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research paper

Three-dimensional printing can provide opportunities to promote coral recruitment on disturbed reefs

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ABSTRACT.—Tropical corals are undergoing population declines due to disturbances. The implications of these trends are modulated by the ability of corals to support population recovery through recruitment. Current research underscores the importance of physical features of benthic surfaces in promoting coral recruitment, which creates opportunities to enhance recruitment by engineering surfaces to replicate these features with the goal of enhancing coral settlement. This study examined the interaction between the settlement of coral larvae and three-dimensional (3D) surfaces and employed 3D printing to enhance recruitment. We tested the effects of the features of microhabitats on the settlement preference, gregariousness, and survival of the brooding coral *Pocillopora acuta*. Grooved microhabitats that are common in the shallow (<7 m depth) backreef of Moorea, French Polynesia, were printed onto tiles made of polylactic acid, and were favored for settlement by freshly released larvae from *P. acuta*. The percent survivorship over 20 d of coral recruits that settled in grooved microhabitats was 16.4% vs none on open flat surfaces. These results underscore the importance of naturally forming benthic features in promoting coral recruitment, and they highlight the potential for duplication of these features through 3D printing to enhance coral recruitment and accelerate reef restoration following damage.

In the midst of the global environmental crises, the United Nations has nominated 2021 to 2030 as the "Decade on Ecosystem Restoration" (Fischer et al. 2021). This has created the impetus to accelerate global restoration efforts on degraded ecosystems (Boström-Einarsson et al. 2018, Hughes et al. 2023). Currently, coral reef restoration, while only considered a short-term solution to reversing declines in coral population sizes (Boström-Einarsson et al. 2020), might be necessary to promote coral recovery on reefs that are experiencing intensifying disturbances with short recovery windows between sequential events (Hughes et al. 2017). Utilizing emerging technologies in ecosystem restoration efforts that are contextualized by empirical ecology has the potential to be valuable in conserving, preserving, and maintaining coral reef function in the face of accelerating environmental disturbances.

An emerging technology being explored as a tool to enhance coral restoration is additive manufacturing (Levy et al. 2022), also known as three-dimensional (3D) printing (Guo and Leu 2013). 3D printing can accurately recreate complex structures that are similar to those naturally forming on benthic habitats (Mohammed 2016), and these structures can be printed with dimensions varying from a few millimeters (Riera 2020) to meters (Lange et al. 2020) in greatest dimension. Unlike conventional methods that manipulate benthic surfaces to modify recruitment (Nozawa 2008), for example, through the costly processes of drilling holes or custom-molding features (Okamoto et al. 2008, Frazier 2014), 3D printing provides a more cost-effective way to replicate complex structures. 3D printing reduces excess material from production that occurs while working with ceramics and casting molds.

Among the factors favoring 3D printing as an effective tool for creating substrata of use in reef restoration is its ability to print using different materials having a variety of physiochemical properties. 3D printers using fusion deposition modeling (FDM) or fusion filament fabrication (FFF) are widespread and a well-known means of printing structures outside the field of marine ecology (Guo and Leu 2013, Bryll et al. 2018), but they are relatively new to coral restoration (Bryll et al. 2018, Ruhl and Dixson 2019). FDM uses thermoplastic material that is derived from starch to create biodegradable polymers such as polylactic acid (PLA) and acrylonitrile butadiene styrene (ABS). FDM can be modified to use liquid or paste material such as ceramics and resin, with the potential to infuse calcium carbonate onto these materials for biological application (Darling and Smith 2021).

Ensuring 3D printing creates ecologically relevant features of proven success in promoting coral recruitment is likely to maximize the potential of this technique to promote the increase in size of coral populations through enhanced recruitment. Given that large-scale (i.e., ≥1 m) habitat structures used in coral restoration often provide flat or homogenous surfaces for settling corals (Loke et al. 2015), the lack of structural complexity on the settlement surface is likely to deter coral recruitment and prevent the potential of this kind of restoration from being realized. The capacity to design, manufacturer, and install "coatings" to these surfaces through 3D printing may be a valuable addition to restoration science seeking to enhance coral recruitment (Randall et al. 2020, 2021, Levy et al. 2022).

The recruitment of corals to coral reefs marks the demographic origin of coral populations, and it is an important process for stocking and replenishing populations (Edmunds 2023). While this process has been studied for nearly a century (de Lacaze-Duthiers 1873, Duerden 1902), there is a renewed appreciation of the importance of the data obtained from analyses of coral recruitment to quantify the response of coral reefs to disturbance, and to evaluate ecological resilience in an increasingly human-disturbed ecosystem (Hughes et al. 2019, Price et al. 2019). Most analyses of coral recruitment use settlement tiles to measure the arrival of coral settlers (Glassom et al. 2004), and these rely on the immersion of small tiles on the reef for fixed periods (Edmunds 2021). Following immersion and subsequent retrieval, coral settlers on the tiles are usually evaluated through microscopic inspection. While scoring recruitment on natural reef surface remains a challenge due to coral settlers being inconspicuous (Babcock et al. 2003), settlement tiles provide a way to quantify the abundance and taxonomic composition of coral settlers, and to describe spatiotemporal trends in recruitment (Edmunds 2023).

Coral recruits (i.e., corals <2 mm diameter) often settle in cracks, pits, and grooves on natural reef surfaces (Edmunds et al. 2014, Doropoulos et al. 2016). This distributional preference can be modulated by the biomass of epilithic algae, the abundance of fish grazers, and the density of coral settlers (Doropoulos et al. 2017, 2018). High biomass of epilithic agal communities can limit available space for coral settlement (Birkeland 1977, Arnold et al. 2010), and high abundances of grazing fishes can lead to direct and indirect mortality of coral recruits on open surfaces (Davies et al. 2013, Gallagher and Doropoulos 2017). Different densities of established coral recruits can influence the rate at which further coral larvae settle, gregariousness of settling larvae, and the degree of clustering of recruits, all of which can lead to enhanced growth and survival of small corals (Puill-Stephan et al. 2012a, Doropoulos et al. 2017, Cameron and Harrison 2020). Gregarious settlement of coral larvae can attract higher intensities of fish corallivory but can also help in the formation of larger chimeric coral colonies that enhance survivorship (Amar et al. 2008).

This study was conducted to advance the ability to employ 3D printing to promote reef restoration through enhanced coral recruitment. We reasoned that a better understanding of the ways in which coral larvae select locations to settle on complex 3D surfaces would lead to a greater ability to reproduce the favored surfaces through 3D printing, thus creating the potential to enhance reef-wide recruitment if these surfaces can be replicated at large spatial scales. Working with brooded larvae freshly released from the common Indo-Pacific coral *Pocillopora acuta*, we tested the hypotheses that settlement preference, gregariousness, and the survival of recruits varies among types of microhabitats on small settlement tiles (34 × 46 × 4 mm) with complex surfaces that were 3D printed using FDM bioplastic. We used the results to describe how 3D printing can be optimized to enhance coral recruitment.

Methods

Study Site.—This study was conducted on the north shore of Moorea, French Polynesia, from 1 April to 14 May, 2022 (17°28.498´S, 149°47.518´W). Moorea has been subject to multiple disturbances in the last few decades, including cyclones, bleaching, and outbreaks of coral predators (e.g., the crown-of-thorns sea star *Acanthaster solaris*; Trapon et al. 2011). *Pocillopora acuta* was used in this study given their high abundance, accessibility on the shallow reefs of Moorea and release of brooded larvae (Johnston et al. 2022).

Larval Collection.—*Pocillopora acuta* was used to supply brooded coral larvae. Parent colonies were collected from 1 m depth on a fringing reef on the north shore. Six colonies were haphazardly collected 3 d before the new moon in April, and 7–12 d before the brooded larvae of this species were expected to be released (Fan et al. 2006). Colonies were placed in plastic bags and transported to the lab in shaded tubs of seawater, where they were placed in individual aquaria modified for the collection of larvae. Aquaria were slowly supplied (ca 60 mL min^{-1}) with free-flowing, sand filtered, seawater (at an ambient temperature of 28 °C) that overflowed into small cups fitted with plankton mesh (110 μm) to retain larvae. Sunlight reaching these buckets was shaded compared to the collection depth of the corals, and the maximum light intensity in the buckets at noon was about 1100 µmol photons s^{-1} m^{-2} (recorded with a cosine-corrected Li-Cor LI 192 sensor).

3D Printed Settlement Tiles.—Custom-made settlement tiles (34 × 46 × 4 mm) were engineered using an FDM printer (MK3S+, Prusa Research a.s., Czech Republic) and were designed to provide refuges to settling coral larvae. Tiles were printed (n = 25) in which microhabitats in the shape of small grooves were printed into the plastic, with each tile having both grooves and an area of smooth surface (Fig. 1). Groove microhabitats were common on benthic surfaces across the backreef of Moorea. 3D printed groove microhabitats were recreated so that the walls of the grooves created angles of 90° at the floor of the grooves and where the walls met the surface of the tiles. Printing features with engineered angles was important given their roles in determining the settlement of barnacle larvae (Le Tourneux and Bourget 1988) and some tropical reef corals (Carleton and Sammarco 1987).

Tiles were printed using polylactic acid (PLA: Prusament PLA; color: Galaxy Silver) and were conditioned in seawater in Moorea for 2 wks to develop a natural biofilm that induces coral settlement (Sneed et al. 2014). Once conditioned, settlement tiles were individually suspended in containers (53 × 119 × 167 mm; hereafter described as chambers) with the grooved surface of the tiles facing downward and about 10 mm above the bottom of the chambers. This positioning placed the grooved surface of the tile in an inverted orientation, which often is a favored position for coral larval settlement (Raimondi and Morse 2000). Each chamber was fitted with a small window of plankton mesh (110 µm) that allowed the exchange of seawater within a larger tank. Twenty-five chambers, each fitted with a settlement tile, were placed in a flow-through seawater table to maintain the ambient temperature (in April) of 28 °C.

On 18 May, 2021, larvae freshly released from three colonies of *P. acuta* (and pooled among colonies) were added to chambers (25 larvae $chamber^{-1}$) that were filled with sand-filtered seawater. While chambers were opaque plastic and allowed natural light to enter their sides, they were shaded by their lids. The larvae were left to settle for 48 hrs on a 12:12 hr dark:light photoperiod to allow the newly settled corals to establish firm attachment to the benthic surface (Fabricius et al. 2017). The settlement location of all the recruits on each tile was mapped to quantify their settlement location (i.e., in grooves or on open surfaces), abundance, and the extent of aggregated settlement. Aggregated settlement was defined as cases where coral larvae settled close enough to allow the tissue of adjacent recruits to touch (after Doropoulos et al. 2017), and it was used to quantify gregarious larval settlement (vs singletons), and subsequent survivorship. Newly settled coral spat on inverted tiles were left in their respective chambers in order to compare survivorship between single and aggregated recruits (i.e., two or more adjacent spat touching) in grooves and on open surfaces. Survivorship was observed in the laboratory, and was evaluated daily for 10 d, and then every other day for 10 more days.

Statistical Analysis.—Data were processed using R Statistical Software (v4.2.2; R Core Team 2023). Settlement in each microhabitat type (grooves and smooth surfaces) were standardized to the number of corals per unit planar area within that microhabitat type, summed within each tile. Settlement densities were not normally distributed, and this distribution could not be corrected through transformation, therefore they were analyzed using the nonparametric Kruskal–Wallis test. To test

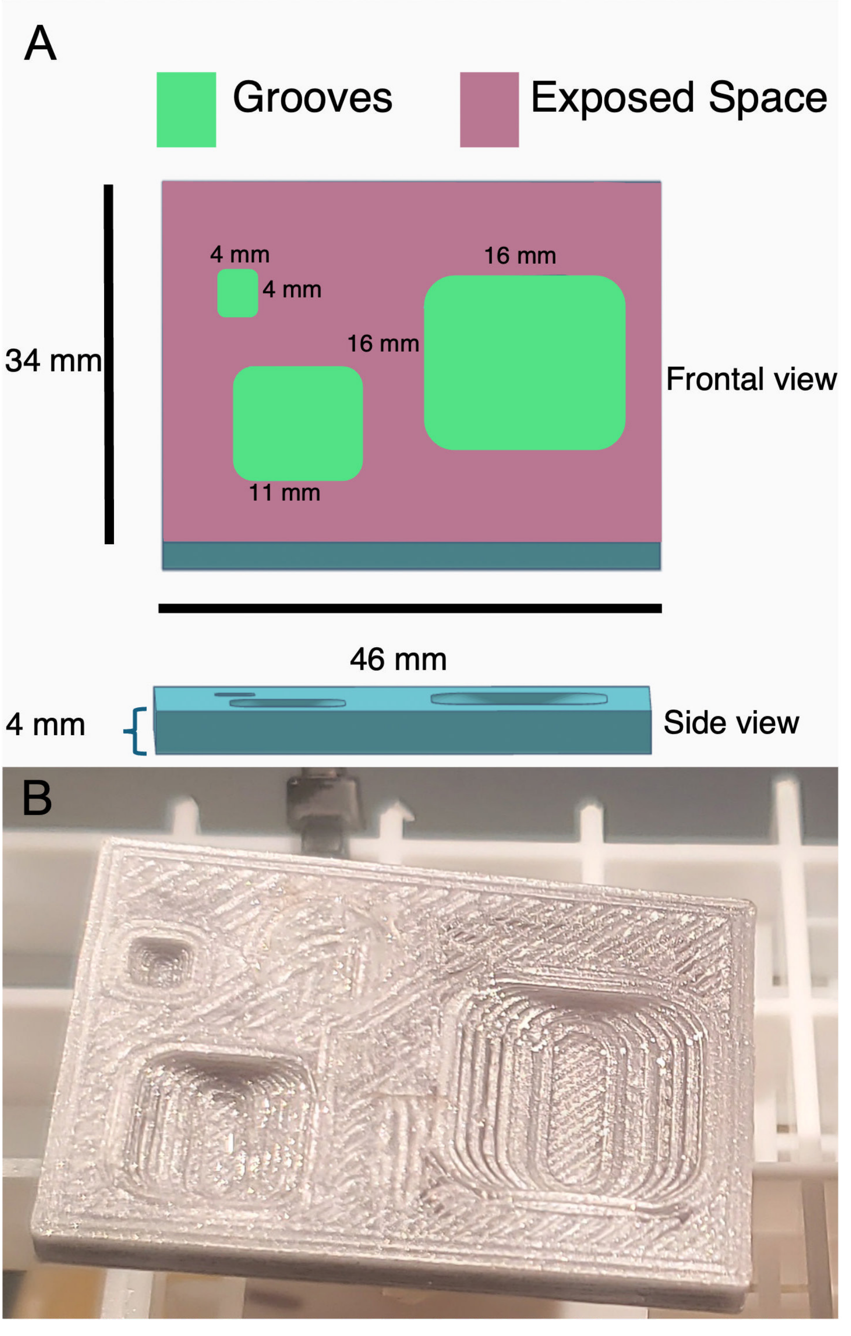

Figure 1. Schematic diagram of 3D printed tiles with surface features. (A) Front and side view of 3D printed tiles with grooves highlighted in green and exposed space in pink. Size of tiles are indicated in mm. (B) Settlement tile printed using PLA filament.

whether gregarious settlement (i.e., solitary vs aggregated) was associated with microhabitat location (i.e., grooves vs smooth surfaces), a 2 × 2 contingency table and chi-square test was used. Survivorship of coral recruits in each microhabitat type (i.e., grooves vs smooth surfaces), and between settlement categories (i.e., solitary vs aggregated) were graphically displayed using Kaplan–Meier (KM) log-rank survivorship curves (Kaplan and Meier 1958). To test whether recruits in different aggregates categories (i.e., solitary vs aggregated) differed in survivorship between microhabitats, a mixed effects Cox proportional hazards model was built (coxme R Package v2.2.18.1; Therneau 2020). In this model, individual recruits were incorporated as a random effect to account for multiple individuals within each microhabitat on each tile. This analysis examined how survival was affected by gregarious settlement and microhabitat type. Post hoc pairwise comparisons between separate groups were completed by analyzing differences in the covariate-adjusted regression coefficients derived from the mixed-effects Cox model (emmeans package; Lenth et al. 2019).

Results

Patterns of Settlement, Gregariousness, and Survival.—During the laboratory experiments, larvae were swimming and favored settling on the inner edges of the groove microhabitats relative to adjacent open spaces. Coral larvae that settled looked healthy after 48-hour exposures to 3D printed settlement tiles. Some coral larvae showed weak adhesion to the PLA-derived settlement tiles, and four coral spat detached when handled during processing (detached spat were excluded from statistical analysis). Settled spat were light to dark brown in color.

Overall, the freshly released larvae from *P. acuta* settled on tiles at a mean (SD) density of 0.216 (0.099) spat cm^{-2} (pooled among microhabitats on each tile; n = 25). Within microhabitats, mean (SD) settlement densities were 0.428 (0.127) spat cm^{-2} in grooves, and 0.003 (0.001) spat cm^{-2} on the smooth surfaces adjacent to the grooves (both n = 25 tiles). Settlement density was significantly higher in grooves than on smooth surfaces (Kruskal–Wallis test: H = 17.60, df = 1, P < 0.01; Fig. 2).

Seventy-three *P. acuta* larvae settled on the 25 tiles, and all were mapped for location on each tile (i.e., in grooves or on smooth surfaces). All other larvae within their respective chambers had metamorphosed in the water column, died, or adhered to the walls of the chambers. Overall, a higher percentage of spat settled in grooves (79.5%) than on open smooth surfaces (20.5%; pooled among tiles). Of the 58 spat within grooves, 46.6% were in aggregates, with these aggregates composed of two, three, or four coral spat that touched one another (Fig. 3). On open smooth surfaces where 15 of the spat were found, 40% were in aggregates of two or three spat touching one another. Overall, the proportion of spat in aggregates did not differ between grooves and open surfaces (χ^2 = 1.39, df = 1, P = 0.247). Survivorship differed between grooves and smooth surfaces (Coxme: χ^2 = 36.71, df = 1, P < 0.001; Online Table S1) and between solitary vs aggregated settlement (Coxme: χ^2 = 38.02, df = 1, P < 0.001; Online Table S1). Pairwise comparison among K-M survivorship curves revealed that solitary settlement in grooves positively affected survival [Coxme: P < 0.05; coefficient of effect size −2.71 (SE 0.26); Online Table S2]. The 20-d survivorship of recruits in grooves was 16.4% (n = 58 recruits), but none survived on open surfaces (n = 15 recruits). After 7 d, tissue fusion appeared to have occurred in two pairs of

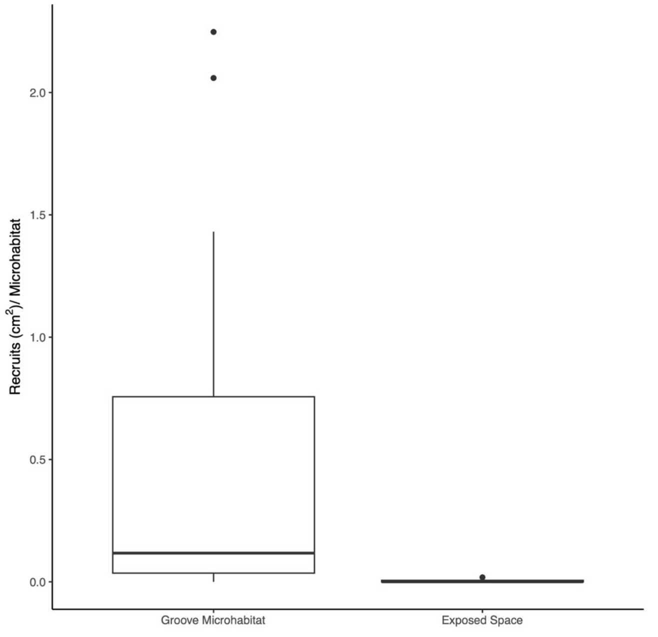

Figure 2. Box plot showing larval settlement of *Pocillopora acuta* on 3D printed tiles with grooves ($n = 58$) and adjacent exposed spaces ($n = 15$). Boxes represent first to last quartile. Points above the box represent outliers 1.5× the interquartile range.

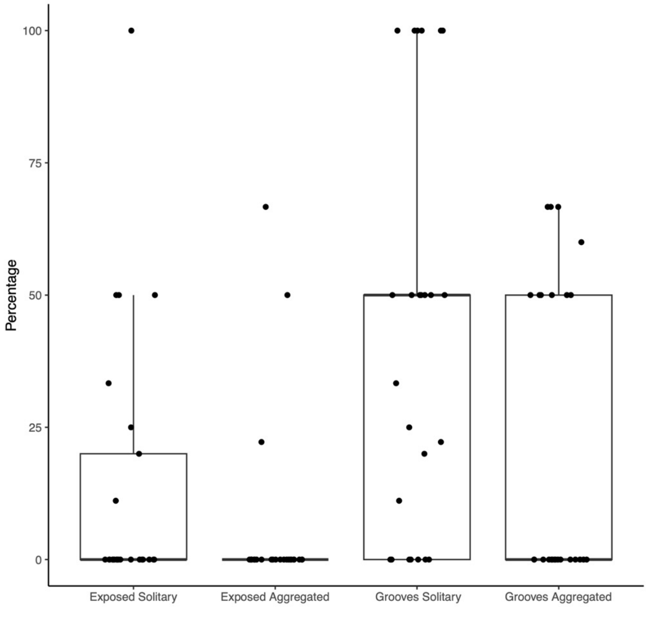

Figure 3. Box plot showing percentage of coral recruits in microhabitats printed on 3D tiles (exposed space vs grooves) separated by aggregation type (solitary vs aggregated). Results obtained from 25 replicate chambers to each of which 25 larvae were added and their final settlement location and aggregation type were expressed as a percentage of the larvae added to each chamber. Boxes indicate the first to last quartile and whiskers show 1.5× the interquartile range of the data. Dots show values jittered for clarity.

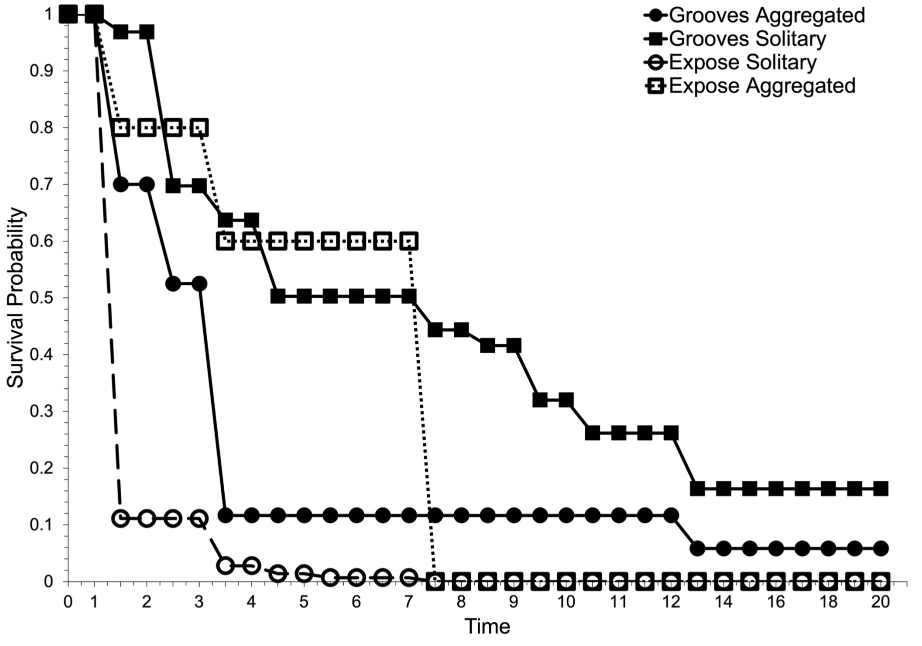

Figure 4. Kaplan–Meier survival curves for *Pocillopora acuta* spat in laboratory conditions for 20 d. Spat were tracked for survivorship on 3D printed tiles where they were found in grooves and on adjacent exposed surfaces and were distinguished as solitary (single) or aggregated (more than two spat touching). Solitary spat (n = 15) had a higher probability of survival than aggregated spat (n = 58).

coral spat that were aggregated. When pooled between microhabitats, survivorship was 26.2% for solitary recruits and 6.3% for aggregated recruits at 12 d, regardless of the number of recruits in the aggregates (Fig. 4). After 12 d all recruits had died, except for those within the grooves printed onto the tiles.

Discussion

Widespread degradation of tropical coral communities (Eddy et al. 2021) highlights the urgency of developing effective restoration methodologies (sensu Hughes et al. 2023) to slow, and perhaps reverse, future trajectories of declining abundance of reef corals. This study applied 3D printing to replicate naturally forming microhabitat features (forming on a scale of ≤1 cm) that were used to test whether patterns of coral settlement and survival varied between microhabitats. *Pocillopora acuta* larvae showed higher settlement in grooves printed on tiles relative to adjacent spaces on the same tiles. The differences in larval settlement location, and the elevated survival of the recruits they form in each microhabitat, supports the use of 3D printed grooves as design features on artificial settlement surfaces to facilitate coral recruitment. Overall, our results reveal the potential to optimize 3D printed artificial surfaces that could be deployed in restorative efforts to enhance coral recruitment and accelerate reef recovery.

In the present study, the larvae of *P. acuta* settled in grooves more often than on adjacent smooth surfaces. Substratum selection by larvae of *P. acuta* in favor of grooves is consistent with previous studies of the settlement of coral larvae (Baird and Hughes 2000, Edmunds et al. 2004, Petersen et al. 2005, Nozawa 2008, Doropoulos et al. 2016, 2017, Randall et al. 2021), in which the suitability of microhabitats for larval settlement is a product of physical (Nozawa 2008, Mallela 2018) and biological cues (Ritson-Williams et al. 2010) that include micro-crevices and crustose coralline algae (CCA), respectively. The increased complexity (i.e., their surface texture) of microhabitat features can influence the settlement behavior of coral larvae (Whalan et al. 2015) possibly because these larvae are rugophilic (sensu Mallela 2018). Substratum texture created by the angular intersections of surface planes on hard substrata might be formed on rocks at scales of meters when boulders and cliffs meet, or at scales of ≤1 cm when the hard surfaces forming microhabitats meet. Evidence that coral larvae favor these features (e.g., the present study) suggests that 3D printed settlement surfaces could be a means to enhance coral recruitment onto these surfaces. This creates the potential to scale up printing of these features for use in reef restoration.

Gregarious settlement is common among marine invertebrates (Hadfield and Paul 2001), and for reef corals, can favor the formations of chimeric colonies that result from fusion of closely located corals (Amar et al. 2008). Such "compound corals" can show augmented physiological performances (i.e., survivorship) through the rapid increase in colony size resulting from joining multiple corals (Foster et al. 2002). Gregarious settlement can reflect a density dependent phenomenon (Suzuki et al. 2012, Doropoulos et al. 2017), where high densities of coral larvae increase the incidence of gregarious settlement (Puill-Stephan et al. 2012a, Shefy et al. 2022), but also the rate at which coral predators (i.e., corallivorous fishes) are attracted to corals settling at high densities (Jayewardene et al. 2009), thus increasing coral mortality (Gibbs and Hay 2015). In the present study, *P. acuta* larvae settling within grooves were slightly more likely to settle in aggregates than when they settle on open surfaces on the same tiles. Aggregation within grooves may be related to our present experimental design, in which coral larvae came from three parent colonies, thus increasing the chance that aggregated larvae were full-siblings, and therefore more prone to fusing (Amar et al. 2008). Elevated frequencies of aggregated settlement can be more common among coral recruits that are genetically related to one another, at least for *Acropora millepora* (Puill-Stephan et al. 2012b). However, results from Shefy et al. (2022) showed that kinship among *Stylophora pistillata* recruits was only a main driver of aggregated settlement of coral recruits in petri dishes with high initial stock densities (>54 per 100 cm^2). Conversely, high abundances of solitary spat in the microhabitats in the present study are comparable to those recorded in settlement experiments with *A. tenuis* (Randall et al. 2021), during which larvae were exposed to tiles fitted with microhabitats and irregular surfaces. Randall et al. (2021) showed that 90% of the coral spat in their experiment originated from solitary settlement (cf 56.9% in the present study). Determining which microhabitat features to recreate through 3D printing at a scale of mm to cm and evaluating their ecological relevance in influencing the settlement behavior of coral larvae warrants further investigation to better understand the effectiveness of printed surfaces in restorative applications.

Grooved microhabitats are associated with higher survival of coral recruits in the present study, and they may provide refuges to reduce exposure to biological and environmental disturbances such as targeted and accidental corallivory (Christiansen et al. 2009), sedimentation (Babcock and Smith 2002), and benthic competition with macroalgae (Ferrari et al. 2012). While the mechanisms that could account for high survival of coral recruits in grooves in the present study are unknown, this pattern could be attributed to the light regime (i.e., photon flux density) in these locations. In our study, the groove microhabitats promoting the elevated survival of coral spat were found close to the edges of the tiles where they may have been exposed to brighter light than on other settlement surfaces further from the edges of the tiles. This type of an "edge effect" was highlighted in Maida et al. (1994) who found higher mortality of coral recruits that settled further from the edges of stacked tiles deployed at 5 m depth at Lizard Island, Great Barrier Reef, Australia.

Our results support the use of 3D printing to create physical features of benthic surfaces to promote the settlement of coral larvae and the survival of the recruits produced (e.g., Tabalanza et al. 2020, Randall et al. 2021, Crawford et al. 2022, Schmidt-Roach et al. 2023). With coral populations globally declining in size (Sully et al. 2022), understanding more of the ways in which novel technologies such as 3D printing can be used to promote coral recruitment has potential to enhance manufacturing techniques used in restorative strategies on tropical coral reefs.

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