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REPORT

Rock and roll: experiments on substrate movement and coral settlement

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Abstract Rubble is ubiquitous on coral reefs and can aggregate into fields, forming a significant component of the reef substrate. Rubble fields often remain unconsolidated, with the component rubble pieces subject to movement that is dependent on hydrodynamic forcing, rubble size, shape, and other factors. Settlement of corals to rubble fields has long been assumed, but the dynamic movement of rubble pieces has been presumed to deter settlement and is thought to contribute to high post-settlement mortality. Rubble often forms on coral reefs following severe disturbances, and is predicted to increase under climate change, with the potential to impact settlement and recruitment-dependent recovery processes. Through a series of laboratory and field experiments, we demonstrate that corals from broadcast spawning species on the Great Barrier Reef will settle on unstable substrates, even those in constant motion. We also observed more coral spat on settlement tiles suspended in the water column than those fixed to the reef using a common approach to censusing settlement. Sampling of natural rubble on the reef 50 days after a mass-spawning event confirmed the presence of similar numbers of coral settlers on rubble and on tiles fixed to the reef. These results suggest that rubble fields are places of significant settlement for broadcast spawning corals. Suspended tiles were also surprisingly effective in collecting coral settlers, demonstrating that a change in sampling protocol can produce significant variation in settlement data and strengthening the argument for standardisation of settlement-monitoring protocols, particularly at a time of growing need for reliable metrics. These results also suggest that movement of rubble is not precluding settlement outright, but rather post-settlement processes (i.e. competition, predation, shading or burial by shifting rubble) are limiting recruitment to rubble patches. Consequently, rubble stabilisation may increase the survival of spat that have settled in these environments.

Keywords Coral settlement · Movement · Rubble · Stability · Recruitment · Recovery

Introduction

Unconsolidated substrates such as sand and rubble are widely distributed across coral reefs and can be the dominant substrate in some reef zones (Rasser and Riegl 2002). While rubble fields are routinely recognised as a major substrate type in reef habitats (Kennedy et al. 2021; Wolfe et al. 2021) that harbour diverse communities (Klumpp et al. 1988; Gischler and Ginsburg 1996), they usually feature reduced structural complexity and hence, at least for macrobiota, lower biodiversity relative to consolidated reef substrate (Ferreira et al. 2023). Colonisation of these unstable habitats by sessile epibenthic organisms may be constrained both by larval settlement preferences and by challenges to post-settlement survival, including from substrate mobility, competition, sediment burial, and light limitation (Jones et al. 2015; Cameron et al. 2016; Kenyon et al. 2020). Yet Scleractinian coral larval settlement and subsequent growth and recruitment to the population is a critical phase of reef recovery,

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which maintains the rich biodiversity found on coral reefs (Edmunds 2023). Hence, it is important to understand how these processes occur on unconsolidated substrates, and how changes in the abundance and distribution of rubble may limit recovery of coral reefs.

It has long been assumed that the settlement of sexually produced coral larvae onto rubble, such as dead coral fragments, is probable (Davies and Hutchings 1983; Hughes et al. 1999). While some coral species adapted to fragmentation are known to persist in rubble habitats if the fragments are large enough to avoid burial (Heyward and Collins 1985; Roff 2008; Cameron et al. 2016), sexually produced coral larvae of many broadcast spawning species produce primary polyps 1 mm in diameter or less (Babcock et al. 2003). Studies of rubble dynamics indicate that lateral movement and overturning of rubble poses an elevated risk to survival of these small coral settlers relative to those on consolidated substrate (Viehman et al. 2018), leading a recent review to characterised rubble beds as killing fields for coral recruits (Fox and Caldwell 2006; Ceccarelli et al. 2020). Yet, quantitative and qualitative data on coral settlement and recruitment to rubble is limited (Cameron et al. 2016). Some movement of rubble may occur daily, particularly in shallow areas of the reef. Consequently, evidence of initial settlement to these substrates can be lost before it can be quantified with confidence. Many in situ studies (e.g. Mumby 1999; Davidson et al. 2019) have used visual census techniques, with lower size detection limits around 4–5 mm diameter being common. Until recent technological advancements (Schmidt-Roach et al. 2008; Roth and Knowlton 2009; Martinez and Abelson 2013; Zweifler et al. 2017; Nativ et al. 2021; Gouezo et al. 2023), even the most careful visual surveys (e.g. Mumby 1999) acknowledge that data for the lowest detectable size class (2–3 mm) were probably underestimates, with counts for 4–5 mm sized recruits more accurate than anything smaller. Corals of this size are likely to be several months old, leaving considerable uncertainty about the scale and composition of initial settlement to rubble beds. When Roth and Knowlton 2009 tackled this problem using in situ fluorescence to detect juveniles down to 1 mm, settlement of corals onto rubble at Palmyra Atoll in the Central Pacific was comparable to that on consolidated reef. This supports earlier predictions that settlement is probable, but there is a lack of comparable studies on reefs in other biogeographic regions to know if broadscale settlement of corals across rubble zones is the norm. The settlement to rubble measured at Palmyra Atoll may not be typical of all reef areas or may require particular environmental conditions.

Rubble pieces, particularly if covered in appropriate biofilms, can represent an attractive microhabitat for the settlement of coral larvae and may not be able to be differentiated from the stable reef matrix by larvae during settlement (Nugues and Szmant 2006; Villanueva et al. 2012; Randall et al. 2024). However, experimental studies of coral settlement have used a variety of static substrates, in the field or on the laboratory bench, that have not factored in movement. It is unknown if movement of substrates, such as that which naturally occurs with dynamic rubble pieces in situ, affects larval behaviour or inhibits larval settlement. Coral spawning events mostly occur during calmer times of year (van Woesik 2010) which could favour less movement of rubble substrates during periods of larval settlement, but some movement is likely even during mild weather, particularly in shallower and windward areas of reefs. Furthermore, species-specific settlement preferences for rubble (Randall et al. 2024) may alter the species composition of recruits in these areas, and depending on post-settlement mortality processes, can consequently impact community composition during reef recovery.

Forecasts of increasing physical and biological disruption to coral reefs (Webster et al. 2005; Cheal et al. 2017; Smale et al. 2019) point to the loss of live coral and an increasing supply of both fine and coarse unconsolidated substrates (Kenyon et al. 2023). Yet there is a limited understanding of what an increase in rubble habitat could mean for coral settlement, recruitment and recovery processes and general reef ecology. Amongst those knowledge gaps, the nuances underpinning coral recruitment dynamics in different rubble bed types and at different stages of stabilisation are important to investigate (Kenyon et al. 2023). In addition, settlement studies on reefs have typically focused on fixed substrates and are often referred to as recruitment studies, although they are more accurately measuring settlement rather than the recruitment of new individuals to the population (Connell 1973). Given the sometimes large and potentially growing amount of mobile rubble on reefs due to climate-changed induced mass-bleaching events, increased erosion and stronger cyclones (Kenyon et al. 2023), improved knowledge of the potential for coral settlement to these dynamic substrates should lead to a more holistic understanding of recruitment. Here, we conducted a series of laboratory and field experiments to better understand the role of substrate mobility on coral settlement. Specifically, we aimed to (1) compare settlement onto fixed and moving/unstable substrates in the laboratory and field, (2) compare settlement behaviour amongst taxa in these environments, and (3) assess natural settlement onto rubble in situ.

Methods

Experiment 1—moving plugs

Two species of gravid scleractinia from the Great Barrier Reef (GBR) were transported to the National Sea

Simulator (SeaSim) at the Australian Institute of Marine Science (AIMS), Townsville as broodstock for a pilot study testing settlement onto moving and static substrates. Six colonies of *Goniastrea retiformis* collected from Manbarra sea Country in the Palm Islands spawned in captivity on 16 November 2019, 4 days after the full moon, beginning at approximately 20:00. Eight colonies of *Acropora millepora* collected from Woppaburra sea Country in the Keppel Islands spawned on 17 November 2019, 5 days after the full moon, beginning at approximately 21:00. Spawning, fertilisation and larval rearing followed standard SeaSim methods, summarised in (Pollock et al. 2017). To compare settlement onto moving versus static substrates, larvae were sourced from bulk cultures at SeaSim and added to each experimental tank at a nominal density of 50 l^{-1}, once > 50% competency was established through standard settlement assays sensu Negri et al. (2001).

For each coral species, 165 aragonite plugs (OceanWonders, 20-mm diameter) mounted in a PVC frame, were conditioned for 6 weeks prior to spawning, in flowing seawater in the SeaSim, to allow biofilm development. Just prior to settlement, sixteen plugs, selected at random, were inserted into clean, individual square PVC frames without any biofilm. The PVC frames also restricted larval access to the upper-facing surface of the plug only. Each PVC frame was deployed in the tank independently, with 8 plugs assigned to each of the still and moving treatments. The plugs were placed haphazardly, but approximately equally spaced (approximately 11 cm apart) in a single 68 L tank holding 60 L of ambient seawater. Plugs were then referred to as 'still' or 'moving'. Each 'still' plug was paired with a 'moving' plug and was stationary on the bottom of the tank while 'moving' pugs were individually suspended on a jute string line, approximately 20 cm below a 37-mm diameter plastic surface float, in the midwater area of the tank, approximately 20 cm above each 'still' plug. To ensure that the 'moving' plugs were constantly in motion, aeration was provided mid-water in the tank via a rigid plastic tube (4 mm interior diameter) venting bubbles in the tank, causing ripples at the water's surface. Delivering constant aeration for the settlement period with vigorous bubbling caused the 37–mm floats connected to the 'moving' plugs to bob continuously throughout the experiment. Observations indicated that the movement of the surface floats provided a slight but constant jiggling motion to the suspended settlement plugs, analogous to that of a teabag. The moving plug substrates were jiggled (i.e. bobbed up and down) 1–2 times s^{-1} and moved a few mm with each jiggle of the float, in the range 1–5 mm (see online Supplementary video).

Approximately 48 h after larval introduction to the tank, all plugs were collected and examined under a stereo light microscope. The numbers of settled (i.e. attached and metamorphosed) spat on the surface of each plug were counted.

Coral settlement was modelled using a generalised linear mixed effects model with a negative binomial distribution and a log link function, using the 'glmmTMB' package (Berg et al. 2017) in R (R Core Team 2022). Treatment (still vs. moving), species (*Acropora millepora* and *Goniastrea retiformis*), and their interaction were modelled as fixed effects and the plug pair (i.e. each set of still and moving plugs) was modelled as a random effect to account for any spatial patterns of settlement within the tank. Model diagnostics were assessed with DHARMa (Hartig 2020) and modelled responses were visualised using ggplot and emmeans.

Experiment 2—Moving rubble

In 2021, the laboratory study described in experiment 1 was repeated with a third common reef building species, *Acropora cf. kenti* (Bridge et al. 2023). In this study, pieces of live reef rubble were used as the settlement substrate rather than coral plugs, to better mimic the natural communities of biofilm that would be present during settlement on rubble in situ.

A. cf. kenti broodstock colonies and natural pieces of rubble were collected from Davies Reef, (18°48′37"S, 147°38′32"E) a typical mid-shelf reef east of Townsville, on the central GBR in Bindal sea Country. The rubble was a natural mixture of shapes although dead branching *Acropora* was common. Similarly-sized pieces of the branching coral rubble were chosen, and cut, using stainless steel bone cutters, into cylindrical pieces between 2 and 3 cm in length (Fig. 1B). The length of each rubble fragment was measured and the rubble curved surface area (SA) was nominally estimated using the equation for a cylinder:

$SA = 2\pi rh$; where r is the radius and h is the height of the coral branch.

Three replicate 68-L tanks were used and the cut rubble pieces distributed as before, with each tank containing 4 pieces lying static on the tank floor and 4 paired pieces suspended under 37-mm diameter floats on pieces of cotton string, for a total of 12 'still' and 12 'moving' replicate rubble pieces. *A. cf. kenti* larvae generated from corals spawned on 23 November 2021, 4 days after the full moon at approximately 18:30, were added to each replicate tank, once competent to settle, as described above. They were allowed 48 h to settle after which the pieces of rubble were removed and the numbers of settled coral spat were counted, excluding those on the ends of the fragments. Spat density (cm^{-2}) was calculated by dividing the number of spat by the SA of each rubble fragment.

Coral settlement was modelled against treatment (still vs. moving) using a generalised linear mixed effects model with treatment considered a fixed effect and replicate pair nested within experimental tank as a random effect. Settlement

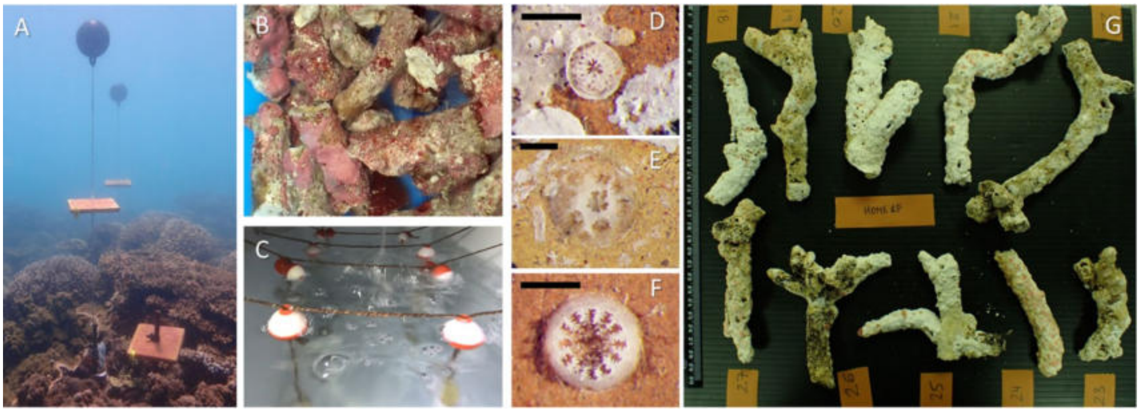

Fig. 1 **A** Paired floating and fixed tiles deployed on Halfway Island reef during Experiment 3. **B** Rubble fragments used in Experiment 2. Natural rubble, consisting mostly of branching coral fragments and encrusted with crustose coralline algae and biofilm was collected from Davies Reef and cut into similar lengths. **C** Experimental settlement tank setup for Experiments 1 and 2 showing the surface floats and aeration enabling the movement of settlement substrates suspended beneath. **D**–**F** Photomicrographs of spat skeletons on settlement tiles. **D** Acroporidae **E** Pocilloporidae and **F** 'other'. Scale bars = 1 mm. **G** Examples of natural rubble fragments collected, bleached and assessed for settlement

density was modelled with a gaussian distribution, using the 'glmmTMB' package (Berg et al. 2017) in R (R Core Team 2022). Model diagnostics and visualisations of estimated marginal means were undertaken as described for Experiment 1.

Experiment 3—Field settlement to fixed and floating tiles

To investigate the role of fixed versus free-floating (i.e. moving and elevated) substrates on coral settlement in situ, we undertook a field experiment. Natural clay fired (terracotta) tiles (11 × 11 × 1 cm, L, W, H; average weight 122 g) were deployed as coral settlement substrates at Halfway Island reef (23°12′5.82″S, 150°58′12.78″E), in Woppaburra sea Country (Keppel Islands) in the southern inshore GBR. Tiles were pre-conditioned in the SeaSim in flowthrough seawater for the development of a biofilm beginning on 11 October, before deployment on 4 November 2021 approximately 20 days ahead of the predicted coral spawning period (realised on 23 November 2021 for colonies collected from this location and spawned in the SeaSim).

Each pair of tiles consisted of a fixed tile and a floating tile and were deployed in five replicate pairs across each of 3 replicate 10 m transects, for a total of 15 tiles of each treatment. Fixed tiles were mounted on steel reinforcement rod (reo) driven into the reef and placed at the height of the surrounding coral canopy, but not in contact with the substrate. Floating tiles were tethered to an individual reo rod adjacent to the fixed tile but were suspended in the water column in a horizontal position, approximately 40 cm above the height of the coral canopy, from a Dyneema® string line fed through the centre of the tile and tied to a 78 mm diameter buoy (Fig. 1A). Tiles were retrieved on 8 Jan 2022 (65 days after deployment and approximately 46 days after spawning), bleached and returned to the laboratory for assessment. The surfaces of each tile were searched twice using a dissection microscope (Leica M60 stereo microscope), and all coral spat skeletons were marked, identified into family categories (Acroporidae, Pocilloporidae, other, or unknown; Fig. 1D–F) and counted as per Babcock et al. (2003). Spat from the family Acroporidae were identified using the following features: (i) porous coenosteum, (ii) prominent septa and (iii) no columella. Pocilloporidae spat were identified by a (i) solid coenosteum, (ii) prominent septa and a (iii) prominent columella. Spat in the other category were defined as an intact spat without the features of either Acroporidae or Pocilloporidae, such as septa with prominent teeth typical of Poritidae and Fungiidae for example, and unknown was defined as an unrecognisable spat due to damage, obscurity, or age of < ~ 1 wk without evident features. All surfaces (upper, lower and sides) of the tile were assessed and quantified separately to investigate whether settlement preferences varied between treatments and by location on the tile.

Coral settlement density was modelled using a generalised linear mixed effects model with treatment (fixed vs. floating), tile position (top, side, or underside), and their interaction as the fixed effects, and tile nested in replicate pair nested within replicate transect as a random effect. Settlement density was used as the response to account for uneven surface areas across tile positions, and to compare with rubble settlement densities. Settlement was modelled using a Tweedie distribution with a log-link function using the 'glmmTMB' package in R, to account for the continuous, non-negative data with a high frequency of zero values and a right-skewed distribution. Total settlement density (over the entire tile) was also compared between treatments (fixed vs. floating) with replicate pair nested within replicate transect as a random effect, as above. Model diagnostics were assessed as described above.

Experiment 4—Settlement to natural rubble

From 8–12 January 2022, (an estimated 46–50 days after the predicted Nov 2021 spawning) approximately 10 rubble pieces were collected from each of six reefs across the Keppel Islands: Humpy Island Reef, Halfway Island Reef, "Home" (i.e. the house reef of the Konomie Island Environmental Education Centre) and Mazie Bay reefs of North Keppel Island (NKI), Clam Bay and Shelving Bay reefs of Great Keppel Island (GKI) (Table 1). The rubble pieces were bleached and dried. The rubble pieces were then laid on their flattest aspect and photographed from above on a contrasting black backdrop with a ruler for scale (Fig. 1F). Using Image J ('versatile tool') to select the boundary of each rubble piece, an upper two-dimensional surface area was calculated. This surface area was then multiplied by two, combining the upper and lower surface areas and approximating the area available for settlement. Each fragment was then examined for coral spat using the method described above for Experiment 3. Once assessed, the number of spat and the available surface area were used to calculate a spat settlement density. We note that this approach likely overestimates the available area for settlement as some underside surfaces may be flush with the benthos, preventing larvae access for settlement. Thus, settlement densities may have been underestimated using this method. Spat densities were compared amongst sites using a generalised linear model with a Tweedie distribution and a log link function, to handle the continuous, non-negative and zero-inflated density data. Model diagnostics and data visualisation were undertaken as described above.

Results

Experiment 1—moving plugs

Coral settlement onto moving plugs was not significantly reduced compared with fixed plugs in either species tested (A. *millepora* and G. *retiformis*) (Fig. 2A; Table 2). Modelled settlement of *A. millepora* was estimated to be 14.4 and 13.9 spat per plug for still and moving plugs, respectively, while settlement of G. *retiformis* was lower overall and was estimated at 7.9 and 5.0 spat per plug for still and moving substrates, respectively.

Experiment 2—moving rubble

Rubble fragments had an average surface area of 1553 mm^2 and ranged from 939 to 2350 mm^2. *A. cf. kenti* settlement onto moving rubble was significantly reduced compared with still rubble, which saw five times higher settlement density than moving rubble (5.9 vs. 1.0 spat cm^{-2} on still and moving rubble, respectively; Fig. 2B; Table 2).

Experiment 3—field settlement to fixed and floating tiles

A total of 759 spat were identified across the 30 tiles deployed at Halfway Island. In situ settlement to floating tiles was approximately 4 times higher than settlement to fixed tiles, with 612 and 147 spat identified on floating and fixed tiles, respectively (Fig. 3A, Fig. 4A; Table 2), and this pattern was consistent across replicate transects. Most settlers were from the family Acroporidae, representing 80 and 92% of spat from the floating and fixed treatments, respectively (Fig. 3B). Pocilloporidae were only found in the floating treatment and only accounted for a small proportion of total recruits identified (12%), whilst the 'other' and 'unknown' categories represented between 3 and 5% of spat in each treatment.

The highest densities of settlers were found on the sides of the tiles (with a mean density of 0.13 and 0.38 spat cm^{-2} on fixed and floating tiles, respectively), and the undersides

Table 1 Waypoints and dates of rubble collection for assessment of natural settlement (Experiment 4)

Site name	Latitude	Longitude	Date of rubble collection (dd/mm/yyyy)
Clam Bay, Great Keppel Island	23°11′11.20"S	150°58′26.69"E	8/1/2022
Halfway Island Reef	23°12′7.10"S	150°58′16.27"E	11/1/2022
Home Reef, North Keppel Island	23°4′58.06"S	150°53′4.70"E	10/1/2022
Humpy Island Reef	23°12′40.66"S	150°57′58.23"E	8/1/2022
Mazie Bay, North Keppel Island	23° 5′7.99"S	150°54′11.43"E	9/1/2022
Shelving Bay, Great Keppel Island	23°11′20.46"S	150°56′1.69"E	10/1/2022

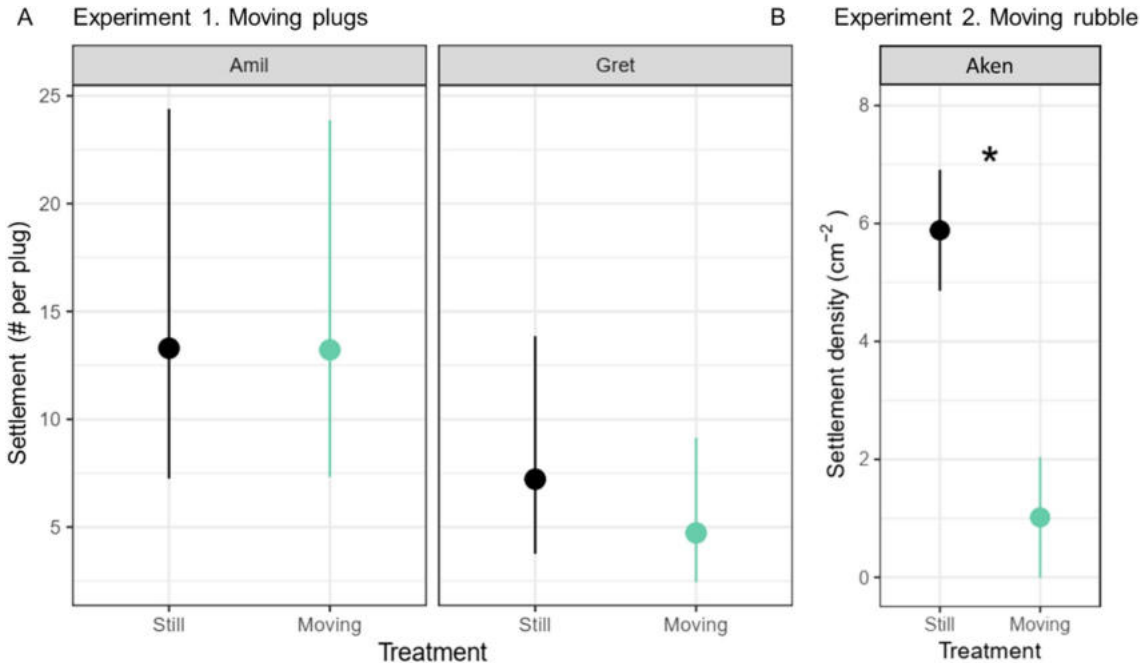

Fig. 2 **A** Experiment 1 coral larval settlement results for two species (Amil, *Acropora millepora*; Gret, *Goniastrea retiformis*) on still versus moving plug treatments. No significant differences were observed between treatments, but G. *retiformis* had significantly fewer settlers than A. *millepora*. **B** Experiment 2 coral larval settlement results for *Acropora cf. kenti* on still versus moving rubble fragments (Fig. 1B, C). * indicates statistically significant differences between treatments ($p < 0.001$)

of floating tiles (0.16 spat cm^{-2} vs. 0.004 spat cm^{-2} on undersides of fixed tiles) (Fig. 3A). The tops of tiles in both positions had very low densities of spat (0.03 and 0.04 spat cm^{-2} for fixed and floating tiles, respectively), while the lowest density observed was on the undersides of fixed tiles, which had negligible settlement (0.004 spat cm^{-2}; Fig. 3A).

Experiment 4—settlement to natural rubble

Between 10 and 17 rubble fragments were sampled from each of the six sites (Fig. 1F, Fig. 4) and a total of 99 spat across 71 rubble fragments were identified. Approximately 2 months after the main mass-spawning event, spat were recorded on 42% of rubble fragments. Settlement to rubble in situ was lower than settlement to the tiles (compare Fig. 3A and Fig. 4A) and averaged 0.02 spat cm^{-2} across sites, again noting that spat density on rubble was likely underestimated due to the method of surface area estimation. The highest average settlement was observed at Mazie Bay and was 2.8 spat per fragment, 14 times higher than the lowest settlement at Clam Bay and Humpy Island, both with an average of 0.2 spat per fragment.

The dominant taxon recruiting to rubble was Acroporidae, representing 72% of spat. Pocilloporidae represented 14% of spat, with 13% identified as other and 1 as unknown. The relative proportion of spat from each family varied amongst sites (Fig. 4C) but the sample sizes were very low at some locations, thus comparisons amongst sites were made qualitatively only.

Discussion

The ability of larvae to detect, attach to, and metamorphose on moving substrates in the experimental system was initially surprising, as both the larvae and the substrata were continually in motion. Kenyon et al (2023) reported that rubble fragments demonstrated rocking motion even at water velocities too low for rubble transport, which they conjectured may prevent coral settlement to small rubble pieces under even low-energy hydrodynamic conditions. However, in the laboratory we demonstrated the settlement of larvae of *Acropora millepora*, *A. cf. kenti* and *Goniastrea retiformis* on substrates experiencing constant fine-scale movements. These results, combined with the in situ settlement observed to natural rubble and floating tiles, suggest that coral settlement can occur on rubble pieces as small as a few centimetres (i.e. those with the greatest likelihood of rubble motion (see Kenyon et al 2023)), even if there is slight to-and-fro movement of the substrate from regular wave action.

The scale of substrate movement in the present laboratory experiments was only a few millimetres per second, comparable to water movement found within reef interstices (Koehl & Hadfield, 2010). Given that larvae are reported

Table 2 Model statistics for each of the four experiments undertaken. Statistically significant terms are bolded ($p < 0.05$)

Experiment	Model	Distribution	Response	Term	Estimate	standard error	*z* valu/*t*value	*p* value
Experiment 1—2019 moving plugs with *Acropora millepora* (Amil) and *Goniastrea retiformis* (Gret)	Settlement ~ Treatment * Species + (1 | Pair)	Negative binomial with log link function	Number of settled spat	Treatment (moving)	−0.035	0.410	−0.086	0.931
				Species (Gret)	−0.602	0.418	−1.439	0.150
				Treatment * Species	−0.419	0.599	−0.699	0.485
Experiment 2—2021 moving rubble with *Acropora cf. kenti* (Aken)	Total density ~ Treatment + (1 | Tank / Pair)	Gaussian	Settlement density	Treatment (moving)	−4.868	0.564	−8.629	**< 0.001**
Experiment 3—2021 in situ floating tile settlement	Habitat-specific density ~ Treatment * Position + (1 | Transect / Pair / Tile)	Tweedie with a log-link function	Settlement density	Treatment (floating)	0.5845	0.423	1.380	0.167
				Position (side)	1.6023	0.370	4.330	**< 0.001**
				Position (underside)	−1.839	0.608	-3.026	**0.002**
				Treatment (floating: position (sides)	0.412	0.481	0.858	0.391
				Treatment (floating): position (underside)	3.132	0.687	4.557	**< 0.001**
	Total density ~ Treatment + (1 | Transect / Pair)	Tweedie with a log-link function	Settlement density	Treatment (floating)	1.631	0.190	8.565	**< 0.001**
Experiment 4—2021 settlement to natural rubble across 6 sites	Density ~ Site	Tweedie with a log-link function	Settlement density	Halfway Island	2.515	1.100	2.287	**0.022**
				Home reef	0.846	1.303	0.649	0.516
				Humpy Island	2.511	1.130	2.221	**0.026**
				Mazie Bay	3.367	1.091	3.085	**0.002**
				Shelving reef	1.428	1.184	1.206	0.228

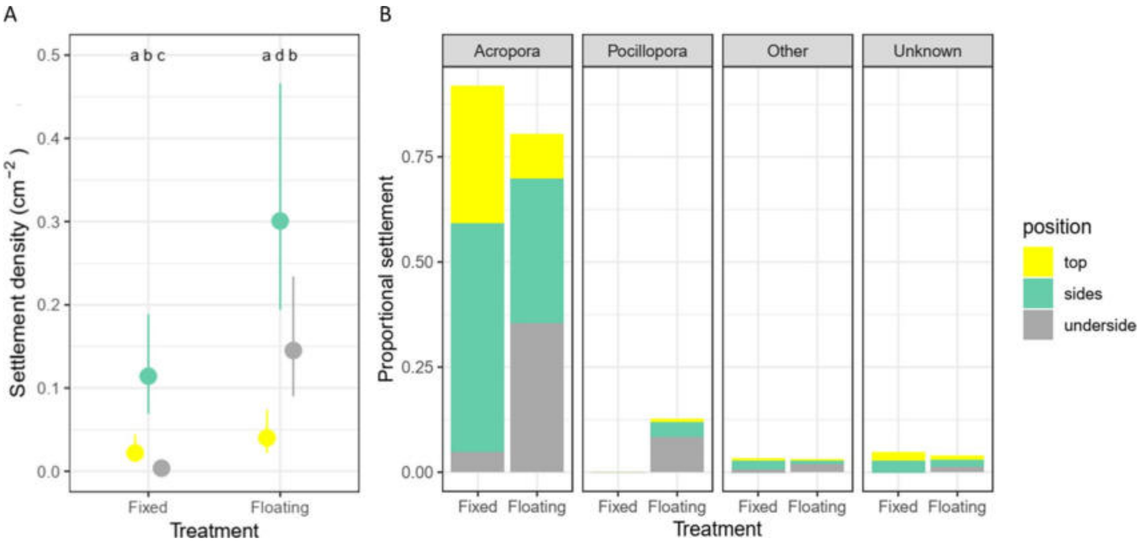

Fig. 3 **A** Results of an in situ experiment (Experiment 3) assessing natural settlement onto fixed and floating tiles (Fig. 1A). Letters in (A) indicate statistically significant differences between treatments from post-hoc pairwise comparisons $p < 0.001$; (Table 2). **B** Proportional settlement of spat onto fixed and floating tiles by family groups (*Acropora*, Acroporidae; *Pocillopora*, Pocilloporidae; Other = other taxa, Unknown = unidentifiable, partial, or damaged spat skeletons). Colours in **B** indicate the position of settlement onto the tile (top, sides or underside)

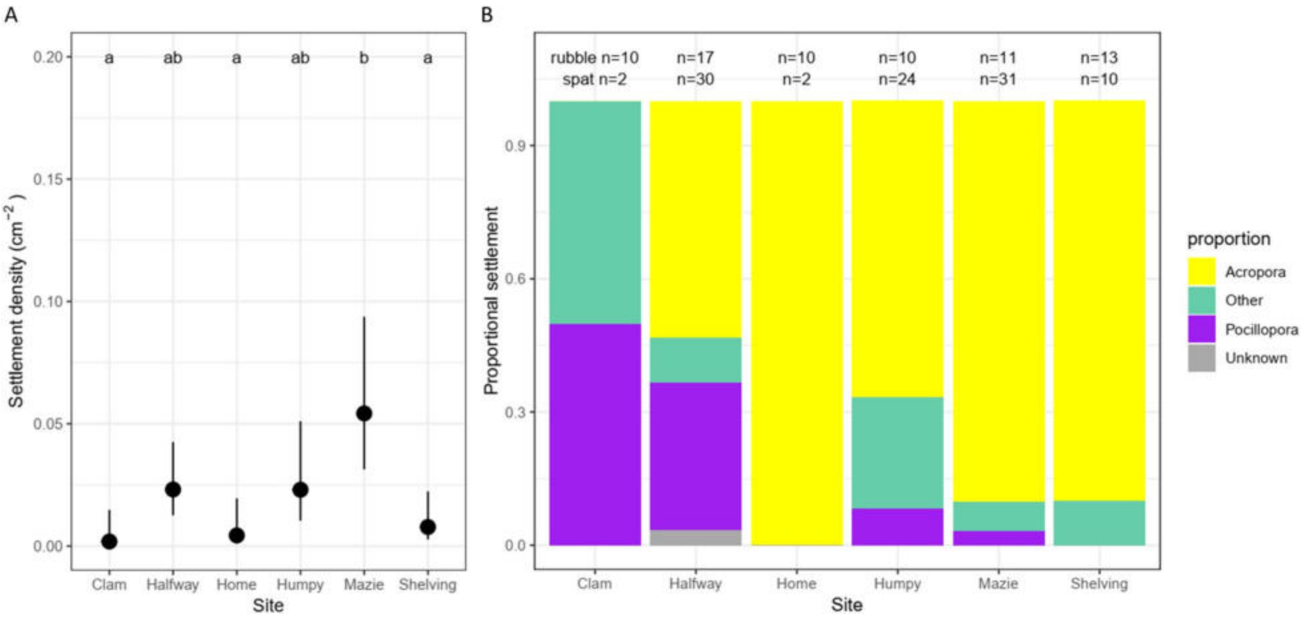

Fig. 4 **A** Coral settlement densities on rubble across six sites (Experiment 4). **B** Proportional settlement of spat onto rubble by family groups (*Acropora*, Acroporidae, *Pocillopora*, Pocilloporidae, Other = other taxa, Unknown = unidentifiable, partial, or damaged spat skeletons), at each of six sites (Table 1). Letters in **A** represent statistically significant differences amongst sites. Rubble sample sizes from each site are indicated above bars in (**B**)

to be poor swimmers and may rely on fine scale turbulence to reach settlement sites within the reef framework (Hata et al 2017; Koehl & Hadfield, 2011), these results suggest that larvae swept into the benthic boundary layer have the ability to settle routinely within rubble fields under normal hydrodynamic conditions. Indeed, the numerous interstices amongst rubble pieces conditioned with appropriate settlement cues present an attractive settlement habitat across a broad range of coral taxa as recently demonstrated by Randall et al. (2024) for 25 taxa from 7 families tested in the laboratory. Our finding of settlement to rubble in situ at six sites is consistent with this view and supports results of Johns et al. (2018) who found comparable settlement on tiles deployed in rubble and consolidated areas. Similar results were also found by Cameron et al (2016) in Florida, where mainly brooding species were observed settling on rubble. These findings suggest that rubble fields should be considered as potential targets for initial coral settlement on a reef, alongside areas of consolidated habitat, by both brooding and broadcast spawning species. The results support the long-held assumption that corals do settle to rubble habitats, and thus slow recovery of corals in rubble fields is likely driven by elevated post-settlement mortality.

As our three experimental species have larval development and settlement processes typical of the majority of broadcast spawners, (e.g. Babcock and Heyward 1986) we hypothesise that larvae may routinely be settling on unconsolidated rubble areas of reef following annual mass spawning events on the GBR. The same is likely to apply to brooding species (see Cameron et al 2016). Nonetheless, species-specific differences in larval settlement preferences in relation to substrate movement are probable, given variation in other settlement preferences (e.g., Baird et al. 2003; Abdul Wahab et al. 2023; Randall et al. 2024) and it remains to be seen if particular taxa favour or avoid these unstable areas. Given that most rubble fields are perceived as highly unfavourable for corals post-settlement (Kenyon et al. 2020; Leung and Mumby, 2024), settling there likely represents a poor choice and a loss of potential new recruits from the arriving cohort (Yadav et al. 2016).

While natural settlement to rubble was observed at all six sites surveyed, there was considerable variability in settler densities amongst sites, with a 14-fold difference between sites with the most and least settlement. These differences are likely due to variation in local conditions, including: (i) hydrodynamics, which can impact larval supply (Hughes et al. 2000; Gouezo et al. 2021), (ii) benthic community composition, which can influence settlement cues and inhibitors (reviewed in Randall et al. 2020) and affect larval supply via allee effects (Teo and Todd 2018) and (iii) sedimentation, which affects larval settlement preferences (Jones et al. 2015; Ricardo et al. 2017), among other factors. While outside the scope of this study, further investigation into the within and between-reef scale drivers of settlement onto rubble is warranted, to understand the limitations to recruitment in these habitats.

A more comprehensive understanding of coral settlement patterns is desirable at a time when coral reefs are in decline (Pandolfi 2003; Hoegh-Guldberg et al. 2007; De'ath et al. 2012; Hughes et al. 2018) and there is heightened interest in measuring coral settlement and recruitment (Hughes et al. 2019; Edmunds 2023). Adequate larval supply and post-settlement success are fundamental for reef renewal, while accurate and comparable measures of settlement provide the means to understand stock-recruit relationships within and between reefs and assess the risks to recovery. Such data are also useful to assess whether interventions to enhance larval supply are warranted or are likely to make a difference (Edwards et al. 2015; Dela Cruz and Harrison 2020; Harrison et al. 2021), and whether methods that restore juvenile corals would be better suited than direct larval delivery to those environments (Chamberland et al. 2015, 2017; Randall et al. 2021, 2022).

There have been numerous studies demonstrating that substrate type (i.e. material and texture) and deployment method (i.e. orientation and conditioning) influence coral settlement (Harriott and Fisk 1987; Maida et al. 1994; Mundy 2000; Edmunds 2023). Our comparison of terracotta tiles fixed to the seabed or suspended in the water column demonstrated both quantitative and qualitative differences in coral settlement between treatments. The approximate fourfold increase in spat on the suspended tiles was unexpected and warrants further investigation, particularly given comparable settlement densities recorded on fixed tiles deployed to the substrate and on racks elevated ~ 15 cm above the reef benthos (Mundy 2000). While it's not clear what drove this fourfold increase in spat on suspended tiles, we propose several potential hypotheses, which are not mutually exclusive. Firstly, it's possible that predation pressure from benthic invertebrates or benthic-associated fish may have been stronger on tiles near the seafloor (Fabricius and Metzner 2004; Wolf and Nugues 2013), reducing apparent settlement. It's also possible that substrate encounter rate by larvae was higher on floating tiles resulting in higher settlement. Stronger allelopathic interactions near the benthos could also have deterred settlement on fixed tiles (Maida et al. 1995; Birrell et al. 2008; Page et al. 2023), as could higher sedimentation (Babcock and Davies 1991; Mundy and Babcock 1998; Ricardo et al. 2017) and/or lower light conditions (Mundy and Babcock 1998; Strader et al. 2015). Given the tile positioning, it is likely that there was a greater area of suitable substrate with preferred light levels on the underside of floating versus fixed tiles. Indeed, settlement to the underside of fixed tiles was very low compared with the underside of floating tiles. Finally, the benthic community composition that developed on suspended and fixed tiles may have varied, leading to differential attractiveness and inductive communities for settlement. Regardless of the mechanism driving these differences, even when a standard method is used to allow comparative settlement rate assessments over time in longitudinal studies, it is probable that the data are only relative and do not fully reflect actual larval supply or settlement to the reef. Variation in protocols used for recruitment census only compound the potential for experimental artefacts, undermining comparative studies. Interestingly however, the average density of spat on fixed tiles (0.03 cm^{-2}) was similar to that observed on rubble (0.02 cm^{-2}), despite their variation in substrate material and benthic community composition, suggesting that the positioning of substrates within the reef environment may be more important to standardise than the substrate type itself. This result also suggests that assessing settlement with substrates fixed to the seafloor may be more representative of settlement on reef substrate, but that larval supply may be more accurately assessed using above-substrate collection methods.

While our laboratory and field experiments supported the notion that larvae can settle onto moving substrates, the results varied amongst experiments and these comparisons may shed light on the fundamental processes that influence settlement. For example, while larvae settled just as well on floating plugs as they did on static plugs in experiment 1, settlement was much higher on static than floating rubble in experiment 2. The reason for this variation is unknown but we propose several potential explanations that warrant further investigation. Firstly, different taxa were tested in these experiments, so it is possible that there were species-specific preferences at play. Yet, *A. millepora* and *A. cf. kenti* larvae typically display similar larval settlement behaviour (Randall et al. 2024) and occupy similar environmental niches so this explanation is considered unlikely. Secondly, the biomass and the community composition of the biofilm, encrusting organisms and bioeroding communities found on the aquarium-reared aragonite plugs and the natural rubble fragments likely varied considerably (Webster et al. 2004; Petersen et al. 2021; Turnlund et al. 2023) and it's possible that the larger biomass of inducers on natural rubble increased the concentration of inductive cues in the water (Koehl and Hadfield 2004), triggering more bottom-seeking behaviour (Szmant and Meadows 2006; Da-Anoy et al. 2017; Antonio-Martínez et al. 2020). In this case, larvae, which can modulate their position in the water column via swimming behaviour, may have come into direct contact with rubble on the bottom of the tank more often than floating rubble, to which they attached and metamorphosed. Finally, it is possible that the variations in shape and size between plugs and rubble affected micro-eddies and currents within the tanks, altering larval retention dynamics as they were moved around the tank (Koehl and Hadfield 2004; Hata et al. 2017). Whether this variation would result in higher retention around rubble than plugs would require testing.

The need for more frequent and multi-year settlement and recruitment studies is recognised (Edmunds 2023), but is currently constrained by the resource intensive nature of diver-based tile deployments and retrievals, as well as microscopic examination of spat. Moving towards an updated and potentially universal approach to settlement assessment, with consideration of methods that are very straightforward and much more cost-effective would support these objectives. Although a small pilot study, our suspended tile results indicate that substrate-attached tiles may not be the only solution. Settlement plates and collectors suspended under moorings have been a common tool in recruitment studies for various marine organisms (i.e. Fuentes and Molares 1994), including corals (e.g. Sammarco and Andrews 1988). Any review of settlement assessment protocols should include some consideration of suspended arrays as an alternative to diver-based methods, and automated image analysis for spat identification. The potential for diver-less settlement censuses around reefs using temporarily anchored floats and suspended settlement substrates is attractive, given cost and safety considerations, and offers an alternative approach to the collection of coral spat on settlement objects for subsequent deployment in restoration efforts.

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Author contribution All authors conceived of and undertook the experiments. CG and AH collected the data. CR analysed the data. AH and CR wrote the manuscript. All authors reviewed, edited, and approved the final version.

Declarations

Conflict of interest On behalf of all authors, the corresponding authors state that there are no conflicts of interest.

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