

RESEARCH ARTICLE

Recruitment Variability of Coral Reef Sessile Communities of the Far North Great Barrier Reef

Heidi M. Luter^{1,2*}, Alan R. Duckworth², Carsten W. Wolff², Elizabeth Evans-Illidge², Steve Whalan^{3,4}

1 NAMRA and the Australian Institute of Marine Science, Arafura Timor Research Facility, Darwin, NT, Australia, **2** Australian Institute of Marine Science, Townsville, QLD, Australia, **3** Central Caribbean Marine Institute, Little Cayman, Cayman Islands, **4** Marine Ecology Research Centre, School of Environment, Science and Engineering, Southern Cross University, Lismore, NSW, Australia

* h.luter@aims.gov.au



Abstract

One of the key components in assessing marine sessile organism demography is determining recruitment patterns to benthic habitats. An analysis of serially deployed recruitment tiles across depth (6 and 12 m), seasons (summer and winter) and space (meters to kilometres) was used to quantify recruitment assemblage structure (abundance and percent cover) of corals, sponges, ascidians, algae and other sessile organisms from the northern sector of the Great Barrier Reef (GBR). Polychaetes were most abundant on recruitment tiles, reaching almost 50% of total recruitment, yet covered <5% of each tile. In contrast, mean abundances of sponges, ascidians, algae, and bryozoans combined was generally less than 20% of total recruitment, with percentage cover ranging between 15–30% per tile. Coral recruitment was very low, with <1 recruit per tile identified. A hierarchical analysis of variation over a range of spatial and temporal scales showed significant spatio-temporal variation in recruitment patterns, but the highest variability occurred at the lowest spatial scale examined (1 m—among tiles). Temporal variability in recruitment of both numbers of taxa and percentage cover was also evident across both summer and winter. Recruitment across depth varied for some taxonomic groups like algae, sponges and ascidians, with greatest differences in summer. This study presents some of the first data on benthic recruitment within the northern GBR and provides a greater understanding of population ecology for coral reefs.

OPEN ACCESS

Citation: Luter HM, Duckworth AR, Wolff CW, Evans-Illidge E, Whalan S (2016) Recruitment Variability of Coral Reef Sessile Communities of the Far North Great Barrier Reef. *PLoS ONE* 11(4): e0153184. doi:10.1371/journal.pone.0153184

Editor: Sebastian C. A. Ferse, Leibniz Center for Tropical Marine Ecology, GERMANY

Received: October 27, 2015

Accepted: March 24, 2016

Published: April 6, 2016

Copyright: © 2016 Luter et al. This is an open access article distributed under the terms of the [Creative Commons Attribution License](https://creativecommons.org/licenses/by/4.0/), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

Data Availability Statement: All relevant data are within the paper and its Supporting Information files.

Funding: This study was funded by the Marine and Tropical Sciences Research Facility, Project 1.3.2: Ecological role and potential economic value of sponges to the Torres Strait.

Competing Interests: The authors have declared that no competing interests exist.

Introduction

Coral reefs exhibit remarkable biodiversity [1]. Although the conspicuous scleractinian corals form key structural components of coral reefs numerous other groups play important functional roles. Notably, reef-consolidating algae [2] and sponges play vital roles in nutrient cycling and aid in benthic-pelagic energy coupling [3]. The underlying resilience of coral reefs, in part, relies on the maintenance and persistence of these coral reef communities through space and time [4], particularly for sessile benthic taxa with dispersive larval or propagule phases.

Knowledge of recruitment, larval dispersal and population connectivity of benthic sessile invertebrates is critical to the management and conservation of coral reefs [5–8]. Population connectivity of marine sessile invertebrates has largely been determined from population genetics [5], which often depicts complicated patterns of larval dispersal. Larval dispersal of coral reef invertebrates is often characterised by endogenous recruitment, but with enough long-distance dispersal to provide variable levels of population subdivision for scleractinian corals [9,10], octocorals [11] and sponges [12,13]. While assessments of larval dispersal are important to establish levels of population maintenance, collecting data on spatio-temporal variability in larval recruitment is also important [8].

Determining the spatial scales of community recruitment contributes to our understanding of resilience, maintenance and persistence of coral reefs, however, there is a large focus on documenting recruitment dynamics of scleractinian corals (e.g. [14–17]). The dedicated effort to understanding population demographics of scleractinian corals has resulted in valuable knowledge aiding how we manage these ecosystems, particularly when data show patterns of reef degradation [18–20].

Scleractinian coral recruitment studies have relied on a combination of the use of recruitment tiles (e.g. [21]) and field surveys (e.g. [15]); while broad scale interpretations of coral recruit variability are difficult, the resilience of reefs is strongly linked to recruitment potential [22,23]. Moreover, the potential for shifting taxonomic states in coral reefs following disturbance, such as coral-algae phase shifts [24], highlights the importance of understanding the dynamics and scales of recruitment variability [22]. Coral recruitment can vary greatly across many spatial scales, including between coral reefs [15,25,26], among reefs patches with reef systems [27], within reef patches [28] and between experimental recruitment tiles [21,29,30]. Recruitment variability also occurs among depths [16] and over time [15,27,31]. Interpreting drivers that contribute to coral recruitment variability is complex, but can include both abiotic (e.g. light intensity and water flow) and biotic (e.g. competition and predation) influences [15,31], as well as spatio-temporal environmental stochasticity [32]. In contrast to the many published studies examining coral recruitment, there are few studies that have investigated recruitment patterns of other sessile organisms, such as sponges, bivalves and ascidians, on coral reefs [33]. Often this recruitment data for non-scleractinian organisms is incidental to more focused coral recruitment studies (e.g. [27,29]). As such, our overall knowledge of non-scleractinian coral reef invertebrates is poorly developed, thereby hindering a broader understanding of community coral reef recruitment.

The broad objective of this study was to begin to meet some of those knowledge gaps of recruitment patterns of benthic coral reef communities (i.e. scleractinian and non-scleractinian coral reef taxa) within a region of Torres Strait, northern Australia. Torres Strait forms the northern most region of the Great Barrier Reef (GBR). While there is limited peer reviewed data on distribution and abundance of sessile coral reef taxa in Torres Strait (e.g. [34,35]), information of non-scleractinian coral reef recruitment studies are, to our knowledge, non-existent in central Torres Strait. Therefore, the specific aim of this study was to examine and quantify recruitment assemblage structure of sessile organisms across a range of spatial and temporal scales, to establish spatio-temporal variability between and within coral reefs in central Torres Strait.

Materials and Methods

Study site and plate deployment

The study was conducted at Masig and Marsden Islands in central Torres Strait, Australia (S1A Fig). Both islands consist of sand cays with fringing coral reefs, with a reef profile typically comprising a slope descending at an angle ranging from 20–60° from 6 m, terminating at a

sand bottom at 15 m. To examine differences in recruitment patterns of sessile invertebrates at a range of spatial scales relevant to the two islands, the design of the study allowed us to examine variation in recruitment patterns at spatial scales from 5 km (between islands), 200 m (between locations), 20 m (between sites), depth (6 m vs. 12 m) and 1 m between tiles (S1B Fig). Settlement plates were deployed at each of the three locations on the northern side of each island. Each location was further divided into three sites, with each site having two depth categories: shallow (6 m) and deep (12 m). Five settlement plates, placed 1 m apart, were deployed at each site x depth combination, using the direct attachment method of [21]. Briefly, 11x11 cm terracotta tiles with pitted surfaces were anchored 1 cm above the reef to provide settlement surfaces on both sides of each plate.

Assessment of temporal patterns was made possible by deploying seasonal sets of plates at the start of the Australasian summer (November) and winter (May). Plates were deployed for six months to allow comparisons over summer and winter over a two-year period (November 2006 to May 2008). At the end of each season, the top and underside of each plate were photographed *in situ* and a new plate was deployed. Representative sponge specimens were removed from tiles during the winter 2007 sampling and preserved in 70% ethanol to facilitate higher taxonomic identifications.

The study area lies within Australian jurisdiction of the Torres Strait Protected Zone, where marine resource management is undertaken by the Australian Fisheries Management Authority (AFMA) under the Torres Strait Fisheries Act 1984. AFMA officers were consulted prior to the commencement of this study, and confirmed that the deployment of settlement of tiles required for this study was not a matter for their regulation, and did not require a permit under their act. The study area also lies within the traditional lands and seas of Torres Strait traditional owners. Their consent to the study was obtained via a consultative process coordinated by the Reef and Rainforest Research Centre, which administered all Torres Strait research conducted through the Marine and Tropical Science Research Facility (MTRSF), which funded the study. This study did not involve endangered or protected species.

Photographic analysis

An underwater close-up frame, adapted to accommodate either an Olympus C-7070 or Canon IXUS 850IS camera in underwater housings, was constructed to photograph settlement tiles at a fixed distance and to record site and tile information. Both cameras have identical lenses and sensor-resolution; hence images produced are comparable in quality and view. The recruitment of sessile invertebrates was determined for both abundance and percent cover. To determine the abundance of each taxon, an overhead transparency marked with a square was overlaid on a PC-screen. All images of tiles were displayed by Microsoft Windows XP "Picture and Fax Viewer™" and enlarged by clicking the zoom-in button sufficient times to identify each organism. To measure the surface area occupied by each taxon, a 40-point grid was overlaid on the PC-screen image. When analysing images for both abundance and percent cover, the square grid was reduced by a 1 cm margin to eliminate any potential edge effects. Identification to species or genus level could not be established for many of the recruits due to their small size, which is not uncommon in recruitment studies [36,37]. Therefore, recruit assemblages were categorized into broad taxonomic groups (e.g. sponges, ascidians, bryozoans, corals, polychaetes, bivalves, algae and diatoms). In addition, sponges were identified to species level if possible.

Data analysis

All statistical analyses were performed at the taxon level (e.g. sponge, algae, polychaeta), with further analysis for sponge species that were positively identified. Multivariate permutational

analysis (PERMANOVA) was used to examine differences in invertebrate recruitment patterns over various spatial scales using a balanced 5-factor nested design. Factors in the model were Season (fixed), Island (fixed), Location (random, nested within Island), Site (random, nested within Location) and Depth (random, nested within Site) and permutations were based on the Bray-Curtis resemblance matrix generated from $\log(x+1)$ transformed data. The unconstrained principal coordinate analysis (PCoA) was used to visually compare recruitment patterns of sessile invertebrates from both islands. Individual PERMANOVA tests (9999 permutations) based on the Euclidean distance matrix were performed to examine variability in recruit abundance, assemblage structure, and the individual taxa between all spatial scales at each season separately. For the individual tests, differences were considered significant at a lower p-value of <0.01 to reduce the risk of a Type 1 error. The nested design used in this study allowed for (pseudo) variance components to be compared between spatial scales and seasons [38,39]. All analyses were performed using PRIMER 6/PERMANOVA+ v1.0.2 (Plymouth, UK). Initial analyses revealed no significant difference in invertebrate recruitment patterns (e.g. recruit abundance and percent cover) between the two years; therefore, only data from the second year (e.g. May 2007 to May 2008) is presented.

Results

While both the top and underside of the settlement plates were photographed, $>90\%$ of the top side was bare space with very low recruitment of unidentified algae; no other organisms recruited to the top of the plate. Due to the very low recruitment on the top side of tiles, only data from the undersides are presented. In total, eight broad taxonomic groups recruited to the tiles over the course of the two-year study, including sponges, ascidians, scleractinian corals, bryozoans, polychaetes, bivalves, algae and diatoms (Fig 1; S2 Fig). Polychaetes were the most numerically dominant taxa observed, with average numeric recruitment abundances being four times higher than any other taxa (Fig 1A). Scleractinian corals displayed the lowest recruitment with an average of ≤ 1 recruit per tile observed (Fig 1A). Although polychaetes were the most numerically abundant taxa, they occupied a very low percentage cover (means ± 1 S.E., $3.0 \pm 0.6\%$) of the settlement tiles (Fig 1B). On the other hand, groups with more encrusting prostrate morphologies such as algae ($22.0 \pm 1.1\%$), sponges ($16.7 \pm 1.4\%$) and ascidians ($16.4 \pm 1.4\%$) comprised a greater percentage of the tile surface (Fig 1B).

Recruitment abundances were similar at the highest spatial scale (e.g. between Islands) and across seasons; however, there was a significant effect of location and depth on recruit abundances (Table 1). Variation in recruitment abundance between locations was more pronounced for certain taxa including polychaetes, algae and diatoms, particularly during summer (Fig 2). This finding was also apparent in the PCoA, with the same groups contributing most to the discrimination (Fig 3A). The PCoA showed 64.6% of the variation explained in the first two axes, with no clear patterns separating recruitment between Islands or Seasons (Fig 3A). When examining assemblages using percent cover data, recruitment was remarkably similar across multiple spatial scales and between seasons, with PERMANOVA revealing depth to be the only significant source of variation (Table 2). This was further demonstrated with PCoA, with the ordination displaying no distinct separation between assemblages at the highest spatial scale (Fig 3B). Sixty percent of the total variation was explained in the first two factors, with algae, sponges, ascidians and bivalves contributing the most to the discrimination (Fig 3B).

When recruitment cover was examined separately for each season, PERMANOVA revealed no significant differences at the higher spatial scales (e.g. islands, locations or sites) for summer or winter (Table 3). In fact, depth was the only significant factor, but only during the summer sampling period (Table 3). Similarly, recruitment abundances were not significantly different

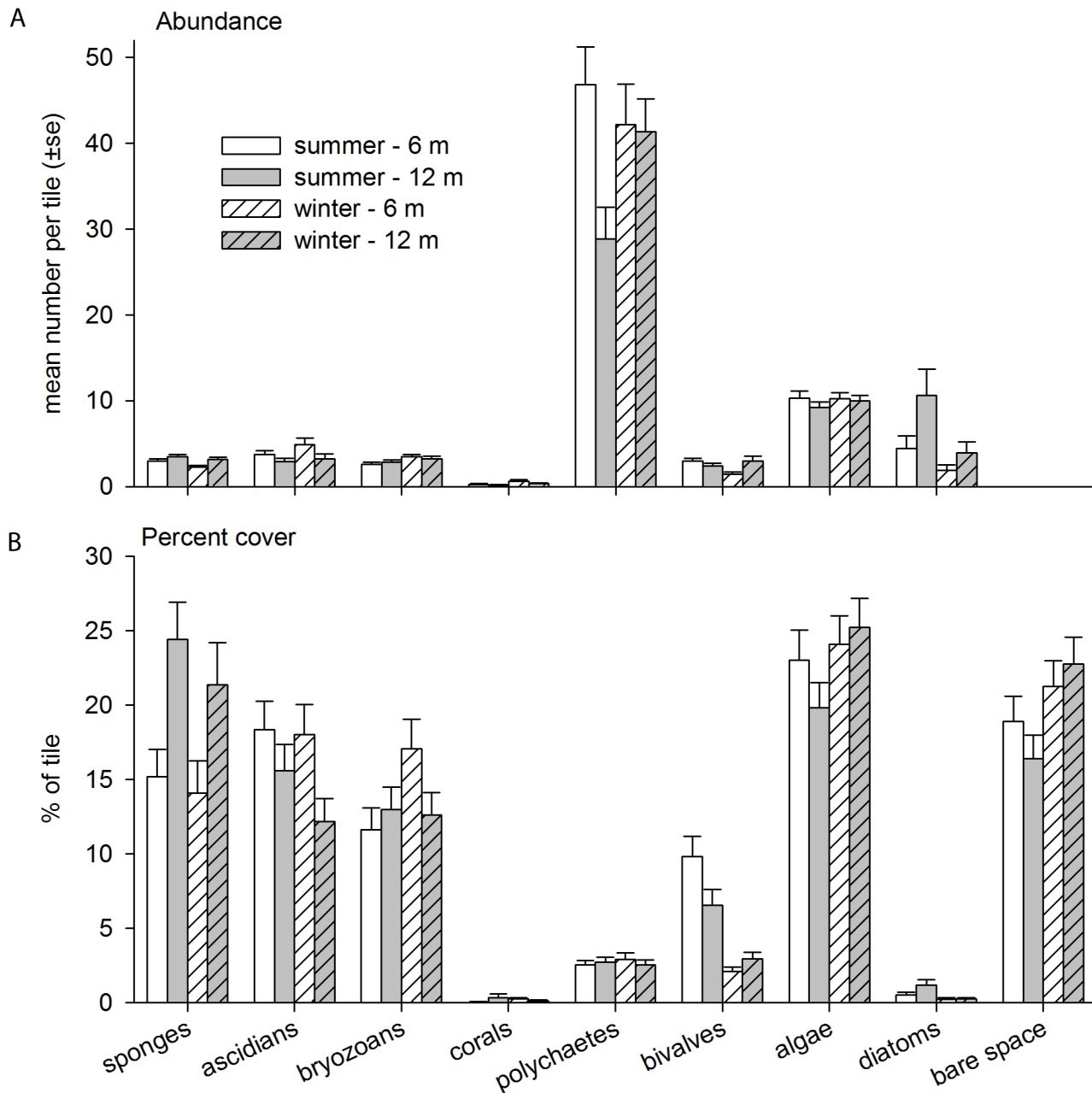


Fig 1. Mean abundance (A) and percent cover (B) of each of the taxa for the year 2 sampling period. Both seasons and depths depicted.

doi:10.1371/journal.pone.0153184.g001

at the highest spatial scale for either season; there was a significant difference between locations during the summer only (Table 3). Examination of the pseudo-variance components from the PERMANOVA model revealed that the largest source of variation could consistently be attributed to the smallest spatial scale (i.e. between tiles, 1-m apart) for both recruitment abundance and percent cover (Fig 4A and 4B). The patterns of variation were inconsistent for both measures between the two seasons. For instance, Site contributed to the variation in abundances during winter, but not during summer (Fig 4A), and location contributed to the variation in percent cover during the summer, yet had no contribution during winter (Fig 4B). The only

Table 1. Results of the multivariate PERMANOVA for abundance data. Permutations were based on a Bray-Curtis similarity matrix generated from log(x+1) transformed data. Significant p-values (<0.05) in bold.

Source	df	Pseudo-F	p
Season	1	6.76	0.249
Island	1	0.41	1
Season x Island	1	0.59	0.59
Location (Island)	4	2.44	0.005
Site (Location)	12	1.06	0.382
Season x Location	4	1.04	0.438
Season x Site	12	0.94	0.65
Depth (Site)	18	2.17	0.001
Season x Depth	18	1.15	0.203

doi:10.1371/journal.pone.0153184.t001

consistent source of variation between both measures and seasons (excluding tiles) was depth; however, it was higher for both during the summer (Fig 4A).

Individual PERMANOVA tests for each taxa revealed that depth was a significant source of variation during the summer for only three out of the seven taxa: algae, sponges and ascidians (Table 3). For instance, sponges covered a larger percentage of deep tiles, whereas ascidians covered a larger percentage of shallow tiles (Fig 1B). During the summer, there was also a significant difference in the cover of bivalves between locations (Table 3). Interestingly, the only significant source of variation in the winter was depth, but only for algae (Table 3).

In total, eight different sponge species were positively identified over the course of the two-year study (S3 Fig). Species spanned six families and included: *Chalinula nematifera*, *Coscinoderma matthewsi*, *Dysidea avara*, *Dysidea* sp. 1 grey, *Haliclona turquiosia*, *Hyrtios erecta*, *Iotrochota purpurea* and *Iotrochota* sp. 1 green. Average recruitment abundances of all species were very low, with *H. turquiosia* recruitment being the highest (Fig 5A). Interestingly, *H. turquiosia* also occupied the highest percentage (overall mean = 2.12%) of the tiles, along with *Dysidea* sp. 1 grey (0.92%) (Fig 5B). *H. erecta* was the least abundant and occupied the smallest percentage (0.03%) of the tile out of all the sponges species identified (Fig 5A and 5B). Notably, higher recruitment of sponges like *Coscinoderma matthewsi* and *Dysidea* species at 12 m compared with 6 m agrees with the abundance patterns of adult sponges across depth [40](Fig 1B).

Discussion

A notable finding of this study was that the highest levels of recruitment variation occurred at the lowest spatial scale examined, with recruitment varying more between experimental tiles 1 m apart than between sites, locations and islands. Recruitment variability of sessile benthic taxa, at small, within-habitat scales is a consistent finding in recruitment studies [38,39,41,42], despite the use of uniformly sized settlement tiles that provide a standardised habitat that limits recruitment variability associated with complex heterogeneous natural reef habitats [33,36]. Interpretations of small scale (i.e. highly localised) recruitment variability can be linked to a range of environmental processes, including competition for space or predation [41,43,44]. Physical processes including, boundary flow hydrodynamics and habitat surface topography can also play roles in recruitment variability at small spatial scales [45–47]. Tiles in this study had similar habitat topography; however, factors such as flow rates and light intensity were possibly different [45], which likely affected recruitment patterns.

The finding of recruitment heterogeneity among experimental tiles provides an important insight into the dynamics of recruitment. Heterogeneity at local scales, covering metres,

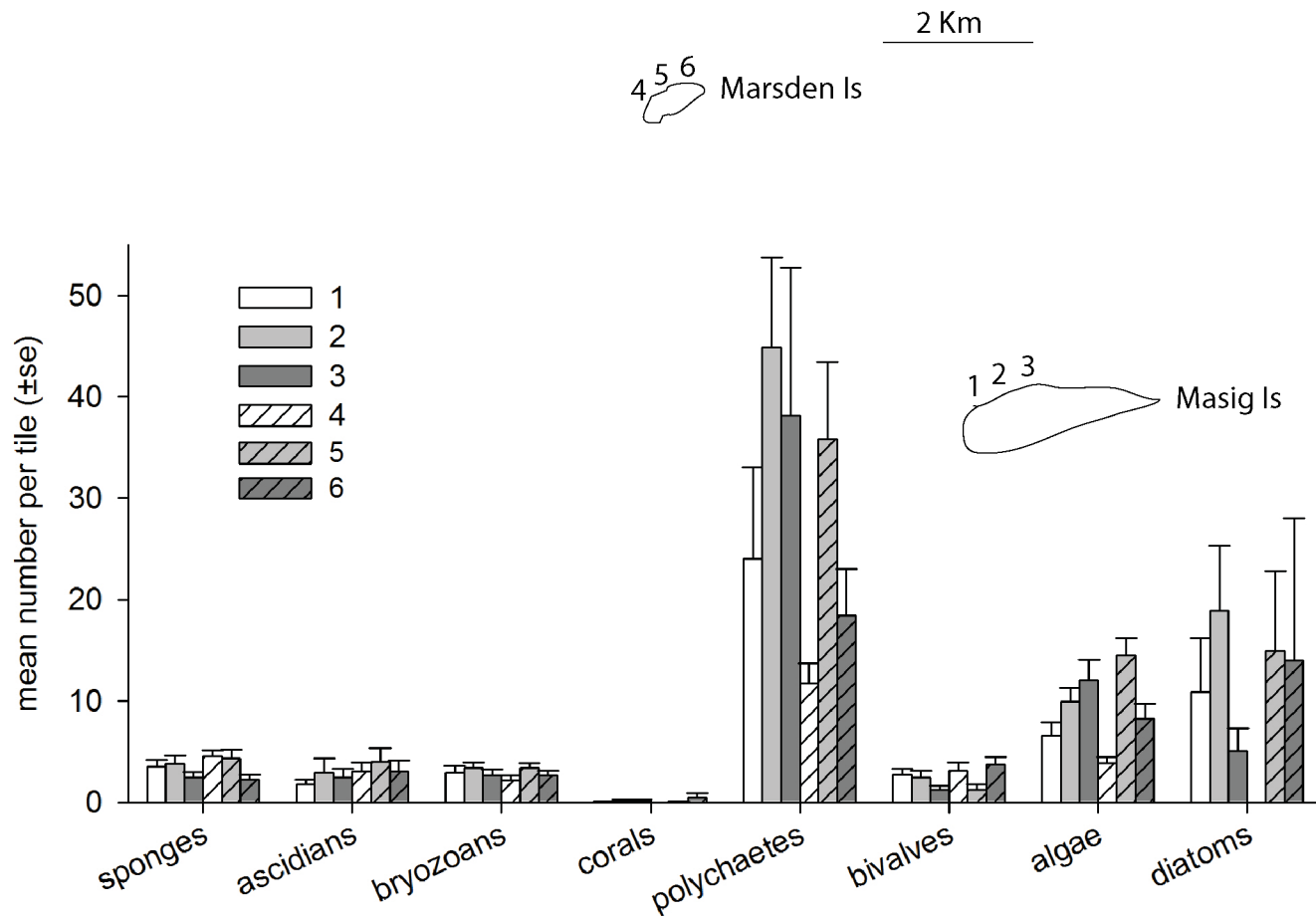


Fig 2. Mean abundance of each taxa, separated by locations, during the summer of the year 2 sampling period. Note locations 1 to 3 are Masig Is and 4 to 6 are Marsden Is. Refer to [S1 Fig](#) for the location of the islands within Torres Strait, Australia.

doi:10.1371/journal.pone.0153184.g002

suggests that local drivers (e.g. predation and competition) play a role in contributing to community assemblages at these spatial scales. Here, grazing (direct and incidental) from herbivorous fish can contribute to coral recruit mortality [14], which arguably translates to recruitment variability. The spatial scale of recruitment variability through predation/grazing may depend on the home range of herbivores. The two conspicuous groups of herbivores on coral reefs, fishes and urchins, show foraging patterns over a range of spatial scales [48,49] with both groups playing likely roles in contributing to recruitment variability over smaller within habitat scales [42], particularly to upper tile surfaces.

In the present study there was little evidence of recruitment to the upper surfaces of tiles. It is likely that the very low recruitment of organisms (e.g. algae) to the upper surfaces of tiles resulted from high grazing pressure and other post-settlement mortality [14]. Although not quantified, the upper surfaces of many tiles in this study possessed noticeable feeding scars. Similarly, nearly all recruits (98.8%) settled to the bottom of the tiles in a study done in the southern Persian Gulf [50]. In comparison, the underside tile surfaces, with clear signs of invertebrate and algal assemblages, potentially provided protection from larger grazers, with this pressure potentially being less important than other processes, including competition. In addition, light no doubt played an important role for coral and algal recruitment. Recruitment to under sides of tiles may also reflect recruitment of cryptic taxa to shaded habitats [42].

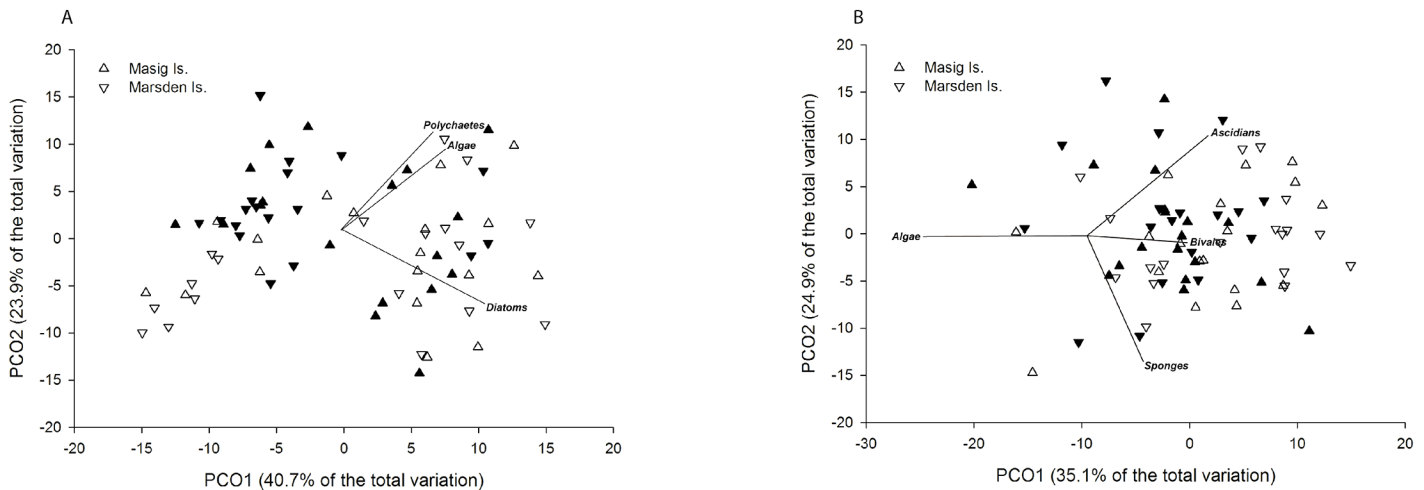


Fig 3. Principle coordinate analysis (PCoA) of invertebrate abundances (A) and assemblage structure, using percent cover data (B), at Masig and Marsden Islands. The five replicate tiles from each depth were pooled prior to constructing a Bray-Curtis similarity matrix. Taxa with a Spearman Rank correlation value greater than 0.6 have been overlaid on the plot as vectors. Summer and winter sampling periods are represented by open and closed symbols, respectively.

doi:10.1371/journal.pone.0153184.g003

The small numbers of scleractinian coral recruits (<1 recruit per tile), to either the upper or bottom surfaces of tiles, was surprising, and is in contrast to other recruitment studies which demonstrate coral recruitment on both upper and under sides of settlement tiles and in higher numbers than observed in this study [16,17,27,29,31]. While patterns of scleractinian coral recruitment to individual experimental tiles can reflect nil, or very low numbers of recruits [17], average numbers of recruits in these comparative studies are conspicuously higher than scleractinian coral recruitment found in the present study, despite the study sites being located within a thriving coral reef community. For instance, coral recruitment on the GBR can range from 36 to 7000 recruits per m² per year depending on the study and method employed (See Table 4, [51]). Incidental grazing from herbivores may be indicative of the low number of recruits, including corals, to the upper surfaces of tiles in this study, and the lower number of coral recruits underneath tiles may be a reflection of competition with other sessile invertebrate taxa [27]. Although not quantified as a part of this study, a relatively low abundance of crustose coralline algae (CCA) was observed on the underside of the tiles, potentially contributing to the low coral recruitment observed.

Table 2. Results of the multivariate PERMANOVA for percent cover data. Permutations were based on a Bray-Curtis similarity matrix generated from log(x+1) transformed data. Significant p-values (<0.05) in bold.

Source	df	Pseudo-F	p
Season	1	9.67	0.256
Island	1	0.34	0.904
Season x Island	1	0.61	0.616
Location (Island)	4	1.78	0.089
Site (Location)	12	1.4	0.142
Season x Location	4	1.32	0.273
Season x Site	12	1.04	0.438
Depth (Site)	18	2.04	0.001
Season x Depth	18	0.903	0.668

doi:10.1371/journal.pone.0153184.t002

Table 3. Results of PERMANOVA tests to examine differences at both time points (i.e. summer & winter) separately. Permutations for abundance and percent cover were based on a Bray-Curtis similarity matrix generated from log(x+1) transformed data, while permutations for the individual taxa (using percent cover data) were based on a Euclidian distance matrix using untransformed data. Significant p-values (<0.01 to account for multiple tests) in bold. Is = Island, Lo = Location and Si = Site. Due to their very low abundances, corals were excluded from the individual PERMANOVA tests.

	Summer								Winter							
	Is		Lo (Is)		Si (Lo)		De (Si)		Is		Lo (Is)		Si (Lo)		De (Si)	
	F	p	F	p	F	p	F	p	F	p	F	p	F	p	F	p
Abundance	0.301	0.907	2.11	0.016	0.746	0.879	2.01	0.001	0.599	0.798	1.88	0.028	1.57	0.033	1.21	0.108
Percent cover	0.368	0.699	2.4	0.017	1.075	0.393	1.7	0.002	0.452	0.897	1.07	0.423	1.58	0.076	1.28	0.111
Algae	0.539	0.504	4.08	0.032	0.482	0.905	3.76	0.001	0.393	0.597	4.89	0.0164	0.7	0.74	2.28	0.004
Sponges	2.5 E2	0.901	1.39	0.282	0.694	0.739	2.11	0.006	3.14	0.097	0.323	0.849	1.52	0.204	0.924	0.553
Ascidians	1.3 E3	1	1.82	0.201	0.903	0.56	2.45	0.002	7.04	0.094	0.189	0.941	1.33	0.278	1.29	0.21
Bryozoans	2.64	0.196	0.148	0.973	1.76	0.132	0.846	0.649	0.424	0.497	1.28	0.328	1.21	0.343	1.36	0.155
Polychaetes	1.73	0.305	0.683	0.629	0.881	0.575	1.39	0.138	1.9 E2	1	2.06	0.131	1.08	0.432	0.918	0.560
Bivalves	0.558	0.599	8.14	0.003	0.565	0.842	1.15	0.314	0.357	0.899	1.40	0.286	1.95	0.087	1.07	0.393
Diatoms	0.432	0.901	3.33	0.031	1.79	0.093	0.689	0.849	1.22	0.394	0.909	0.479	2.09	0.060	0.667	0.878
Total significant		0		2		0		5		0		0		0		1

doi:10.1371/journal.pone.0153184.t003

Polychaetes were by far the most abundant taxa observed, with abundances four times higher than any other taxa. However, this group occupied less than 5% of the tile surface. Polychaetes are known to recruit to dead coral in northern Australia [52] and are often found dominating recruitment of artificial structures [36,53]. This is an interesting finding given polychaetes are not a conspicuous group occurring on substrata in the immediate vicinity of experimental recruitment tiles. The immediate sessile reef community is predominantly comprised of cnidarians and sponges [34]. Nevertheless, polychaete diversity, and the apparent common occurrence of this group within coral reef micro habitats, is noted at Lizard Island, northern GBR [54]. That polychaetes, and to a lesser extent diatoms, dominate recruitment tiles may be a reflection of these groups excelling as colonisers rather than competitors. The dynamic between colonisers and competitors is routinely reported, particularly when recruitment surfaces represent bare space [36]. Therefore, tiles deployed for the six months in this study are likely to confer advantages to important colonising taxa such as polychaetes. However, the fact that polychaetes occupy a small area of space on tiles suggests less capacity for polychaetes as competitors, particularly when compared to taxa with noted encrusting habits or allopathic capacities such as ascidians, sponges and bryozoans resulting in overgrowth of poor spatial competitors [55–57].

Spatial recruitment variability was not evident beyond the smallest scales examined in this study (experimental tiles), suggesting that recruitment between islands and among locations within islands is less heterogeneous. While processes such as predation contribute to coral reef recruitment patterns at both small and large spatial scales, it is more likely that processes governing larval supply, and larval dispersal, are more uniform between islands or among locations within islands thereby contributing to less differentiation in overall recruitment. Despite the distance of several kilometres between islands, or among locations within islands, it is likely that there is enough localised dispersal and recruitment, limiting spatial heterogeneity among sessile groups. Larval dispersal for many coral reef sessile invertebrates can be highly endogenous, but with enough long-distance dispersal and recruitment to maintain population connectivity over regional scales [9,58].

This study also examined recruitment variability between shallow (6 m) and deep (12 m) sites. In this case, depth was found to be an important factor influencing recruitment during

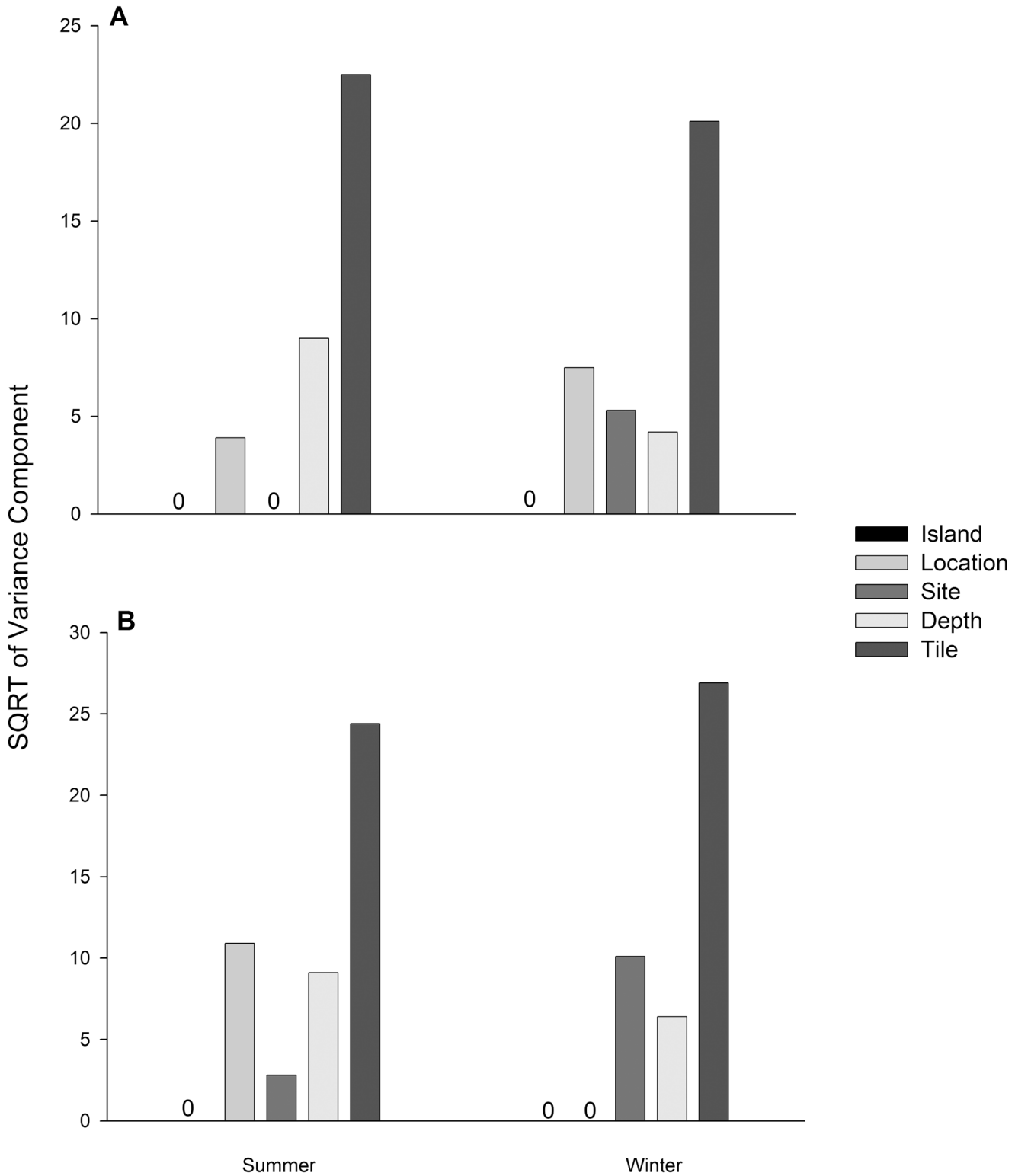


Fig 4. Variance components for (A) abundance and (B) percent cover for the Year 2 summer and winter. Note the different y-axis scale bars.

doi:10.1371/journal.pone.0153184.g004

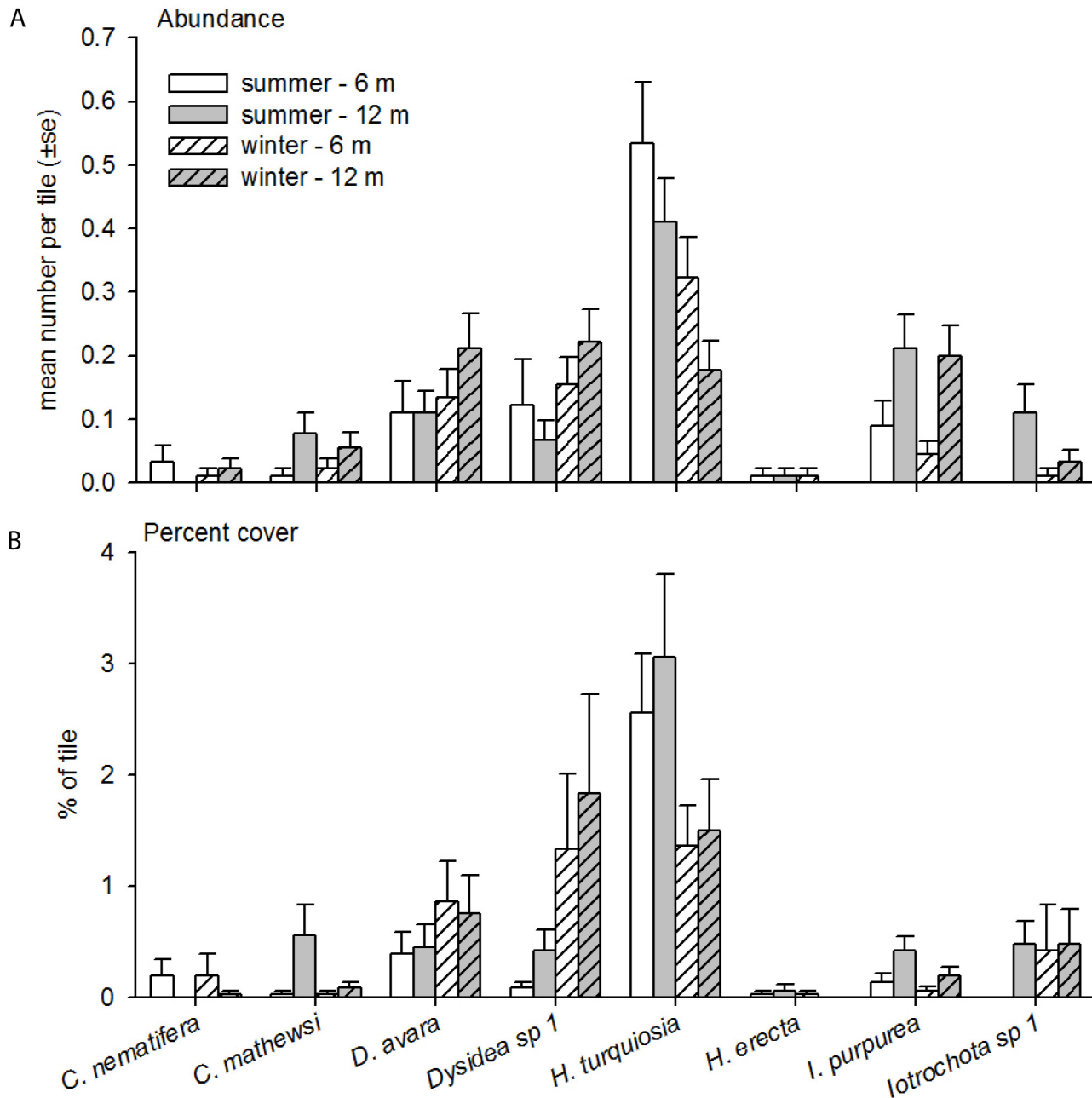


Fig 5. Mean abundance (A) and percent cover (B) of each sponge, positively identified to species level, for the year 2 sampling. Both seasons and depths depicted.

doi:10.1371/journal.pone.0153184.g005

the summer, particularly for algae, sponges and ascidians. Sponge recruits were more prevalent and occupied a greater percentage of tiles at deeper sites, while ascidians on the other hand dominated shallow sites. While information of ascidian distribution patterns is unknown within Torres Strait, sponge distribution patterns are well documented [34,59]. The finding of higher sponge recruitment numbers at deeper sites (12 m) is consistent with adult distributions where sponges are most commonly observed between 12–15 m [34,59,60]. Interpreting processes that contribute to higher sponge abundance at deeper sites is complex. However,

physical factors such as flow rates and light intensity would likely be different [59], which might affect recruitment patterns. Moreover, larval dispersal for some sponges can be driven by clear larval settlement behaviours that can cue larvae to settle in accordance to light and reef associated environmental/habitat cues [61–66]. Key environmental settlement cues suitable to sponges may be more commonly encountered at deeper sites and therefore may play important contributing roles to successful recruitment there.

Conclusions

The finding that recruitment variability was highest at the smaller spatial scales examined in this study highlights the heterogeneity that occurs within habitats (i.e. at spatial scales of metres). While a range of both biotic and abiotic processes may contribute to patterns of recruitment in marine benthic community assemblages over small and regional scales, the higher variability within habitats suggests localised processes associated with competition and predation may play important roles in the heterogeneity of community assemblages on very fine scales. Torres Strait is situated at the northern boundary of the GBR with shallow reef habitats dominated by scleractinian corals. The very low numbers of coral recruits found in this study, and that it differs from other recruitment studies undertaken on the GBR, identifies a need for further work to bridge the complex temporal and spatial patterns of recruitment on coral reefs [51]. The low presence of organisms on the surface of tiles and encrusting organisms on the underside of tiles further highlights the potential role of both predation (through incidental grazing) and competition in defining the community assemblages. The documentation of non-coral sessile invertebrate recruitment patterns provides much-needed information on these groups within the northern GBR and more broadly coral reef systems. In addition, this study provides knowledge of key performance indicators related to coral community recruitment patterns that depict variability over time and space, which are valuable to how coral reefs are managed and conserved.

Supporting Information

S1 Fig. Map of the central Torres Strait, showing the two study Islands: Masig and Marsden (A). Diagram of the nested hierarchical study design (B).
(TIF)

S2 Fig. Mean abundance (A) and percent cover (B) of each of the taxa from Masig and Marsden Is. over the two-year sampling period. Both seasons and depths depicted.
(TIF)

S3 Fig. Mean abundance (A) and percent cover (B) of each for sponges, positively identified to species level, over the two year sampling. Both seasons and depths depicted.
(TIF)

S1 Table. Abundance data. Raw abundance data for the year 2 sampling (May 2007 to May 2008).
(XLSX)

S2 Table. Percent cover data. Raw percent cover data for the year 2 sampling (May 2007 to May 2008).
(XLSX)

S3 Table. Sponge species data. Raw abundance and percent cover data for the sponge species identified in the year 2 sampling (May 2007 to May 2008).
(XLSX)

Acknowledgments

We thank J. Morris, S. Lowatta, S. Lui, T. Hyndes, E. Matson and the crew of the RV 'Cape Ferguson' who helped out with the diving and initial tile deployment for this study. We also thank the indigenous community Masig Island for allowing us to conduct this study in their traditional sea country.

Author Contributions

Conceived and designed the experiments: AD SW EEI. Performed the experiments: HL CW AD SW. Analyzed the data: HL CW AD SW. Contributed reagents/materials/analysis tools: EEI. Wrote the paper: HL SW. Edited the manuscript: HL AD CW EEI SW.

References

1. Small AM, Adey WH, Spoon D. Are current estimates of coral reef biodiversity too low? The view through the window of a microcosm. *Atoll Research Bulletin*; 1998; 458: 1–19.
2. Steneck RS. The ecology of coralline algal crusts: convergent patterns and adaptive strategies. *Annual Review of Ecology and Systematics*. 1986; 17: 273–303.
3. De Goeij JM, van Oevelen D, Vermeij MJA, Osinga R, Middelburg JJ, De Goeij AFPM, et al. Surviving in a marine desert: the sponge loop retains resources within coral reefs. *Science*. 2013; 342: 108–110. doi: [10.1126/science.1241981](https://doi.org/10.1126/science.1241981) PMID: [24092742](https://pubmed.ncbi.nlm.nih.gov/24092742/)
4. Hughes TP. Climate change, human impacts, and the resilience of coral reefs. *Science*. 2003; 301: 929–933. doi: [10.1126/science.1085046](https://doi.org/10.1126/science.1085046) PMID: [12920289](https://pubmed.ncbi.nlm.nih.gov/12920289/)
5. Cowen RK, Sponaugle S. Larval dispersal and marine population connectivity. *Annual Reviews*. 2009; 1: 443–466. doi: [10.1146/annurev.marine.010908.163757](https://doi.org/10.1146/annurev.marine.010908.163757)
6. Shanks AL, Grantham BA, Carr MH. Propagule dispersal distance and the size and spacing of marine reserves. *Ecological Applications*. 2008; 13: 159–169. doi: [10.1890/1051-0761\(2003\)013\[0159:PDDATS\]2.0.CO;2](https://doi.org/10.1890/1051-0761(2003)013[0159:PDDATS]2.0.CO;2)
7. Palumbi SR. Population Genetics, demographic connectivity, and the design of marine reserves. *Ecological Applications*. 2008; 13: 146–158. doi: [10.1890/1051-0761\(2003\)013\[0146:PGDCAT\]2.0.CO;2](https://doi.org/10.1890/1051-0761(2003)013[0146:PGDCAT]2.0.CO;2)
8. Lowe WH, Allendorf FW. What can genetics tell us about population connectivity? *Molecular Ecology*. Blackwell Publishing Ltd; 2010; 19: 3038–3051. doi: [10.1111/j.1365-294X.2010.04688.x](https://doi.org/10.1111/j.1365-294X.2010.04688.x)
9. Ayre DJ, Hughes TP. Genotypic diversity and gene flow in brooding and spawning corals along the Great Barrier Reef, Australia. *Evolution*. Blackwell Publishing Ltd; 2000; 54: 1590–1605. doi: [10.1111/j.0014-3820.2000.tb00704.x](https://doi.org/10.1111/j.0014-3820.2000.tb00704.x)
10. Underwood JN, Smith LD, van Oppen MJH, Gilmour JP. Multiple scales of genetic connectivity in a brooding coral on isolated reefs following catastrophic bleaching. *Molecular Ecology*. Blackwell Publishing Ltd; 2007; 16: 771–784. doi: [10.1111/j.1365-294X.2006.03187.x](https://doi.org/10.1111/j.1365-294X.2006.03187.x)
11. Lasker HR, Porto-Hannes I. Population structure among octocoral adults and recruits identifies scale dependent patterns of population isolation in The Bahamas. *PeerJ*. PeerJ Inc; 2015; 3: e1019. doi: [10.7717/peerj.1019](https://doi.org/10.7717/peerj.1019)
12. Whalan S, de Nys R, Smith-Keune C, Evans BS, Battershill C, Jerry DR. Low genetic variability within and among populations of the brooding sponge *Rhopaloeides odorabile* on the central Great Barrier Reef. *Aquat Biol. Inter-Research*; 2008; 3: 111–119. doi: [10.3354/ab00066](https://doi.org/10.3354/ab00066)
13. Bell JJ, Smith D, Hannan D, Haris A, Thomas L. Isolation and characterisation of twelve polymorphic microsatellite markers for *Xestospongia* spp. and their use for confirming species identity. *Conservation Genet Resour*. Springer Netherlands; 2014; 6: 105–106. doi: [10.1007/s12686-013-0015-5](https://doi.org/10.1007/s12686-013-0015-5)
14. Penin L, Michonneau F, Baird AH. Early post-settlement mortality and the structure of coral assemblages. *Marine Ecology*. 2010; 408: 55–64.
15. Edmunds PJ, Steneck R, Albright R, Carpenter RC, Chui APY, Fan TY, et al. Geographic variation in long-term trajectories of change in coral recruitment: a global-to-local perspective. *Marine and Freshwater Research*. CSIRO Publishing; 2015; 66: 609–622. doi: [10.1071/MF14139](https://doi.org/10.1071/MF14139)
16. Adjeroud M, Penin L, Carroll A. Spatio-temporal heterogeneity in coral recruitment around Moorea, French Polynesia: Implications for population maintenance. *Journal of Experimental Marine Biology and Ecology*. 2007; 341: 204–218. doi: [10.1016/j.jembe.2006.10.048](https://doi.org/10.1016/j.jembe.2006.10.048)
17. Edmunds PJ, Leichter JJ, Adjeroud M. Landscape-scale variation in coral recruitment in Moorea, French Polynesia. *Marine Ecology Progress Series*. 2010; 414: 75–89.

18. Bruno JF, Selig ER. Regional decline of coral cover in the indo-pacific: timing, extent, and subregional comparisons. Freckleton R, editor. PLoS ONE. Public Library of Science; 2007; 2: e711. doi: [10.1371/journal.pone.0000711](https://doi.org/10.1371/journal.pone.0000711)
19. Gardner TA, Côté IM, Gill JA, Grant A, Watkinson AR. Long-term region-wide declines in Caribbean corals. *Science*. American Association for the Advancement of Science; 2003; 301: 958–960. doi: [10.1126/science.1086050](https://doi.org/10.1126/science.1086050)
20. De'ath G, Fabricius KE, Sweatman H, Puotinen M. The 27-year decline of coral cover on the Great Barrier Reef and its causes. *Proc Natl Acad Sci USA*. National Acad Sciences; 2012; 109: 17995–17999. doi: [10.1073/pnas.1208909109](https://doi.org/10.1073/pnas.1208909109)
21. Mundy CN. An appraisal of methods used in coral recruitment studies. *Coral Reefs*. Springer-Verlag; 2000; 19: 124–131. doi: [10.1007/s003380000081](https://doi.org/10.1007/s003380000081)
22. Hughes TP, Graham NAJ, Jackson JBC, Mumby PJ, Steneck RS. Rising to the challenge of sustaining coral reef resilience. *Trends in Ecology & Evolution*. 2010; 25: 633–642. doi: [10.1016/j.tree.2010.07.011](https://doi.org/10.1016/j.tree.2010.07.011)
23. Doropoulos C, Ward S, Roff G, González-Rivero M, Mumby PJ. Linking demographic processes of juvenile corals to benthic recovery trajectories in two common reef habitats. Orejas C, editor. PLoS ONE. 2015; 10: e0128535–23. doi: [10.1371/journal.pone.0128535](https://doi.org/10.1371/journal.pone.0128535) PMID: [26009892](https://pubmed.ncbi.nlm.nih.gov/26009892/)
24. McManus JW, Polsenberg JF. Coral–algal phase shifts on coral reefs: Ecological and environmental aspects. *Progress in Oceanography*. 2004; 60: 263–279. doi: [10.1016/j.poccean.2004.02.014](https://doi.org/10.1016/j.poccean.2004.02.014)
25. Harriott VJ, Fisk DA. Recruitment patterns of scleractinian corals: a study of three reefs. *Marine and Freshwater Research*. CSIRO Publishing; 1988; 39: 409–416. doi: [10.1071/MF9880409](https://doi.org/10.1071/MF9880409)
26. Hughes TP, Baird AH, Dinsdale EA, Moltschaniwskyj NA, Pratchett MS, Tanner JE, et al. Supply-side ecology works both ways: the link between benthic adults, fecundity, and larval recruits. *Ecology*. 2000; 81: 2241–2249. doi: [10.1890/0012-9658\(2000\)081\[2241:SSEWBW\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2000)081[2241:SSEWBW]2.0.CO;2)
27. Dunstan PK, Johnson CR. Spatio-temporal variation in coral recruitment at different scales on Heron Reef, southern Great Barrier Reef. *Coral Reefs*. Springer-Verlag; 1998; 17: 71–81. doi: [10.1007/s003380050098](https://doi.org/10.1007/s003380050098)
28. Harriott VJ. Coral growth in subtropical eastern Australia. *Coral Reefs*. Springer-Verlag; 1999; 18: 281–291. doi: [10.1007/s003380050195](https://doi.org/10.1007/s003380050195)
29. Baird AH, Hughes TP. Competitive dominance by tabular corals: an experimental analysis of recruitment and survival of understorey assemblages. *Journal of Experimental Marine Biology and Ecology*. 2000; 251: 117–132. doi: [10.1016/S0022-0981\(00\)00209-4](https://doi.org/10.1016/S0022-0981(00)00209-4) PMID: [10958904](https://pubmed.ncbi.nlm.nih.gov/10958904/)
30. Glassom D, Zakai D, Chadwick-Furman NE. Coral recruitment: a spatio-temporal analysis along the coastline of Eilat, northern Red Sea. *Marine Biology*. Springer-Verlag; 2004; 144: 641–651. doi: [10.1007/s00227-003-1243-0](https://doi.org/10.1007/s00227-003-1243-0)
31. Green DH, Edmunds PJ. Spatio-temporal variability of coral recruitment on shallow reefs in St. John, US Virgin Islands. *Journal of Experimental Marine Biology and Ecology*. 2011; 397: 220–229. doi: [10.1016/j.jembe.2010.12.004](https://doi.org/10.1016/j.jembe.2010.12.004)
32. Dornelas M, Connolly SR, Hughes TP. Coral reef diversity refutes the neutral theory of biodiversity. *Nature*. 2006; 440: 80–82. doi: [10.1038/nature04534](https://doi.org/10.1038/nature04534) PMID: [16511493](https://pubmed.ncbi.nlm.nih.gov/16511493/)
33. Colvard NB, Edmunds PJ. Decadal-scale changes in abundance of non-scleractinian invertebrates on a Caribbean coral reef. *Journal of Experimental Marine Biology and Ecology*. 2011; 397: 153–160. doi: [10.1016/j.jembe.2010.11.015](https://doi.org/10.1016/j.jembe.2010.11.015)
34. Duckworth AR, Wolff C, Evans-Illidge E, Whalan S, Lui S. Spatial variability in community structure of Dictyoceratida sponges across Torres Strait, Australia. *Continental Shelf Research*. 2008; 28: 2168–2173. doi: [10.1016/j.csr.2008.03.024](https://doi.org/10.1016/j.csr.2008.03.024)
35. Haywood MDE, Pitcher CR, Ellis N, Wassenberg TJ, Smith G, Forcey K, et al. Mapping and characterisation of the inter-reefal benthic assemblages of the Torres Strait. *Continental Shelf Research*. 2008; 28: 2304–2316. doi: [10.1016/j.csr.2008.03.039](https://doi.org/10.1016/j.csr.2008.03.039)
36. Watson DI, Barnes DKA. Temporal and spatial components of variability in benthic recruitment, a 5-year temperate example. *Marine Biology*. Springer-Verlag; 2004; 145: 201–214. doi: [10.1007/s00227-003-1291-5](https://doi.org/10.1007/s00227-003-1291-5)
37. Todd CD, Turner SJ. Ecology of intertidal and sublittoral cryptic epifaunal assemblages. I. Experimental rationale and the analysis of larval settlement. *Journal of Experimental Marine Biology and Ecology*. 1986; 99: 199–231. doi: [10.1016/0022-0981\(86\)90224-8](https://doi.org/10.1016/0022-0981(86)90224-8)
38. Underwood AJ, Chapman MG. Scales of spatial patterns of distribution of intertidal invertebrates. *Oecologia*. 1996; 107: 212–224.

39. Smale DA. Multi-scale patterns of spatial variability in sessile assemblage structure do not alter predictably with development time. *Marine Ecology Progress Series*. 2013; 482: 29–41. doi: [10.3354/meps10273](https://doi.org/10.3354/meps10273)
40. Duckworth AR, Wolff C. Bath sponge aquaculture in Torres Strait, Australia: Effect of explant size, farming method and the environment on culture success. *Aquaculture*. 2007; 271: 188–195. doi: [10.1016/j.aquaculture.2007.06.037](https://doi.org/10.1016/j.aquaculture.2007.06.037)
41. Fraschetti S, Terlizzi A. Patterns of distribution of marine assemblages from rocky shores: evidence of relevant scales of variation. *Marine Ecology Progress Series*. 2005; 296: 13–29.
42. O'Leary JK, Potts DC. Using hierarchical sampling to understand scales of spatial variation in early coral recruitment. *Coral Reefs*. Springer-Verlag; 2011; 30: 1013–1023. doi: [10.1007/s00338-011-0789-4](https://doi.org/10.1007/s00338-011-0789-4)
43. Wahl M. Small scale variability of benthic assemblages: biogenic neighborhood effects. *Journal of Experimental Marine Biology and Ecology*. 2001; 258: 101–114. doi: [10.1016/S0022-0981\(00\)00348-8](https://doi.org/10.1016/S0022-0981(00)00348-8) PMID: [11239628](https://pubmed.ncbi.nlm.nih.gov/11239628/)
44. Maida M, Sammarco PW, Coll JC. Preliminary evidence for directional allelopathic effects of the soft coral *Sinularia flexibilis* (Alcyonacea: Octocorallia) on scleractinian coral recruitment. *Bulletin of Marine Science*. 1995; 56: 303–311.
45. Mullineaux LS, Butman CA. Recruitment of encrusting benthic invertebrates in boundary-layer flows: A deep-water experiment on Cross Seamount. *Limnology and Oceanography*. 1990; 35: 409–423. doi: [10.4319/lo.1990.35.2.0409](https://doi.org/10.4319/lo.1990.35.2.0409)
46. Metaxas A. Behaviour in flow: perspectives on the distribution and dispersion of meroplanktonic larvae in the water column. *Canadian Journal of Fisheries and Aquatic Sciences*. NRC Research Press Ottawa, Canada; 2011; 58: 86–98. doi: [10.1139/f00-159](https://doi.org/10.1139/f00-159)
47. Whalan S, Wahab MAA, Sprungala S, Poole AJ, de Nys R. Larval settlement: The role of surface topography for sessile coral reef invertebrates. Harder T, editor. *PLoS ONE*. Public Library of Science; 2015; 10: e0117675. doi: [10.1371/journal.pone.0117675](https://doi.org/10.1371/journal.pone.0117675)
48. Tuya F, Boyra A, Sanchez-Jerez P. Relationships between rocky-reef fish assemblages, the sea urchin *Diacema antillarum* and macroalgae throughout the Canarian Archipelago. *Marine Ecology*. 2004; 278: 157–169.
49. Welsh JQ, Bellwood DR. How far do schools of roving herbivores rove? A case study using *Scarus rivulatus*. *Coral Reefs*. Springer-Verlag; 2012; 31: 991–1003. doi: [10.1007/s00338-012-0922-z](https://doi.org/10.1007/s00338-012-0922-z)
50. Bauman AG, Baird AH, Burt JA, Pratchett MS, Feary DA. Patterns of coral settlement in an extreme environment: the southern Persian Gulf (Dubai, United Arab Emirates). *Marine Ecology Progress Series*. 2014; 499: 115–126. doi: [10.3354/meps10662](https://doi.org/10.3354/meps10662)
51. Martin R, Walsh WJ. The West Hawai'i Coral Recruitment Project—recruitment dynamics of scleractinian corals along the Kona Coast of the Big Island of Hawai'i. 2014 p. 24 pp. Report No.: P13AC00436.
52. Hutchings PA. Polychaete Recruitment onto Dead Coral Substrates at Lizard Island, Great Barrier Reef, Australia. *Bulletin of Marine Science*. University of Miami—Rosenstiel School of Marine and Atmospheric Science; 1981; 31: 410–423.
53. Holloway MG, Keough MJ. An introduced polychaete affects recruitment and larval abundance of sessile invertebrates. *Ecological Applications*. 2002; 12: 1803–1823. doi: [10.1890/1051-0761\(2002\)012\[1803:AIPARA\]2.0.CO;2](https://doi.org/10.1890/1051-0761(2002)012[1803:AIPARA]2.0.CO;2)
54. Ribas J, Hutchings P. Lizard Island Polychaete Workshop: sampling sites and a checklist of polychaetes. *Zootaxa*. 2015; 4019: 7–34. doi: [10.11646/zootaxa.4019.1.4](https://doi.org/10.11646/zootaxa.4019.1.4) PMID: [26624064](https://pubmed.ncbi.nlm.nih.gov/26624064/)
55. Jackson JBC, Buss L. Alleopathy and spatial competition among coral reef invertebrates. *PNAS*. National Acad Sciences; 1975; 72: 5160–5163.
56. Jackson J. Competition on marine hard substrata: The adaptive significance of solitary and colonial strategies. *American Naturalist*. 1977; 111: 743–767.
57. Osman RW. The Establishment and Development of a Marine Epifaunal Community. *Ecological Monographs*. 1977; 47: 37. doi: [10.2307/1942223](https://doi.org/10.2307/1942223)
58. Whalan S, Johnson MS, Harvey E, Battershill C. Mode of reproduction, recruitment, and genetic subdivision in the brooding sponge *Haliclona* sp. *Marine Biology*. Springer-Verlag; 2005; 146: 425–433. doi: [10.1007/s00227-004-1466-8](https://doi.org/10.1007/s00227-004-1466-8)
59. Duckworth AR. Substrate type affects the abundance and size of a coral-reef sponge between depths. *Marine and Freshwater Research*. CSIRO Publishing; 2015. doi: [10.1071/MF14308](https://doi.org/10.1071/MF14308)
60. Wilkinson CR, Cheshire AC. Patterns in the distribution of sponge populations across the central Great Barrier Reef. *Coral Reefs*. Springer-Verlag; 1989; 8: 127–134. doi: [10.1007/BF00338268](https://doi.org/10.1007/BF00338268)

61. Ettinger-Epstein P, Whalan S, Battershill CN, de Nys R. A hierarchy of settlement cues influences larval behaviour in a coral reef sponge. *Marine Ecology Progress Series. Inter-Research*; 2008; 365: 103–113. doi: [10.3354/meps07503](https://doi.org/10.3354/meps07503)
62. Whalan S, Ettinger-Epstein P, Battershill C, de Nys R. Larval vertical migration and hierarchical selectivity of settlement in a brooding marine sponge. *Marine Ecology Progress Series. Inter-Research*; 2008; 368: 145–154. doi: [10.3354/meps07573](https://doi.org/10.3354/meps07573)
63. Abdul Wahab MA, de Nys R, Webster N, Whalan S. Larval Behaviours and Their Contribution to the Distribution of the Intertidal Coral Reef Sponge *Carteriospongia foliascens*. Bell J, editor. *PLoS ONE. Public Library of Science*; 2014; 9: e98181. doi: [10.1371/journal.pone.0098181](https://doi.org/10.1371/journal.pone.0098181)
64. Whalan S, Webster NS, Negri AP. Crustose coralline algae and a cnidarian neuropeptide trigger larval settlement in two coral reef sponges. Ferse SCA, editor. *PLoS ONE. Public Library of Science*; 2012; 7: e30386. doi: [10.1371/journal.pone.0030386](https://doi.org/10.1371/journal.pone.0030386)
65. Whalan S, Webster NS. Sponge larval settlement cues: the role of microbial biofilms in a warming ocean. *Sci Rep.* 2014; 4: 4072. doi: [10.1038/srep04072](https://doi.org/10.1038/srep04072) PMID: [24518965](https://pubmed.ncbi.nlm.nih.gov/24518965/)
66. Abdul Wahab MA, de Nys R, Whalan S. Larval behaviour and settlement cues of a brooding coral reef sponge. *Coral Reefs. Springer-Verlag*; 2011; 30: 451–460. doi: [10.1007/s00338-011-0727-5](https://doi.org/10.1007/s00338-011-0727-5)