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Research

The influence of habitat and adults on the spatial distribution of juvenile corals

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Population distributions are affected by a variety of spatial processes, including dispersal, intraspecific dynamics and habitat selection. Within reef-building coral communities, these processes are especially important during the earliest life stages when reproduction provides mobility among sessile organisms and populations experience the greatest mortality bottlenecks both before and immediately after settlement. Here, we used large-area imaging to create photomosaics that allowed us to identify and map the location of 4681 juvenile (1–5 cm diameter) and 25 902 adult (>5 cm diameter) coral colonies from eight 100-m² plots across the forereef of Palmyra Atoll. Using metrics of density, percent cover and the relative location of each colony within each plot, we examined abundance and spatial relationships between juvenile and adult coral taxa. Within coral taxa, juvenile density was generally positively related to the numerical density and percent cover of adults. Nearest neighbor analyses showed aggregation of juveniles near adults of the same taxon for two of the focal taxa (*Pocillopora* and Fungiids), while all other taxa showed random spatial patterning relative to adults. Three taxa had clustered distributions of juveniles overall. Additionally, we found that on a colony level, juveniles for five of nine focal taxa (accounting for >98% of all identified juveniles) associated with a specific habitat type, with four of those five taxa favoring unconsolidated (e.g. rubble) over consolidated substrata. The general lack of clustering in juvenile corals contrasts with consistent clustering patterns seen in adult corals, suggesting that adult spatial patterns are largely driven by processes occurring after maturity such as partial colony mortality, including fission and fragmentation. The association of many taxa with unconsolidated habitat also suggests that corals may play an important role in colonizing natural rubble patches that could contribute to reef stabilization over time.

Keywords: clustering, nearest neighbor, Palmyra Atoll, photomosaic, recruitment, spatial patterns, variance to mean

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Introduction

Large-scale characterizations of spatial patterns are used widely to explore factors that drive population structure. Species can have random, clustered or over-dispersed distributions, and identification of these patterns provides insight into competitive dynamics, dispersal distances and habitat associations within and among species. For instance, distance dependent mortality during the most vulnerable early life stages, as predicted by Janzen–Connell effects, may lead to over-dispersion (Janzen 1970, Connell 1971), while asymmetric competition and spatially clustered resource availability can lead to various degrees of aggregation (Perry et al. 2008). For sessile organisms, spatial patterns may also be linked to dispersal capabilities, as seen in terrestrial systems where dispersal limitations of seeds for tree species lead to highly aggregated adult populations (Hubbell 1979, Condit et al. 2000).

Dispersal limitation may have less influence on spatial patterns for sessile marine organisms, especially those capable of long distance dispersal through broadcast spawning or mobile larval stages. Corals have diverse life histories that employ various reproductive strategies (Bak and Engel 1979). A majority of Indo-Pacific species and roughly half of all Atlantic species use broadcast spawning as their major form of reproduction (Baird et al. 2009) while brooding species produce competent planulae allowing settlement within meters of an adult colony (Nishikawa et al. 2003, Vermeij 2005), and budding in Fungiid corals produces new individuals asexually directly from adult tissues (Kramarsky-Winter and Loya 1996) contributing to highly aggregated adult populations (Carlon and Olson 1993, Kramarsky-Winter and Loya 1998). Greater asexual reproduction creates populations with reduced genetic diversity, leaving them vulnerable to environmental change (Honnay and Bossuyt 2004, Baums et al. 2006). Additionally, variability in larval competencies allows for both self-recruitment and long-distance dispersal within reproductive cohorts (Connolly and Baird 2010), further confounding the impact of dispersal on spatial patterning.

As individual colonies develop through time, they are subjected to a variety of intraspecific interactions in the form of density and distance dependent mechanisms. Intraspecific effects during settlement can lead to positive density dependent settlement (Doropoulos et al. 2017), which may contribute to aggregated settlement patterns for some coral species. However, after settlement, corals have shown negative density (Vermeij and Sandin 2008) and distance dependent mortality (Vermeij 2005) in relation to adult colonies. The mechanism of distance dependent mortality has been attributed to microbial communities of adult conspecifics, providing evidence for Janzen–Connell effects in corals (Marhaver et al. 2013). Given the large bottleneck of mortality that occurs both before and immediately after settlement, processes that control survivorship during these early life stages can shape spatial distributions of these organisms.

Early life-stage organisms can also be structured spatially based on specific habitat features. Unlike generally passive seeds of terrestrial plants, larvae of sessile benthic organisms

demonstrate selective settlement, relying upon chemical cues (Pawlik 1992) from benthic organisms such as crustose coralline alae (CCA) (Heyward and Negri 1999, Price 2010, Doropoulos et al. 2017) and selection for small scale, cryptic refugia (Fisk and Harriott 1990, Edmunds et al. 2004, Roth and Knowlton 2009, Trapon et al. 2013, Brandl et al. 2014) which provide protection from direct predation or incidental grazing by herbivores (Penin et al. 2011, Gallagher and Doropoulos 2017). However, survivorship can be higher on exposed surfaces once size thresholds are reached to escape predation (Doropoulos et al. 2016). At larger scales, reefscapes are often a consortium of stable consolidated habitat and unconsolidated reef (e.g. rubble), the latter of which is physically unstable and has the potential to cause abrasion and burial of juvenile corals. The benthic environment is highly heterogenous in species composition and habitat complexity, therefore, the distribution of other organisms or habitat types which induce or impede the settlement and survivorship of early life-stage colonies likely plays a role in the spatial patterning of corals.

While large-scale mapping in terrestrial systems is used to determine the mechanisms that influence population and individual based spatial patterns, equivalent studies are limited in marine systems due to methodological challenges in mapping individuals across broad spatial scales. However, recent advances in large-area imaging of coral reef benthic communities allows for the mapping of individual colonies at landscape scales, creating the opportunity to explore colony level spatial patterns (Burns et al. 2015, Edwards et al. 2017). The developmental stages of corals are a period of high mortality for individuals, which can influence distribution patterns of adults (Hunt and Scheibling 1997). Therefore, the spatial patterns that emerge following this period can be informative in understanding the processes which may influence spatial patterns of future adult populations. While recent settlers and recruits (<1 cm diameter) are difficult to study in situ, juvenile colonies (1–5 cm diameter) are more readily tracked and represent recruits that survived the bottleneck of post-settlement mortality and the rising generation of adults. Using a large-area imaging technique, we explore correlative relationships between the abundance of juvenile corals and the cover of two distinctive habitat types, as well as the abundance of adult corals. Next, by mapping individual colonies within sites, we examine finer scale spatial patterns. In particular, we test for evidence of 1) habitat affinity, 2) effects of adult presence on distribution of juveniles and 3) taxon-specific patterns of juvenile clustering.

Methods

Study location

Data were collected on Palmyra Atoll (5°52′N, 162°06′W) located in the Northern Line Islands in the Central Pacific. Palmyra Atoll is a National Wildlife Refuge in the Pacific Remote Islands Naitonal Monument and maintains a healthy

coral reef community (Smith et al. 2016) with strong resilience following thermal stress (Fox et al. 2019). In 2013, eight 10×10 m plots were established to document the densities and spatial distributions of hard coral populations on the forereef at 10 m depth along the north and south sides of the atoll, with plots positioned to obtain broad spatial coverage (Fig. 1).

Photomosaic collection

The entirety of each 100-m^2 plot was surveyed using methods of large-area image reconstruction. Composite large-area imagery covers landscape scales while maintaining high resolution, allowing detailed analysis of benthic reef communities (Lirman et al. 2007, Edwards et al. 2017). Plot boundaries were marked using permanent stainless steel pins with temporary lead markers placed at each corner. The boundary markers were used as reference points of known distances for post processing and scaling purposes. Each plot was imaged using a diver operated camera system consisting of two cameras mounted to a custom frame. One camera used a wide angle lens set to an 18 mm focal length to maximize overlap between images, while the other camera used a 55 mm focal length lens to provide higher resolution imagery used

for taxonomic classifications and manual detection of juvenile corals. Each camera operated on time-lapse, capturing one image per second as the diver swam in a gridded pattern approximately 1–1.5 m from the substrate in both the longshore and inshore/offshore direction to ensure coverage of the plot area. At each site approximately 2500 images were captured by each camera, with images taken using the wide angle (18 mm) lens camera used to create a composite photomosaic image of the plot area using methods previously established (Gracias and Santos-Victor 2000, Lirman et al. 2007, 2010).

Image processing

As juvenile corals are visible in mosaic imagery but not easily identified, we used high-resolution images (55 mm focal lens) linked to the photomosaics to identify and map the location of all juvenile corals, defined here as colonies with maximum diameters ranging from 1 to 5 cm (Fig. 2). Colony size was determined with the aid of the scaled photomosaic and using lasers mounted to the mosaic frame which provided scale within high-resolution images. These high-resolution images could be tracked within the photomosaic as images were taken sequentially in a grid-like pattern, allowing the location of juvenile colonies to be mapped onto the
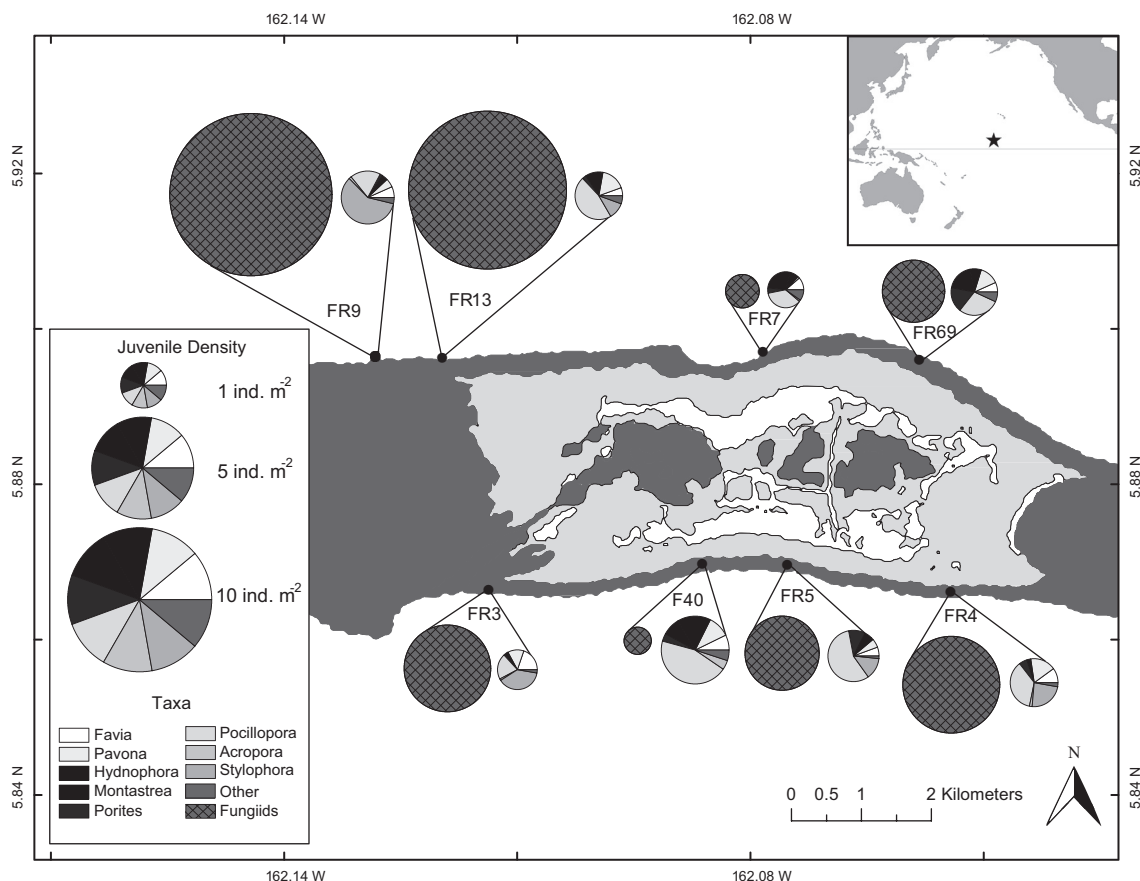

Figure 1. Map of Palmyra Atoll with the density of juvenile corals for each of the major taxa at each site. At each site, density of Fungiids (grey hashed circles) is displayed separately to ensure taxonomic detail of other juvenile colonies.
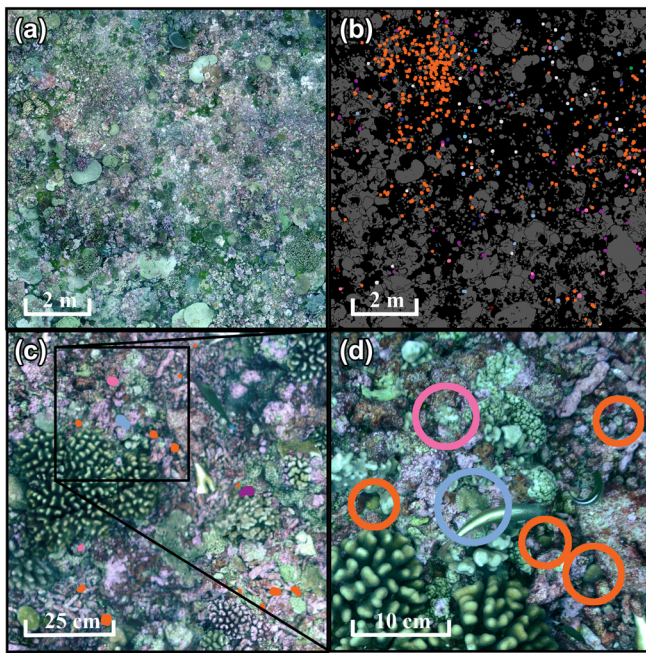
Figure 2. Processing of 100-m² photomosaic plot at FR3. (a) Undigitized plot, (b) digitized plot. Juvenile colonies are mapped with colors indicating different taxa and juvenile colonies have been enlarged to show location. Adult colonies are digitized in grey. (c) Close up of digitized photomosaic showing juvenile colony digitizations. (d) High resolution image used to find and identify juvenile corals, with individual colonies circled using taxon-specific color notations. Pink indicates, *Pocillopora*; orange indicates Fungiids, and blue indicates *Favia stelligera*.

photomosaic. Care was taken to exclude colonies produced by partial mortality, fission or fragmentation (Supplementary material Appendix 1 Fig. A1), therefore encrusting taxa such as *Montipora* spp., *Pavona varians* and *Porites superfusa* were excluded due to high fragmentation seen in these taxa. Our ability to detect and identify juveniles was limited by image resolution and the inability to search through algal mats or under overhangs as with in situ surveys. However, high overlap between successive images and adjacent passes together with variations in camera pose, results in 5–30 images and angles of any given area of the plot, increasing our capacity to find colonies beyond the 2-dimensional plane.

Ecological post-processing of photomosaic imagery was conducted in Adobe Photoshop CC (Fig. 2). Each juvenile (1–5 cm diameter) and adult (defined as a patch of contiguous live coral tissue >5 cm diameter) colony, and each patch of the abundant calcareous algae *Halimeda* spp. was manually segmented and classified to the most resolved taxonomic resolution enabled through visual surveys using preset color designations. Most taxa were identified to species, with some at the genus level including two–three representative species (Williams et al. 2008). For the genus level groupings used here, each consisted of morphologically similar species. Within the study plots, the genus *Pocillopora* was mainly comprised of the species *Pocillopora meandrina*

and *Pocillopora verrucosa*, with *Pocillopora eydouxi* occurring rarely (<3% of adults, Edwards et al. 2017). The genus *Porites* included the massive species *Porites arnaudi*, *Porites lobata* and *Porites lutea*, and the genus *Pavona* predominantly included *Pavona duerdeni*, *Pavona clavus* and *Pavona gigantea*. Fungiids here include species from *Fungia* and *Cycloseris*, both of which are solitary and free-living, which allows for limited mobility that is often facultative. Of the coral taxa examined, *Stylophora pistillata* and *Fungia fungites* are known to be brooding corals, with all other taxa characterized as spawning corals (Baird et al. 2009). Despite the lack of species level identification for some taxa, these designations are constrained with regards to life histories and functional traits, the latter of which are ideal for understanding patterns in community ecology (McGill et al. 2006). Adult encrusting species were included in the analysis despite exclusion during detection of juvenile colonies to account for their space occupancy in spatial analyses. Imagery was also segmented by habitat type, defined broadly as unconsolidated or consolidated reef. Unconsolidated reef was classified as any area of loose reef, often dead coral branches or colonies broken off from the substrate. These habitat designations were confirmed through visual assessments of large area images collected for the same plots in subsequent years, which showed the displacement and movement of individual rubble pieces. Although sand was rare in these plots (<1% total area), it was included in the unconsolidated reef category and mostly consisted of dead *Halimeda* segments. All other areas were designated as consolidated habitat.

Each taxonomic group of adults and juvenile coral colonies, as well as the two habitat types and *Halimeda* spp. patches were separated into individual layers and exported as separate .PNG files. Individual colonies were defined as contiguous patches of pixels with the same RGB value and given unique identifiers using an approach previously described by the authors (Edwards et al. 2017). Images were analyzed for percent cover, density and relative location of colonies for each taxonomic and life stage grouping for corals, as well as the percent cover of each habitat type and *Halimeda* spp.

Statistical analysis

We used correlation analyses to assess the relationship between juvenile density and habitat type. Specifically, we examined the relationship between habitat type and the density of each juvenile taxon as well as total juvenile density, using plots as replicates. For all correlations we used non-parametric Spearman rank correlation as data violated assumptions of normality, even after transformation.

Associations with unconsolidated or consolidated habitat for each taxon were tested using χ^2 analysis. Data were pooled across all sites for each taxon to determine habitat associations. For each taxonomic analysis, the expected value for each habitat type was the resultant sum of the percent cover of the corresponding habitat type multiplied by the number of juvenile colonies at each site. The number of juveniles found on each of the habitat types across all sites was

summed together as the observed value for each taxon. The same analysis was repeated for adult taxa to determine habitat associations of adult colonies.

We examined the relationships between juvenile and adult corals by comparing the density of juvenile corals relative to both density and percent cover of adults. A separate correlation analysis was performed for each taxon, using plots as replicates. Cross-site analyses were performed only for taxa with juvenile colonies present at five or more of the eight plots. As with previous juvenile and habitat correlations, we used non-parametric Spearman rank correlation as data violated assumptions of normality. The same correlation analysis was repeated for adjusted juvenile densities after removing *Halimeda* spp. cover, testing for potential bias resulting from the inability to quantify juveniles that might reside underneath *Halimeda* spp. mats.

The spatial distribution of juveniles near adults of the same taxon was determined using mean nearest adult neighbor distances (Clark and Evans 1954). The nearest adult distance for each juvenile was defined as the Euclidean distance between the juvenile centroid and the closest edge of the nearest adult of the same taxon. Distances were averaged across all sites to determine the mean nearest neighbor distance by taxon. Only juveniles in the center 5 × 5 m area of the photomosaics were used to account for edge effects, however, adults residing in the 2.5 m buffer region around the core were used as neighbors. Analysis was only conducted on taxa with at least five juvenile colonies across all sites, which after implementing the buffer included eight of the nine focal taxa. We used a bootstrapping approach to analyze whether the spatial patterns of juveniles near adults of the same taxon deviated from null random spatial configurations. The null distribution was created by simulating juvenile distributions under conditions of complete spatial randomness (CSR). For each bootstrapped replicate, all juveniles were randomly redistributed across each plot with any area occupied by adult coral colonies excluded from placement to account for space occupancy of variably sized adult colonies. The mean nearest neighbor distance was calculated and the process repeated for 1000 replicates to create the null distribution. If the calculated sample value was less than the 2.5 percentile or greater than the 97.5 percentile of the null distribution, it was determined to significantly deviate from randomness. Values above the 97.5 percentile indicate an over-dispersed distribution while values below the 2.5 percentile indicate clustering.

The overall spatial distribution of juvenile corals by taxon on a 1-m scale was examined using the variance to mean ratio (VMR) (Dale 1999, Dale et al. 2002, Edwards et al. 2017). Each 100-m^2 plot was divided into 100 1-m^2 subplots. The mean (μ), variance (σ^2) and VMR were calculated using the number of juvenile colonies in each subplot. The ratios across all plots were averaged to determine the VMR of each taxon. This metric can be used to interpret spatial distributions, with values >1 indicating clustering, equal to one indicating randomness, and <1 signifying over-dispersion. The same bootstrapping approach used previously for nearest neighbor analyses was used to determine statistically significant deviations from randomness in overall juvenile spatial distributions to again account for space occupancy of adult colonies. All statistical analyses were performed using R ver. 3.4.0 (<www.r-project.org>).

Data deposition

Data are available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.18f9q5d> (Pedersen et al. 2019).

Results

In total, 4681 juvenile colonies were identified across the eight plots. The mean density of juvenile corals was 5.85 ± 1.69 individuals m^{-2} (mean ± SE). The Fungiids accounted for over 79% of all juvenile colonies. Other focal taxa found in order of decreasing abundance include *Pocillopora*, *Stylophora pistillata*, *Pavona*, *Montastrea curta*, *Favia stelligera*, *Hydnophora microconos*, *Porites* and *Acropora*. Rare taxa present at less than four of the eight sites accounting for <2% of the total number of juveniles (*Favites*, *Turbinaria reniformis*, *Platygyra*, *Hydnophora exesa*, *Leptoseris*, *Leptastrea* and *Lobophyllia hemprichii*) were omitted from subsequent analyses. We found large variation in the abundance of juvenile corals among sites. The density of juvenile colonies ranged from 13.74 ind. m^{-2} at FR9 to 1.15 ind. m^{-2} at FR7 (Fig. 1).

A total of 25 902 adult colonies were identified and mapped, with a mean density across sites of 32.4 ± 5.2 ind. m^{-2} (± SE) and a mean percent cover of 20.0 ± 2.5% (± SE). Unconsolidated habitat cover was variable, ranging from 4.8% to 26.2% with an average of 14.8%. Consolidated habitat on average comprised the remaining 85.2% of reef area. *Halimeda* spp. covered 9.7 ± 2.5% (mean ± SE) of reef area.

There were no significant correlations between juvenile density and cover of each habitat type for any taxon. However, significant positive relationships were found between juvenile density and adult percent cover for four of the taxonomic groupings, including *Favia stelligera* ($\rho = 0.71$, p = 0.05), Fungiids ($\rho = 0.79$, p = 0.02), *Montastrea curta* ($\rho = 0.74$, p = 0.04) and *Stylophora pistillata* ($\rho = 0.93$, p < 0.001) (Table 1, Supplementary material Appendix 2 Fig. A2). Similarly, positive relationships were found between juvenile density and adult density for these four taxa, *Favia stelligera* ($\rho = 0.81$, p = 0.02), Fungiids ($\rho = 0.93$, p < 0.001), *Montastrea curta* ($\rho = 0.86$, p < 0.01) and *Stylophora pistillata* ($\rho = 0.85$, p < 0.01) with the addition of *Acropora* ($\rho = 0.73$, p = 0.04) (Table 1, Supplementary material Appendix 2 Fig. A3). Repeated correlations between juvenile density and adult metrics of density and percent cover after accounting for *Halimeda* spp. percent cover showed no large differences in the results described above, indicating no major bias overall or between taxa associated with undetectable juveniles hidden beneath this algal genus.

Table 1. Spearman rank correlation analysis of juvenile and adult corals using both percent cover and density metrics for adult abundances. Results of correlation analysis between juvenile and adult abundances include the correlation coefficient (ρ) and p-values. Significant correlations in bold.

Taxa	Percent cover		Density	
	ρ	p	ρ	p
Hydnophora microconos	0.639	0.088	0.675	0.067
Montastrea curta	0.738	**0.037**	0.857	**0.007**
Pavona	0.635	0.091	0.683	0.062
Favia stelligera	0.708	**0.050**	0.805	**0.016**
Stylophora pistillata	0.927	**<0.001**	0.854	**0.007**
Porites	−0.611	0.108	0.024	0.955
Pocillopora	−0.190	0.651	0.476	0.233
Fungiids	0.786	**0.021**	0.929	**<0.001**
Acropora	0.281	0.500	0.730	**0.040**

Results from χ^2 analysis showed significant habitat preferences, with juvenile colonies at each site found disproportionately on unconsolidated rather than consolidated habitat. *Porites* ($\chi^2 = 44.53$, $p < 0.001$), *Acropora* ($\chi^2 = 6.52$, $p = 0.01$), *Stylophora pistillata* ($\chi^2 = 4.65$, $p = 0.03$) and Fungiids ($\chi^2 = 2571.20$, $p < 0.001$) all showed significant positive associations with unconsolidated habitat (Fig. 3), while only *Pocillopora* ($\chi^2 = 8.00$, $p < 0.01$) showed a significant positive association with consolidated habitat. *Hydnophora microconos*, *Montastrea curta*, *Pavona* and *Favia stelligera* showed no disproportionate association with either habitat type.

All adult taxa showed significant habitat associations with consolidated habitat except for the Fungiids, which associated with unconsolidated habitat (Supplementary material Appendix 3 Fig. A4).

Nearest neighbor analysis revealed differences in juvenile spatial relationships to adults of the same taxon. *Pocillopora* ($p < 0.001$, $n = 94$) and Fungiids ($p < 0.001$, $n = 1076$) both had lower mean nearest neighbor distances than expected, indicating clustering near adults of the same taxa (Fig. 4a). The remaining taxa had mean nearest neighbor distances consistent with a random distribution of juveniles around adults, with none of the taxa displaying overdispersed spatial patterns.

The VMR analysis of juvenile patterns showed three taxa with clustered distributions, with the remaining five taxa randomly distributed (Fig. 4b). All taxa exhibited variance to mean ratios at or above 1, indicating no over-dispersed distributions. Fungiids ($\sigma^2/\mu = 7.50$, $p < 0.001$), *Pocillopora* ($\sigma^2/\mu = 1.16$, $p = 0.01$) and *Stylophora pistillata* ($\sigma^2/\mu = 1.19$, $p = 0.01$) all displayed significant clustering. The dispersion patterns of *Favia stelligera*, *Pavona*, *Hydnophora microconos*, *Montastrea curta* and *Porites* did not differ from spatial randomness.

Concerns over a potential detection bias of smaller juvenile colonies led to examination of the size frequency distribution of juvenile corals, which revealed a lower than expected number of juveniles with maximum diameters between 1 and 2 cm
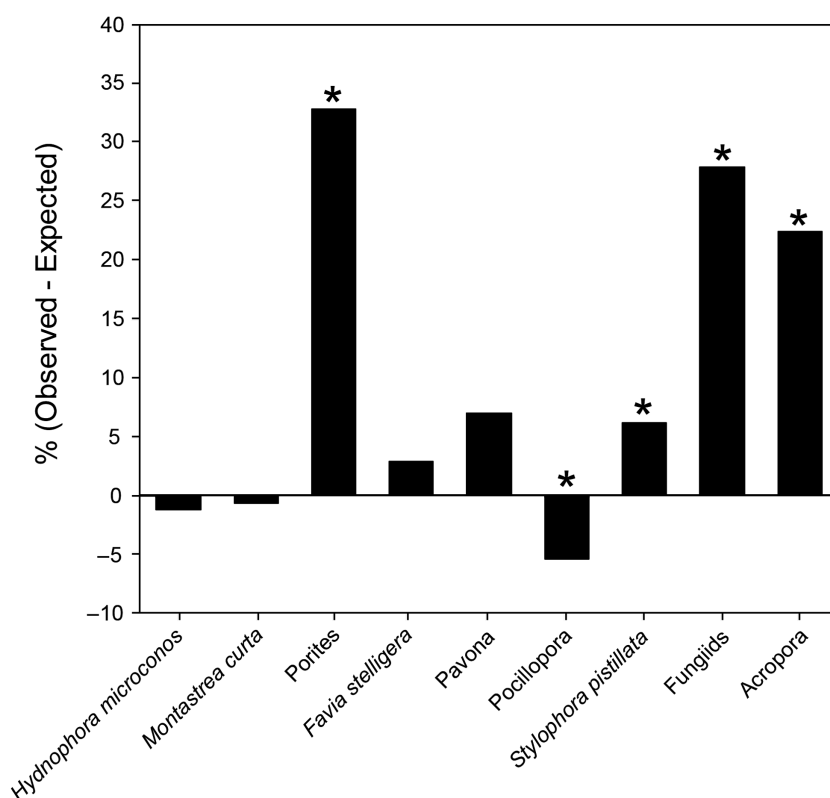

Figure 3. Habitat associations of juvenile corals. Proportional difference between the observed and expected number of individuals located within unconsolidated habitat. Positive values indicate association with unconsolidated habitat, negative values indicate association with consolidated habitat. Asterisks indicate significant habitat association.
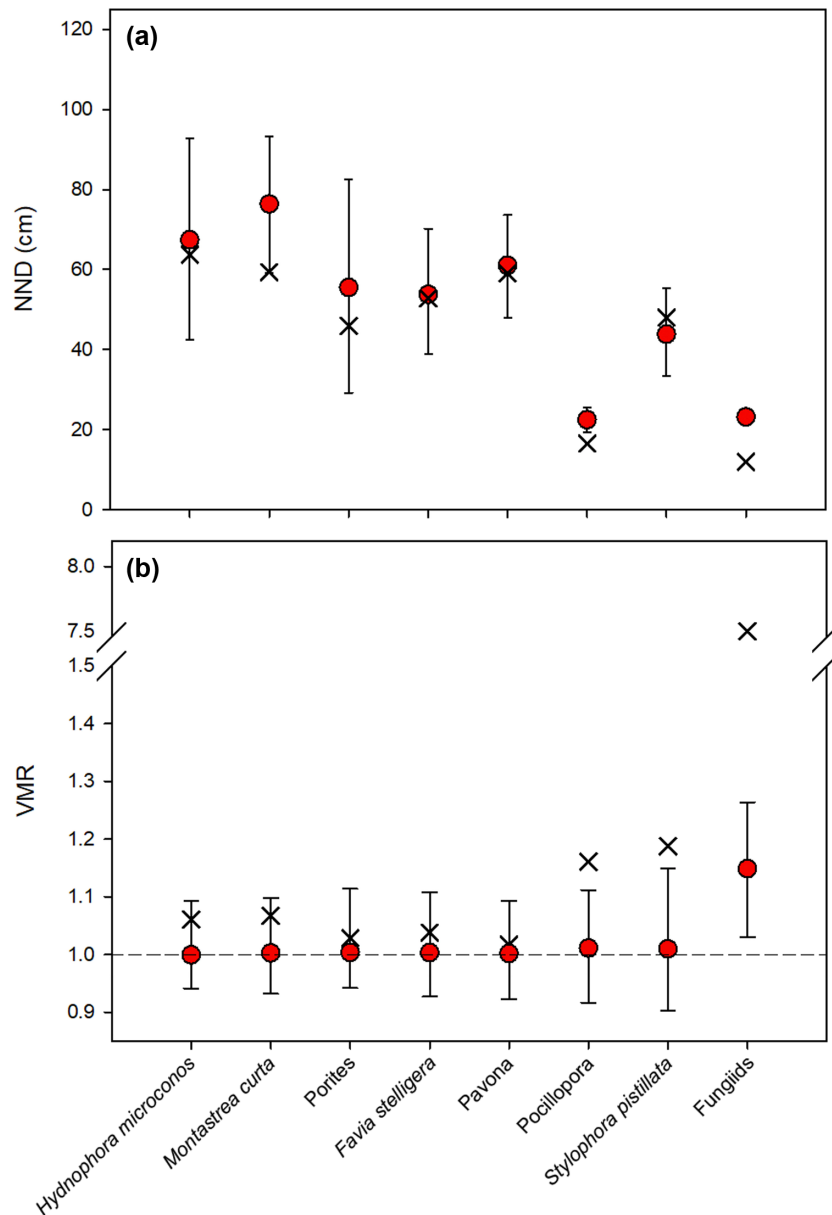
Figure 4. (a) Spatial pattern of juveniles associated with their taxon-specific adults using nearest neighbor distances (NND). (b) Spatial distribution of juvenile corals represented by the variance to mean ratio (VMR). Black crosses indicate the observed value and red circles represent the mean given by the null distribution, with error bars indicating the 95% CI.

following the assumptions of a type-III survivorship curve (Supplementary material Appendix 4 Fig. A5). As such, all analyses were repeated using only juveniles with a maximum diameter between 2 and 5 cm. There were no qualitative differences in the results using the 2–5 cm diameter range, therefore the analyses with all juveniles from 1 to 5 cm in diameter were used to maintain higher power.

Discussion

We explored spatial distribution patterns of juvenile corals. Specifically, we mapped juvenile and adult coral colonies at a landscape scale using large area imaging to examine how variation in habitat and adult community structure were linked to juvenile spatial patterns. While juvenile coral density did not correlate with percent cover of habitat types across sites, the location of individual juvenile colonies showed more habitat specificity, with four of nine taxa associated with unconsolidated habitat and one taxon (*Pocillopora*) associated with consolidated habitat (Fig. 3). Spatial relationships between juvenile and adult corals were more variable, with only two taxa showing strong clustering and the remainder being random. Similarly, while the dispersion patterns of some juvenile coral taxa were clustered across our plots, most were random. Interestingly, spatial distributions of adult corals from Palmyra Atoll showed consistent clustering across most taxa (Edwards et al. 2017). The contrast of spatial

patterns across life stages from random to clustered suggests that mechanisms leading to adult clustering are likely linked to events experienced during the adult life phase.

This study showed positive relationships between juvenile density and percent cover and density of adults for half of the examined taxa. Self-recruitment may be more common amongst corals than expected based on the dynamics of larval competencies alone (Figueiredo et al. 2013). *Stylophora pistillata* and Fungiid corals displayed some of the strongest relationships between juveniles and adult cover or density which may reflect their brooding (*Stylophora pistillata*) and budding (Fungiids) reproductive strategies indicative of semi-closed or closed populations. These taxa also have life history strategies promoting rapid generation times associated with species described as weedy, or r-selected (Szmant 1986). Variation in site-level abundance could also be driven by environmental variation across Palmyra Atoll (Williams et al. 2013, Gove et al. 2015) where site level conditions may be advantageous for taxa with certain life history strategies (Darling et al. 2012).

Individual juvenile colonies showed strong spatial patterning across the benthic landscape, with surprisingly many taxa more abundant within unconsolidated habitat. Unconsolidated habitat is considered unsuitable as a settlement substrate as movement can result in the injury or death of coral colonies (Fox et al. 2003). However, natural rubble fields can have juvenile densities comparable to their stable counterparts (Cameron et al. 2016). The association of adult taxa with consolidated habitat may be an indication that loose rubble generates a demographic bottleneck, as mortality can be high in unconsolidated habitat (Chong-Seng et al. 2014). However, organisms such as sponges, *Halimeda*, CCA, and even the corals themselves help stabilize loose substrate, increasing survivorship of these vulnerable colonies (Wulff 1984, Rasser and Riegl 2002). Successful survival and growth of juvenile colonies may contribute to future cementation and generation of consolidated substrate, thus creating a mosaic landscape of dynamic unconsolidated and consolidated substrate existing at various geologic successional states.

Despite the unstable nature of unconsolidated substrate, there may be beneficial characteristics which attract juvenile colonies. Reef rubble often has lower coral cover (Chong-Seng et al. 2014), decreasing competition with established adult colonies. Rubble contains dead coral branches and fragments which induce metamorphosis of coral larvae (Heyward and Negri 1999) and at Palmyra are often colonized by an abundance of CCA, which provides cues for settlement and metamorphosis of larvae (Harrington et al. 2004, Price 2010). The presence of many dead coral branches also creates cryptic habitat that provides refugia for settlers (Edmunds et al. 2004). Our results suggest that the benefits of settling on unconsolidated reef habitat may outweigh the negative risk of injury or death in natural rubble zones.

Habitat preferences may reflect the influence of physical tolerances in determining where colonies are located.

Specifically, free-living Fungiids may have an advantage in unconsolidated habitat because they do not need to physically attach to the substratum. Their tolerance for high stress environments, limited mobility and propensity for asexual reproduction via budding especially when subjected to environmental and physical disturbances (Kramarsky-Winter and Loya 1996), makes them suitable for this habitat type. Conversely, *Pocillopora* was the only taxon found disproportionately on consolidated habitat which may reflect more specific microhabitat preferences with higher water flow and reduced impacts from sedimentation (Lenihan et al. 2011). In this study, *Pocillopora* appeared to be the only taxon capable of colonizing dead *Acropora* tables. These open, elevated, structurally smooth areas may represent a niche for which *Pocillopora* is well suited.

Nearest neighbor distances were at or below expectations of randomness. While juveniles of *Stylophora pistillata* had expectations of clustering near taxon-specific adults due to reduced dispersal distances associated with brooding, the average distance from a juvenile to its nearest adult was roughly 0.5 m, lower than the potential dispersal range of brooded planulae. Additionally, no corals displayed overdispersion relative to adult colonies as predicted by the Janzen–Connell hypothesis. However, Janzen–Connell effects in corals have been shown amongst larvae and settlers (Marhaver et al. 2013), long before individuals reach the juvenile stage. Mortality associated with the abundance of turf algae (Vermeij and Sandin 2008) and predation (Doropoulos et al. 2016), as well as selective settlement may mask any distance-dependent effects before settlers reach the juvenile size limit used here. Differentiating spatial patterns of settlement and mortality resulting from taxon-specific effects in contrast to other benthic community impacts will help determine the role of within taxon distance-dependent influences on juvenile communities.

Clustering of juvenile colonies near adults of the same taxon could be due to common habitat associations across life stages. Juvenile Fungiids showed a strong association with unconsolidated habitat, and even as adults these individuals are found within unconsolidated substrate such as rubble fragments and sandy bottoms (Hoeksema 1988, Hoeksema and Moka 1989), additionally seen here with Fungiid adults associated with unconsolidated habitat. Additionally, *Pocillopora* juveniles were the only taxon associated with consolidated habitat, which is the same habitat association of all sessile adult taxa. All other juvenile taxa showed associations with unconsolidated habitat or an indifference to habitat, which contrasts with adult associations with consolidated habitat. Therefore, the clustering pattern seen in Fungiids and *Pocillopora* near adults may be a result of conserved habitat associations across multiple life stages.

Most juvenile taxa had random spatial distributions overall, suggesting additional processes occurring during later life stages which may contribute to the consistent clustering seen across adult taxa at Palmyra (Edwards et al. 2017). Spatially driven patterns of adult mortality within a

heterogenous environment could contribute to the clustered patterns seen amongst adult corals. For instance, the association of sessile adult taxa with consolidated reef could indicate high mortality of colonies within unconsolidated habitat that could drive the clustering patterns of adult taxa. However, adult spatial patterns are consistent with non-homogenous or homogenous cluster processes rather than non-homogenous Poisson processes (Edwards et al. 2017). This suggests that habitat filtering, or in this instance, mortality driven spatially by heterogeneity in consolidated and unconsolidated reef alone does not best describe the clustered patterns seen in adults. The clonal nature of corals allows asexual reproduction through fragmentation and fission to be major strategies for reproduction (Highsmith 1982), which will likely strengthen patterns of clustering in corals (Edwards et al. 2017) as multiple daughter colonies are created and likely to remain in close proximity of the original coral colony. As clonal individuals, large adult corals are less likely to experience full colony mortality, instead experiencing a reduction in size or division into multiple colonies through partial mortality and fragmentation processes (Jackson and Hughes 1985). It is therefore more likely that the shift in juvenile and adult spatial patterns from random to clustered are a result of fragmentation and fission amongst adult populations.

The three juvenile taxa that showed clustered spatial patterns were the taxa with the highest juvenile densities. For coral taxa characterized by rapid development, high population and short life spans typical of ruderal or r-selected species (MacArthur and Wilson 1967, Grime 1977), sexual reproduction is more likely the predominant strategy used to create new individuals. For these taxa with high rates of reproduction, settlement selectivity or higher survivorship on preferred habitat within a heterogeneous environment may lead to clustered patterns for *Pocillopora* and the Fungiids, which showed strong associations with consolidated and unconsolidated reef respectively. However, juvenile colonies of *Stylophora pistillata* did not show an association with either habitat despite having a clustered distribution, which could indicate that heterogeneity of specific microhabitats (CCA or crevices) influence clustered patterns in juvenile corals. This suggests multiple mechanisms through which clustered patterns are created in adult spatial patterns, whereby taxa with high reproductive investment have clustered patterns driven by habitat heterogeneity, with all additional clustering reinforced through fragmentation for all taxa during the adult stage.

The use of large-area imagery to map individual coral colonies across landscape scales provides a powerful approach to examine spatial patterns at a community scale. The many juvenile taxa we observed showing positive associations with unconsolidated habitat suggests that early stages of succession whereby corals colonize and consolidate loose rubble patches, may contribute to overall reef stability in addition to reef growth. Habitat heterogeneity is likely one driver of spatial clustering for taxa which invest heavily in reproduction, with fission and fragmentation processes occurring during adult life stages providing a strengthening mechanism for clustering in corals. The influence of habitat heterogeneity on clustering within coral communities is congruent with patterns identified in tropical forests (Condit et al. 2000), however, the proposed process which predominantly drives clustering in corals, fission and fragmentation resulting from their clonal nature, diverges from dispersal limitations identified as a key spatial determinant in forest systems (Hubbell 1979, Condit et al. 2000). The creation of spatially explicit maps of individual distributions across life stages allows for crucial insights to be gained about the patterns and process which spatially structure these coral reef communities.

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Supplementary material (available online as Appendix ecog-04520 at <www.ecography.org/appendix/ecog-04520>). Appendix 1–4.