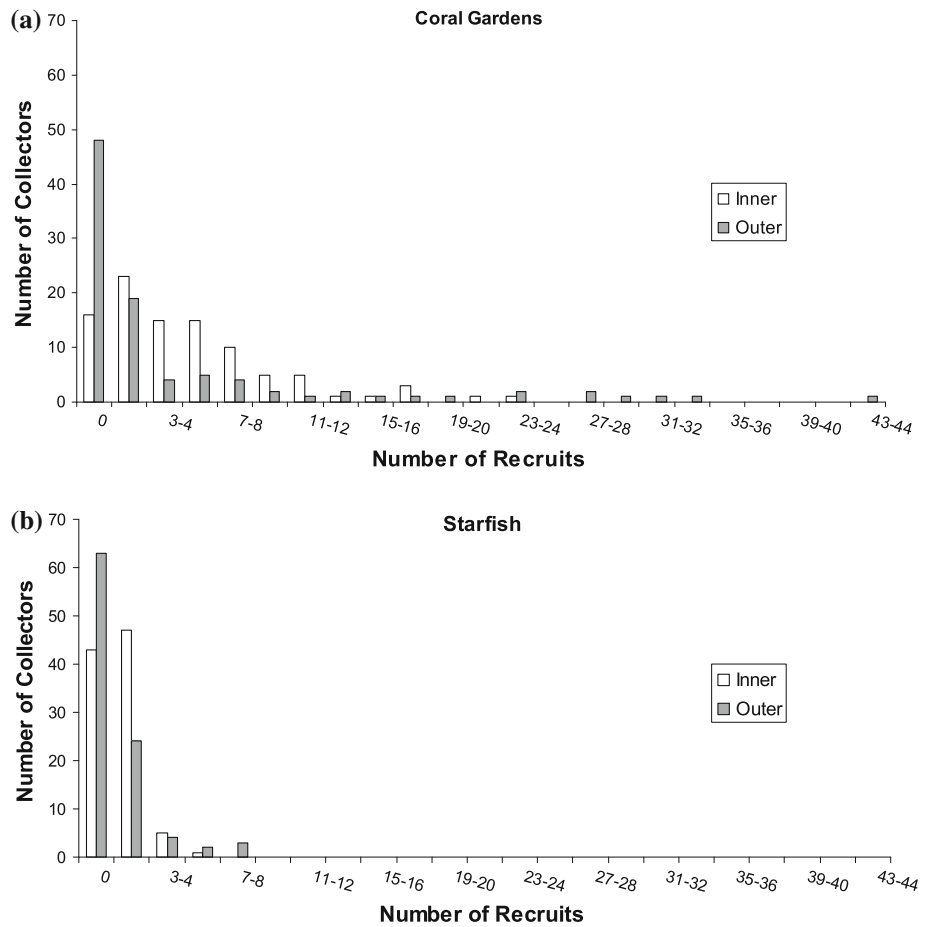


Fig. 3 Components of variation (%) in coral recruitment at each spatial scale on inner (open bars) and outer (solid bars) surfaces

Fig. 4 Frequency distribution of numbers of corals per collector on inner (open bars) and outer (solid bars) surfaces for (a) Coral Gardens and (b) Starfish sites. N = 96 collectors/site (pooling 48 from each time period)



with zero corals on outer surfaces than with zero corals on inner surfaces (16; Fig. 4a).

The total number of recruits was much lower at the Starfish site, but the frequency distributions were similar to those at Coral Gardens (inner surfaces: median = 1, kurtosis = 5.6; outer surfaces: median = 0, kurtosis = 7.9; Fig. 4b). The maximum number of recruits on a collector at Starfish was 8 on outer surfaces and 6 on inner surfaces, and again, there were more collectors with zero corals on outer surfaces (63) than on inner surfaces (43; Fig. 4b).

On outer surfaces at both sites, a small number of collectors had large numbers of recruits, but there were also many more outer collectors with zero recruits than for inner surfaces (Fig. 4). In contrast, recruitment on inner surfaces was more uniform, with fewer collectors having large numbers of recruits, and fewer collectors with zero recruits.

Adult coral populations

Despite large differences in the total number of coral recruits at Coral Gardens (938) and Starfish (161), there

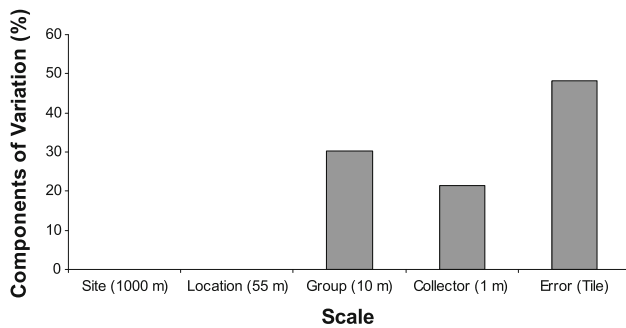


Fig. 5 Components of variation (%) in numbers of fish bites on the outer surfaces of tiles during the first deployment period (November–January)

was no significant difference in total cover of adult corals at each site (one-way ANOVA, $df = 1,25$, $F = 2.5$, $P = 0.13$). Similarly, pocilloporid cover (square root transformed) did not differ between sites (one-way ANOVA, $df = 1,25$, $F = 1.6$, $P = 0.22$). Adult pocilloporid cover was very low at both sites, representing only 0.8% of total cover and 2.6% of coral cover at Coral Gardens, and 0.04% of total cover and 0.2% of coral cover at Starfish.

Potential effects of fish grazing and predation

Recruit size (number of polyps per recruit) was significantly different between inner and outer surfaces of tiles. Recruits were larger on average on the inner tile surfaces (2.9 ± 2.5 SD.) than the outer surfaces (2.1 ± 1.7 SD.; one-way ANOVA $df = 1,207$, $F = 7.7$, $P = 0.006$). The maximum size of recruits on inner surfaces (11 polyps) was also greater than on outer surfaces (8 polyps). Approximately one quarter of all recruits on outer surfaces were damaged (part of the calyx was missing), while every recruit on inner surfaces was intact.

The pattern of variance components in fish bites (fish scars/collector) showed that all variation was at small spatial scales, with $\sim 30\%$ of variation at the 10 m scale, $\sim 20\%$ at the 1-m spatial scale, and $\sim 50\%$ between tiles on a collector (the error term; Fig. 5). None of the variation was attributable to either the location (55 m) or site (1,000 m) scales. Thus, effects of fish grazing appeared to be patchy at small spatial scales of 10 m or less, while being very similar at larger spatial scales.

Discussion

The spatially explicit hierarchical design allowed us to investigate the spatial scales at which recruitment is regulated in a seascape. The approach is valuable as many small-scale studies have high unexplained variation due to local differences between sites that cannot be partitioned

without a nested sampling design (Hughes et al. 2002). In our study, most variation in recruitment was attributable to two scales: the largest (1,000 m, between sites) and the smallest (1 m, between collectors). Which scale had the largest variance differed between inner and outer tile surfaces. We used the differences between tile surfaces to generate hypotheses about processes affecting recruitment that can then be tested in future studies. Inner surfaces, which presumably represented an “undisturbed” environment, had both higher average recruit densities and more even distributions of recruits. Outer surfaces, exposed to grazing fishes, had patchy recruit distributions: while some tiles had very high numbers of recruits, most tiles had zero recruits.

Two potentially confounding factors when comparing inner and outer surfaces in our design were differences in light and water flow. The presence of more recruits on inner surfaces may be due to settlement preferences for crevices or darker microhabitats. However, to explain the patchiness of coral recruitment on outer tile surfaces, light or flow would have to be spatially variable at relatively small scales of 1–10 m. This seems unlikely at least for light, as all collectors were at similar depths, were oriented in the same direction, and thus should have had similar light conditions on outer tile surfaces. Water flow has been demonstrated to affect settlement of other invertebrate larvae including abalone, where higher flow rates negatively influenced larval ability to attach to settlement substrates (Boxshall 2000). It is thus possible that the design of our collectors helped entrain larvae and resulted in more even recruitment on inner tile surfaces or that variable flow contributed to patchy settlement on outer tile surfaces.

Our design eliminated several other major factors likely to affect recruitment, e.g., substrate differences, overgrowth, and physical disturbance. Substrate, especially crustose coralline algae, is an important inducer of settlement for many corals (Harrington et al. 2004; Price 2010). We used new tiles at the start of each 1.5-month sampling period, and large substrate differences did not develop between inner and outer surfaces. When recovered after 1.5 months, all surfaces had similar covers of patchy coralline algae, sparse algal turf, and algal/microbial films, and coral recruits were found on both coralline algae and in areas of algal film. Substrate-related differences in settlement patterns may also be unlikely given that pocilloporid recruits tend to be non-selective of habitat during settlement (Harrison and Wallace 1990; Baird and Hughes 2000; Harrington et al. 2004, but see Putnam et al. 2008). The short duration of the experiment reduced the likelihood of coral death due to overgrowth by other organisms. The only other organisms found growing on tiles were the above-mentioned sparse coralline and turf algae and algal films with no visible evidence of competitive interactions

between them and coral recruits. We also did not observe any discoloration or tissue sloughing in coral polyps that could indicate coral disease. As the tiles were raised above the substrate, there were no interactions with adult corals, and physical disturbances on the surface of tiles (e.g., sand scour, moving rubble) were avoided.

The high variation in recruitment at the smallest scale on outer tile surfaces is consistent with other work showing that coral recruitment is often patchy at a finer scale than that of site (Baird and Hughes 2000; Dunstan and Johnson 1998; Glassom et al. 2004; Hughes et al. 2000). While our experiment cannot determine the mechanism behind the patterns observed, two lines of evidence indicate that predation by grazing fishes may have altered initial settlement on outer surfaces. First, coral recruits were smaller (fewer polyps/recruit) on outer surfaces, and the only damaged recruits were on outer surfaces. It is possible that the light or other conditions on outer surfaces were less optimal for coral growth. However, in a separate study, we found that pocilloporids on shallow reefs in Kenya grew more rapidly on the exposed outer sides of cement blocks than on the shaded inner sides (J.O. pers. obs.). It is possible that recruits on outer surfaces were younger, and hence smaller, due to replacement of older recruits through grazing mortality. Second, only outer surfaces had fish bite scars and the scale of variation in recruitment on outer surfaces was at a small scale, similar to the variation in fish grazing. These indications of predation differ from the findings of a study done on the Great Barrier Reef, where tiles left out for 8 weeks had few signs of predation (Hughes et al. 2000). However, a number of other studies have shown that intensive fish grazing can kill early coral recruits (Sammarco 1985; Fisk and Harriott 1990; Gleason 1996; Christiansen et al. 2009; Penin et al. 2010). We conducted this study in a fisheries closure where most large grazers are herbivorous fishes, notably surgeonfish and parrotfish (McClanahan and Shafir 1990; O'Leary and McClanahan 2010). In a study in Moorea, there was a clear link between mortality of coral recruits and the abundance of grazing parrotfish (Penin et al. 2010). While we found no correlation between the number of fish bite scars and the number of recruits on outer surfaces (one-way ANOVA $df = 1, 92$; $F = 0.38$; $P = 0.54$), this does not exclude a causal relationship as fish grazing occurs on a shorter temporal scale than coral settlement. Fish bite scars counted on the tiles probably persist for no more than a few days (based on algal turnover rates), while coral recruitment represented accumulation over 1.5 months. Because our design does not exclude factors such as irradiance and flow that may have influenced recruitment, in future studies, the grazing hypothesis generated here could be tested by a hierarchical spatial sampling design using caging on half the replicates at each scale to exclude fishes. If grazing is a major cause

of post-settlement mortality in corals, there may be a cost-benefit ratio between the benefits of algal removal by grazers and the costs of coral mortality (Penin et al. 2011).

The coral recruits settling on the tiles were almost entirely pocilloporids, a pattern consistent with the outcomes of two other studies of coral settlement in the Mombasa MPA, in which pocilloporids also were the main recruits on collection tiles (Tamelander et al. 2000; Mangubhai et al. 2007). Most recruits in our experiment probably belonged to the genus *Pocillopora* since the pocilloporid genera *Stylophora* and *Seriatopora* are uncommon in Kenya (Mangubhai et al. 2007). At the Coral Gardens, which received the most recruitment, the mean density of recruits (averaged across both tile surfaces) was 132 per m^2 . This recruit density is similar to that found in a previous study between 2003–2005 in the Coral Gardens which found 101 recruits per m^2 settled on uninoculated settlement tiles during a 3-month period (Mangubhai et al. 2007).

Lower overall recruitment densities should not affect patterns of variation at different scales. We found ~ 7 times more recruits at Coral Gardens than at Starfish on both inner and outer collector surfaces (Fig. 2). The only previous work comparing coral recruitment at the two sites within the Mombasa MPA also reported significantly higher settlement rates at the Coral Gardens site than at the Starfish site, and it was attributed to the higher water flux at Coral Gardens (Tamelander et al. 2000). We hypothesize that differential larval delivery (possibly reflecting differences in currents, water residence times, and sources of recruits) is influencing variation at the site scale, though other factors (e.g., local larval production) may also be contributing. Our experiment cannot determine the specific mechanisms behind the settlement patterns. The low density of adult pocilloporid corals at both sites, but much higher recruit density at the Coral Gardens site, indicates that recruits may not be produced locally, that there were differences in coral fecundity between sites (Hughes et al. 2000), or that there is greater post-settlement mortality at the Starfish site on both inner and outer surfaces. Coral Gardens lies in close proximity to a channel to the open sea, so that recruits produced in other areas may have been transported to the Mombasa MPA where they settled upon reaching suitable substrate at the Coral Gardens site. Pocilloporids can have long-lived larvae competent for up to 100 days, making seeding of distant areas possible (Richmond 1988; Mangubhai et al. 2007). Our results and those of Tamlander et al. (2000) suggest that proximity to the open sea, and perhaps greater flow, may increase recruitment. However, a hydrodynamic study in the Great Barrier Reef concluded that lower flushing rates increase settlement of coral larvae (Sammarco and Andrews 1989). We were unable to identify any source of post-settlement mortality that differed between the two sites, and we did not attempt to evaluate differences in fecundity.

If higher settlement at the Coral Gardens site is normal in most years, it does not appear to translate to a higher density of pocilloporid adults. This suggests that post-settlement mortality is an important factor in determining coral distribution in this system. High mortality in the first 3 months post-settlement is known in other coral species (Vermeij and Sandin 2008), with survival increasing after 6–12 months (Mundy and Babcock 2000). Few larger (and hence older) pocilloporid recruits (1–10 cm diameter) were found on natural substrata in the Mombasa MPA (Tamelander et al. 2000), and adult pocilloporids are uncommon and patchy at both sites. This suggests that pocilloporids in the Mombasa MPA experience high mortality early in their life histories and that mortality remains high at least to the 10-cm size class, potentially explaining the low density and patchy distribution of adults. On natural substrates, fish grazing, competition with other organisms, coverage by sediments, and disease may contribute to post-settlement mortality.

Variances in recruitment did not increase or decrease consistently across sequential spatial scales, indicating that different ecological processes generate variability at each scale. We conducted this study on relatively small spatial scales ranging from 1 to 1,000 m to develop hypotheses about mechanisms that could explain patterns in delivery and post-settlement mortality. Variation in recruitment at the 1,000 m scale has been found in other studies that considered a range of spatial scales and has been attributed to larval delivery patterns (Dunstan and Johnson 1998; Hughes et al. 2000; Glassom et al. 2004). However, our results suggest that grazers and predators can create small-scale variability and be a dominant force driving recruitment patterns. Variation at very small spatial scales is common in both marine systems (Fraschetti et al. 2005) and terrestrial communities (Garcia et al. 2005). In a review of a number of benthic marine species, nearly all populations had patchy distributions at small spatial scales of centimeters to meters (Fraschetti et al. 2005). Across ecosystem types, patchiness at small scales may reflect variation in biotic interactions (as proposed here and in other studies, e.g., Adjeroud et al. 2007), or variation in physical factors ranging from micro-topography to geology (Connell et al. 1997; Nathan and Muller-Landau 2000; Glassom et al. 2006).

In the absence of differential post-settlement mortality, recruitment patterns should mimic settlement patterns. However, relatively small changes in demographic parameters during very early life-history phases can result in major changes in persistent recruitment. A diverse array of grazers, from terrestrial ungulates to aquatic invertebrates and fishes, has been shown to alter the spatial structure of populations of habitat-forming species (Gelwick and Matthews 1997). Due to post-settlement

mortality, optimal places for rapid growth (e.g., outer collector surfaces with more light) may not be the most successful locations for survival (Birkeland 1977). Fishes may play a dual role in coral recruitment dynamics, e.g., by grazing on algae, they prevent shading of coral recruits and open up recruitment space, but if their grazing also causes recruit mortality, fish grazing can reduce ultimate recruitment success (Penin et al. 2010). Large herbivores often have highly variable patterns of habitat use and grazing intensity and hence may strongly influence patterns of prey dispersion on small scales (Menge et al. 1994).

Small-scale spatial variability in recruitment can ultimately affect a number of critical ecological factors including the distribution of biogenic habitat; the growth, fecundity, and productivity of adults; and variation in the strength of both intra- and inter-specific interactions. Variability at small scales should not be considered simply statistical noise that masks larger scale patterns (Coleman 2002). Models of ecological processes should consider a range of spatial scales (including small scales) to determine the levels at which key ecological processes occur that drive patterns in populations and communities.

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References

- Adjeroud M, Penin L, Carroll A (2007) Spatio-temporal heterogeneity in coral recruitment around Moorea, French Polynesia: Implications for population maintenance. *J Exp Mar Biol Ecol* 341: 204–221
- Angwenyi CM, Rydberg L (2005) Wave-driven circulation across the coral reef at Bamburi Lagoon, Kenya. *Estuar Coast Shelf Sci* 63:447–454
- Babcock RC, Baird AH, Piromvaragorn S, Thomson DP, Willis BL (2003) Identification of scleractinian coral recruits from Indo-Pacific Reefs. *Zool Stud* 42:211–226
- Baird AH, Hughes TP (2000) Competitive dominance by tabular corals: an experimental analysis of recruitment and survival of understorey assemblages. *J Exp Mar Biol Ecol* 251:117–132
- Birkeland C (1977) The importance of rate of biomass accumulation in early successional stages of benthic communities to the survival of coral recruits. *Proc 3rd Int Coral Reef Symp* 1:15–21
- Boxshall AJ (2000) The importance of flow and settlement cues to larvae of the abalone, *Haliotis rufescens* Swainson. *J Exp Mar Biol Ecol* 254:143–167
- Caffey HM (1985) Spatial and temporal variation in settlement and recruitment of intertidal barnacles. *Ecol Monogr* 55:313–332

- Carr MH, Syms C (2006) Recruitment. In: Allen LG, Pondella II, Horn MH (eds) *The Ecology of California Marine fishes*. University of California Press, Berkeley, CA, pp 411–475
- Christiansen N, Ward S, Harii S, Tibbetts I (2009) Grazing by a small fish affects the early stages of a post-settlement stony coral. *Coral Reefs* 28:47–51
- Coleman MA (2002) Small-scale spatial variability in intertidal and subtidal turfing algal assemblages and the temporal generality of these patterns. *J Exp Mar Biol Ecol* 267:53–74
- Collinge SK (2001) Spatial ecology and biological conservation - Introduction. *Biol Conserv* 100:1–2
- Connell JH, Hughes TP, Wallace CC (1997) A 30-year study of coral abundance, recruitment, and disturbance at several scales in space and time. *Ecol Monogr* 67:461–488
- 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
- Fisk DA, Harriott VJ (1990) Spatial and temporal variation in coral recruitment on the Great Barrier Reef - implications for dispersal hypotheses. *Mar Biol* 107:485–490
- Fraschetti S, Terlizzi A, Benedetti-Cecchi L (2005) Patterns of distribution of marine assemblages from rocky shores: evidence of relevant scales of variation. *Mar Ecol Prog Ser* 296:13–29
- Gaines SD, Bertness MD (1992) Dispersal of juveniles and variable recruitment in sessile marine species. *Nature* 360:579–580
- Garcia D, Obeso JR, Martinez I (2005) Spatial concordance between seed rain and seedling establishment in bird-dispersed trees: does scale matter? *J Ecol* 93:693–704
- Gelwick FP, Matthews WJ (1997) Effects of algivorous minnows (*Camptostoma*) on spatial and temporal heterogeneity of stream periphyton. *Oecologia* 112:386–392
- Glassom D, Zakai D, Chadwick-Furman NE (2004) Coral recruitment: a spatio-temporal analysis along the coastline of Eilat, northern Red Sea. *Mar Biol* 144:641–651
- Glassom D, Celliers L, Schleyer MH (2006) Coral recruitment patterns at Sodwana Bay, South Africa. *Coral Reefs* 25:485–492
- Gleason MG (1996) Coral recruitment in Moorea, French Polynesia: the importance of patch type and temporal variation. *J Exp Mar Biol Ecol* 207:79–101
- Harrington L, Fabricius K, De'Ath G, Negri A (2004) Recognition and selection of settlement substrata determine post-settlement survival in corals. *Ecology* 85:3428–3437
- Harrison PL, Wallace CC (1990) Reproduction, dispersal and recruitment of scleractinian corals. In: Dubinsky Z (ed) *Ecosystems of the world: Coral reefs*. Elsevier, Amsterdam, pp 133–207
- Heyward AJ, Smith LD, Rees M, Field SN (2002) Enhancement of coral recruitment by in situ mass culture of coral larvae. *Mar Ecol Prog Ser* 230:113–118
- Hughes TP, Baird AH, Dinsdale EA, Moltshaniwskyj 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, Moltshaniwskyj NA, Pratchett MS, Tanner JE, Willis BL (2000) Supply-side ecology works both ways: the link between benthic adults, fecundity, and larval recruits. *Ecology* 81:2241–2249
- Hughes TP, Baird AH, Dinsdale EA, Harriot VJ, Moltshaniwskyj NA, Pratchett MA, Tanner JE, Willis BL (2002) Detecting regional variation using meta-analysis and large-scale sampling: latitudinal patterns in recruitment. *Ecology* 83:436–451
- Hunt HL, Scheibling RE (1997) Role of early post-settlement mortality in recruitment of benthic marine invertebrates. *Mar Ecol Prog Ser* 155:269–301
- Jones GP, Almany GR, Russ GR, Sale PF, Steneck RS, van Oppen MJH, Willis BL (2009) Larval retention and connectivity among populations of corals and reef fishes: history, advances and challenges. *Coral Reefs* 28:307–325
- Keough MJ, Downes BJ (1982) Recruitment of marine invertebrates - the role of active larval choices and early mortality. *Oecologia* 54:348–352
- Kinlan BP, Gaines SD (2003) Propagule dispersal in marine and terrestrial environments: a community perspective. *Ecology* 84:2007–2020
- Levin SA (1992) The problem of pattern and scale in ecology. *Ecology* 73:1943–1967
- Levin LA (2006) Recent progress in understanding larval dispersal: new directions and digressions. *Integr Comp Biol* 46:282–297
- Levin SA, Pacala SW (1997) Theories of simplification and scaling in spatially distributed processes. In: Tilman D, Kareiva PM (eds) *Spatial Ecology: the role of space in population dynamics and interspecific interactions*. Princeton University Press, Princeton, NJ, pp 271–295
- Mangubhai S, Harrison PL (2008) Asynchronous coral spawning patterns on equatorial reefs in Kenya. *Mar Ecol Prog Ser* 360:85–96
- Mangubhai S, Harrison PL, Obura DO (2007) Patterns of coral larval settlement on lagoon reefs in the Mombasa Marine National Park and Reserve, Kenya. *Mar Ecol Prog Ser* 348:149–159
- McClanahan TR, Arthur R (2001) The effect of marine reserves and habitat on populations of east African coral reef fishes. *Ecol Appl* 11:559–569
- McClanahan TR, Shafir SH (1990) Causes and consequences of sea-urchin abundance and diversity in Kenyan coral-reef lagoons. *Oecologia* 83:362–370
- McClanahan TR, Ateweberhan M, Omukoto J (2008) Long-term changes in coral colony size distributions on Kenyan reefs under different management regimes and across the 1998 bleaching event. *Mar Biol* 153:755–768
- Menge BA, Berlow EL, Blanchette CA, Navarrete SA, Yamada SB (1994) The keystone species concept - variation in interaction strength in a rocky intertidal habitat. *Ecol Monogr* 64:249–286
- Mundy C, Babcock R (2000) Are vertical distribution patterns of scleractinian corals maintained by pre- or post-settlement processes? A case study of three contrasting species. *Mar Ecol Prog Ser* 198:109–119
- Nathan R, Muller-Landau HC (2000) Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends Ecol Evol* 15:278–285
- O'Leary JK, McClanahan TR (2010) Trophic cascades result in large-scale coralline algae loss through differential grazer effects. *Ecology* 91:3584–3597
- Penin L, Michonneau F, Baird AH, Connolly SR, Pratchett MS, Kayal M, Adjeroud M (2010) Early post-settlement mortality and the structure of coral assemblages. *Mar Ecol Prog Ser* 408:55–64
- Penin L, Michonneau F, Carroll A, Adjeroud M (2011) Effects of predators and grazers exclusion on early post-settlement coral mortality. *Hydrobiologia* 663(1):259–264
- Pineda J, Reynolds N, Starczak V (2009) Complexity and simplification in understanding recruitment in benthic populations. *Popul Ecol* 51:17–32
- Price N (2010) Habitat selection, facilitation, and biotic settlement cues affect distribution and performance of coral recruits in French Polynesia. *Oecologia* 163:747–758
- Putnam HM, Edmunds PJ, Fan TY (2008) Effect of temperature on the settlement choice and photophysiology of larvae from the reef coral *Stylophora pistillata*. *Biol Bull* 215:135–142
- Quinn GP, Keough MJ (2002) *Experimental design and data analysis for biologists*. Cambridge University Press, Cambridge, UK
- Richmond RH (1988) Competency and dispersal potential of planula larvae of a spawning versus a brooding coral. *Proc 6th Intl Coral Reef Symp* 2:827–831

- Sammarco, P. W., 1985. The Great Barrier Reef vs. the Caribbean: comparisons of grazers, coral recruitment patterns and reef recovery. *Proc 5th Int Coral Reef Congr* 4: 391–397
- Sammarco PW, Andrews JC (1988) Localized dispersal and recruitment in Great Barrier Reef corals - the Helix experiment. *Science* 239:1422–1424
- Sammarco PW, Andrews JC (1989) The Helix experiment: differential localized dispersal and recruitment patterns in Great Barrier Reef corals. *Limnol Oceanogr* 34:896–912
- Soong K, Chen M, Chen C, Dai C, Fan T, Li J, Fan H (2003) Spatial and temporal variation of coral recruitment in Taiwan. *Coral Reefs* 22:224–228
- Strathmann RR, Hughes TR, Kuris AM, Lindeman KC, Morgan SG, Pandolfi JM, Warner RR (2002) Evolution of local recruitment and its consequences for marine populations. *Bull Mar Sci* 70: 377–396
- Tamelander J, Visram S, Obura DO (2000) Prospects for coral recovery through transplantation and natural recruitment, Kenya. *Proc 9th Intl Coral Reef Symp* 2:991–996
- Underwood AJ, Chapman MG (1996) Scales of spatial patterns of distribution of intertidal invertebrates. *Oecologia* 107:212–224
- Vermeij MJA, Sandin SA (2008) Density-dependent settlement and mortality structure the earliest life phases of a coral population. *Ecology* 89:1994–2004
- Wenny DG (2000) Seed dispersal, seed predation, and seedling recruitment of a neotropical montane tree. *Ecol Monogr* 70: 331–351
- Wiens JA (1989) Spatial scaling in ecology. *Funct Ecol* 3:385–397